Insects on Palms

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and

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CABI *Publishing* is a division of CAB *International*

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A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data
Insects on palms / by Forrest W. Howard … [et al.].
p. cm.
Includes bibliographical references and index.
ISBN 0-85199-326-5 (alk. paper)
1. Palms--Diseases and pests. 2. Insect pests. 3. Insect pests--Control. I. Howard, F. W.

SB608.P22 I57 2001
634.9′74--dc21
00-057965

ISBN 0 85199 326 5

Typeset by Columns Design Ltd, Reading
Printed and bound in the UK by Biddles Ltd, Guildford and King's Lynn

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List of Boxes

All boxes by Forrest W. Howard unless otherwise noted

Authors and Contributors

> Nowher so bisy a man as he ther n'as,
> And yet he semed bisier than he was.
> …
> But all be that he was a philosophre,
> Yet hadde he but litel gold in cofre.
>
> (Geoffrey Chaucer (1340–1400), English poet. *The Canterbury Tales*)

The Authors

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Acknowledgements

We thank our colleagues in entomology, botany, horticulture, plant pathology and other sciences who have helped us improve this book by sharing their knowledge and ideas with us. Many of them generously provided us with photographs to help illustrate our discussions.

Scientists who helped us improve our book by reviewing sections of the manuscript include: Dr Abdulaziz Al-Ajlan, King Faisal University, Al-Hasa, Saudi Arabia; Dr Emanuel D. Aterrado, Philippine Coconut Authority (PCA), Davao; Dr Richard Baranowski, University of Florida (UF), Homestead; Dr Bradley C. Bennett, Florida International University, Miami; Dr Carlos Chinchilla, ASD de Costa Rica, San José; Dr Michel Dollet, Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), Montpellier, France; Dr Joseph Eger, Dow AgroSciences, Tampa, Florida; Dr Marc E. Epstein, Smithsonian Institution, Washington, DC; Dr Priyanthie Fernando, Coconut Research Institute of Sri Lanka, Lunuwila; Ms Joana María Santos Ferreira, Empresa Brasileira de Pesquisa Agropecuaria (EMBRAPA), Aracajú, Sergipe, Brazil; Dr Jack Fisher, Fairchild Tropical Garden (FTG), Miami; Dr Imre Foldi, Musée National d'Histoire Naturelle, Paris; Dr Adalgisa Guglielmino, Dipartimento di Protezione delle Piante, Università della Tuscia, Viterbo, Italy; Dr Penny J. Gullan, Australian National University, Canberra; Dr Susan Halbert, Florida Department of Agriculture and Consumer Services (FDACS), Gainesville; Mr Hugh Harries, Centro de Investigación Científica de Yucatán (CICY), Mérida, Mexico; Dr Nigel Harrison, UF, Fort Lauderdale; Dr James Howell, University of Georgia, Tifton; Dr Dennis Johnson, Cincinnati, Ohio; Dr Phil Jones, Rothamsted Experimental Station, Harpenden, UK; Dr Jean-François Julia, CIRAD, Montpellier, France; Dr Meir Klein, Agricultural Research Organization, Bet-Dagan, Israel; Dr Dominique Mariau, CIRAD, Montpellier, France; Dr Douglass R. Miller, Systematic Entomology Laboratory, Agricultural Research Service, US Department of Agriculture (ARS, USDA), Beltsville, Maryland; Ing. Agron. Sigifredo Mora, Universidad Nacional de Colombia, Bogotá; Dr Charles W. O'Brien, Florida A & M

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The following generously provided information, drawings or photographs: Mr Edwin Abreu, University of Puerto Rico; Mr E.R. Asokan, CPCRI, Kayangulam, Kerala, India; Dr Basil Been, Coconut Industry Board, Kingston, Jamaica; Dr Daniel Blumberg, Volcani Research Centre, Israel; Dr Claudio Carrai, Agenzia Regionale per lo Sviluppo e l'Innovazione nel settore Agricolo-forestale, Pisa, Italy; Ing. Aron. Humberto Carrillo Ramírez, Instituto Nacional de Investigaciones Agropecuarias, Chetumal, Mexico; Dr Mary Carrington, UF, Immokalee; Dr M.J.W. Cock, CAB Biosciences, Silwood Park, UK; Ms Mary Collins, FTG, Miami; Mr James V. DeFilippis, UF, Fort Lauderdale; Dr John Dransfield, Royal Botanical Gardens, Kew, UK; Ms Dee Duzak, UF, Vero Beach; Dr Simon Eden-Green, Natural Resources Institute, Chatham, Kent, UK; Dr Dan Enobakhare, University of Benin, Nigeria; Dr Gregory W. Erdos, UF, Gainesville; Dr Carlos Flechtmann, Universidade de São Paulo, Brazil; Mr Mike Foale, Commonwealth Scientific and Industrial Research Organization, Australia; Dr J. Howard Frank, UF, Gainesville; Dr Saeed Gassouma, Ministry of Agriculture and Fisheries, Dubai, United Arab Emirates; Mr Martin Gibbons, The Palm Centre, Ham, Richmond, Surrey, UK; Doña Susi Gómez i Vives, Estación Phoenix, Elche, Spain; Don Antonio González, Consejería de Agricultura, Pesca y Alimentación, Puerto de la Cruz, Tenerife, Canary Islands, Spain; Dr Avas Hamon and Dr John Heppner, FDACS, Gainesville; Dr Madeline Harley, Royal Botanical Gardens, Kew; Mrs Gloria and Ms Martha Howard, Fort Lauderdale; Mr Richard Illingworth, Hacienda Victoria, Costa Rica; Dr Moshe Kehat, Volcani Research Centre, Israel; Dr Paris Lambdin, University of Kentucky; Dr W.H. Lange, University of California, Davis; Dr J. LaSalle, CABI Biosciences; Ms A.A. Loyola, PCA, Davao, Philippines; Ms Katherine Maidman, FTG, Miami; Dr Eric Matthews, South Australian Museum, Adelaide; Ms Dorothy Miller and Aramco World, Houston, Texas; Dr Lois O'Brien, Florida A & M University, Tallahassee; Drs Carlos Oropeza and Roger Orellana, CICY, Mérida, México; Ms Ester Pacumbaba, PCA, Albay, Philippines; Ing. Agron. Eduardo Peña, Instituto Colombiano Agropecuario, Tumaco, Colombia; Ms Patricia Piña Quijano, CICY, Mérida, México; Dr Bob Prior, Papua New Guinea Cocoa and Coconut Research Institute, Rabaul; Dr C. Prior, CABI Biosciences; Dr John Randles, University of Adelaide, Australia; Dr Georges Remaudière, Musée National d'Histoire Naturelle, Paris; Dr Renato Ripa, Instituto Nacional de Investigaciones, Centro Nacional de Entomología La Cruz, Chile; Mr David Romney, Romney Farms, Homestead, Florida, USA; Ms Erlinda P. Rillo and Ms Nemesia San Juan, PCA, Philippines; Dr Laura Sampedro R., Universidad de Colima, Mexico; Ms Dalva Luiz de Queiroz Santana, EMBRAPA, Aracajú, Brazil; Dr S. Ahmed Siddig, Shambat Research Station, Khartoum North, Sudan; Mr A. Thirakul, Chumphon Horticultural Research Centre, Chumphon, Thailand; Dr Darryl Thomas, Goldsmith Seeds, Gilroy, California, USA; Dr Michael Thomas, FDACS, Gainesville; Dr Dulce Warwick, EMBRAPA, Aracajú, Brazil; Dr Thomas Weissling, ARS, USDA, Miami; Dr Robert Woodruff, FDACS, Gainesville; Dr Scott Zona, FTG, Miami. Our special thanks to Ms Emma Critchley, Ms Zoe Gipson and Mr Tim Hardwick, CABI *Publishing*, for editorial assistance and much valuable advice; Mr John B. Kramer, UF, Fort Lauderdale, for assistance with computer technology.

Major funding for colour photographs in this book was provided by gifts from the South Florida and Palm Beach Chapters of the International Palm Society to the

University of Florida Foundation, Inc. – SHARE. Additional support was provided from gifts to SHARE from the Florida Pest Control Association; Howard Fertilizer Co., Inc., Groveland, Florida; and Richard Illingworth, Hacienda Victoria, Costa Rica.

Preface

The authors of this book have long studied the insects and related animals that live on palms. Our respective interests were initially focused on the coconut spike moth (Abad), palm weevils (Giblin-Davis), potential lethal-yellowing vectors (Howard) and coconut mites (Moore). As each of us broadened his scope, he became aware of important similarities and interesting dissimilarities in the palm-associated insect faunas of various regions and of pervasive patterns in the relationships between insects and the palm family. We found that colleagues concerned with insect pest management on palms in disparate regions shared with us many common interests and problems Of particular concern were insect pests of limited distribution that were potential pests elsewhere: we felt that all palm workers should become aware of the more serious of these.

We thus saw a need for a reference book on insects of palms from a world standpoint. The book that we now present is intended for members of the far-flung community of entomologists concerned with pest management in palms, as well as to a broader readership, including horticulturists, tropical ecologists, biological conservationists, plantation managers, palm gardeners and students of the natural history of warm regions.

The book is not an identification manual or a complete compilation of every insect species reported on palms We concentrated on better-known ‘representative species’ to illustrate general principles and patterns. Lists of significant species on palms were compiled for some families as a measure of their relative importance on palms and for reference use.

The information included in this book is based on the literature on palm insects published from the early 1800s to the present. Although early naturalists and entomologists lacked such modern tools as statistical control of data, they seem to have been astute, patient observers and careful thinkers, and much of the information that they provided seems reliable. Many of their observations have been confirmed by recent workers. We greatly condensed the information contained in many excellent papers published on palm insects in recent decades. This was especially true of highly specialized topics. Hopefully, our literature citations will be helpful to those wishing to pursue these topics further.

Being limited in language capabilities and lacking a budget for translation services, we limited our study mostly to works published in English and the Romance languages. We thus remain intrigued by what appear to be some very worthy publications on palm insects in various languages in which we are not competent.

The authors worked on the book intermittently while managing research programmes involving specific field and laboratory projects at our own facilities or in distant countries, developing and teaching college courses and dealing with the daily incidences of communication with growers and palm horticulturists, students of various academic levels and the public at large. Attention to these demands stretched completion of the book beyond more than a few years, but we hope that our frequent involvement with insects and palms during the writing of the book has resulted in an insightful interpretation of the literature and that our close contact with diverse people has increased our awareness of what information was of broadest interest and therefore worth emphasizing.

It was rewarding to communicate with palm entomologists in different countries and include their very useful and interesting information in the book. Another reward of preparing this book was that it expanded our personal knowledge of insects of palms. We hope that our readers will be similarly rewarded.

Forrest W. Howard
Dave Moore
Robin M. Giblin-Davis
Reynaldo G. Abad

1

The Animal Class Insecta and the Plant Family Palmae

Forrest W. Howard

Es una antorcha al aire esta palmera,
Verde llama que busca al sol desnudo.
(It is a torch in the air this palm, a green flame searching for the naked sun.)
(Miquel de Unamuno (1864–1936), Spanish philosopher and author. Lines of a poem)

The Class Insecta

Insects (class Insecta) are the most diverse and ubiquitous of metazoans. They occur in nearly all terrestrial environments that are favourable for life and are prominent in freshwater aquatic environments.

Insects have traditionally been considered a class of Arthropoda, a phylum of invertebrate animals characterized by a rigid integument, which serves as an exoskeleton, and by the presence of paired appendages (such as legs and antennae). Movement on these animals is possible because the integument is not uniformly rigid, but divided into plates (sclerites) and segments, between which are membranous areas in which the cuticle is flexible. The appendages of arthropods are thus referred to as 'jointed'. Arthropods have bilateral symmetry, a ventral nerve cord and a dorsal heart. The heart is basically a musculated tube that pumps blood forward into an open, rather than a vascular, circulatory system. Arthropods are poikilothermic ('cold-blooded') animals, that is, their internal temperature varies with ambient temperature, although they are capable of some degree of temperature regulation. Arthropods are generally dioecious, i.e. with reproduction requiring the mating of males and females.

Major subphyla of arthropods include the Crustacea (lobsters, crabs, shrimps, etc.), Chelicerata (spiders, ticks, mites, scorpions, etc.) and Uniramia (insects, centipedes, millipedes, Collembola, etc.). The insects constitute the class Insecta.

In recent years, the taxonomy of the arthropods has been debated intensely. Currently, there are many differences of opinion regarding the status of the various major taxa of this phylum and even regarding the validity of conserving them in a single phylum. In this book, we follow the traditional and familiar system, in which Arthropoda is the phylum as described above. The vast majority of species of this phylum belong to the class Insecta.

In the basic plan of a mature individual (adult, or imago) of the class Insecta, there are three body regions, namely the head, thorax and abdomen. The head is a centre for sensory activity and feeding. It bears paired structures, namely the antennae, compound eyes and mouth-parts. The antennae are usually the olfactory organs. The principal mouth-parts are the labrum and labium (upper and lower 'lip', respectively), the maxillae, all of which hold or manipulate food, and the mandibles, which bite and crush food. These structures are highly modified in some insect taxa. For example, in the order Hemiptera, the mouth-parts are modified to pierce tissue and suck fluids. The thorax is packed with muscles and is the centre of locomotor activities. It consists of three segments, namely the prothorax, mesothorax and metathorax. Each segment bears a pair of legs, so that an insect has a total of six legs. The mesothoracic and metathoracic segments each bear a pair of wings. The abdomen has nine to 11 segments. It houses most of the organs involved in digestion, excretion and reproduction. The digestive, excretory, reproductive, circulatory, nervous, endocrine and other vital systems of arthropods are basically similar, but in insects the respiratory system is unique. Air is taken into the insect's body through openings (spiracles) and distributed via a tracheal system.

The egg, larval and, in some taxa, pupal stages constitute the immature stages of insects. The larva is the stage in which growth takes place. Because of the rigidity of the insect integument, insects grow by increments, shedding their old cuticles (exuviae) and developing new ones at each step. For example, the newly hatched larva (first instar) grows to a certain point and then moults. This is typically followed by four additional increments (instars), each culminating in the moulting process.

All but the most primitive insects undergo one of two types of development (metamorphosis) from egg to imago. In incomplete, or gradual, metamorphosis, the fifth and final moult initiates the imago stage. The orders for which this type of metamorphosis is characteristic are referred to as *exopterygote* orders, in reference to the presence of rudimentary wings, which develop externally in later instars. Larvae of exopterygotes have a general form similar to that of the imago, with compound eyes, mouth-parts, legs, etc., but are smaller and lack functional wings and reproductive structures. Both the larvae and the imagos of exopterygotes typically occupy the same hosts and habitats. Exopterygotes include two major groupings: the orthopteroid orders, which include Orthoptera and related orders, and the hemipteroid orders, which include Hemiptera and related orders.

In complete metamorphosis, the larvae are generally vastly different morphologically from the imago. In fact, the larvae are often wormlike, while the imagos are among the most active and specialized insects. The drastic change from larva to imago takes place via an intermediate stage, the pupa. This is a non-feeding, relatively inactive stage, during which tremendous morphological and physiological changes take place in the insect. The pupal stage culminates in the eclosion, or emergence, of the imago. Because the precursors of the wings of the imago develop internally in the larvae, insects that undergo complete metamorphosis are categorized as *endopterygotes*. The larvae and imagos of endopterygotes occupy different hosts and habitats. Endopterygotes are considered more advanced than exopterygotes. The four largest orders of insects, namely Hymenoptera, Lepidoptera, Diptera and Coleoptera, are endopterygote orders. Each is larger than Orthoptera or Hemiptera, the two largest exopterygote orders. Over 80% of the species of insects are endopterygotes.

The developmental stages of insects that develop by gradual metamorphosis are widely known by the term 'nymph', but some entomologists apply this term only to the penultimate and ultimate instars in which wing rudiments become visible. In French, the term 'nymphe' refers to the pupal stage of endopterygote insects. 'Prosopon', 'prosopide' and 'neanide' have been proposed as preferable terms for the developmental stages of Hemiptera, but none of these have caught on. We follow the practice of many entomologists in applying the term 'larva' to developmental stages of insects in general, including those of Hemiptera and other exopterygotes.

Insecta are relatively small animals. Most fall within a range of perhaps 2–50 mm in length. Insects of 100 mm or more in length are considered unusually large. Females, which bear and lay (oviposit) eggs, are usually slightly larger than the males of their species and live longer. In this book, we generally omit measurements for the male.

Insects tend to reproduce prolifically, ovipositing on or near the host or habitat that the larvae will occupy when eggs hatch. After mating, the principal activity of the female is to disperse eggs to a maximum number of suitable sites. Most species do not remain with the eggs, and parental protection and care involve little more than finding a suitable site for eggs and hiding the eggs by, for example, inserting them in host tissue or constructing a shelter of fibres over them. Thus, the immature stages are generally the most susceptible to loss, due to various biotic (e.g. predators and parasitic insects) and abiotic factors (e.g. weather). Populations of particular species increase or decrease in response to pressure by these factors.

Most of the damage and most of the beneficial effects of insects on agriculture are related to their feeding, the greater portion of which takes place in the larval stage. The degree of benefit or damage by feeding is related to the population density of the insect species.

Insects are the most diverse class of animals, and there is a multitude of exceptions to all of the general rules outlined above.

Only about one-third of the insect orders contain a substantial number of phytophagous species, that is, species that feed on living vascular plants. Most orders consist predominantly of insects that feed on dead organic matter, fungi or algae or are predacious or parasitic. However, phytophagous taxa are generally highly diverse. In fact, the largest orders in terms of species – Orthoptera, Hemiptera, Diptera, Hymenoptera, Lepidoptera and Coleoptera – are mostly phytophagous or have large phytophagous families. So, while a minority of insect orders are phytophagous, over half of the known species of insects are phytophagous. Thus, the relatively few major insect taxa that utilize vascular plants as food and habitat would appear to have overcome formidable plant defences or other obstacles and, having surmounted these, found an environment favourable for vast speciation (Strong *et al.*, 1984).

An important part of knowledge of insects of palms is the geographical distribution of different species. Here we are confronted with the problem that insect biogeography lacks standardized placenames. The faunistic realms of zoogeographers (e.g. the neotropical, Ethiopian, oriental, etc.) were conceived for birds (Sclater, 1858), were later used for vertebrate animals in general and are somewhat inapt for insects. Furthermore, some entomologists have altered these concepts, for example, defining the neotropics as the tropical lowlands of the Americas, while in vertebrate zoology the term refers to all of South America, including the frigid areas of the high Andes and the extratropical regions of southern Chile and Argentina. The term 'Ethiopian region', corresponding to the African continent, is seldom seen in entomological works. Floristic regions (e.g. Takhtajan, 1986) seem to coincide better with the broad trends of insect distribution; thus insects are often referred to as being distributed in the Caribbean, Amazonian, Mediterranean, etc., regions. Within regions, one often resorts to names that denote political or cultural divisions (e.g. southern Europe, Kerala State, the Philippines).

In this book, precise localities are listed for some species that are highly endemic or known only from a few records. Otherwise, we have not attempted to describe the distribution of insect species precisely. Precise distributional data are not known for many insects and, in any case, may become out of date rapidly. Thus, insects that we refer to as being distributed in the Caribbean, the western hemisphere, tropical America, etc., may be known only in a portion of those broad regions. In most cases in which insects are known from a political division of an island (e.g. Haiti, Irian Jaya), we list their locality as the island (e.g. Hispaniola, New Guinea). We use current place names, except when an earlier name provides historical clarity.

The poikilothermic condition of insects and their small size (making desiccation a risk) would seem to imply that humid tropical environments are most suitable for insect life. Indeed, it has been quite well established that insect diversity is generally higher in the humid tropics than in other regions. However, contrary to popular belief, the numbers of individual insects per unit area are similar or higher in certain temperate-zone habitats than in the humid tropics (Penny and Arias, 1982).

To understand the natural history of palms, to protect them in cultivation and to conserve them in the wild, it is important to try to understand their relationships with insects. This book is about phytophagous species of insects that select palms (family Palmae, or Arecaceae) as their hosts. Mites (Acari) constitute the only taxon of arthropods besides insects with phytophagous species. A minority of families of Acari are phytophagous, but, as in Insecta, the phytophagous families are the largest. Because these two arthropod taxa have a similar impact on human activity, the science of mites, acarology, is closely allied to the science of insects, entomology. However, in this book, we focus on insects, discussing only some of the more important mites on palms.

The Palm Family

Palms constitute one of the most familiar of plant families. They and their products have been an integral part of the culture of peoples of the warmer regions of the earth since ancient times. Over the centuries, numerous palm species have been developed into crop plants and are important sources of food and materials for local economies. Three species – coconut palm (*Cocos nucifera*) (Colour Plate 1a, b, Figs 1.1, 1.4e and 1.15), African oil palm (*Elaeis guineensis*) (Colour Plates 2b and 3c) and date palm (*Phoenix dactylifera*)[1] (Figs 1.2 and 1.19) – are the bases of major world agricultural industries. Palms are favourite ornamental plants wherever they can be grown – in outdoor landscapes in warm regions, indoors in cooler regions – partly because, more than any other plant group, palms represent the lure and romance of the tropics. Their consistent presence in tropical forests implies that they are essential components of these ecosystems.

The Palmae are one of the most easily recognized plant families, being distinguished from most other angiosperms by distinctive leaves, or fronds, and by the fact that they constitute one of the few monocotyledonous plant families with arborescent species. They constitute one of the largest botanical families, with about 2800 species.

General Ecology of Palms

Palms are essentially tropical plants. They grow continuously throughout the year, lacking dormancy mechanisms. The family reaches its maximum diversity and distribution in warm, humid lowlands of the tropics (Af and Aw climates – see Box 1.1). About 75% of the species of palms occur in rainforests (Dransfield, 1978) and many species are adapted to swamps. Palms are often a conspicuous feature of tropical savannahs, but here, too, they are most often restricted to the wetter sites. There are no true xerophytes among the palms. Species associated with arid regions (BW climate – see Box 1.1), such as *Brahea* spp. and *Washingtonia* spp. of the Sonoran Desert and adjacent areas and the date palm of North Africa and the Middle East, grow around oases or where there are under-

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[1] The date palm, coconut palm and African oil palm as well as other well-known plants in cultivation (e.g. bananas, mangoes, coffee) are referred to in this book by their vernacular names. Complete scientific names of plants and insects, with the taxonomic authorities, are listed in the index.

Fig. 1.1. Coconut palm (*Cocos nucifera*), Florida Keys.

Fig. 1.2. Date palms (*Phoenix dactylifera*), Saudi Arabia. Courtesy of Dorothy Miller and Aramco World.

ground water sources (Colour Plate 2a). There are a few palms adapted to high altitudes, such as *Calamus gibbsianus*, found at about 3000 m in Borneo, and species of *Parajubaea*, *Geonoma* and *Ceroxylon*, found at altitudes over 3000 m in the Andes (Moraes, 1996). Species of *Ceroxylon* are found at up to 4000 m (Uhl and Dransfield, 1987). Outside the tropics, the number of species of palms dwindles to extratropical species, such as *Sabal palmetto* (Colour Plate 1d, e), *Sabal minor*, *Serenoa repens* (Fig. 1.3a) and *Rhapidophyllum hystrix*, all native to the coastal plains of the south-eastern USA; *Chamaerops humilis* (Colour Plate 2f), which occurs naturally in the Mediterranean region; and *Butia capitata* and *Jubaea chilensis*, the latter of which is native as far south as about 35°S latitude in South America (Uhl and Dransfield, 1987). Cultivation has artificially extended the range of the palm family. For example, many species of palms native to tropical localities are cultivated in southern Florida, surviving frost damage once every several years (Goldstein, 1989). A surprising diversity of palms is grown in gardens in Britain (Cooper, 1983). Two of the most cold-hardy palms, T*rachycarpus fortunei*, native to the mountains of south-central China, and *R. hystix,* survive in cultivation in areas visited by winter snows. In Britain, *T. fortunei* is found as far north as southern Scotland (Martin Gibbons, personal communication).


a
c
b

Fig. 1.3. (*and opposite*) Palms with palmate or costapalmate fronds. (a) *Serenoa repens*, Florida Everglades. (b) *Sabal umbraculifera*, Santo Domingo, Dominican Republic. (c) *Borassus aethiopium*, Fairchild Tropical Garden, Miami. (d) *Licuala* sp., Fairchild Tropical Garden. (e) *Washingtonia robusta*, Fort Lauderdale, Florida. (f) *Bismarckia nobilis*, Fairchild Tropical Garden.

Box 1.1. The regions of perpetual summer: a primer on tropical and near-tropical climates.

> They were approaching the region of perpetual summer.
>
> (Henry Wadsworth Longfellow (1802–1882), American poet. *Evangeline*)
>
> It's so damp here, I can't tell whether you're applauding or splashing.
>
> (Bob Hope, American comedian, to an outdoor audience in the Panama Canal Zone, December 1960)

Most species of palms are adapted to the warm, humid climates of relatively low elevations within the tropical zone (the belt between 23.5°S and 23.5°N). A minority grow in the cool climates of higher elevations within the tropics and a handful of cold-hardy species may be grown outdoors in northern Europe and other cool regions, but these are oddities. Indeed, along with physical factors (mean monthly and annual values of temperature and precipitation), the native plant associations are considered in classifying the climate of a region. A diversity of palms is one indicator of a tropical climate.

Most modern climate classification systems are based on a system developed by Wladimir Köppen (1846–1940). Categories of the Köppen system of most interest to palm culture include the following:

- A – tropical climates
  - Af – tropical wet climate
  - Aw – tropical wet and dry climate
  - Am – tropical wet climate with a short dry season
- Cs – Mediterranean climate
- BW – desert climate

The tropical wet (Af) climate is the climate of the equatorial lowlands in, for example, the western part of the Amazon basin, mainland South-East Asia, Indonesia and West (equatorial) Africa. Here, within a few degrees of the equator, are found most of the world's tropical rainforests. Moisture is brought to this zone – the intertropical convergence zone – by the north-easterly and south-easterly trade winds, which converge here. Surface winds are infrequent. The general motion of the warm, moist air is aloft. As it reaches high altitudes, it cools and its moisture condenses. The sky is frequently cloudy and rainfall is frequent all year. Most species of palms and undoubtedly most species of palmivorous insects are adapted to this climate.

Poleward from the equator, continuous rainfall grades into seasonally distributed rainfall. The tropical wet and dry (Aw) climate is characteristic of the lowlands bordering the equatorial zone. A classic example is the monsoon climate of southern Asia. The monsoon is a wind system characterized by seasonal reversal of wind direction. During warmer months, the land of southern Asia accumulates heat at the surface faster than does the Indian Ocean. As a result, the air over the land rises and is replaced by cooler, moisture-laden air from the ocean, which in turn flows upward. The condensed moisture falls, often as quite heavy rain. This phase is called a wet monsoon. In the winter, the cooling of the Indian Ocean lags behind that of the continent. As a result, the air over land becomes relatively dense and flows offshore. With no moisture input from the ocean, southern Asia now experiences a dry monsoon, i.e. a dry season.

All climates classified as Aw are variations of this system. Winters are the dry season, summers the wet season. Upward air movements over land peak during the hottest part of the day, precipitating afternoon thunderstorms, a highly characteristic feature of Aw and other tropical climate types.

In addition to southern Asia, the lowlands of northern South America, Central America, Mexico, the West Indies, most of tropical West Africa (outside the equatorial zone), islands in the Pacific within the tropics but outside the equatorial zone and the northern peninsulas of Australia (e.g. Cape York Peninsula) experience some version of the Aw climate. Some special places outside the tropics also have this kind of climate, as explained below. Although more palm species occur in regions with an Af climate, a great diversity of palms occurs in regions with an Aw climate.

The local climates of coastal areas involve a reversal of air movement that is a small-scale version of a monsoon climate. Sea breezes blow from oceans and other large bodies of water over the land during the day and air flows offshore from the land during the night. Again, the mechanisms depend on greater accumulation of heat at the land surface relative to the surface of the ocean by day, with resulting upward air movement over land and afternoon showers, which are often a little inland from the shore. The flow reverses at night because of the lag in cooling of the ocean relative to land. This pattern is especially pronounced in coastal areas of the tropics and is characteristic of the habitat of the coconut palm and other maritime palms.

Box 1.1. *continued*

There is a general movement of air across the oceans from about 20° and 35° north and south latitudes towards the low pressure of the intertropical convergence zone. The earth's spin deflects it so that the movement is from the north-east towards the south-west in the northern hemisphere and from the south-east towards the north-west in the southern hemisphere. These prevailing winds, the trade winds, are gentle and relatively constant. They bring moisture from the sea to eastern coasts of continents, but away from western coasts.

Ocean currents bring tropical climates to some localities outside the tropics. Southern Florida at 25–27°N (i.e. south of Lake Okeechobee) has a tropical wet and dry (Aw) climate. Tropical species are amply represented in both the native and the exotic flora, and the catastrophic frosts that come at intervals of years are not severe enough to permanently alter the vegetation. The climates of the Bahamas and Bermuda at 32°N are similar but without frosts. These localities lie in or near the path of a major current, part of the clockwise circulation of the North Atlantic, which brings warm water from the tropical belt northward. The impetus in the tropical zone for this general movement is the drag effect of the trade winds, which causes a westward current, which enters the Caribbean Sea and ultimately the Gulf of Mexico. Water that piles up in the Gulf escapes through the Florida Straight between Florida and Cuba and then flows north. This, the Florida current, greatly moderates the climates of the localities mentioned. The coconut palm, a good indicator plant of a tropical climate, thrives in the Bahamas, Florida and Bermuda. At higher latitudes, the current is deflected increasingly eastward, so that its effect on the coast of North America decreases. Between North Carolina and Newfoundland, the Florida current joins an easterly oceanic movement, which corresponds to the flow of air at those latitudes. Here the current, called the Gulf Stream, carries enough heat for the climate of England to be much warmer than that of Labrador at the same latitude. This permits cold-hardy palms to be grown in Britain.

The paradox of tropical climates outside the tropical zone is matched by that of non-tropical climates within the tropical zone. Temperatures decrease with increasing elevation, culminating in polar-like climates on the higher mountain peaks. Vegetation becomes sparser and shorter with increasing elevation, the maximum for palms being about 4000 m, where *Ceroxylon* species are found.

Tropical cyclones, a factor in some tropical regions, are categorized according to their minimum sustained wind speeds, 75 miles (120.7 km) per hour being the threshold for those identified as hurricanes (or typhoons in the north Pacific Ocean). The torrential rains and coastal flooding often accompanying these storms are factors that often rival their wind speed in their effects on land areas.

Tropical cyclones form in three different regions: (i) in or near tropical latitudes of the Atlantic Ocean, from where they move toward the west and north, often traversing the Caribbean or adjacent waters or land areas and often reaching eastern coastal regions of North America; (ii) in the Indian Ocean and adjacent waters, moving towards southern Asia; and (iii) in some regions of the Pacific Ocean, often reaching South-East Asia. South America and Africa rarely experience them.

Within the zones traversed by tropical cyclones each year, their extent, paths, intensities and frequency are variable and unpredictable, so that localities are affected to varying degrees or may escape effects for years. But, during the intervals, local weather may be influenced by a range of effects related to them.

The tropical wet climate with a short dry season (Am) is similar to the Af climate, but with a very short dry season. It is characteristic of the Amazon delta, French Guiana and some of Suriname.

The Mediterranean (Cs) climate is characteristic of lower middle-latitude coastal areas that border desert areas, mostly on western sides of continents. It has cool to mild, rainy winters and a hot, dry summer. Examples include most of the coastal areas of the Mediterranean basin, some coastal strips of Australia, the southern coast of Chile and California, USA. Palms adapted to this climate type tend to be cold-hardy, e.g. *Chamaerops humilis, Washingtonia* spp. and several *Phoenix* spp. Most tropical palms are not well adapted to this climate.

The desert climate (BW), characterized by extremely low amounts of precipitation, supports sparse, xerophilous plants or is barren. In the Sahara, Arabian and Thar deserts, widely dispersed oases support date palms and other vegetation.

The BW climate is characteristic of the western sides of continents in a zone between 20° and 35° north and south latitudes. This is where air flowing at high altitudes polewards from the equator has expended its moisture and become cool enough to subside. Deflected westward, the air mass cannot bring moisture from the oceans to western coasts. The Sahara, Arabian, Thar, Kalahari, Sonora and Atacama deserts and the deserts of Western Australia are examples. Similarly, the south-western coastal areas of islands in the Caribbean are relatively dry and the north-eastern coasts relatively wet.

Box 1.1. *continued*

The El Niño event *sensu stricto* is a climatic phenomenon that affects the coast of Peru. It is part of a larger complex interplay of atmospheric and oceanic forces affecting global climate, known as the El Niño southern oscillation (ENSO) phenomenon. It involves the oscillation of high and low atmospheric pressure between the eastern and western portions of the Pacific Ocean. Normally, pressure is lower in the western Pacific and the south-eastern trade winds move generally in that direction. The shift every 3–7 years of low pressure to the eastern Pacific weakens the westward movement of wind and water, triggering the complex ENSO phenomenon. Decreased rainfall in parts of the Asia–Pacific region is among several of its important effects on world climate, and this in turn exerts an influence on populations of certain insects associated with palms in the region.

General Structure of Palms

Fronds

Leaves of palms, cycads (Cycadales) and ferns (Filicopsida) are often referred to as fronds. Although the two terms are often used interchangeably, frond may often be preferable, in order to emphasize the uniqueness of this structure, while leaf is a more general term, is employed in terms referring to structures, etc. (e.g. leaf base) and is preferable when emphasizing the similarities between palm leaves and leaves of other kinds of plants. A frond consists of a blade, or lamina, a petiole and a base.

There are two general forms of fronds, categorized by the shape of the laminae: palmate (fanlike) and pinnate (featherlike). In the simplest palmate form, leaf segments radiate from where the petiole joins the blade so as to form a flat, fanlike structure (Fig. 1.3). In the palmate form known as costapalmate, the petiole is continuous with a rachis, which extends well into the leaf blade. The rachis of a costapalmate frond is typically arched (Fig. 1.3b). In the pinnate form, the leaflets or pinnae (which are morphologically homologous with leaf

Fig. 1.4. (*and opposite*) Palms with pinnate fronds. Fort Lauderdale unless otherwise noted. (a) Royal palm, *Roystonea regia*. (b) *Ptychosperma elegans*. (c) *Phoenix reclinata*. (d) *Gastrococos crispa*, Havana, Cuba. Photo by Dave Moore. (e) Coconut palms, Kerala, India. Photo by Mr E.R. Asokan. (f) *Ceroxylon* sp., Colombian Andes. Photo by Gloria Howard.

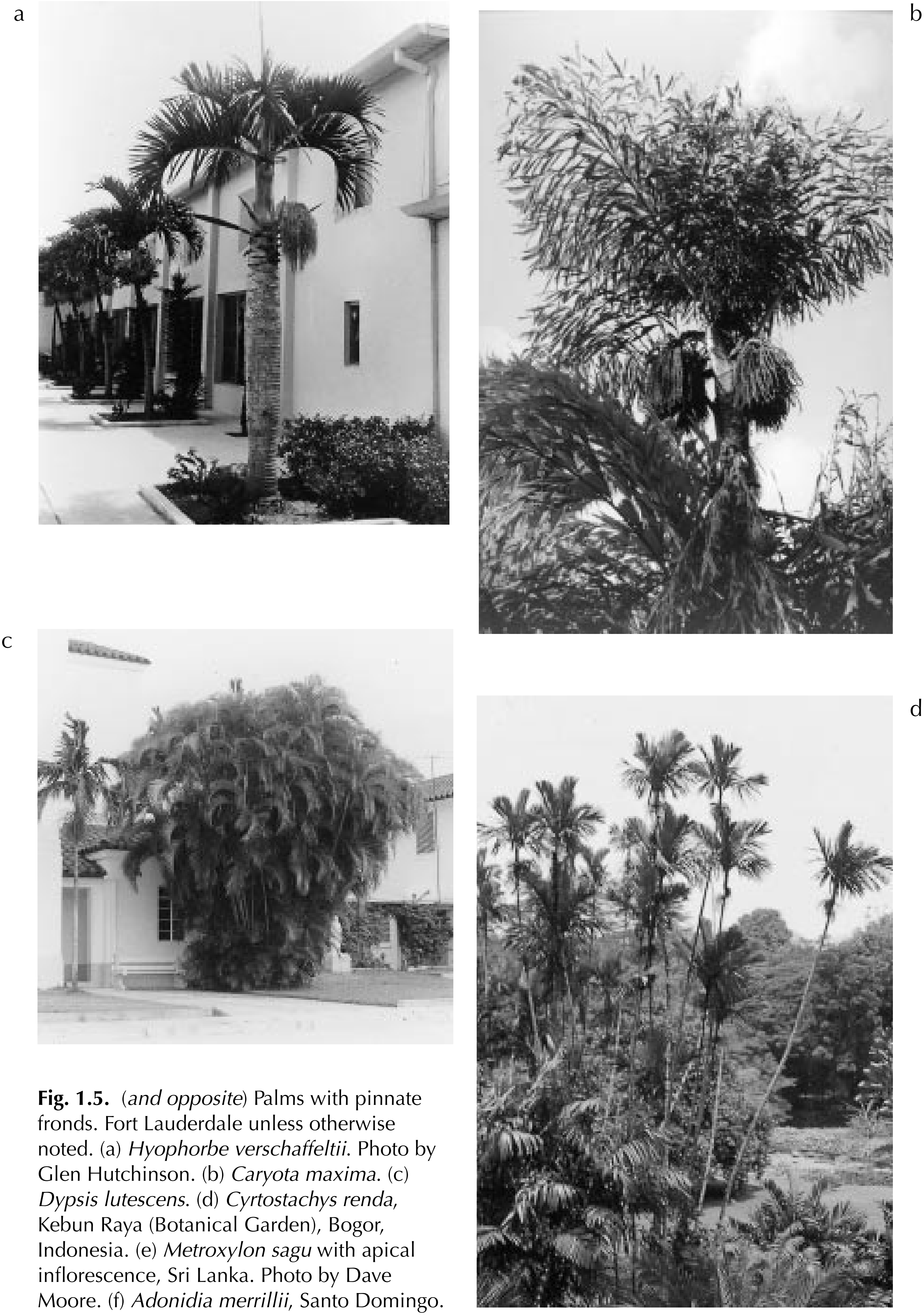

Fig. 1.5. (*and opposite*) Palms with pinnate fronds. Fort Lauderdale unless otherwise noted. (a) *Hyophorbe verschaffeltii*. Photo by Glen Hutchinson. (b) *Caryota maxima*. (c) *Dypsis lutescens*. (d) *Cyrtostachys renda*, Kebun Raya (Botanical Garden), Bogor, Indonesia. (e) *Metroxylon sagu* with apical inflorescence, Sri Lanka. Photo by Dave Moore. (f) *Adonidia merrillii*, Santo Domingo.

segments of palmate fronds) arise more or less equidistantly along each side of the rachis to form a featherlike structure (Figs 1.1, 1.2, 1.4 and 1.5). Each of the two forms is represented in large subfamilies of palms, but pinnate fronds are characteristic of cycads and ferns, in addition to palms.

Variations within these general forms include palmate fronds with entire or divided margins, undivided pinnate (pinnately ribbed) fronds, bipinnate fronds and plumose fronds, the latter being basically pinnate fronds with the pinnae in more than one plane. The references listed at the end of the section 'Classification of the Palm Family' contain illustrations and details of the many variations in palm fronds.

In the leaf segments or pinnae of most palms, the laminae fold down from the midvein so that the structure is Λ-shaped in cross-section. Fronds of this type are referred to as the reduplicate type. In the leaf segments or pinnae of palms of almost all members of the subfamily Coryphoideae and of the tribe Caryoteae, the laminae fold upward from the midvein so that the structure is V-shaped in cross-section, in which case fronds are referred to as induplicate. Date palms, for example, have induplicate pinnae (Fig. 1.6).

The petioles of palm fronds are typically thick and tough and are normally rigid, but, when large fronds are subjected to heavy wind loads, the petioles show amazing flexibility. The waving fronds of coconut palms on windy beaches are a familiar example of this. Many kinds of palms survive powerful tropical storms with their fronds intact. Petioles of some species and, less often, the rachides and more prominent veins bear armature, such as sawtooth margins, prominent teeth or spines.

The base of the petiole (i.e. leaf base) clasps the stem or trunk, forming a ringlike to cylindrical sheath. Conspicuous differences in this structure make it useful for identifying palms. It is particularly conspicuous in the species in which it is a long tubelike structure, which, when the frond desiccates, splits on the side of the stem opposite the petiole and the whole frond falls. Palms with this type of leaf base are said to have *a crown shaft* (e.g. Fig. 1.5f). In other palm species, as new fronds continue to develop after the formation of a sheath, the softer tissue of the

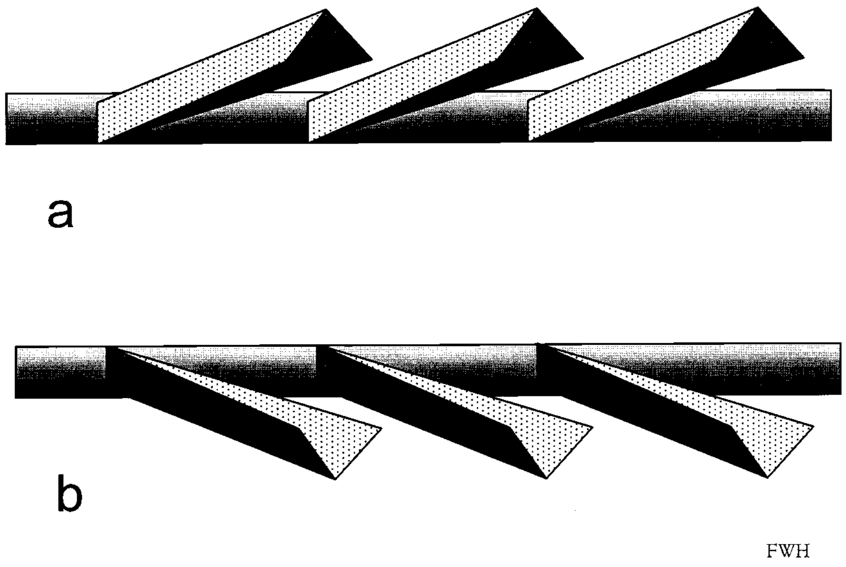

Fig. 1.6. Arrangement of pinnae on rachis in pinnate palms, with pinnae truncated distally, showing (a) reduplicate and (b) induplicate orientation.

sheath disintegrates, leaving a network of fibres encircling the petioles of subsequently formed fronds.

The living fronds are clustered as a crown in an alternate arrangement at the upper end of the stem. Fronds are produced in a meristem, often called the bud, or heart, located at the apex of the stem, i.e. in the centre of the crown. The tender whitish bud consists of a tightly packed series of primordial fronds, each enclosing the one preceding it in age. Periodically, a lance-shaped unfolded frond grows upwards from the bud. This is commonly referred to as the spear or sword leaf. The spear leaf is evident in, for example, Figs 1.3f and 1.5a. The interval between the emergence of two spear leaves varies with species; for example, it is about once a month in coconut palm, about every 16 days in the African oil palm and once every 9 months in *Lodoicea maldivica* (Corner, 1966). As a new spear leaf emerges, the oldest frond dies and may persist or be shed, according to the species. Thus, a fairly constant number of living fronds is maintained on any individual palm as long as conditions remain the same. During droughts, for example, palms may shed older fronds prematurely and thus have fewer fronds in the crown.

Notwithstanding much phenotypic variation and variation over time in the same individual, different species of palms have a characteristic number of open fronds (e.g. ten or less in the small *Chamaedorea* species, 12 in the extremely large, palmate *L. maldivica*, 22–36 in coconut palm and up to 200 large plumose fronds in *Phoenix canariensis*) (Corner, 1966; Fisher and Theobald, 1989; Fisher and Dalrymple, 1994).

In young seedling palms, fronds are two-ranked. As successive fronds emerge and develop, in most palms they take on a spiral arrangement around the apex of the stem, as seen from above. Each successively older frond arises from a point lower on the stem. In work in which the relative ages of fronds are a consideration, they may be numbered according to age. The spear leaf may be designated as 0, the most recently opened frond as no. 1, the second oldest open frond as no. 2, and so on to the oldest frond, which may be no. 36 in the case of a coconut palm growing under good conditions in the tropics (Fig. 1.7; Corner, 1966).

In the coconut palm, any open frond is on the opposite side of the stem and just to one side, i.e. at an angle of about 140–160° from another frond that is either 1 month older or 1 month younger. The younger of the two may be recognized by its higher position in the crown.

Only a basic understanding of phyllotaxy (leaf arrangement) is necessary for

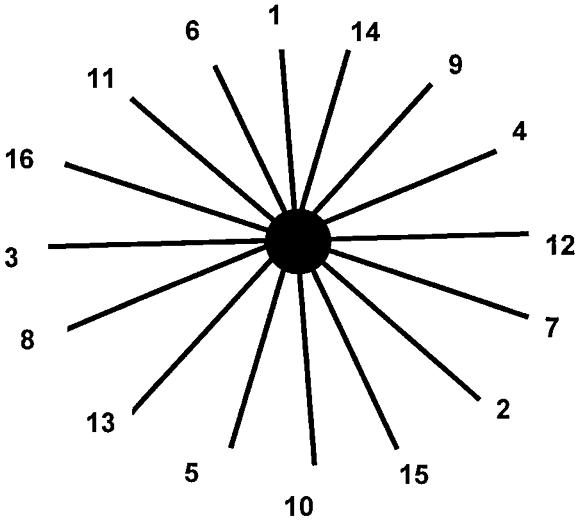

Fig. 1.7. Phyllotaxy of the coconut palm as seen from above, lines representing fronds extending out from the central bud. The fronds are numbered according to age, with no. 1 being the youngest. Each frond is on the opposite side and at about 160° from the frond preceding it in age.

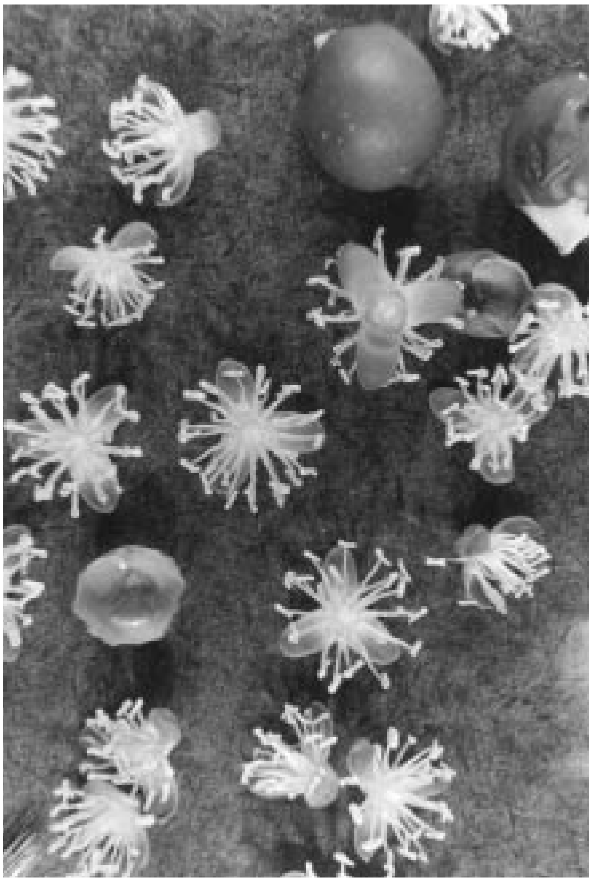

Fig. 1.8. Fallen flowers, perianth and fruits of *Ptychosperma elegans*. Note trimerous arrangement of floral parts, characteristic of monocotyledons.

most entomological work on palms. *Dypsis decaryi* has a 1/3 phyllotaxis, meaning that three fronds are encountered in one rotation around the palm stem. In this palm, the fronds are in three ranks, giving the crown a peculiar triangular appearance (hence the vernacular name triangle palm). In a palm with a 2/5 phyllotaxis, the fronds are arranged so that five are encountered in two rotations and the sixth frond encountered is almost directly below the first. A 3/8 phyllotaxis indicates eight fronds in three rotations around the stem, and there are other combinations up to 13/34 in *Copernicia*. All arrangements seem to ensure exposure of the fronds to sunlight (Tomlinson, 1990; Romney, 1997).

Flowers

The flowers of most species of palms are unisexual, and most palms are monoecious, a minority being dioecious. Monoecious palms may be cross-pollinated, particularly in palms in which the male and female flowers bloom out of phase (for example, some types of coconut palms).

With few exceptions, palm flowers (Fig. 1.8) have the basic trimerous structure of monocotyledons. The perianth has three petals and three similar tepals. Male flowers have three stamens in each of two whorls. Female flowers are hypogynous with three carpels, which may be coalescent. Individual palm flowers are relatively small and inconspicuous. Their petals are most commonly white, with the colours of tepals commonly similar to that of the species' or variety's petiole, i.e. green, yellowish, apricot or sometimes whitish. Their attractiveness to insects may depend partly on the vast numbers of flowers borne on large inflorescences, which would seem to compensate for the lack of showiness of the individual flowers. Also, some palm flowers are highly fragrant.

The inflorescence (Colour Plate 13b, Fig. 1.3a) is a specialized flower-bearing branch, which develops from the central bud area. It consists of the stalk, or peduncle; the rachis; the flower-bearing branches;

Fig. 1.9. *Gaussia maya,* infructescences.

and bracts, most of which subtend branches or flowers. Typically, one of the lower peduncular bracts is large enough to enclose the entire inflorescence as it develops. Horticulturists refer to this structure as the spathe, in this case a term applied somewhat imprecisely (Uhl and Dransfield, 1987). In some species, the spathe falls as the flowers open, but in other species it persists and splits open to release the inflorescence. Each inflorescence may bear up to hundreds or even thousands of flowers, according to the species. Male flowers are usually the more numerous and are short-lived. Fertilized female flowers persist and potentially develop into fruit, although a proportion of fertilized flowers or developing fruits are shed.

Fruit and seed

Palm fruits occur in an infructescence (Colour Plate 3d, Figs 1.9 and 1.19). Most fruits of palms are classifiable as drupes and most contain one seed. The mesocarp is essentially fleshy, as in dates of the date palm and in the orange, fleshy, oil-producing layer in African oil palm, or fibrous, as in coconuts (Fig. 1.10). Seeds often have very hard endocarps (e.g. the coconut 'shell') and a hard, white endosperm (e.g. coconut and oil palm kernel), which is rich in oil and carbohydrates and has some protein. The structures commonly referred to as palm seeds are actually comparable to the stones of drupes, such as apricots, i.e. the endocarp enclosing the seed. In the coconut palm, part of the endosperm is in liquid form ('coconut water') in a central

Fig. 1.10. Coconuts harvested from a plantation in Jamaica.

Fig. 1.11. *Corypha umbraculifera,* a hapaxanthic palm, in bloom. USDA Subtropical Horticultural Research Station, Miami.

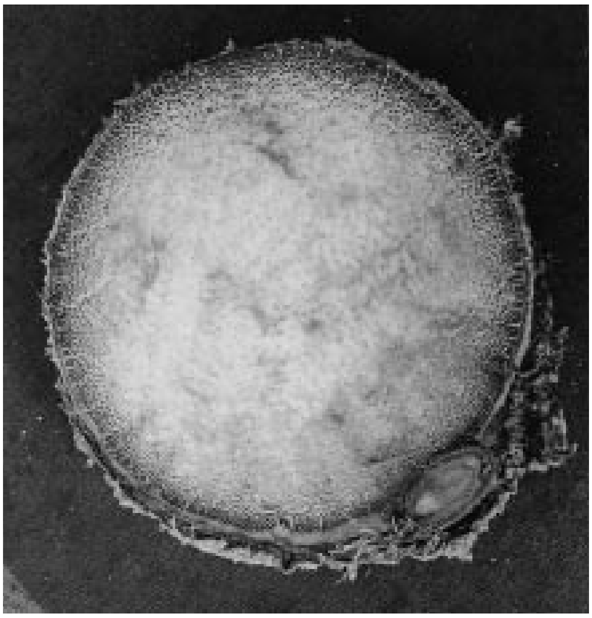

Fig. 1.12. Cross-section of stem of *Caryota mitis,* with dispersed vascular bundles characteristic of monocotyledons.

cavity. Fruits and seeds vary widely across the spectrum of the palm family in shape, colour, size and other characteristics.

The embryo appears as a small plug on the endosperm. Under conditions favourable for germination, which generally include relatively high temperatures and moisture, the embryo produces its first leaf, or plumule, which in most species precedes the production of the root.

Most palms are pleonanthic, i.e. once maturity is achieved they flower periodically. The age at which a palm comes into bearing is determined by genetics and secondarily by environmental factors. For example, a particular species may typically begin producing flowers and fruit at 10 years, but environmental factors may delay or accelerate maturation by a year or two. In most palms, once fruit production is initiated, it becomes an annual event. For example, the date palm flowers in spring and fruits are mature by autumn. Under the best conditions for production, coconut palms initiate fruit development about monthly, coinciding with the monthly production of fronds, so that coconuts can be harvested throughout the year. Some palms are hapaxanthic, flowering and fruiting once after many years of development, after which the stem dies. Since *Corypha* (Fig. 1.11) and *Metroxylon* are single-stemmed hapaxanthic palms, the entire plant dies after fruiting. Some species of *Caryota (*Fig. 1.5b) have multiple stems per plant, in which case only the stem that bears flowers dies.

Stem

Most species of palms produce solitary stems. Other species branch below ground to produce multiple stems, but stems of a very few species (e.g. *Dypsis lutescens*) branch above ground.

All of the growth of the stem takes place from the apical meristem. Palms do not possess a cambium and thus their stems do not grow radially, but they may thicken

Fig. 1.13. Trunk of *Cryosophila warscewiczii*. Morphologically, the spines are adventitious roots.

slightly due to anatomical changes (Rich, 1987). Stem heights range from a few centimetres to more than 65 m in some *Ceroxylon* spp. (Corner, 1966). Stems vary in diameter from less than a centimetre (e.g. *Wendlandiella gracilis*, some *Chamaedorea* spp.) to 1.8 m in *Jubaea chilensis* (Hoyos Fernández and Braun, 1984).

In cross-section, the palm stem is typical of monocotyledons (Fig. 1.12). The vascular tissues develop from procambial strands of the apical meristem. Xylem and phloem are organized into bundles sheathed in thick-walled sclerenchyma fibres. The vascular bundles are scattered among parenchyma tissue. The interior of the stem is soft and moist in living palms, due to the high ratio of parenchyma to vascular bundles. The density of the vascular bundles with their sheathing sclerenchyma increases toward the outside of the stem, forming a cortex that is extremely hard in some species of palms Some variation in diameter, once the stem is formed, may be due to expansion or contraction of cells of the ground tissue due to environmental factors, especially water relationships. Additionally, the stems of some palms thicken slightly with age due to anatomical changes in the cortex, including cell-wall thickening and sclerification in fibres and in some parenchyma cells. These anatomical changes also result in increased stiffness and strength in the old, basal parts of stems of mature palms (Rich, 1987).

Because they do not have secondary growth, palm stems lack bark homologous to that of dicotyledonous trees. However, a corky covering is eventually formed on the stems of some palm species. The surface of the stem of each species has a characteristic texture and colour, and may have rings or other patterns formed by frond-base scars. Many palms have very smooth stems, but stems of some species bear spines, persistent fronds, leaf bases or fibres (Fig. 1.13).

The frequent twists, curves and dramatic sweeps in the stems of coconut palms on tropical beaches are adjustments to beach erosion and wind and the search for light (Colour Plate 1a). The stems of palms with multiple stems curve out from the centre of the stem (*Cyrtostachys*). Species with usually straight stems curve as they search for openings in a forest canopy or, if felled by wind, form pronounced bends as they grow upwards. Various types of swellings of the stem are characteristic of particular species (Fig. 1.4a, d, *Gastrococos*). In some palm species, e.g. *Washingtonia* spp., the dead fronds are persistent for years. In other species, persistent dead fronds may break off at the petiole, so that the stems are characteristically covered with dead frond bases, giving them a rough or bumpy surface (Fig. 1.20).

Because palms lack cambial growth, they do not produce the annual growth rings seen in cross-sections of the stems of dicotyledonous trees of the temperate zones. However, the regularity of frond production, together with permanent and very conspicuous frond scars in some species, can be utilized in estimating the age of some palms. This is done by determining the number of frond scars (or persistent frond bases) on the stem, plus the number of living fronds. The total is divided by the average number of fronds produced per year by the species under study (a parameter that may differ somewhat, according to local environmental conditions). Added to this is the estimated time lapse between sprouting and formation of the stem (i.e. the average period of establishment growth, which is known or can be determined for each species). However, in some palms, the frond scars eventually become too indistinct to be useful for such purposes. In any case, the procedure described is not easy to implement and is probably seldom used by experienced palm entomologists, who, if they do not know the age of the palms that they work with, can usually make a reasonably accurate estimate based on their height, general appearance and growing conditions.

Roots

Palms do not produce tap roots, but numerous primary roots of virtually the same thickness. These radiate from a meristematic zone at the base of the stem below ground and are connected by newly initiated vascular elements to new fronds developing in the apical meristem. Once a root initiates growth, it elongates but undergoes virtually no radial growth and little branching. The first order of roots radiate great distances from the base of the stem. Lateral roots are eventually produced, which branch up to four orders. These smallest ultimate roots are the feeder roots. Most palms do not have root-hairs. Water and nutrients are absorbed principally in a small zone near each root tip. Air is taken in through small pneumatophores. In some older palms, adventitious roots may develop from the stem above ground. Some species are adapted to poorly drained soils by stilt roots, and in some species which do not normally have stilt roots, when grown on shallow soils or for long periods in containers, the roots grow so as to lift the stem off the ground. Roots are constantly dying and being replaced by new roots.

Classification of the Palm Family

According to the system of Uhl and Dransfield (1987), the palm family consists of six subfamilies, distinguished principally by floral characteristics, as well as by morphological characteristics of fronds and other structures.

- Coryphoideae. The coryphoid palms, with 39 genera, include all palms with palmate or costapalmate fronds (Fig. 1.3). The date palm genus *Phoenix* is an exception in this subfamily in having pinnate fronds. Leaf segments or leaflets of coryphoid palms are induplicate. Examples of palmate and costapalmate palms include the massive *Corypha* of Asia (Fig. 1.11) and the diminutive *Licuala* (Fig. 1.3d), most species of which are understorey plants in Asia and Oceania.
- Calamoideae. There are 21 genera of Calamoideae. The fruits of calamoid palms are unique, being covered with imbricate scales. Examples of calamoid palms include *Calamus* (Fig. 1.14), *Raphia, Metroxylon* (Fig. 1.5e) and *Salacca*.
- Nypoideae. The Nypoideae contain a single monotypic species, *Nypa fruticans*, a palm with prostrate dichotomously branched stems and long, reduplicate, pinnate fronds. The species occurs in brackish marshes in South-East Asia and the western Pacific (Colour Plate 1f).
- Ceroxyloideae. The Ceroxyloideae contain ten genera, including *Ceroxylon* of the Andes, among the tallest palms (Fig. 1.4f). *Chamaedorea* spp. are diminutive palms of the understorey of tropical forests of the western hemisphere, many species of which are popular ornamental plants for interiorscapes.

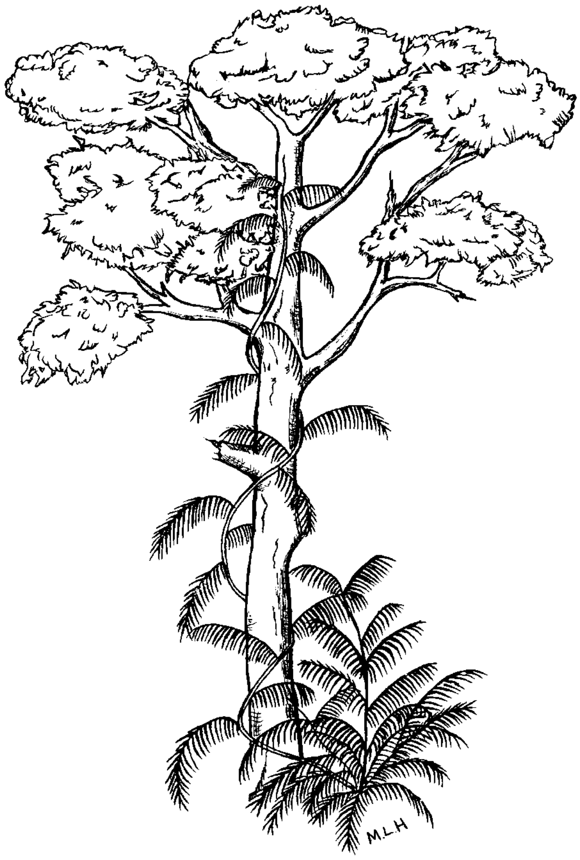

Fig. 1.14. *Calamus scipionum*, a climbing rattan palm of the Malay Peninsula, Sumatra and Kalimantan. Redrawn by Martha Howard from Sastrapradja *et al.* (1978).

- Arecoideae. The Arecoideae are a highly diverse subfamily with 123 genera, including coconut palm, *Areca catechu*, *Caryota* spp. (Fig. 1.5b), *D. lutescens* (syn. *Chrysalidocarpus lutescens*) (Fig. 1.5c), *Roystonea* spp. (Colour Plate 2d, Fig. 1.4a) and *Ptychosperma* spp. (Fig. 1.4b).
- Phytelephantoideae. The Phytelephantoideae are a small subfamily of three genera that occur from north-western South America to the Isthmus of Panama. Their unique fruits yield *tagua*, or vegetable ivory, which is used for artistic carvings.

There is a high degree of endemism in palms, the distribution of many species being restricted to very limited localities, such as islands. More than half of the known genera of palms contain five or fewer species and more than a third are monotypic (Tomlinson, 1979).

More thorough and detailed treatments of palm biology, morphology and taxonomy can be found in the following references: Corner (1966), Moore (1973), Tomlinson (1979, 1990) and Uhl and Dransfield (1987). Useful books on coconut palm culture include Menon and Pandalai (1960), Piggot (1964), Frémond *et al.* (1966), Bourgoing (1991), Mahindapala and Pinto (1991), Romney (1997) and Ohler (1999). Useful reference books on the culture of African oil palm are by Hartley (1988) and Ortiz and Fernandez (1994). Culture of date palms is reviewed by Nixon and Carpenter (1978). Books on the culture of other crop palms are cited in the discussions of these species in this book. There are many useful books on the identification, distribution, ecology, culture, products and landscape use of palms of the world, and by region and taxonomic grouping, e.g. McCurrach (1960), Braun (1968), Stevenson (1974), Hoyos Fernández and Braun (1984), Blombery and Rodd (1989), Dowe (1989), Balick and Beck (1990), Jones (1990a, b, 1995), Boyer (1992), Hodel (1992), Meerow (1992), Quero (1992), Dransfield and Beentje (1995), Henderson (1995), Henderson *et al.* (1995), Iorenzi *et al.* (1996), Kahn (1997) and Broschat and Meerow (2000). Internet web sites maintained by the International Palm Society, Fairchild Tropical Garden and many similar organizations are also excellent sources of information on palms.

Palms as Hosts of Insects

An important feature of palms as hosts of insects is that they are reliable as sources of food. Not only are they evergreen plants, but leaves of various ages, from young to old, are present on individual palms continuously throughout the year. Some insects prefer young foliage of palms, while other species prefer older foliage. The amount of food available likewise does not change materially, because the size of the fronds and the number of fronds in the crown stay basically the same, once the crown is fully formed (Howard, 1999b).

The shape of palm fronds offers particular advantages for small arthropods. The large size of most palm fronds makes them easy targets for wind-dispersed arthropods. The broad palmate frond, with the ridges and furrows formed by adjacent leaf segments, provides exceptional protection from the heaviest rains and the most desiccating sunlight, while the rooflike reduplicate leaflets of pinnate fronds are also well suited as shelters for small arthropods.

Here it is instructive to contrast palm fronds to leaves of dicotyledons. In the latter, the leaf laminae generally extend horizontally from the midvein, so the abaxial surfaces are generally the lower surfaces, although many leaves, such as those at the ends of branches, hang vertically so that the abaxial surfaces face horizontally.

In contrast, in palms the youngest frond extends vertically in the centre of the crown, so that its abaxial surface faces towards the horizontal. Even so, the very youngest fronds offer some degree of protection from above because of their corrugated nature. Better protection from above is provided as the frond ages and assumes a more horizontal position in the crown.

In September 1998, we initiated a simple test to demonstrate that palm fronds offer a high degree of protection from above. Rectangles 10 mm × 20 mm were cut from manila herbarium paper. These were glued with a water-soluble glue to abaxial and adaxial surfaces of horizontal fronds of *Licuala spinosa*, *Acoelorraphe wrightii*, *Coccothrinax argentata* (all with palmate fronds), *S. palmetto* (with costapalmate fronds) and *Dypsis cabadae*, *Ptychosperma macarthurii, Syagrus schizophylla* and *Dypsis lastelliana* (all with pinnate fronds). Over 200 mm of rain fell during the next 24 h. All of the rectangles on the abaxial surfaces remained dry and the glue hardened, while those on the adaxial surfaces were washed off by the rains. Surprisingly, when examined 110 days later, which included about 12 days with rain, the rectangular strips remained glued to the abaxial surfaces of two of the palmate palms (*L. spinosa* and *C. argentata*) and one of the pinnate-frond palms (*D. cabadae*).

Most species of insects that feed on palm fronds show a decided preference for the abaxial surfaces. This provides protection not only from abiotic factors, as noted above, but probably from many predatory vertebrate animals as well. Birds and lizards, for example, can easily alight on or jump to and search the adaxial surfaces of palm fronds that are in the horizontal position, but the abaxial surface cannot serve as a landing platform for most vertebrate animals. Also, it seems reasonable, but is conjectural, that the generally thicker wax layer of the adaxial surfaces of fronds is more difficult for insects to penetrate than the thinner wax layer of abaxial surfaces. Induplicate leaves (Fig. 1.6), such as in the date palm, might seem less suitable if it were assumed that the furrows formed by their laminae always faced skyward. In fact, this is true only of the medium-aged (horizontal) fronds, but insects that feed on foliage of *Phoenix* spp. often prefer the adaxial (‘upper’) surfaces (see, for example, *Parlatoria blanchardi*).

Insects seldom inhabit or rest on the highly flexible distal tips of leaflets, preferring the portions closer to the rachis, which are broader and more rigid and move less in the wind. They generally prefer the sheltering portions close to leaflet midveins, although many kinds of caterpillars chew at the margins of laminae.

Colonization may in many cases be facilitated because palms have relatively few large leaves instead of numerous small leaves. The ease by which an infestation can spread from a single fertilized female scale insect along a 3 m long coconut palm frond can be contrasted with the problem of colonizing individual conifer needles or the leaves of most dicotyledonous trees. The difference is that colonization of a palm frond can proceed without interruption, while natural barriers must be crossed to infest each needle of a conifer or leaf of a dicotyledonous tree.

Many insects associated with palm foliage are usually found only on palms that have reached some degree of height

Fig. 1.15. Coconut seedling bed, Jamaica.

and maturity, and are seldom found on young seedling palms (Fig. 1.15). Insects associated with young seedlings are often primarily associated with nearby low vegetation and are seldom found on taller palms.

Palm flowers produce great quantities of pollen, and all species are probably anemophilous to some extent. However, insects are the principal pollinators or, at least, highly important in pollinating some species, and this may be generally true throughout the palm family. Among the advantages for insects are that palm flowers are shallow, thus easily visited, usually pale in colour and occurring in conspicuous aggregations and sometimes highly fragrant or fetid, serve as copious sources of pollen and nectar and usually undergo anthesis during the day.

Insects that utilize flowers of palm species as nectar or pollen sources must often be opportunistic, since most species flower during a specific period of the year. During the rest of the year, other plants must serve as nectar or pollen sources. Hapaxanthic palms provide flowers only once in their lifetime. A palm that flowers repeatedly throughout the year is a more reliable nectar source. Arthropods with some degree of preference or specificity may visit flowers of such palms. In fact, African oil palm flowers follow this phenology and the several species of beetles identified as pollinators of this palm in its native home of West Africa are highly specific to it.

Only opportunistic insects may utilize fruits of most palm species. In contrast, some species of arthropods that attack fruits of coconut and oil palms, which are available continuously throughout the year, are virtually monophagous.

In many plants, abnormal growths, known as galls, may be formed when certain organisms invade their tissues and introduce chemicals that react with the plant's growth hormones. Plant galls appear in many different shapes and colours, each corresponding to the species that induces it. Most gall-makers are insects or mites. Insect gall-makers are usually species of Psyllidae, Aphididae and of certain families of Hymenoptera and Diptera. Some plant families, e.g. Fagaceae and Rosaceae, are rich in galls. Galls are rarely formed in palms. This may be partly due to the poor representation of gall-making taxa on palms. However, two gall-making families, namely Asterolecaniidae and Eriophyidae, which are well represented on palms, do not induce galls on their palm hosts. Palm aphids (*Cerataphis*) induce galls on dicotyledonous hosts, but not on their palm hosts.

Lacking cambium or bark, palms are not

attacked by cambium borers or bark beetles. The hard ‘rind’ created by the dense fabric of fibre-sheathed vascular bundles toward the outside of the stem has no counterpart in dicotyledonous trees. This is extremely hard in some species and undoubtedly offers a degree of protection to the stem. Although palms tend to store most of their carbohydrates in the trunk, palms in general are relatively free of trunk borers, and there are not many species of insects that bore living palm trunks. Some of those that do initiate attack in the relatively soft apical meristem tissue, from which they bore into the soft central tissues of the trunk. Palms growing under stress are most susceptible to most borers.

Like roots of dicotyledonous trees in general, roots of palms are not usually prime targets of attack by arthropods. They are not centres of carbohydrate storage, and tender growing tissue is located only at the tips. *Sagalassa valida* (Lepidoptera: Glyphipterigidae) is one of the few insect pests of palm roots. Its original hosts in South America are *Bactris* spp., but it has become a pest of African oil palm (Philippe *et al.*, 1999). Cicadas, whose immature stages feed on roots of diverse flora, and termites, which are subterranean insects that exploit any sources of cellulose they may encounter, are examples of insects that may feed on palm roots. Mealybugs are sometimes associated with roots of palms grown in containers, in which case a large surface area of the roots at the edge of the root ball is exposed to air, but mealybug–root associations may be less frequent in palms grown in the field.

Most knowledge of arthropod–palm relationships is derived from studies of pests of economically important palms, especially coconut, date- and African oil palms and, increasingly, the wide array of palm species grown as ornamental plants. Insects associated with wild palms are the least studied. Lepesme (1947) commented that the insect fauna of about 85% of the palm genera was completely unknown, and the present situation is probably similar.

Whether we compare different species of palms in the same region, palms of different regions or even palms and some arborescent monocotyledons other than palms (Fig. 1.16), we may often find strong similarities in their insect fauna. Hemiptera, Coleoptera and Lepidoptera are the best-represented orders among palmivorous insects, and within these orders certain families are especially well represented. Taxa that are represented by one or a few species in one region usually have a similarly low representation in other regions. Also, there are some small families restricted to palms that are present in several regions. Finally, the distribution of some species of insects on palms has been extended via human traffic, and these are now found in the insect fauna of palms in more than one region. Thus, one may expect to find similarities in, for example, the insect communities on coconut palms in Fiji and Florida and on date palms in Morocco.

The scope of this book does not include the fascinating world of insects that frequent palms for resources that these plants provide indirectly. Detritus that accumulates in leaf axils supports many saprophagous and mycetophagous insects. Leaf axils of some palms hold water, thus creating aquatic microhabitats (phytotelmata) for aquatic insects (Paine, 1943; J. Howard Frank, personal communication). Insects such as Psocoptera are found on trunks and older leaves, where they presumably feed on algae or mosses. Many insects feed on honeydew produced by palmivorous Hemiptera.

Economic Importance of Palms

Palms have many uses (Balick, 1988; Balick and Beck, 1990; Johnson, 1998). Two species of palms are foremost in importance in international commerce: the coconut palm and the African oil palm. Third in international importance is the date palm. Most of what is known about the insects associated with palms has come from research on these three species.

Coconut palm (Colour Plate 1a, b, Fig. 1.1), referred to by Michener (1959) as ‘that

Fig. 1.16. Arborescent monocotyledons other than palms. (a) Dragon-tree, *Dracaena draco* (Agavaceae), Tenerife, Canary Islands. Courtesy of Don Antonio González. (b) *Pandanus utilis* (Pandanaceae), Fort Lauderdale. (c) Traveller-palm, *Ravenala madagascariensis* (Strelitziaceae), Fort Lauderdale. (d) Banana, *Musa* × *paradisiaca* (Musaceae), Dominica, Lesser Antilles. Plastic bag protects fruits from insects.

one essential, that miraculous sustainer of tropical life', was listed as one of the 20 most important crop species upon which human life depends (Mangelsdorf, 1966; Vietmeyer, 1986). Since remote times, peoples of the Malay Peninsula and the South Pacific have cultivated it. A transportable water source, coconuts probably provided the means for early peoples to wander the Pacific and populate its islands. From its region of origin in the Pacific, the coconut palm was disseminated by humans throughout the tropical lowlands of the world. It has a recorded history of 2000–3000 years in Sri Lanka and southern India. From there it was distributed along the coasts of Africa. In the 1500s, the Spanish and Portuguese brought it from West Africa to the Caribbean and coasts of tropical America. Some evidence suggests that coconut palms may have been present on the Pacific side of the Americas before the arrival there of Europeans (Beccari, 1917; Hill, 1929; Purseglove, 1968; Harries, 1971, 1978, 1990).

Coconut palms are currently grown commercially in more than 90 countries on a total area of 12 million ha (Persley, 1992), i.e. an area approximately equivalent to that of Nicaragua. About 85% of the coconut crop is grown in Asia and Oceania. Major producers are the Philippines, Indonesia, India, Papua New Guinea and other Pacific islands and Sri Lanka. Major producers in the Americas are Mexico and Brazil. Tanzania and Mozambique are major producers in Africa (Persley, 1992). In addition to its use as a crop tree, it is one of the most common plants grown around any residence or settlement in the humid lowland tropics. Being perhaps the most esteemed palm for creating a tropical look in the landscape, it has found a home as an ornamental plant in many localities outside its commercial range. It thrives and produces fruits abundantly in southern Florida. It grows well, but is less productive, in Bermuda and the Canary Islands. In Australia, it grows on both eastern and western coasts as far south as 29°S, but is productive only to 25°S (Mike Foale, personal communication). Its latitudinal distribution on both coasts of South America is similar. Distinct varieties of coconut and other major economic species are recognized (Box 1.2).

The most important product of the coconut palm is the coconut, i.e. the fruit (Colour Plate 3a, b, Fig. 1.10). The fruit consists of a thick husk, composed of long, tough fibres enclosing the shell, the latter being analogous to the stone of a stonefruit. Coconut shell is one of the hardest botanical substances known (Corner, 1966). Interior to the shell is the endosperm, which consists of a white fleshy layer (the kernel) and an almost clear liquid contained within a cavity.

Coconut kernel serves as an important food source in the tropics. In non-tropical countries, it is consumed principally in confectionery products. Fresh coconut kernel is about 50% moisture and deteriorates rapidly unless dried to form copra. Dried to 15% moisture, the composition of kernel is about 4% crude fibre, 6% protein, 15% carbohydrates and 60% oil. Copra production is the principal activity of the coconut industry. The world production of coconuts is estimated at 50 billion year^{-1}, 55% of which is converted into copra (Punchihewa, 1995). Coconut-oil is one of the world's most important vegetable oils, used in the manufacture of many pharmaceutical, industrial and food products (Fig. 1.17).

The fibres of the husk (coir) have excellent qualities for making mats, ropes and

Fig. 1.17. A sampling of coconut products.

Box 1.2. Varietal names of palms.

> No one definition has yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species… The term 'variety' is almost equally difficult to define; but here community of descent is almost universally implied though it can rarely be proved.
>
> (Charles Robert Darwin (1809–1882), English naturalist, *The Origin of the Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 1859)

In the relatively few species of palms grown as crop plants, agriculturists have recognized naturally occurring distinct populations of individuals or, in some cases, have selectively bred such groupings. These are referred to as varieties, cultivars, ecotypes and populations by different authors and in reference to different kinds of palms. For simplicity, we shall refer to them all as varieties.

The many varieties of coconut palm fall into two general types, namely tall and dwarf (Narayana and John, 1949). Coconut palms of the tall type have robust trunks, long fronds with thick petioles and large coconuts. They begin producing fruit at 7–10 years of age. The dwarf type has a more slender stem, shorter fronds with thin petioles and smaller coconuts, which they begin to produce as early as 4 years of age. Mature palms of the tall type have a maximum height of about 25 m, compared with 15 m in the dwarf type (Jack and Sands, 1929; Romney, 1997).

There are many varieties of each of the two types. As with many crop plants, the varieties of coconut often carry place-names, sometimes combined with a descriptive term (e.g. 'Laguna Tall', 'Jamaica Tall', 'Rangiroa Tall', 'Fiji Dwarf', 'Malayan Red Dwarf', 'Malayan Green Dwarf', etc. These may or may not reflect their true origins.

Some entities named as separate varieties may in fact be synonymous with other varieties. For example, the variety known as 'Malayan Red Dwarf' in Jamaica and many other countries is referred to in Florida as the 'Malayan Golden Dwarf' (Colour Plate 3a). Apparently this same variety is called 'El Dorado de la India' in Cuba (Jack and Sands, 1929; Harries, 1971; McCoy *et al.*, 1983; Romney, 1997).

All species of *Phoenix* are dioecious and therefore individuals must be cross-pollinated. But date palm varieties have been developed over the centuries in different oases and kept pure by vegetative propagation from offshoots. Several systems of classification of varieties are used, all based on characteristics of the fruit. Some growers classify date varieties as yellow or red, according to the colour of the fruits just before ripening. More commonly, date varieties are classified as: (i) wet, semi-dry or dry; or (ii) soft or hard, reflecting their physical character when ripe for harvest (Popenoe, 1973; Nixon and Carpenter, 1978).

Most date varieties have names from Arabic, Berber, Farsi and other North African, Middle Eastern and southern Asian languages, which are usually descriptive of characteristics of the variety, e.g. 'Deglet Noor' (translucent seedling), 'Halawy' (sweet), 'Medjool' (unknown, or possibly firm of flesh), 'Raghawi' (which makes one's mouth frothy), etc. (Popenoe, 1973).

Three different forms of African oil palm are recognized, based on fruit characteristics. These are the tenera (thin-shelled), dura (thick-shelled) and pisifera forms The latter term means 'pea-bearing' and refers to the nature of the endocarp. Within these general forms are many selections.

Varieties are also recognized in the peach palm (*Bactris gasipaes*), areca-nut palm (*Areca catechu*) and other palms grown as crop plants.

similar products. Coconut palms grown in southern India and Sri Lanka are a particularly important source of fibre products. The shell, which is used to fashion drinking vessels, scoops, etc., for local use, is exported for making fine charcoal. The liquid portion of the immature endosperm, i.e. coconut water, serves as a refreshing beverage, generally consumed directly from the coconut (Colour Plate 3b). On some islands, it is the only source of fresh water. Sales of coconut water are an important business in many tropical countries. Lumber and many other 'wood' products are made from the stem (Fig. 1.18; Cornelius, 1973; Purseglove, 1985; Persley, 1992; Punchihewa, 1995).

The African oil palm, native to West Africa, is grown as a crop plant there and in extensive plantations in tropical Asia

Fig. 1.18. House constructed of coconut palm 'wood' with roof thatch of fronds of *Nypa fruticans*. Courtesy of Philippine Coconut Authority.

and the Americas (Colour Plates 2b and 3c). Two kinds of oil are obtained from it. The pulp (mesocarp) of the fruit yields the product known as palm-oil. A different product, palm-kernel oil, which is extracted from the kernel, is similar in composition to coconut-oil. African oil palm can produce up to about 9 t ha^{-1} $year^{-1}$. This is about three times the production of coconut. In contrast, annual oil-crop plants, such as groundnuts and soybeans, seldom produce more than 2 t oil ha^{-1} $year^{-1}$. The oils from African oil palm and coconut are used in the manufacture of pharmaceuticals, cosmetics, soaps and a variety of other industrial products, including synthetic resins, rubber substitutes, insulating materials, safety glass, nitroglycerine, animal feeds and even a special lubricant for jet engines. Coconut-, palm- and palm-kernel oil are used in certain food processing, but this accounts for only a small percentage of the total consumption of these oils, and in most countries they are only a small part of the saturated fats in the diet (Cornelius, 1973).

The major product of the date palm is the fruit, known as the date (Figs 1.19 and 1.20). It is the fleshy mesocarp that is consumed. Date palms, cultivated in the

Fig. 1.19. Date fruits. Saudi Arabia. Strings help support weight of mature fruits. Courtesy of Dorothy Miller and Aramco World.

Fig. 1.20. Date harvest, Saudi Arabia. Courtesy of Dorothy Miller and Aramco World.

Middle East and North Africa for at least 6000 years (Zohary, 1982), are a main staple in the diet of these regions. They have probably been grown in northern India and Pakistan since prehistoric times, but are a less important part of the culture (Popenoe, 1973). They have been cultivated in Spain at least since the Middle Ages (Ferry and Greiner, 1999; Frutos and Rodríguez, 1999). A small but important date industry, centred in the arid (but irrigated) Coachella Valley of southern California, was established at the end of the 19th century (Nixon and Carpenter, 1978).

Many additional species of palms furnish products that are indispensable in local economies and, in many cases, important in international commerce. The diversity of palm products is amazing (Box 1.3).

Palm 'wood' is obtained mostly from the relatively hard periphery of the stems. The especially hard wood of palms such as *Astrocaryum standleyanum* (known as black palm), *B. gasipaes*, *Borassus flabellifer* and *Iriartea deltoidea* can be cut into durable planking, flooring and other types of lumber (which is drilled and joined by pegs or screws, as it cannot be effectively nailed). The entire stems of some palms are used for poles, posts and piers.

Rattans are vine-like palms that climb trees in the forests of tropical Asia and Africa (Fig. 1.14). They are also grown horticulturally. Their smooth, thin stems of up to 200 m long are strong and supple. Rattans include many species each of *Calamus* and *Daemonorops*, the two most important genera. Entire stems of about 2.5 cm in diameter are used in 'bentwood' furniture. Backings of 'cane' furniture are woven of splints from the outer rind of various rattan species. The softer inner core may be used in 'reed' furniture. In tropical America, *Desmoncus* is a genus of climbing palms somewhat resembling and filling a niche similar to that of the Asian rattans, but not equal to them as a source of stems of desirable qualities (Dahlgren, 1944). Certain palms of Yucatán, Mexico, are potential rattan substitutes (Orellana *et al.*, 1999).

Palm fronds are used for roof thatching throughout the tropics, each locality having its preferred species (Colour Plate 3f, Fig. 1.18). Fashioning these roofs, with either palmate fronds or the pinnae of pinnate fronds, takes skill. Some thatched roofs last up to 15 years (Bradley Bennett, personal communication). The large fronds with entire margins of *Manicaria* are preferred in much of the Amazon region. The palmate fronds of the relatively small palm, *Lepidocaryum gracile* (syn. *Lepidocaryum tenue* var. *gracile*) are the source of the most common thatch in Peru (Kahn, 1997). *Nypa fruticans* is a common source in the Malay Archipelago and western Pacific (Dahlgren, 1944; Tinambunan, 1992). On many Pacific islands, coconut palms are the only palm abundant enough to provide material for thatching. In the Caribbean, fronds of *Thrinax* spp. are highly desirable, but palms of *Sabal* spp.

Box 1.3. A use for every day of the year.

> The young leaves of the coconut wave.
> Wave, wave, they wave.
> The leaves of the rattan cut and twist.
> Twist, twist, cut and twist.

(From a traditional Philippine ceremonial dance, in Willard R. Trask, 1966,
The Unwritten Song, Macmillan, New York)

The diversity of products derived from coconut palms is well known. According to Indonesian folklore, there are as many uses for this palm as there are days of the year (Punchihewa, 1995). A sample of some of the less well-known products derived from coconut and other palms follows.

People of the Amazon region are astute at finding uses for diverse palms: corks for demijohns are cut from the petioles of *Mauritia flexuosa*, blowpipes are made from the slender stems of *Iriartea deltoidea* and *Bactris gasipaes* and arrowheads are made from the hard 'wood' of *Wettinia* spp. and *Socratea exorrhiza* (Anderson, 1978; Barfod and Balslev, 1988; Kahn, 1997). Small bows are made from the hard but springy wood of *B. gasipaes* and large bows from *Astrocaryum* sp. (Beckerman, 1977; Bennett, 1992).

Coconut shell, one of the hardest known plant materials, is processed to make carbon electrodes for batteries (Banzon, 1984). The same material finds a whimsical role in *la quiebra de cocos* (coconut cracking), a game played for generations in Venezuela during the Easter season. Players select coconuts to strike against the coconuts of other players. The winning coconut is the one that survives without cracking (Braun, 1968).

Coconut fibre is sold commercially as an additive to be incorporated in the surface of horse-riding arenas for increasing traction and durability (Dulae, 1996). A horticultural use is as an excellent amendment in potting soil (Meerow, 1992, 1994; Abad *et al.*, 1993).

Coconut husk was shown to be effective in absorbing dyes from solutions and thus is potentially useful for cleaning waste waters discharged from certain kinds of industrial facilities (Low and Lee, 1990).

In his study of folk-ways of Bali, Miguel Covarrubias (Covarrubias, 1937) described a unique method, utilizing a half coconut shell with a hole drilled in it, for timing certain tasks. The duration of the task was measured against the time it took for the shell to fill up with water and sink.

Coconut water is used in medical research in culture media for studying protozoa (Trypanosomatidae) that cause Chagas' and similar diseases (Marzochi *et al.*, 1988, 1996).

In the Philippines, diesel engines were run on crude coconut oil during the 1940s and, in recent times, diesel has been blended with 5–10% coconut-oil as a part of a national energy conservation programme. In one test, an Isuzu diesel-powered jeepney was run on coconut-oil for 10,500 km (Banzon, 1984). However, engines run on pure coconut-oil are difficult to start in cold temperatures and filters are easily clogged. Processing of the coconut-oil can remedy these difficulties (Arida *et al.*, 1984).

The flower of *Pholidocarpus majadum*, a large palm of eastern Kalimantan, is used to add a pleasant aroma to rice (Sastrapradja *et al.*, 1978).

The hard, heavy trunks of *I. deltoidea*, perhaps Ecuador's most common palm, are used as support poles for banana plants in that country's extensive banana plantations (Pedersen and Balslev, 1992).

Palm trunks can be split lengthways and the softer inner core hollowed out, leaving the harder rind. In Vanuatu, trunks of *Veitchia macdanielsii* (syn., *V. arecina*) are thus fashioned into sections of aqueducts that may carry water tens of kilometres. The practice is centuries old (Dowe, 1996).

For protection from the midday sun, the Warao people of the Orinoco delta (Venezuela) fashion a type of cap from the pouchlike cover of the spathe of the inflorescence of *Manicaria saccifera*, a palm widely distributed in tropical America (Wilbert, 1980). They use the large, entire-margined fronds as sails for canoes (Kahn, 1997).

In Elche, Spain, a traditional craft involves covering newly emerged fronds of date palms so that they remain chlorotic. These fronds, called *palma blanca* (white palm), are widely marketed in Spain for use on Palm Sunday (Gómez i Vives and Ferry, 1999b).

Some palms are even musically inclined: in Ecuador, stems of *I. deltoidea* and *B. gasipaes* are used for marimba keys (Barfod and Balslev, 1988).

are usually more common. *Sabal palmetto*, which in Florida has provided thatching since remote times, has a modern role in roofs of picturesque kiosks at luxury hotels and other resort areas. Ecotourism in tropical countries has created a market for thatching for lodges (Bradley Bennett, personal communication).

Frond material of many different species of palms are used in weaving mats, hammocks, hats, baskets, bags and similar products in almost all tropical countries. Strips of palmate fronds and midveins of pinnae of pinnate palms are commonly used. Coconut palm, *A. standleyanum*, *Attalea*, *Corypha* and *Mauritia flexuosa* are among the many palms that serve as sources of useful fibres. Raffia is a fibre used in weaving and cordage obtained by pealing the adaxial epidermis of the frond of *Raphia ruffia*, of Madagascar. Frond midribs of various palms are used in brushes and brooms. Splints for weaving can be separated from petioles of *Corypha*, *Sabal* and other palms.

Piassava refers to petiole fibres (i.e. vascular bundles) that hang as a long fringe from the petiole scars on the trunk of some palm species after the petiole falls. Useful for mats and many other products, it is obtained from *Leopoldinia piassaba*, *Attalea funifera* and other palms of South America (Dahlgren, 1944; Putz, 1979; Kahn, 1997).

The spathes that enclose the inflorescences of palms are not overlooked. They furnish scoops, trays and other utensils, the large spathes of *Maximiliana* being a notable example (Dahlgren, 1944).

Chamaedorea tepejilote is a common forest palm of Central America and northern South America, which is cultivated in Guatemala for its edible inflorescence. Known as *pacayas*, the inflorescences are common in Guatemalan markets and a minor amount is exported (Castillo Mont *et al.*, 1994).

Fruits of many palm species are edible. The quality and palatability of fruits vary from species to species. Notable palms additional to coconut, date and African oil palm that are cultivated principally for their fruit are *Bactris gasipaes*, *Salacca zalacca* and *Borassus flabellifer*.

Bactris gasipaes, known as peach palm, has been cultivated for thousands of years in the American tropics and is known only in cultivation (Mora Urpí *et al.*, 1997). It is one of the most important crop plants in local areas of the region, e.g. the lowlands of Ecuador (Pedersen and Balslev, 1992). The fruits, which superficially resemble peaches, can be consumed fresh, cooked or canned. They are said to contain carbohydrates, protein, oil, minerals and vitamins in nearly perfect proportions for the human diet (Anon., 1975; Vietmeyer, 1986). A portion of the fruits are used to make *chicha*, a fermented beverage consumed since ancient times.

As an indication of the importance of peach palm, the Instituto Nacional de Investigaciones Agropecuarias of Ecuador has a germplasm collection of 4000 varieties of this species (Pedersen and Balslev, 1992).

The salak (*S. zalacca*) bears a pear-shaped fruit, which 'tastes like pineapple, and is covered by the most perfect imitation snakeskin' (Covarrubias, 1937). The fruits are widely marketed in tropical Asia, where it is native (Colour Plate 3e).

The palmyra (*Borassus flabellifer*), ubiquitous in India, yields clusters of fruits weighing 22.5–45 kg. Red-brown to orange when ripe, they taste like mangoes but are somewhat oily (Dahlgren, 1944). *Borassus aethiopum* (Fig. 1.3c) is a similar species, of immense importance in local economies in West Africa (Johnson, 1984).

Fruits of many wild palms are consumed locally. In tropical South America, these include *Aiphanes* spp., *Ammandra dasyneura*, *Astrocaryum aculeatum*, *Jessenia* spp., *Maximiliana maripa*, *Mauritiella aculeata*, *M. flexuosa* and *Phytelephas tenuicaulis*. Juice is extracted from fruits of *Jessenia bataua*, *Oenocarpus* spp. and *Euterpe oleracea* (Braun, 1968; Atchley, 1984; Pedersen and Balslev, 1992; Kahn, 1997).

As sources of vegetable oil, several species additional to African oil palm and coconut are important. These include the babassu (*Orbignya martiana*), which produces an abundance of fruit containing up to 70% oil (Anon., 1975). This palm is an important resource for over 300,000 families in the state of Maranhão, Brazil (Pinheiro and Ferro Frazão, 1995). Additional species of *Orbignya* are rich sources of oil, as are *Astrocaryum* spp., *Scheelea* spp., *Oenocarpus* spp., *Jessenia* spp. and many other palms.

The extremely hard endosperm of *Phytelephas* has a consistency reminiscent of ivory, for which reason it is called 'vegetable ivory'. It was formerly a major export item from Ecuador and used extensively for manufacturing buttons. Plastics have largely supplanted this use. It is now used for carvings, some of which show exquisite skill (Barfod, 1989; Dalling *et al*., 1996). The hard endosperm of some species of *Metroxylon* (syn. *Coelococcus*) are similarly carved.

Fruits and other parts of plants have biologically active compounds, i.e. that may be either toxic or medicinal at certain concentrations. The toxicity of a biologically active compound depends upon its concentration. In fruits of some palms, naturally occurring concentrations of some substances are toxic. Needle-shaped crystals of calcium oxalate in the mesocarp cause dermatitis in people that handle some palm fruits, and the concentration of these differs widely among species (Broschat and Latham, 1993).

In recent years, saw palmetto, *Serenoa repens*, has become one of the best-known medicinal plants. Medical researchers have shown that an extract of the fruits (referred to in the trade as 'berries') is effective in treatment of benign prostatic hyperplasia, a malady common in men of 50 years of age or older. This is an example of an ancient folklore herbal remedy that has been validated by science (Elehambry and Hansel, 1969; Braeckman, 1994; Carraro *et al*., 1996; Plosker and Brogden, 1996; Bombardelli and Morazzoni, 1997). Currently, about 6.8 million kg of the fruits are harvested per year in Florida. Although *S. repens* is the most abundant palm in its native range in the south-eastern USA, fruit collecting from wild palms poses a conservation problem, since they are an important food for native black bears and several other forms of wildlife (Bennett and Hicklin, 1998). A possible solution may be to cultivate saw palmettos in 'orchards'.

Trachycarpus fortunei has long been considered to be a medicinal plant in China, and several compounds from this species have been researched in modern times (Essig and Dong, 1987). The roots of *Syagrus inajai* are used in traditional medicine in Amazonia (Kahn, 1997). Undoubtedly, many compounds of medicinal value await discovery in the palm family.

The fruits of the areca-nut palm, *Areca catechu*, are prepared by wrapping parings of the palm fruit in the leaf of a vine, *Piper betle*. These are consumed in some parts of Asia and Oceania as betel-nuts, a mild stimulant. The palm is thus an economic plant and the horticulture, pests and diseases of this palm are subjects of scientific research. Unfortunately, consumption of betel-nuts may adversely affect human health (Winstock *et al*., 2000).

The hearts (buds, or apical meristem) of most palm species are edible and the flavour and consistency of some species, including coconut palm, *Astrocaryum jauari*, *Sabal palmetto, Euterpe* spp., *B. gasipaes* and others, are superior. A disadvantage of this use of palms is that destruction of the meristem is fatal. *Bactris gasipaes*, however, is a cespitose (multiple-stemmed) palm and thus orchards can be sustained by removing only selected stems at harvest.

Hapaxanthic palms, such as sago palm (*Metroxylon sagu*), accumulate starch in the parenchyma of the stem for 10–25 years. The peak quantity of starch just prior to flowering may amount to 250 kg. Thought to be native to New Guinea and the Moluccas, the sago palm is naturalized and is a main source of carbohydrates throughout South-East Asia. The starch is harvested by felling entire palms (Sastrapradja *et al*., 1978). After starch production, the palms can be used for palm-weevil grub production (see Box 5.3). The palms are thus far abundant, but, as pressure is placed on this resource, steps should be taken to ensure their conservation.

The sap of various species of palms may be fermented to make beverages, such as beer or wine, variously known as toddy, *tuba* and *sagueir* (Siebert, 1999). Distillation of fermented sap yields arrack, a potent liquor. Sap may be boiled down to jaggery (unrefined palm sugar). In India, the wild date palm (*Phoenix sylvestris*) is tapped by clearing an area of the crown of fronds and cutting a cavity, where the sap collects. The flow can be kept going for several weeks. The Canary Islands date palm (*P. canariensis*) is similarly tapped in the Canary Islands. Other palms, e.g. *Borassus flabellifer*, are tapped by cutting the stalk of the male inflorescence and bruising it by gentle malleting for several days (Romera, 1968). The black sugar palm, *Arenga pinnata*, in tropical Asia and the African wine palm, *Raphia vinifera*, are tapped in this way. A somewhat similar method is used to tap coconut palms in the Philippines. Cut inflorescences of nipa palms (*N. fruticans*) yield 1–2 l sap day^{-1}. Extensive swamps populated by this palm border many islands and coastal areas of Asia. Since the palms are of short stature, the sap can be collected without climbing and can usually be transported by water. Nipa swamps are a potentially rich source of energy (Dahlgren, 1944; Corner, 1966).

The fronds of the carnauba wax palm (*Copernicia prunifera*) have an unusually thick coating of wax, which is thought to be an adaptation to its arid habitat in north-eastern Brazil. Harvesting is carried out by pruning the fronds and putting them through a process that loosens the wax. Carnauba wax is much esteemed for furniture, vehicle and floor polishes, and was formerly used extensively in gramophone records (Dahlgren, 1944; Johnson, 1998).

Palm flowers are generally visited by bees, and some palm species are considered important melliferous plants. In Florida, ‘palmetto honey’ is preferred by many people.

Finally, an important category of use of palms is as ornamental plants. No more than about 4% of the species are of widespread importance in environmental (i.e. ornamental) horticulture. These are species that are relatively easy to propagate, in most cases fast-growing, adaptable to urban landscapes or interiorscapes and reasonably resistant to pests and diseases. However, amateur and professional palm growers, motivated by curiosity and enthusiasm for these plants, have brought a large diversity of species under cultivation in public botanical gardens and private collections of living palms. For example, the living palm collection of Fairchild Tropical Garden in Miami, Florida, contains 193 genera and 500 identified species of palms All palm species have potential value as ornamental plants, as each is interesting and attractive in its own way.

2

Defoliators of Palms

> There is no more effective eating machine than the caterpillar devouring a leaf; and no more effective reproducing machine than the female moth.
>
> (Howard Evans, American entomologist. *Life on a Little-known Planet.* University of Chicago Press, 1948)

There are three general ways in which insects utilize living leaves of plants as a food resource: (i) by rasping the exterior surfaces so as to release plant juices and imbibe them; (ii) by piercing into the tissue to feed on plant juices; and (iii) as defoliators, i.e. by chewing and consuming the tissue itself.

Defoliators possess at the anterior of the mouth a pair of unsegmented and strongly sclerotized appendages, known as mandibles (Fig. 2.15c). Mouth-parts of this type are often referred to as 'chewing' or 'biting' mouth-parts. Insect mandibles operate transversely (i.e. swinging like gates) to bite, cut and crush material and, in insects such as certain Hymenoptera (Fig. 2.8), mandibles are used to hold objects so they can be moved and positioned, to shape nest material, groom antennae and legs, etc. Mandibles are tapered toward the mesal edge, which typically is serrated, facilitating cutting action.

Defoliators conform to the basic plan of the class Insecta as that of an animal that eats solid food. The mouth-parts of those that feed on liquids, e.g. the tubelike mouth-parts of adult Lepidoptera, the piercing–sucking mouth-parts of Hemiptera, the sponging mouth-parts of some Diptera, etc., are considered specialized mouth-parts that have evolved from chewing mouth-parts.

The presence of chewing mandibles is characteristic of the majority of the orders. In endopterygote orders, in which the imagos have specialized mouth-parts (i.e. Lepidoptera, Diptera), the immature stages have chewing mandibles or very similar structures.

For hundreds of millions of years, myriad pairs of insect mandibles have constituted a great natural force that has shaped life on this planet. The mandibles are typically the strongest and hardest major structures of insects, enabling different species to bore dense wood, penetrate hard seedcoats, lacerate the cuticles of arthropod prey and construct galleries in compacted soil. They are ideal tools for chewing leaf tissue.

As food sources of insects, palm fronds have the advantages of abundance and availability throughout the year, but a disadvantage is their fibrous nature. Basically, the photosynthetic tissue of palms is contained in extremely large leaves, which arise from a central stem, rather than, for example, small leaves supported by woody branches that seek the sunlight, as in arborescent dicotyledonous plants. Because they are required to support their own weight and sometimes strong wind loads, palm fronds tend to require relatively strong internal support, which is provided by a relatively high density of sclerenchymous fibres. The fibres and thus the weight of a palm frond are concentrated in the petiole and rachis. In most palms, these are exceedingly tough and strong and yet flexible. The long, narrow pinnae of pinnate palms are supported by lengthways-running fibres, which are well distributed across the lamina, although concentrated in the midveins and, to a lesser extent, in marginal veins. Leaf segments of palmate palms are similarly fibrous.

The fibrous nature of palm-leaf tissue would appear to be a challenge to mandibulate phytophagous insects, and could be a major reason why representatives of relatively few insect orders have evolved adaptations to utilize palms.

The major orders of chewing insects that are of primary significance as plant defoliators are the exopterygote orders Orthoptera and Phasmida and the endopterygote orders Lepidoptera, Coleoptera, Diptera and Hymenoptera. All but the last two orders are significant on palms. The order Lepidoptera is the most widely represented on palms in different regions and contains the larger number of pestiferous species. Second in importance is Coleoptera. Several species of Orthoptera and Phasmida are defoliators on palms in Oceania, and species of Orthoptera are occasionally pests of palms elsewhere. Sawflies (Hymenoptera: Symphyta) are the main group of Hymenoptera that feed on plants. They are unknown on palms. In the American tropics, leaf-cutter ants (Hymenoptera: Formicidae) are sometimes defoliators of palms and many dicotyledonous trees. However, they do not actually consume leaf tissue but utilize it to culture a fungus, which is their food source. Many Diptera attack plants, usually as fruit flies, stalk borers or leaf-miners. Some fruit flies attack palm fruits (Lepesme, 1947), but otherwise the order is not represented by phytophagous insects on palms.

Lepidoptera

Forrest W. Howard and Reynaldo G. Abad

Imagos in the order Lepidoptera are clothed with overlapping flat setae, or scales (Fig. 2.1). Most Lepidoptera imagos have elongate bodies and functional wings, which are large in relation to the body, and functional mouth-parts, with the galea of the maxillae greatly elongated, grooved internally and coupled to form a tubular proboscis, through which liquids are drawn, including plant nectars, water from puddles and many other liquids (Scoble, 1992). The larvae of most species are phytophagous.

Systematic and biogeographical considerations

The Lepidoptera, which include the butterflies and moths, are one of the largest orders of insects, with perhaps 200,000 described species and as many as 500,000 described and undescribed species.

Butterflies and moths have long been recognized in popular cultures as two distinct but related kinds of insects, e.g. *les papillons* and *les papillons de nuit*, respectively. Earlier entomologists placed butterflies in the suborder Rhopalocera (clubbed antennae) and the moths in the suborder Heterocera (variable antennae), and an impression that they are the two major and more or less equal divisions of the Lepidoptera persists among non-specialists. Perhaps this is partly due to biased observations: although butterflies constitute only one of 41 superfamilies of this order and perhaps about 10% of the species, they are diurnal and conspicuous; moths predominate, but they are nocturnal and a large proportion of them are small and drab.

In another earlier classification, three suborders were recognized, namely the

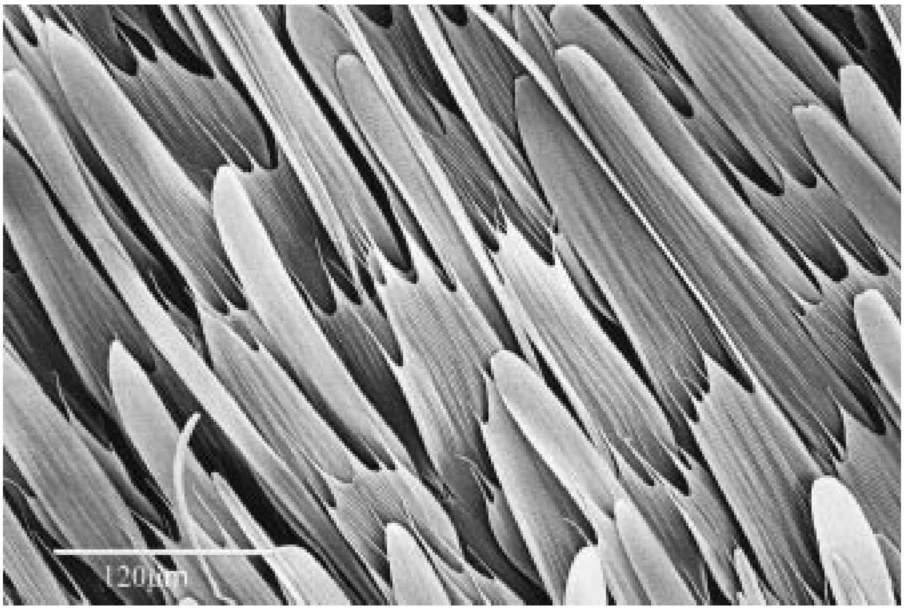

Fig. 2.1. Scales (SEM view) of the imago of *Thosea* sp. (Lepidoptera: Limacodidae), a palmivorous species of the Philippines. The scales that cover the body and wings of imagos of Lepidoptera are modified (flattened) setae, which are unique to this order of insects.

Jugatae, Frenatae and Rhopalocera, the first two of these suborders being separated on the basis of structures that couple the fore- and hind-wing, and the Rhopalocera constituting the butterflies, as in the system previously mentioned.

According to a recent concept (Scoble, 1992), the more primitive families, which correspond roughly to the Jugatae, are referred to as monotrysian, while two advanced assemblages are the lower and higher Ditrysia. (The term 'Ditrysia' refers to the presence in the females of two genital apertures, one that receives the male intromittent organ during copulation and the other through which eggs pass during oviposition. Monotrysian Lepidoptera use one aperture in both functions.) The lower and higher Ditrysia include 98% of known species of Lepidoptera.

The lower Ditrysia, together with the monotrysian groups, constitute what some authors refer to as the Microlepidoptera. They are relatively small, often dull brown or greyish-coloured moths and their caterpillars have a proclivity towards concealed feeding as borers, web-makers or leaf-miners. The higher Ditrysia are known by some authors as Macrolepidoptera. This assemblage includes larger, often more colourful, moths, such as the Geometridae, Noctuidae, Saturniidae, Hesperiidae and the superfamily Papilionoidea.

Thus, the majority of species of Lepidoptera, i.e. moths, are generally nocturnal. The antennae are usually filiform, but there are variations, such as pectinate antennae, and the antennae of the males of many species are plumose. When at rest, the wings are tectiform (rooflike) or wrapped around the body.

In the butterflies, the terminal segments of the slender antennae are dilated, giving them a club shape. They generally have large, colourful wings and are day fliers. The wings of Papilionoidea are held out horizontally or vertically when at rest.

Of the 41 superfamilies and 107 families of Lepidoptera recognized by Scoble (1992), ten families contain species considered to be significant defoliators of palms. In fact, only Limacodidae, Hesperiidae and perhaps Nymphalidae could be said to be amply represented by species on palms. This seems a small representation of Lepidoptera for a large plant family that is distributed throughout the warm regions of the world, where insect diversity is highest. In contrast, species of at least three times as many families of Lepidoptera have been reported as defoliators of one dicotyledonous genus, *Quercus* (Fagaceae), which has about 300 species (Covell, 1984; Johnson and Lyon, 1991). Of course, some collecting bias may be assumed, since *Quercus* is of immense economic interest and is distributed mostly in the north temperate zone. Large families of Lepidoptera that are well represented among arboreal defoliators, but not among palm defoliators, include the Geometridae (loopers) and Noctuidae, which together contain about 25% of known Lepidoptera (Scoble, 1992). Additional large families that are often associated with dicotyledonous trees but rarely, if at all, among palm defoliators are the Tortricidae, Gelechiidae and Gracillariidae. Several species of Arctiidae and Lymantriidae, large families with many tree defoliators, are listed by Lepesme (1947), but these are rarely mentioned in other studies of insects of palms. In summary, fewer families of Lepidoptera are represented on palms than might be expected, given such advantages to insects as the continual availability of foliage throughout the year and the excellent protection offered by the fronds. The superfamilies and families of importance on palms are listed in Table 2.1.

In tropical Asia, Oceania and Africa, eight families are important on palms, namely Nymphalidae (subfamilies Amathusiinae and Satyrinae), Hesperiidae, Psychidae, Oecophoridae, Agonoxenidae, Zygaenidae, Limacodidae and Pyralidae. Six of these families of Lepidoptera are represented among defoliators of palms in the American tropics. Psychidae, Oecophoridae, Limacodidae and Hesperiidae are represented in the fauna on palms in both hemispheres.

Table 2.1. Defoliators of palms.

Lower Ditrysia	Higher Ditrysia
Tineoidea	Hesperioidea
Psychidae	Hesperiidae
	Hesperiinae
Gelechioidea	
Oecophoridae	Papilionoidea
Agonoxenidae	Nymphalidae
Coleophoridae	Amathusiinae
	Brassolinae
Zygaenoidea	Satyrinae
Zygaenidae	
Limacodidae	
	Bombycoidea
Pyraloidea	Saturniidae
Pyralidae	
Pyraustinae	

The Nymphalidae are represented among defoliators of palms in both eastern and western hemispheres, but by different subfamilies, namely Amathusiinae and Brassolinae, respectively. Satyrinae are distributed worldwide, but are more prominent on palms in the eastern hemisphere.

In summary, Lepidoptera are generally better represented on palm foliage in Asia than in the Americas and have the poorest representation in Africa. This pattern follows that of the diversity of palms in these respective regions, as discussed by Corner (1966). Four families are well represented on palms in both hemispheres.

General bionomics and relationships of Lepidoptera with palms

All but a small minority of species of Lepidoptera are phytophagous in the larval stage. They are among the most important pests of agricultural crops, forest trees and ornamental plants. Larvae of Lepidoptera, called caterpillars, are eruciform (wormlike), with a well-defined head, thorax and abdomen. The heavily sclerotized head capsule bears powerful mandibles for crushing leaf tissue. The labium bears a spinneret, which produces silk, which the caterpillar uses as a sort of safety line to prevent being blown out of trees, for ballooning (i.e. riding air currents), for tying leaves and for spinning cocoons. A distinct thorax bears three pairs of legs. In most families abdominal segments 3 to 6 plus segment 10 bear prolegs. This is an adaptation for feeding externally on plants, for caterpillars can attach to surfaces that can be penetrated by their tarsal claws and the crochets, i.e. tiny hooks on their prolegs (Fig. 2.2). Because the prolegs are short in relation to the body, the caterpillar clings closely to the plant. Caterpillars of the family Limacodidae are further modified for close contact with the plant surface by the loss of the prolegs. With speed of long legs sacrificed for stability on plant surfaces and compensated for by the mobility provided by their silk lines, caterpillars are adapted for life on aerial plant parts, particularly in the arboreal habitat. Less specialized caterpillars feed externally on leaves, but many species are specialized to utilize main stems, twigs, fruits, seeds and other plant parts. In cryptophagic caterpillars, i.e. those that bore within plant tissue, legs and prolegs are usually absent or not well developed.

In most species of Lepidoptera, the prepupal caterpillar forms a cocoon around itself and then passes into the pupal stage. It is during the culmination of larval

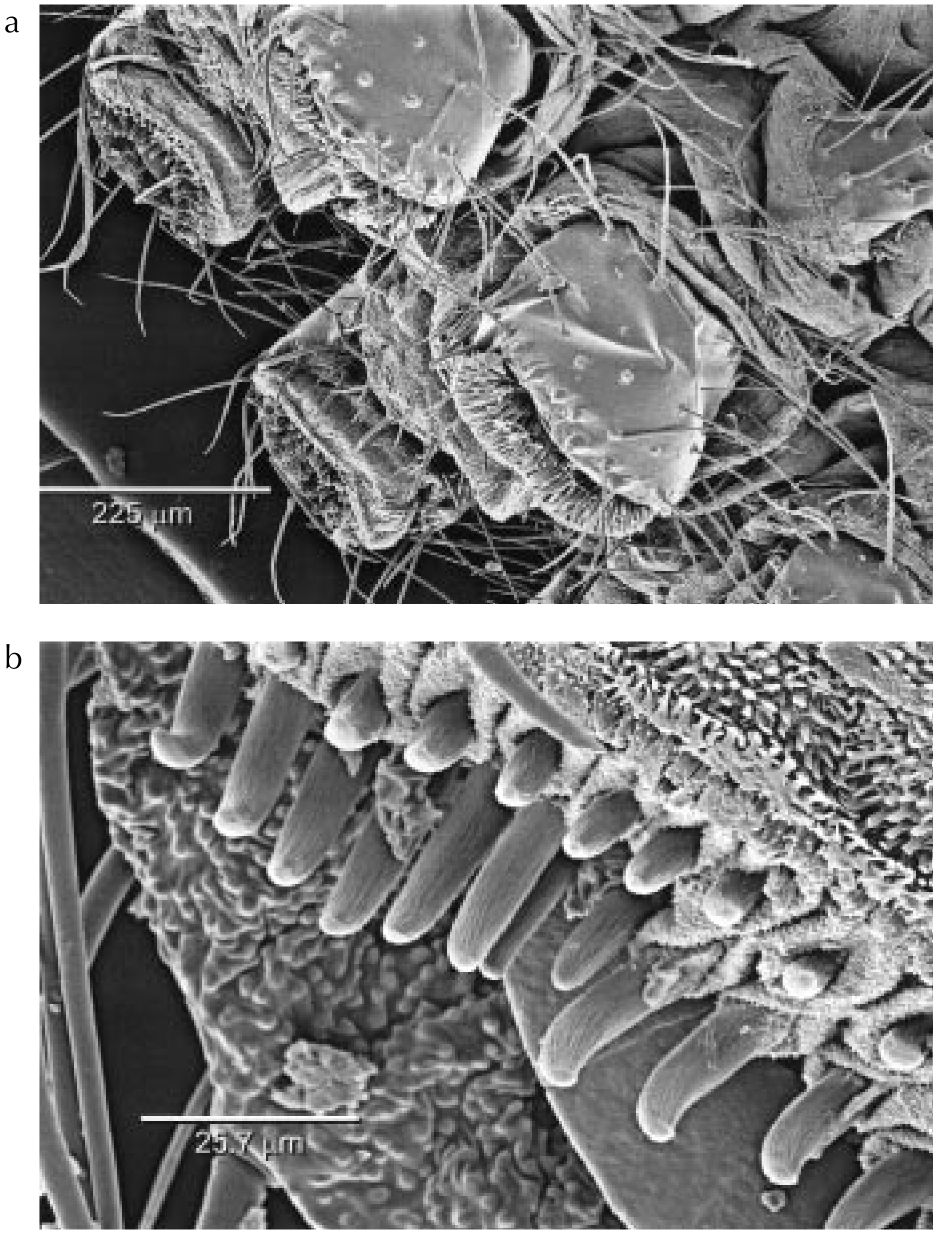

Fig. 2.2. The larvae of Lepidoptera that feed externally on plants move on prolegs, which bear hooked crochets. SEM views showing (a) prolegs of caterpillar of *Automeris io* (Lepidoptera: Saturniidae), and (b) detail of crochets. This species attacks palms in Florida.

development that caterpillars spin silk to fabricate the cocoon, in many species incorporating leaf fragments and other debris. The pupal stage of butterflies (higher Ditrysia) has a special name: the chrysalis. The chrysalis is typically exposed, rather than enclosed in a cocoon, and is suspended from host plants or other objects by caudal hooks, known collectively as the cremaster. The prepupa spins a ‘silken girdle’ and attaches it to the object, providing stability. However, some species of skippers make a thin cocoon in the larval shelter or in litter underground.

Host-plant specificity may be viewed as an evolutionary advancement. Caterpillars of the less advanced moth taxa, e.g. lower Ditrysia, are more often polyphagous, while those of more advanced families, e.g. Hesperiidae and Papilionoidea, have narrower host ranges. Psychidae, a lower ditrysian family that is represented on palms by several species in different zoogeographical regions, have broad host ranges. Those that attack palms are polyphagous, utilizing dicotyledonous as well as monocotyledonous hosts. Limacodidae, one of the best-represented families on palms, is a somewhat more advanced family of lower ditrysian moths. Based on what is known of limacodids, some species apparently have quite narrow host ranges, while others are highly polyphagous. But, while they are not always restricted to monocotyledons, they are particularly well adapted to them; apparently, many species of the family prefer palms (Godfray *et al.*, 1987; Holloway *et al.*, 1987). Other large to medium lower ditrysian families, i.e. Oecophoridae, Coleophoridae, Zygaenidae and Pyralidae, are represented on palms by one or a few species that are highly specific to this plant family. The Agonoxeninae, a subfamily of the small lower ditrysian family Agonoxenidae, occurs only on palms. The higher ditrysian families Hesperiidae and Papilionoidea, the species of which tend to have narrow host ranges, are each represented on palms by several species that are restricted to monocotyledons and, in some cases, to palm hosts. However, few, if any, lepidopterous defoliators of palms are truly monophagous, i.e. restricted to a single palm species.

Brassolinae and Satyrinae are two closely related subfamilies of the Nymphalidae (Papilionoidea), which utilize monocotyledons as larval hosts. Caterpillars of Brassolinae feed on leaves of Musaceae, Marantaceae and Palmae, and those of Satyrinae on Palmae and Gramineae. Young (1980) postulated that the narrow host ranges of species of these families may be adaptations to forests in which palms are major components, or to secondary forests with large patches of grasses and other monocotyledons. In contrast, highly polyphagous species would seem to be best adapted to forests with diverse angiosperms and with a lower proportion of palms. These forests may be the original habitat of the more polyphagous Lepidoptera that attack palms, such as Psychidae and Limacodidae.

Caterpillars that feed on foliage of palms and other monocotyledons have overcome certain barriers associated with this resource, the most formidable of which would appear to be its low nutritional value, as a high percentage of it consists of indigestible cellulose fibres. The larval stages of palmivorous Lepidoptera are of relatively long duration, typically more than a month, a characteristic that Godfray *et al.* (1987) suggested may be related to the low nutritional value of the highly fibrous tissue of palm foliage. Indeed, caterpillars develop more slowly on artificial diets rich in cellulose, because it acts as a diluent of dietary nutrients (Wheeler and Slansky, 1991). However, in comparing larval development of an insect species on different host plants, it would be difficult to isolate the influence of fibre content from that of other chemical and physical factors. In fact, other factors may surpass fibre content in importance. For example, in comparing the larval development of the polyphagous *Automeris io* on excised foliage of three monocotyledonous and two dicotyledonous species previously reported as hosts of this caterpillar, survival rate was higher and the pupal stage was reached earlier on two of the monocotyledons, namely coconut palm (highly fibrous) and banana (relatively tender). Survival was poorest and the larval stage of survivors most prolonged on date palm and tamarind. The most obvious characteristic of date palm foliage that could deter larval development is its high fibre content, i.e. toughness. Poor survival on excised tamarind foliage was perhaps related to plant chemistry or to relatively high water loss of the excised foliage (F.W. Howard, unpublished). Experiments with intact foliage of the same species might reveal a different array of host-plant preferences, but with the same difficulty of isolating fibre content as a factor.

The caterpillars of many species of Limacodidae bear urticating setae, as do the few species of Saturniidae associated with palms (Colour Plates 4e, f and 5f, Figs 2.9, 2.11 and 2.15d, e). The tissues of all life stages of many species of the family Zygaenidae, a few species of which are important on palms, secrete a defensive chemical. Godfray *et al.* (1987) suggest that the powerful defence of the urticating setae of limacodids may be an especially important adaptation for these larvae, because they remain exposed for relatively long periods of development. Stated another way, protection by urticating setae may have evolved in response to predator pressure against the relatively long larval stadium. This combination of characteristics could have evolved as an adaptation to life on palms or on other arboreal hosts, making it possible for limacodids to invade palms. That is, a short larval stage is probably not possible on fibrous palm foliage; thus the protective mechanisms that may have evolved on other arboreal hosts may have been an important adaptation that permitted them to utilize palm foliage.

The urticating spines of caterpillars are like tiny injection needles with poison glands at their bases (see especially Fig. 2.15). One needs only to brush against one of them to get a dose of a substance that causes, in most people, a low, burning pain, inflammation and swelling. A large portion of the venom of saturniids appears to be a protease, i.e. an enzyme that breaks down proteins, but there are other components, such as histamine, a highly irritating substance, which is a major component of the venom of some wasps and bees and is also produced by cells of the human body in response to certain stresses.

One might think that the stings of caterpillars, fire ants, bees and wasps are basically the same, but biochemists so far have found that, although venom of different species may contain substances in common, such as histamine, the combination of different substances is unique for each species. Thus, we would expect that a person may tolerate the venom of some species and be highly sensitive to those of other species. And, of course, individuals differ in their sensitivity to insect venoms in general. Since these stings are irritating, but otherwise are not well understood chemically, it is a good policy to avoid contact with these caterpillars as much as possible. The spines of some species readily break off in the skin, and thorough rinsing of an affected site with water may dislodge fragments and prevent a reaction. We have found that antihistamine swabs, sold for first-aid treatment of stings of wasps and bees, alleviate the swelling, redness and pain of caterpillar stings. Some medical doctors recommend meat tenderizers, containing papain (a compound in papaya), which may act on the proteins in the venom. Possibly sap from freshly cut papaya may have similar effects, although this itself may be allergenic to some people. Aloe sap also seems to help alleviate the effects of some caterpillar stings.

Caterpillars with protective spines or which are otherwise distasteful or toxic to predators commonly have combinations of bright colours in patterns that are conspicuous against palm fronds. These are generally thought of as aposematic, or ‘warning’, colours, which birds, lizards and other higher predators learn, through experience, to avoid. Caterpillars that are not well protected by chemical defences are likely to be camouflaged by colours that blend well with leaf surfaces.

Caterpillars of the family Psychidae (bagworms), which are represented by a few species that utilize palm foliage, protect themselves by strong bags, which they weave of silk, incorporating plant fibres and other materials. Insects can also be protected by various behavioural traits, for example, confining feeding activity to the hours of darkness.

In summary, adaptations that protect the insect during a long period of exposure, while not unique or highly specialized, seem to be especially important advantages for defoliating caterpillars associated with palms.

Caterpillars tend to attack the older, rather than the younger, fronds of palms. Corbett (1932) suggested that this may be related to the greater protection from sun and other elements afforded by horizontal, as opposed to vertical, fronds. Similarly, they prefer the shelter of the abaxial surfaces. A notable exception, *Zophopetes cerymica*, typically feeds on the adaxial surface of older palm fronds.

There have been few cases in which lepidopterous defoliators of palms have been introduced far outside their ranges (but see *Opisina arenosella* and *Homaledra* sp.). Most are native to their respective regions. Although caterpillars of various species are common in plantations, they normally occur at low population densities, regulated by biotic factors, with which they have presumably co-evolved, usually including parasitic species of Braconidae, Chalcidae, Ichneumonidae and other families of the order Hymenoptera, and species of the family Tachinidae and perhaps other families of the order Diptera. Microbial pathogens, including especially fungi and viruses, are known to attack many species of these Lepidoptera and, in some species, are considered to be of major importance in regulating populations. Predators, such as reduviid bugs (Hemiptera), spiders, etc., attack caterpillars on palm foliage but generally make less of an impact on the host populations than do parasitoids.

Significant damage to plantation palms by caterpillars is usually in the form of occasional outbreaks, which probably occur when natural population regulation deteriorates for some reason. These outbreaks can be devastating and difficult to manage. Insects whose populations on crops are usually insignificant but which occasionally explode to pest levels may be more damaging than perennial pests. This is because a farmer is apt to have a system in place for managing predictable perennial pests, but may be unprepared to contend with a problem caused by a different pest that develops suddenly.

Pesticides have become an important tool in agriculture, because of the ease, rapidity and economy with which they can be used to control pest populations and their damage. But, although pesticides may quickly and effectively reduce the target pest population, the adverse effects on natural enemies have often outlasted this benefit (Wood, 1968; Syed and Shah, 1977).

The fact that the damage caused to a plantation by a caterpillar outbreak increases with the duration of the outbreak provides incentive for early intervention with pesticides. On the other hand, the longer an outbreak continues, the more likely it becomes that natural enemies will begin bringing the pest population under control. This is a common dilemma in pest management.

Although pesticides are believed to have indirectly caused many of the outbreaks of caterpillars on palms, some outbreaks of caterpillars have been observed in plantations where pesticides were not used. Thus, other factors have been considered.

Dry conditions seem to be conducive to high population density of caterpillars on palm foliage. This is particularly well known in limacodids, e.g. *Darna nararia* in India and Sri Lanka (Menon and Pandalai, 1960), *Mambarilla rotunda* in India and *Birthosea bisura* in various localities in South-East Asia (Holloway *et al.*, 1987). Outbreaks of *Darna catenatus* in Sulawesi and New Guinea were observed in the dry season and in Sulawesi were associated with dry years (Lever, 1979; Holloway *et al.*, 1987). During an atypical drought, which lasted from December 1982 to May 1983, in the Philippines, there were several outbreaks of *Penthocrates zelaznyi* on coconut palm on Mindanao and an outbreak of *Penthocrates rufofascia* on coconut palm on Luzon (Holloway *et al.*, 1987). This drought affected a large area of South-East Asia and is thought to have been linked to the El Niño southern oscillation phenomenon (Salafsky, 1994). Outbreaks of the coconut palm zygaenid, *Artona catoxantha* (Zygaenidae), have usually occurred during drier months (Lever, 1953). The chief effect of drier weather may be to inhibit the activity of natural enemies. Dry conditions are generally known to be unfavourable for the development of entomogenous fungi. Parasitic wasps and flies may also be adversely affected. For example, in southern India, populations of *Trichospilus pupivora*, a natural enemy of a coconut caterpillar, *O. arenosella* (Oecophoridae), became extremely sparse during the dry season from March to May and flourished during and immediately after the rains from July to February (Anantanarayanan, 1934). Dry weather may also be favourable to caterpillars, because they are not subjected to the direct effects of rain. Heavy rains may decimate the weak adult moths of *Hidari irava* (Hesperiidae). *Birthamula chara* (Limacodidae) has occurred in outbreaks in September at the beginning of the rainy season in Sumatra (Holloway *et al.*, 1987), but possibly the major population increase was in the preceding dry season.

Outbreaks of caterpillars of various species in plantations have followed elimination of ground cover by herbicide treatments and by wildfires. Herbaceous ground cover may provide important nectar sources for adult Hymenoptera that as larvae parasitize caterpillars (Gabriel, 1976; Syed and Shah, 1977).

The closure of the canopy as a plantation matures, thus facilitating the movement of caterpillars between palms, and the occasional emergence of genetic strains of moths prone to epizootics have been suggested as additional possible factors that may lead to outbreaks (Syed and Shah, 1977).

Although caterpillar outbreaks have been attributed to the indirect effects of factors described above, Syed and Shah (1977) pointed out that caterpillar populations often remain stable in palm plantations in spite of the prevalence of a condition such as drought, lack of ground cover or application of a broad-spectrum pesticide. They interpreted this as evidence that outbreaks may usually be the result of combinations of such factors, rather than a single factor.

If insecticides are used at all, their use should be limited, so as to minimize direct loss of natural enemies and to leave tolerable reserves of populations of the pest insect to serve as hosts for the natural enemies. Insecticide use may be reduced or eliminated by monitoring caterpillar populations and applying insecticides only when census figures indicate that treatment is economically justified. Wood (1968) describes census methods for caterpillar pests of oil palms, which include periodic field visits and counts of caterpillars on fronds of palms near predetermined census points. The number of caterpillars on two fronds each of three adjacent palms are determined. Visits may be trimestral when there is no outbreak, and more frequent when the census indicates an important population increase. Insecticides are applied when the numbers of insects reach a certain index that indicates economic damage. These have been recommended for numerous species of caterpillar pests of palms. They have been based mostly on intuitive interpretation of field observations.

Pest management methods applicable to plantations may be likewise applicable to controlling lepidopterous defoliators on ornamental palms in certain situations, such as field nurseries, which typically consist of blocks of single species, and city landscapes in which a particular plant species is predominant. Such monocultures are likely to be conducive to outbreaks of defoliators similar to those experienced in plantations. In general, the incidence of such outbreaks is expected to be less in landscapes in which palms are incorporated with dicotyledonous trees and in which a diversity of palms is planted. Occasional attacks by caterpillars on such palms would not usually cause sufficient aesthetic damage to warrant treatment. However, in areas of high recreation use, such as around resort hotels, parks and other tourist facilities, there may be a low tolerance for caterpillars, especially limacodids, because of the possibility of injury due to their urticating setae. In such situations, pests may often be manageable with simple mechanical control, e.g. hand-picking.

Important lepidopterous defoliators of palms

Tineoidea

The Tineoidea are the most primitive superfamily of the Ditrysia, with more than 10,000 known species. Important distinguishing characteristics of the very small to medium-sized adult moths is that the proboscis is reduced or lacks scales, there are some erect scales on the frons and the wings are often narrow, with reduced venation. The caterpillars are concealed feeders in portable cases, tunnels, silken tubes, etc. Clothes moths (*Tinea* spp.) are familiar examples of this superfamily.

Psychidae

The Psychidae, known as bagworms, are one of the most important tineoid families, with about 6000 spp., most of which are native to the eastern hemisphere. The adult males are small to medium, typically dull-coloured, winged moths. Females of most species are apterous (wingless). The caterpillars live in bags, which they construct by spinning silk, often incorporating plant fibres or other matter (Colour Plate 4a). The tubelike bag is open anteriorly to allow feeding and posteriorly to permit ejection of frass (solid excrement, usually in the form of finely ground plant tissue). The bags are built up in size as the caterpillar grows, until finally the insects undergo pupation in these bags. The winged males leave the bag after eclosion from the pupal case, but the apterous females remain in the pupal case within the bag. Males have extensible abdomens for penetrating the bag to mate with the female. Females lay eggs inside their pupal case within the bag. The abdomen of the female bears a tuft of deciduous setae, which are shed at oviposition and become mixed with the eggs. Most psychids feed on angiosperms, but a few attack gymnosperms, lichens and mosses. Some bagworm species commonly observed on trunks of palms in Florida and perhaps elsewhere do not attack palm foliage, but are thought to feed on lichens or mosses on the trunks.

Since females are apterous, they do not disperse, but oviposit on the host plant on which they developed. Larvae of *Metisa plana* tend to remain on the same palm frond where they hatched, but move to new hosts in response to high population pressure (Rhainds *et al.*, 1998). Dispersal in the caterpillar stage is mostly by young instars before they begin construction of the bag. In palmivorous species, caterpillars disperse to new palms either: (i) by crawling down the stem, over the ground and up the stem of the new palm, or across fronds that are in contact with adjacent palms; or (ii) by swinging on their silk strands or ballooning (Syed and Shah, 1977). Caterpillars swing on their silk threads to move between fronds of the same or adjacent palms. They may crawl to the tips of leaflets and spin strands of about 1 m in length and be carried to new plants. The dispersal of bagworms is obviously facilitated where palms are densely planted.

The unusually high fecundity and the apterous condition of the females of Psychidae seem somehow connected as a survival strategy. In most Lepidoptera, the female, with good host-finding abilities, constitutes the main dispersal stage. In Psychidae, reliance on ballooning larvae for dispersal must result in high losses to the population. The female's unusually high fecundity may compensate.

Bagworms of several species attack palms in tropical regions. In South-East Asia, three species are of primary importance: *Mahasena corbetti*, *M. plana* and *Cremastopsyche pendula* (syn. *Pteroma pendula*) (Syed, 1978).

Mahasena corbetti, the coconut case caterpillar, occurs in South-East Asia and some islands of the Pacific, where it is a serious pest of African oil palms. The adult male moth is brown, with a wing-span of 25–30 mm. Females and immature stages have the typical characteristics of Psychidae, described above, including the concealed habit in a silk bag, to which overlapping pieces of leaf are loosely attached. Maximum length of caterpillars is 44 mm for caterpillars that develop into females and 30 mm for those that develop into males (Sankaran, 1970).

Reported hosts, in addition to African oil palm, include *Areca* sp., *Arenga* sp., coconut palm and diverse dicotyledonous species (Corbett, 1932). It is a pest of banana in the Philippines (Ostmark, 1974). In a survey to determine the extent of infestation of this insect in Sabah, localized infestations of *M. corbetti* were observed on African oil palm and *Areca catechu*, but not on coconut palm. Among dicotyledonous hosts, infestations were particularly common on two leguminous trees, namely *Albizzia* sp. and *Delonix regia*. In the laboratory, the insect developed on several legume species, as well as other dicotyledonous species (Syed, 1978).

Mating is typical of psychids. The female, which may occupy the host plant or another substrate, remains in the pupal case within the silk bag. Within 24 h after mating, the female begins to oviposit inside the pupal case. Fecundity is relatively high, compared with most Lepidoptera, Wood (1968) reporting a maximum of over 3000 and Syed (1978) a mean of 2009 eggs deposited per female. The egg incubation period is 16 days. The larvae pass through 11 or 12 instars during 101–124 days (Syed, 1978).

As caterpillars mature, they turn around in the bag, changing from a feeding position with their heads orientated toward the plant surface, to a position more typical of Lepidoptera pupae, i.e. with their heads toward the distal portion of the bag, and pupate. The pupal stage lasts 26 days (Syed, 1978).

The early-stage caterpillars scarify the abaxial surfaces of fronds. Caterpillars of later instars chew the entire leaf tissue, forming holes, and finally feed at the leaf margins, causing notches (Corbett, 1932). In addition to the holes and notches caused by bagworm feeding, dried necrotic areas are formed where they have fed on the surface. Bagworms attack the middle and oldest fronds of palms, the younger fronds usually remaining free of damage.

According to Wood (1968), the importance of *M. corbetti* in relation to other species of bagworms on oil palms declined after the 1930s in the Malay Peninsula, but it remained the principal pestiferous bagworm of these palms in Indonesia (Hartley, 1988) and Sabah (Syed and Shah, 1977). Outbreaks of the coconut case caterpillar are occasional but often severe. In outbreaks in Sabah, 300–500 of these caterpillars were commonly observed on a single frond (Wood, 1968). It is common as a pest of coconut seedlings in the Philippines (Bigornia, 1977; Blancaver *et al.*, 1977) and may attack older coconut palms.

A complex of natural enemies normally regulates populations of *M. corbetti*. The relative importance of species of this complex varies with locality (Wood, 1968; Sankaran and Syed, 1972; Kamarudin *et al.*, 1996). Outbreaks of this insect in recent decades have been attributed to the elimination of large segments of populations of natural enemies by pesticides applied to control various foliar pests. Contact pesticides are believed to be especially inappropriate for bagworm control, as they seem to have a differential effect, favouring these well-protected caterpillars at the expense of the relatively more exposed parasitoid populations (Ostmark, 1974). Some systemic insecticides applied by trunk injection are effective (Wood *et al.*, 1974; Singh, 1986). Flooding and other factors that reduce ground cover may result in population increases of the pest (Siburat and Mojiun, 1998). Conversely, maintaining ground cover with nectariferous plants enhances populations of natural enemies of *M. corbetti* (Lay, 1996).

Entomopathogenic fungi (Siti-Ramlah *et al.*, 1994) and viruses (Ali *et al.*, 1996) have been isolated from *M. corbetti* and are being studied for control of this pest. Applications of *Bacillus thuringiensis* have thus far not been effective (Basri *et al.*, 1994).

Because dispersal of bagworms is limited to the larval stage, adhesive bands wrapped round the stem have been used to prevent the caterpillars from crawling up into the foliage (Blancaver *et al.*, 1977). Hand-picking has been effective in controlling incipient infestations, e.g. on palm seedlings in germination beds or container nurseries.

When insecticides have been employed to attempt to control large outbreaks of *M. corbetti*, some difficulties have been encountered. The caterpillars of this species feed on the abaxial surface of fronds, a factor that may have reduced the effectiveness of aerial applications (Wood, 1968).

In the mid-1900s, two similar species of bagworms, namely *C. pendula* and *M. plana*, surpassed *M. corbetti* as important bagworm pests of African oil palm in the Malay Peninsula. *Metisa plana* became dominant in that region (Wood, 1968) and is also a pest of bananas in the Philippines (Ostmark, 1974). Syed (1978) published detailed observations on these three species.

Additional bagworms on palms in India and South-East Asia include the following species:

- *Acanthopsyche cana* on coconut in Sri Lanka.
- *Cryptothelea cardiophora* on African oil palm in Malaysia.
- *Dappula tertia* on African oil palm in Malaysia.
- *Metisa hypoleuca* (syn. *Acanthopsyche hypoleuca*) on coconut in Sri Lanka.
- *Metisa* (syn. *Acanthopsyche*) *griseoalba* on *Nypa fruticans* in Vietnam.
- *Pteroma* (syn. *Acanthopsyche*) *nipae* on *N. fruticans* in Vietnam (Lepesme, 1947; Lever, 1979; Zhang, 1994).

Oiketicus kirbyi occurs in the Americas from Mexico to Argentina (Colour Plate 4a; Genty *et al.*, 1978; Zhang, 1994). In the West Indies, it was reported from Cuba (Hochmut and Manso, 1982). The adult males are similar to those described for *M. corbetti*, but larger, with a wing expanse of 32–52 mm. Maximum length of the apterous female is 60 mm (Genty *et al.*, 1978).

A polyphagous insect, *O. kirbyi* is a pest of various crops grown in areas with a tropical wet (Af) or tropical wet and dry (Aw) climate (see Box 1.1), being especially destructive to banana and plantain plantations (Stephens, 1962; Ostmark, 1974; Ponce *et al.*, 1979). A forest pest, it defoliates eucalyptus in plantations in Brazil (Campos Arce *et al.*, 1987) and destroyed up to 80% of the foliage of a mangrove forest in Ecuador (Gara *et al.*, 1990). In the 1970s, it was recognized as a pest of African oil palm (Genty *et al.*, 1978). *Oiketicus kirbyi* is a prolific species, with a maximum egg production of 10,000 eggs per female (Genty *et al.*, 1978).

The sex pheromone of *O. kirbyi* has been identified (Rhainds *et al.*, 1994). In the usual lepidopteran mechanism, sex pheromone is released from abdominal glands until mating occurs. The bagworm mechanism is different. In the several species that have been studied, including *O. kirbyi*, females expel pheromone-impregnated scales into the posterior end of the bag to attract the males. It is not yet known how males differentiate between mated and unmated females. Possible explanations are that the pheromone dissipates relatively quickly from the scales and thus the females are attractive for a limited period, or that, upon mating, the females are marked by an inhibitory semiochemical produced by either the male or the female. Males prefer larger females and females that are positioned at relatively high sites on palms (Rhainds *et al.*, 1995a, b).

Oiketicus kirbyi is attacked by various natural enemies (Ponce *et al.*, 1979; Delvare, 1992). Leguminous ground cover, e.g. *Pueraria phaseoloides, Centrosema pubescens, Calopogonium* spp., etc., is thought to enhance parasitoid populations by providing nectar sources (Mexzón and Chinchilla, 1999). The burning of debris under palms should be discouraged, because smoke may interfere with natural enemies.

Some principles learned from experience in controlling bagworms on bananas (Ostmark, 1974) seem applicable to bagworms on palms. Because the caterpillars attach the bags to the leaf surface and feed from within it, the bag remains attached even if the larva dies. Dead and live caterpillars cannot be distinguished by the appearance of the bag. Therefore, monitoring dead and live bagworms to determine the impact of natural enemies and thus make decisions on timing of sprays or to determine the degree of control with an insecticide involves the difficulty of opening the bags of each specimen to observe the condition of the larva. Studies of bagworms as pests of bananas also revealed that late-instar caterpillars tend to be resistant to pesticides, possibly because of a high lipid content or because the caterpillars may remain in their bags and cease feeding after the first contact with an insecticide (Ostmark, 1974).

Thyridopteryx ephemeraeformis, a highly polyphagous bagworm in eastern North America, sometimes lives on the foliage of *Sabal palmetto* in Florida (Johnson and Lyon, 1991). *Oiketicus abbotti* has been reported on palms in Florida and Jamaica (Lepesme, 1947).

Gelechioidea: Oecophoridae

The Oecophoridae are the largest family of the superfamily Gelechioidea, with about 4000 species, most of which are native to Australia and other areas of the eastern hemisphere. The adult moths are small to medium-sized. The caterpillars are often leaf-miners or borers in other plant parts (Scoble, 1992).

Opisina arenosella (syn. *Nephantis serinopa*), the coconut leaf-eating caterpillar or coconut blackheaded caterpillar, is native to southern India and Sri Lanka, where it is a major pest of coconut palms (Fig. 2.3). It was first described from specimens collected in Sri Lanka in 1898 and reported for the first time in southern India in 1909. By 1923, it had apparently spread to Bangladesh and Myanmar (Burma). The expansion in coconut plantations during the 20th century probably encouraged the spread of this insect. Details of the bionomics, distribution and biological and other methods of control of this insect published in the decades of the 1920s to the 1950s were reviewed by Nirula (1956). Ramachandran *et al.* (1979) and Cock and Perera (1987) published more recent reviews.

The medium-sized, light-greyish adult female moths have a wing-span of 20–25 mm. The males are smaller and have a slender abdomen, terminating in a prominent tuft of scales, which provides a useful means of separating the sexes. The caterpillars (Colour Plate 4b) are greenish yellow in the earlier instars and increasingly more greenish in later instars. Their head capsules and thoracic plates are black. Nirula (1956) published a detailed description of all stages, including all five larval instars.

Although the insect is best known as a pest of coconut palm, palmyra (*Borassus flabellifer*) is presumed to be the original host of *O. arenosella*. Palmyra is native to southern India and is commonly infested with this insect, even in areas where coconut palms are not grown. In a study comparing four plants, the insect's order of preference for oviposition and feeding was palmyra, coconut and banana, while *A. catechu* was rejected (Murthy *et al.*, 1995). Additional reported hosts include *Caryota urens*, *Corypha umbraculifera*, *Phoenix sylvestris*, *Hyphaene* sp. and *Roystonea oleracea* (Jayaratnam, 1941; Nirula, 1956; Menon and Pandalai, 1960; Dharmaraju, 1963).

The imagos generally emerge from the pupal case in the early morning hours, but rest during the day on foliage or trunks of palms or other objects near palms. When on leaflets, moths typically align themselves parallel to the margins, with the head directed upwards. The imagos regularly imbibe nectars (Nirula, 1956). A sex pheromone of the female moth has been identified (Mumford *et al.*, 1986) and attraction of males to virgin females in the

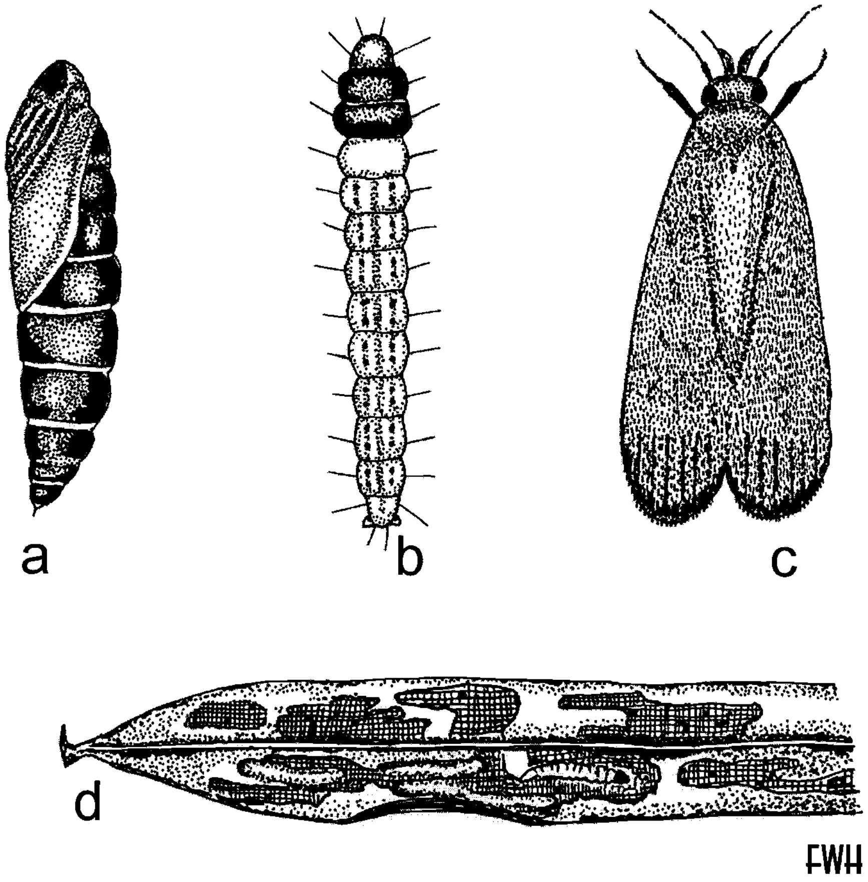

Fig. 2.3. *Opisina arenosella* (Lepidoptera: Oecophoridae), a pest of coconut palm in Sri Lanka and India. (a) Pupa. (b) Larva. (c) Imago. (d) Damage to coconut leaflet. Redrawn from P.M. Somasirimudali, in Mahindapala and Pinto (1991).

field has been observed (Fernando and Chandrasiri, 1997). The sexes mate at dusk one or a few days after eclosion and females oviposit at dusk, beginning a day after mating, continuing for about 2 days. The behaviour of the imagos has been described as 'sluggish' (Ramachandran *et al.*, 1979). They cling fast to palm foliage tossed by winds or during moderately heavy rains. They are poor fliers, a factor that may have contributed to their relatively slow rate of spread and the localized nature of infestations. However, it is said that strong winds prevalent in coastal areas may carry imagos long distances.

The females lay 60–250 small, inconspicuous eggs (about 0.3 mm × 0.7 mm) near the tips of leaflets of usually older fronds. The eggs hatch within a week. The caterpillar wanders for a time after hatching and then spins a silken shelter on the abaxial frond surface, remaining in it while feeding (Nirula, 1956; Menon and Pandalai, 1960).

Aggregations of first-instar larvae occur on the oldest fronds. Larvae tend to move to younger fronds as they develop. Dense populations of second to fourth instars may occur on fronds 12–14 months of age, while the fifth and sixth instars occupy fronds of 2 months of age (Perera, 1987).

The total larval period of five or six instars is about 40 days, during which the caterpillar grows from a length of about 1.5–3.5 mm to about 20 mm. The sluggish, pink prepupa spins an ovoid cocoon on the abaxial surface of the frond. The pupal stage lasts 9–14 days. The complete life cycle takes about 2–2½ months (Nirula, 1956; Menon and Pandalai, 1960; Lever, 1979).

Opisina arenosella attacks palms from the seedling stage to maturity (Ramachandran *et al.*, 1979). The caterpillars destroy abaxial leaf-surface tissue by their feeding, causing parchment-like necrotic patches. Population density may reach five to ten larvae per leaflet, in which case feeding results in extensive desiccation of foliar areas and presumed reduction in yield. Extraordinarily dense populations have been observed, e.g. 100 first-instar larvae per leaflet and 20–30 third- to fifth-instar larvae per leaflet (Priyanthie Fernando, personal communication). Damage can be recognized as characteristic patchy necrosis, with silk shelters and frass deposits (Nirula, 1956; Menon and Pandalai, 1960).

Reports of *O. arenosella* as a pest of coconut palm were rare prior to the 1920s. In recent times, it has been considered to be the most serious defoliator of coconut palm in India and Sri Lanka. There were 159 outbreaks in Sri Lanka during 20 years (1965–1985) (Ramachandran *et al.*, 1979; Cock and Perera, 1987; Perera, 1987). In Sri Lanka, most outbreaks occur between October and February, when cooler temperatures inhibit the development of parasitoids (Perera, 1987; Priyanthie Fernando, personal communication).

Natural control of *O. arenosella* usually keeps this insect at tolerable levels. It becomes a pest suddenly and temporarily in localities where natural control temporarily breaks down. Pest populations are most often associated with dry conditions, which are presumed to be detrimental to fungi and other natural controls (Cock and Perera, 1987). For example, on the south-western coast of India, the insect builds up to pest levels most often during the dry season (January–April). Populations diminish quickly with the onset of the south-west monsoon (May–August) (Nirula, 1956; see Box 1.1).

Many species of insects are natural enemies of the larval and pupal stages of *O. arenosella*. These include parasitic Hymenoptera in the families Bethylidae, Braconidae, Chalcidae, Elasmidae, Eupelmidae, Eurytomidae and Ichneumonidae and Diptera in the families Phoridae and Tachinidae. Predators include species of Acari, Hemiptera (Reduviidae and Anthocoridae), Coleoptera (Carabidae) and Hymenoptera (Formicidae) (Cock and Perera, 1987).

In Sri Lanka, Way *et al.* (1989) observed that at least 11 species of ants nested in coconut palm spathes and some of these are predators of eggs of *O. arenosella*. Some species, such as *Oecophylla smaragdina* (Fig. 2.8), which has a reputation as a fearsome general predator, and *Paratrechina longicornis*, were dominant in some palms and were mutually exclusive. Although they preyed on the eggs of *O. arenosella*, other ants, such as *Monomorium floricola*, *Technomyrex albipes* and *Crematogaster* sp., were more effective in controlling *O. arenosella*. However, the general impact of the ants was insufficient to control the pest effectively.

Species of bacteria and fungi also infect larvae and pupae of *O. arenosella*. *Serratia marcescens*, a bacterium that was observed to infect larvae in laboratory cultures of the moth, caused 70% mortality of larvae that fed on sprayed leaflets (Antony, 1961; Muthukrishnan and Ranagarajan, 1974). Significant mortality was associated with a nuclear polyhedrosis virus in Kerala (Philip *et al.*, 1982). In nature, fungi are believed to cause high mortality of *O. arenosella* during wet seasons (Nirula, 1956).

Different species of natural enemies are important in different parts of the range of *O. arenosella,* and the importance of species in particular localities changes over time. Even where natural control is usually adequate, it may occasionally deteriorate, leading to local outbreaks. The extensive literature on the subject was reviewed by Cock and Perera (1987).

As early as the 1920s, workers in India became interested in augmenting natural control by rearing and releasing natural enemies of *O. arenosella.* To control the spread of outbreaks in the south-west coastal region in 1924/25, *Trichospilus pupivora* (Eulophidae), *Goniozus nephantidis* (syn. *Perisierola nephantidis*) (Bethylidae), *Elasmus nephantidis* (Elasmidae) and *Bracon brevicornis* (Braconidae) were reared in massive numbers in government laboratories. A network of canals, streams and lakes extends over a zone of about 900 km^2, known as 'the backwaters' of Kerala (Fig. 1.4e). One rearing laboratory was mounted on a boat, which circulated the backwaters. Populations of *O. arenosella* diminished to 'the irreducible minimum' and the biological control effort was terminated in 1931 (Nirula, 1956).

Several similar efforts have since been conducted in various areas of southern India and Sri Lanka. These efforts appear to have resulted in varying degrees of success (Nirula, 1956; Ramachandran *et al.*, 1979; Cock and Perera, 1987; Jayaraj, 1989). Cock and Perera (1987) concluded that *Argyrophylax fugipennis* (Tachinidae), a parasitoid of *A. catoxantha* in Java, merited investigation as a possible biological control agent of *O. arenosella*, because it was thought that it could successfully parasitize the larvae hidden in silk tubes, has a high reproduction rate and can survive on other caterpillars when *O. arenosella* populations are low.

Preliminary studies in Gujarat, India, suggested that *O. arenosella* consumed less leaf tissue of a local green dwarf variety than of two other types: the predominant local tall variety and a hybrid (Kapadia, 1981). However, even in the most resistant of these three varieties, about one-third of the leaf surface was damaged, compared with about half of that of the more susceptible tall varieties.

Chemical control of *O. arenosella* has been investigated for many years (Pillae and Kurian, 1960; Sathiamma and Kurian, 1970). An enduring problem has been that insecticides generally disrupt natural or biological control agents. A trunk-injection technique with monocrotophos was reported to control *O. arenosella* effectively (Nadarajan and Channa Basavanna, 1981). The authors judged this technique to be appropriate for use by farmers and compatible with biological control. Monocrotophos injected into the trunk reaches the foliage in 6 h, and persists in tissues for 4 months (Priyanthie Fernando, personal communication). Because palms do not heal holes made in the trunk, workers plug injection holes to prevent entry of fungi and other deleterious organisms.

Stenoma impressella (syn. *Stenoma cecropia*) causes serious damage to African oil palm in Colombia and Ecuador.

The wing-span of the female is 25–30 mm. Both sexes are similar in appearance. The forewing is brown, with pale violet zones and two fine transverse dark lines. The hind-wing is grey distally and bright rose-orange or yellow-orange near the margins. A conspicuous feature is a thick tuft of dark brown scales on the thorax. Caterpillars are pale yellow, with purple longitudinal stripes, and 20–25 mm when full-grown (Genty *et al.*, 1978).

Stenoma impressella is highly polyphagous, attacking, in addition to African oil palms, many species of forest trees, as well as important crop trees, such as cacao, coffee, guava and citrus (Genty *et al.*, 1978).

The moths rest in lower vegetation by day, becoming active nocturnally. They mate while on young foliage. An unusual characteristic is that the females lay eggs on the adaxial frond surfaces singly and often in a line along leaflet midveins on the distal zones of fronds of the upper half of the crown. In contrast, most defoliators of palms oviposit on the abaxial frond surfaces. Eggs hatch in 3–5 days. Soon after hatching, the larva selects a site, usually against a leaflet midvein, and begins spinning a shelter of silk and incorporated frass, the construction of which is continuous as the larva grows. Since new construction proceeds anteriorly, corresponding with the increasing size of the larva, the shelter takes on a narrow, conical shape. The larva remains protected by the shelter while feeding. Early feeding damages the abaxial frond surface, except for secondary veins. In later feeding, the entire leaf tissue, except for midveins, is consumed. The larva extends the shelter as necessary to reach new tissue. The larval period of eight instars lasts 57–67 days.

During its development, a single larva consumes a mean of 40–50 cm^2 of leaf material. Populations of 1500–2000 caterpillars per frond were observed on African oil palm. Sparse but repeated infestations also cause considerable damage, such as stripping of the distal half of fronds, except for leaflet midveins. Infestations were observed to spread over hundreds of hectares in two generations.

Rhysipolis sp. (Hymenoptera: Braconidae) was identified as the most important natural enemy of *S. impressella*, but the rate of parasitism was low, i.e. 7–18% in Genty *et al.*'s (1978) observations. Additional hymenopterous parasitoids (Chalcidae, Ichneumonidae) and predators (Coleoptera, Hemiptera and Hymenoptera) were still less effective. A high incidence of mortality of young caterpillars was observed during dry periods.

Control with *B. thuringiensis* was effective experimentally. Synthetic chemicals have been used effectively in some plantations. Genty *et al.* (1978) stressed the importance of timing of applications, indicating that a reduction of 95–100% of caterpillars was achieved if treatments were applied in the first 15 days after caterpillars hatch.

Gelechioidea: Agonoxenidae

The family Agonoxenidae contains relatively few species. One subfamily, the Agonoxeninae, is of interest because all four known species are associated with palms and distributed almost completely allopatrically in the Pacific region from Australia to the Hawaiian Islands. The adult moths are small and narrow-winged (Fig. 2.4). The caterpillars feed beneath a flimsy silken web (Bradley, 1966; Nielsen and Common, 1991).

Agonoxena argaula, the coconut flat moth, is a pest of coconut palm in Fiji (Hinckley, 1961) and has been reported from many islands of the Pacific (Bradley, 1966; Dharmaraju, 1980a, b; Walker, 1989).

The adult moths are small, 5–9 mm in length, and of a general yellow-brown colour, with light stripes. The early-instar caterpillars are yellow, later-instar caterpillars becoming green. The pupal stage is passed in a whitish cocoon, attached to the palm-frond surface or, if the caterpillar drops, on undergrowth. The caterpillars

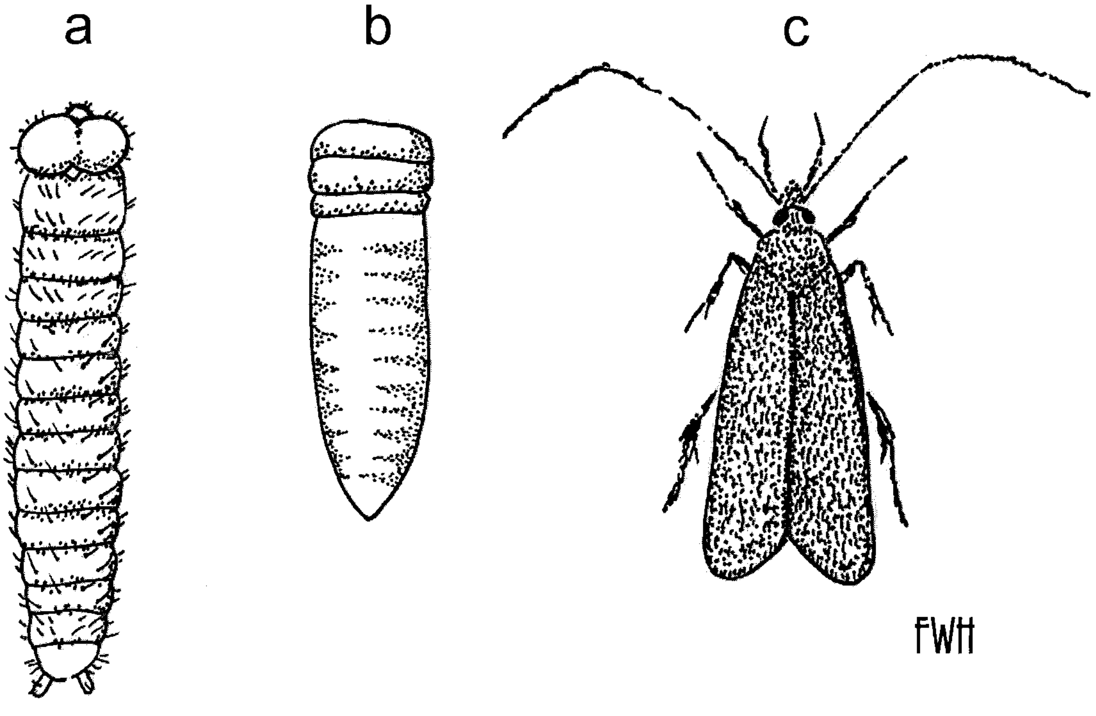

Fig. 2.4. *Agonoxena* sp. (Lepidoptera: Agonoxenidae). This small genus is represented on palms in Oceania. (a) Larva. (b) Pupa. (c) Adult. After Risbec, in Lepesme (1947).

develop in 16–22 days and the pupal stage lasts 9–10 days (Singh, 1951).

In addition to coconut palm, this species has also been reported from *Metroxylon* and from *Clinostigma* (Bradley, 1966). The latter is a genus of palms of the western Pacific, usually found in dense montane rainforests (Uhl and Dransfield, 1987).

The imagos are active nocturnally. The females oviposit on the abaxial frond surfaces, often near feeding scars and beneath the webs of caterpillars of previous generations. The newly hatched larvae spin a flimsy protective web, beneath which they feed on the abaxial surfaces of fronds. They feed between parallel veins, consuming all but the adaxial epidermis, thus leaving a rectangular scar. The damage may be especially severe when high populations of the insect infest young palms (Lever, 1979).

Natural enemies native to Fiji attack caterpillars of *A. argaula*, including species of *Apanteles, Bracon, Agathis* (Hymenoptera: Braconidae) and *Tongamyia* (Diptera: Tachinidae). Other parasitoids attack the pupa, including *Brachymeria* sp. (Chalcidoidea), which is indigenous to Fiji. Lever (1979) reported a parasitization rate of nearly three-quarters of the caterpillars, about half of which was due to *Apanteles*.

In Fiji, native natural enemies of the caterpillars have been supplemented by the introduction of two parasitoids of *Agonoxena pyrogramma*. These are *Elachertus agonoxenae* (Hymenoptera: Eulophidae) from New Guinea and *Actia painei* (Tachinidae) from New Britain. *Macrocentrus* sp. (Braconidae), which was introduced into Fiji from Java, attacks the pupa, supplementing control imposed by *Brachymeria* sp.

Two additional species of *Agonoxena*, neither of economic importance, are associated primarily with coconut palm (Bradley, 1966). *Agonoxena pyrogramma* is distributed in Java, New Britain, New Guinea, Solomon Islands and Mariana Islands. *Agonoxena miniana* is known from Java, and was reportedly introduced into the Hawaiian Islands (Zhang, 1994). *Agonoxena phoenicia* was described from imagos reared from caterpillars collected from a palm, *Archontophoenix alexandrae*, in northern Queensland, Australia (Bradley, 1966).

Gelechioidea: Coleophoridae

Coleophoridae (case-bearer moths) are very small moths with linear wings fringed with setae. The caterpillars of most species mine leaves and make distinctive cases out of the plant material. The subfamily Batrachedrinae (q.v.) contains species that mine in fruits of palms, and the following species, which are leaf skeletonizers in Florida, the West Indies and possibly elsewhere in the American tropics.

Homaledra sabalella is reported throughout peninsular Florida, the Dominican Republic, Puerto Rico and the nearby island of Vieques (Wolcott, 1936; Martorell, 1976; Zhang, 1994).[1]

The imagos are typical coleophorids: small, dull tan-coloured moths. The well-developed proboscis indicates that it feeds on nectars or other liquids. The caterpillar has a cream-coloured body, with the thorax and head a darker yellow and the mandibles brown. The fully developed caterpillar is about 15 mm long.

The caterpillars are 'skeletonizers', feeding on tissues of the abaxial frond surface, leaving the veins intact (Colour Plate 4c). The tissue of the adaxial surface above the skeletonized areas desiccates. The caterpillars spin a tough silk tube, in which they incorporate their fine, brown frass, extending the tube as they grow and feed over an increasingly larger area of the frond surface. The pupal stage is passed in a small, spindle-shaped cocoon within the tube. Creighton (1937) described *H. sabalella* larvae as gregarious, living in colonies of 35–100 individuals beneath a common web.

Homaledra sabalella larvae are present throughout the year and complete five generations per year in northern Florida. The larval stage may take about a month in early autumn and about 3 months during winter (Creighton, 1937).

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[1] *Homaledra sabalella* was identified in California, near San Diego, in March 2001; it has not been determined whether this species is established in that state (John Heppner, personal communication, March 2001).

Homaledra sabalella has been reported from diverse palm species (Martorell, 1976; Schmutterer, 1990). There is a single record from *Beaucarnea recurvata* (Agavaceae) in central Florida. Creighton (1937), whose observations were probably mostly in the Gainesville area, reported that *S. palmetto* was the most heavily infested native palm species and *Phoenix canariensis* the most heavily infested exotic species. According to plant inspection records obtained over several decades by the Florida Department of Agriculture and Consumer Services, the species had been most frequently observed on the native palmate palms *Acoelorraphe wrighti, S. palmetto* and *Serenoa repens*, as well as on *Washingtonia robusta*, which is a palmate palm native to Mexico but commonly planted in Florida. *Phoenix canariensis* has also been frequently reported as a host. Our impression from field observations of palms since the 1970s in Florida and some localities in the West Indies was that it was more frequent on palmate than pinnate palms.

Natural enemies of *H. sabalella* larvae in Florida include six hymenopterous parasitoids and a predator, *Plochinus amandus* (Carabidae) (Creighton, 1937).

A second species of this genus, *Homaledra heptathalama*, is known in Florida only on *S. palmetto* (John Heppner, personal communication). In contrast to *H. sabalella*, the larvae of this species are solitary (Lepesme, 1947).

Fig. 2.5. *Homaledra* sp. (Lepidoptera: Coleophoridae), an undescribed species recently found in Florida and Puerto Rico. SEM view of head of imago showing coiled tubelike proboscis, a characteristic of Lepidoptera.

In recent years, we have noticed that coconut palms are increasingly attacked by a leaf skeletonizer in southern Florida (Figs 2.5 and 2.6). We initially assumed that this insect was *H. sabalella*, but its behaviour differs from this species in preferring coconut palms to *Washingtonia* sp. and *P. canariensis*, and in that the larvae are solitary rather than aggregated. It differs from *H. heptathalama* in host preferences. Of 20 species of palms examined, extensive damage was seen only on coconut palm (F.W. Howard, unpublished). A leaf skeletonizer that has recently become a pest of coconut palms in Puerto Rico may be the same species (Edwin Abreu, personal communication). Efforts are now under way to identify this species and to investigate whether it is the same as an unidentified species of *Homaledra* reported on coconut palm from Guerrero, Mexico (Noriega *et al.*, 1991; John Heppner, personal communication).

On coconut palm in Florida, caterpillars of the species occur singly in a tube. A damaged area, often of about 2 cm × 20 cm, eventually surrounds the tube, indicating that the larvae leave the tube to feed. Damage is not present on the two youngest open fronds of coconut palm. Twenty or more skeletonized areas, each the damage of one caterpillar, are often found on the third frond. Succeeding fronds often have over half of their leaflets damaged by the caterpillars (F.W. Howard, unpublished).

Coconut palm foliage was protected from damage by this species by applications of a product containing azadirachtin (neem-seed extract), repeated at about 14-day intervals for 10 months (F.W. Howard, unpublished). Further work is being conducted to develop practical methods of controlling this pest.

Zygaenoidea

The moths of the superfamily Zygaenoidea are usually small to medium-sized. The

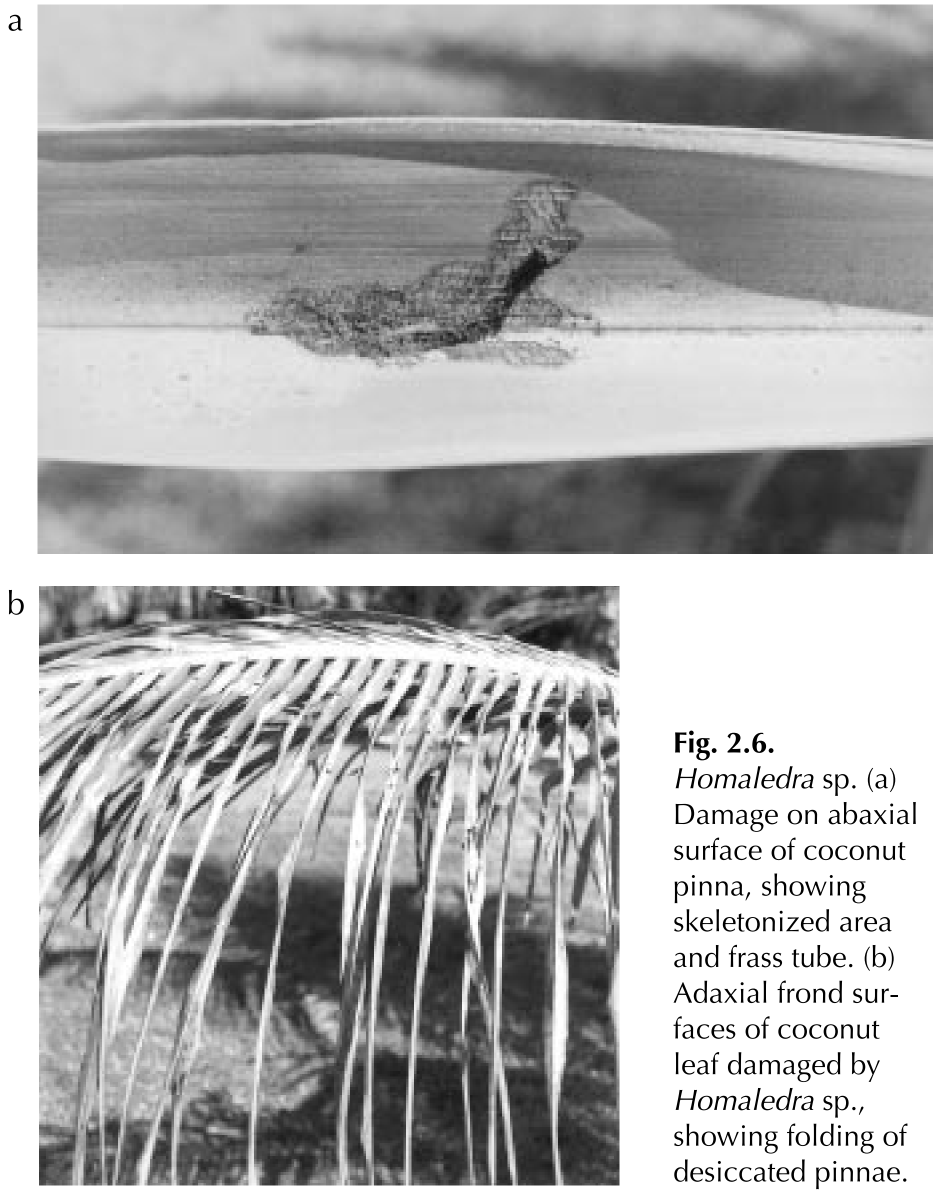


Fig. 2.6. *Homaledra* sp. (a) Damage on abaxial surface of coconut pinna, showing skeletonized area and frass tube. (b) Adaxial frond surfaces of coconut leaf damaged by *Homaledra* sp., showing folding of desiccated pinnae.

caterpillars are stout and sluglike and tend to possess some form of chemical protection, accompanied by aposematic colouring. Two families of zygaenoids, the Zygaenidae and the Limacodidae, contain important defoliators of palms. Dalceridae and Megalopygidae are also represented by important palmivorous species in some localities (Epstein, 1998).

Zygaenidae

The Zygaenidae (burnet and forester moths) are a widely distributed family of about 1000 species, most of which are tropical (Marc E. Epstein, personal communication). The moths are diurnal and brightly coloured. Unlike limacodids, zygaenids have well-developed probosci and feed on nectar. Caterpillars of many zygaenids have been shown to be cyanogenic, i.e. capable of synthesis of cyanoglucosides, which form a component of a viscous material stored in specialized cuticular cavities. This material is released in response to aggression and breaks down to yield hydrogen cyanide, which has toxic or antifeedant properties, depending on the concentration (Rothschild *et al.*, 1970). In some zygaenids, the caterpillars feed on cyanogenic plants but synthesize their own cyanogenic compounds independently. Caterpillars with well-developed chemical protection mechanisms often have aposematic colour patterns.

Cyanogenic compounds are widely distributed in plants and in arthropods (Nahrstedt, 1985), including many families of Lepidoptera. However, cyanogenesis has been found to be especially well developed in the Zygaenidae (Witthohn and Naumann, 1987). The species of Zygaenidae that are associated with palms may be presumed to possess this adaptation, but this has not been investigated.

Artona catoxantha (syn. *Zeuxippa catoxantha*, *Brachartona catoxantha*), the coconut leaf moth or coconut zygaenid, has long been known as a pest of this palm in South-East Asia. The imagos (Fig. 2.7) are small brown and greyish moths, with yellow bands on the anterior margins of the fore- and hind-wings and a wing-span of 13–16 mm (Gater, 1926; van der Vecht, 1950).

The first-instar caterpillars are translucent yellow, becoming greenish after feeding. The colour of the larva does not change materially until the third larval stage, when a median dorsal line becomes visible. The fifth-instar caterpillars are green, with a dark purplish mid-dorsal line and fainter lateral lines and with three rows of tubercles along each side, with one tubercle per segment. The tubercles bear tufts of short setae. The head is retracted in the prothorax.

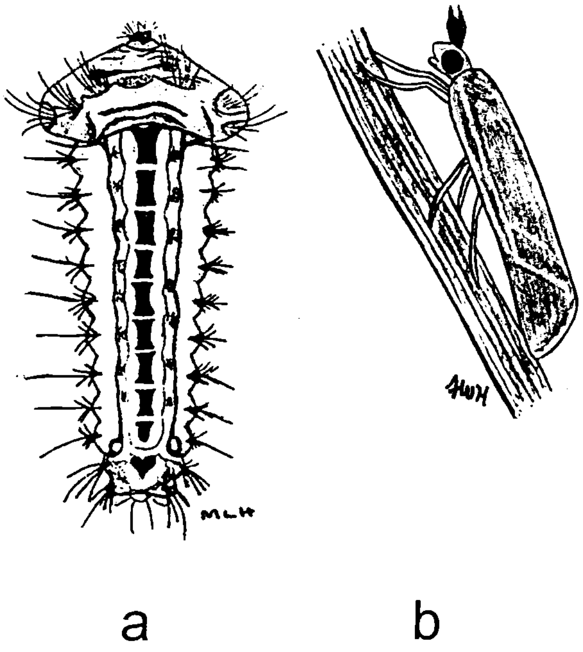


Fig. 2.7. *Artona catoxantha* (Lepidoptera: Zygaenidae), a species that attacks palms in South-East Asia. (a) Larva, redrawn by Martha Howard after Gater (1925). (b) Adult, redrawn after Puan Hamidah Suhaimi and Encik Ng Beng Cheng, in Ooi (1977).

The pupal stage, which typically lasts 9 days, is passed in a whitish, flattened cocoon of the consistency of paper, usually located at the bases of leaflets and of fronds.

The preferred hosts are coconut palm and *Metroxylon sagu*. Additional hosts include African oil palm, *Arenga pinnata, Calamus* sp., *Oncosperma* sp., *Livistona rotundifolia*, *N. fruticans* and *Salacca zalacca*. It is not a pest of African oil palm in Asia, and does not feed on *Areca catechu* (van der Vecht, 1950; Lever, 1979), although it was reported on that host (Gater, 1926). The insect attacks bananas when in outbreak conditions on nearby palms (van der Vecht, 1950).

Artona catoxantha was a pest of coconut palm in central Java as early as the mid-1800s (van der Vecht, 1950). It was probably present throughout much of South-East Asia, but was not noticed in most areas until an outbreak occurred (Merino, 1938). It is now known to be distributed in the Malay Peninsula, Indonesia (Bali, Java, Kalimantan, Sumatra), Myanmar, New Guinea, Philippines (Palawan), Singapore and many smaller islands (Merino, 1938; van der Vecht, 1950; Lever, 1979).

The imagos of *A. catoxantha* are diurnal nectar-feeders and most active during the early morning and afternoon. During outbreaks, many of these moths fly in and around the crowns and feed from flowers of coconut palm (Kalshoven, 1950/51, cited by Lever, 1979). When not flying, they tend to rest on vertical objects (Fig. 2.7). In plantations, their flight is rapid and erratic. Resting moths that are disturbed typically fly a short distance and return to the same place. During outbreaks, probably in response to crowding and exhaustion of food sources, large numbers of the male and female moths may disperse from highly infested plantations (van der Vecht, 1950). S. Leefmans (unpublished, cited by van der Vecht, 1950) observed flights of about 150,000 moths day^{-1} from a grove of infested coconut palms. They are capable of flying over distances of 1.5 km over open country and storms can spread them over greater distances (van der Vecht, 1950). They live up to 13 days in captivity. Some early researchers were intrigued by the observation that males and females sometimes exhibited a pronounced attraction to tobacco smoke (van der Vecht, 1950).

Mating is believed to involve a sex pheromone. Females are thought to begin to oviposit the day after mating in the late afternoon towards dusk, and repeat this behaviour daily for several days. Eggs are yellow, oval, about 0.5 mm × 0.6 mm and somewhat flattened. Females oviposit a mean of about 40 eggs, in irregular groups of three to 12 eggs each, on the abaxial surface of the fronds (van der Vecht, 1950).

The caterpillars grow from a length of about 0.5 mm in the first-instar to up to 12 mm in the fifth and final instar. Newly hatched first-instar larvae consume the chorions of their own eggs, a common behavioural trait in Lepidoptera, and then feed on the abaxial surface of the frond near where they hatched. This feeding results in pinhole-size damage. The second- to fifth-instar caterpillars feed on broader areas between veins, resulting in strips of damaged leaf tissue parallel to the major leaf veins. Fifth instars rest on the abaxial frond surface, but feed on the margin of the leaflet, consuming areas of 340–580 mm^2. Single caterpillars consumed a mean of 628 mm^2 of leaf tissue, about two-thirds of which is consumed in the fifth instar (van der Vecht, 1950).

The caterpillars prefer mature fronds and do not attack younger fronds except when populations are extremely dense. Fronds highly damaged by the caterpillars wither and droop, and this is followed by abnormally high shedding of immature coconuts (Merino, 1938; van der Vecht, 1950).

Within its range, *A. catoxantha* is apparently under a high degree of natural control. It is usually scarce, and seldom abundant in coconut plantations. Locally and at varying intervals of years, larval populations typically increase suddenly to pest levels. For example, an outbreak on Palawan, Philippines, affected 10,000 coconut palms (Merino, 1938). Eventually, these abnormally high populations decline precipitously, after which the insect persists at low population levels.

Based on records of 48 outbreaks of *A. catoxantha* that occurred during a total of 20 years from 1923 to 1952 on the Malay Peninsula, the preponderance of outbreaks occurred during the drier months of the year. Outbreaks usually ended at the beginning of the wet monsoon, which involves a relatively abrupt onset of wet conditions, with high winds (Gater, 1926; Merino, 1938; van der Vecht, 1950; Lever, 1953). Some early observers believed that fires in or near coconut palm plantations made conditions conducive to outbreaks of *A. catoxantha* (Gater, 1926).

During the first half of the 20th century, investigators identified many natural enemies that attack *A. catoxantha* during these outbreaks and established their importance in regulating populations of the caterpillar (Gater, 1926; S. Leefmans, R. Awibowo and J.R. Pootjes, unpublished, reviewed by van der Vecht, 1950). The parasitoids judged to be most important in controlling *A. catoxantha* included two species of Tachinidae (Diptera), one species each of Ichneumonidae and Braconidae and four species of Eulophidae. Predators include *Callimerus arcufer* (Cleridae) and occasionally other predacious insects and vertebrate animals (Gater, 1926).

Bessa remota (Diptera: Tachinidae) (Fig. 6.2) is considered to be the most effective of the several insect species that regulate populations of *A. catoxantha* (Gater, 1926; Lever, 1953, 1979; Ooi, 1977). For example, in the Malay Peninsula, of 6196 pupae of *A. catoxantha* examined, 48% were parasitized by *B. remota* (Gater, 1926).

The imagos of *B. remota* (Fig. 6.2) are diurnal and feed on flowers. They are good fliers, capable of dispersal over long distances. Flights of *A. catoxantha* and *B. remota* are often simultaneous and the tachinid parasitizes most of the caterpillars in the population at about the same time, so there is little subsequent overlapping of generations (van der Vecht, 1950).

Female flies usually produce 25 to 30 eggs and oviposit on the fourth or fifth instars of the caterpillar, laying one egg per larva. The parasitoid maggot develops internally in the host and, by its third instar, devours all internal organs of the host. *Bessa remota* parasitizes various Lepidoptera and other insects additional to *A. catoxantha*. Thus, when *A. catoxantha* is scarce, the parasitoid may live on other hosts.

Apanteles earthen (Braconidae) is second in importance to *B. remota* in some areas and more important than *B. remota* in Java (Lever, 1953, 1979). The braconid imago oviposits one egg on the second instar of the caterpillar, i.e. one stage earlier than *B. remota*. The parasitoid larva feeds internally, emerges from the third instar of the host and spins a cocoon beneath the caterpillar. It parasitizes lepidopterous species additional to *A. catoxantha*.

Caduricia leefmansi (Tachinidae) has somewhat different bionomics from that of the other tachinid and is more important in Java than in the Malay Peninsula, but is similarly most active during later phases of outbreaks of *A. catoxantha*.

Fourteen species of Chalcidoidea and two species of Ichneumonidae are exclusively hyperparasitoids that attack parasitoids of *A. catoxantha*.

An entomogenous fungus, *Beauveria bassiana* (Deuteromycotina), may make an impact on *A. catoxantha* populations under certain conditions, and attempts have been made to spread it artificially to control the pest (Lever, 1953), but, like entomogenous fungi in general, its effectiveness is undoubtedly highly sensitive to environmental conditions.

The importance of limiting insecticide use to conserve the natural enemy complex was stressed by earlier workers (van der Vecht, 1950). Ooi (1975) demonstrated control of *A. catoxantha* in experiments with trunk injections of a systemic insecticide, monocrotophos. The insecticide, 6 ml active ingredient per palm, was administered by pouring it into a hole drilled at 45° to the trunk. Holes were then plugged. Bioassays indicated that the insecticide was active in the leaves within 24 h after trunk injection and persisted there for 10 weeks. Residue analyses revealed levels of less than 0.02 p.p.m. of monocrotophos in the water and kernel, which was considered a safe level for consumers of these products. The authors recommended that the first application of insecticides be administered while the caterpillars are in the first and second instar. In this way, the caterpillars would be killed before they were attacked by *B. remota*. This tachinid would then survive in caterpillar hosts on untreated palms, such as *N. fruticans*, in the vicinity.

Early in the 20th century, *A. catoxantha* played a critical role in a famous biological control campaign against a closely related zygaenid, *Levuana iridescens,* in Fiji (see Box 2.1).

Homophylotis catori (syn. *Chalconycles catori*) (Zygaenidae) attacks coconut palm in West Africa. It is of less importance on African oil palm. The imagos, small moths with blue spangles and a wing-span of about 30 mm, are short-lived, poor fliers. They are active during the day, mating within 24 h to a few days after emerging. Females oviposit on palm fronds from the first to the fourth day after mating. The first- and second-instar caterpillars feed on the abaxial surface, leaving intact the adaxial epidermis and the main veins. Later instars, still feeding on the abaxial surface, consume large pieces of the lamina, including the adaxial epidermis. The duration of different life stages of *H. catori* and of the complete life cycle (about 50 days) are similar to those of the important Asian Zygaenidae on palms, namely *L. iridescens* and *A. catoxantha* (Cachan, 1959).

Based on his detailed field observations in Côte d'Ivoire, Cachan (1959) reported that *H. catori* larval populations tended to develop on palms of 15 years or older on

Box 2.1. The winged weapons from Elephant Stone: classical biological control of the *Levuana* moth.

Early in the 20th century, Viti Levu, the largest of the Fiji Islands, was one of the few islands of Melanesia where coconut palms were not a conspicuous feature of the shoreline. The impediment to the cultivation of coconuts was a species of Lepidoptera, the adult stage of which was a pretty blue moth, *Levuana iridescens* (Zygaenidae) (Colour Plate 5a). The larval stage was a voracious consumer of coconut foliage. Since the 1870s, one outbreak of the moth had followed another, each time spreading damage through plantations like a scorching flame. This pest was finally brought under control in 1925 in one of the most dramatically successful campaigns in the history of biological control.

Known for many years only on Viti Levu, in the early 1920s *L. iridescens* spread to some neighbouring islands, which were potential stepping-stones to Vanau Levu, the main coconut-growing island of Fiji. Because of its restricted distribution and its lack of natural enemies, entomologists assumed that *L. iridescens* was an introduced pest. If so, and if its origin could be located, its natural enemies could be found and imported into Fiji to control the pest.

In 1923, H.W. Simmonds, the government entomologist in Fiji, and A.M. Lea, of the Adelaide Museum, searched the main island groups between Fiji and Singapore and much of Queensland without finding *L. iridescens.* Lea also searched for natural enemies of *Artona catoxantha*, a zygaenid moth that had been known on coconut palms in Malaya (now Malaysia) and the Malay Archipelago for generations. *Artona catoxantha* was under natural control, undergoing outbreaks only occasionally. Because the two moth species were in the same family and had similar life histories, it seemed possible that the natural enemies of *A. catoxantha* might be effective for controlling *L. iridescens* in Fiji.

In Malaya in 1924, G.H. Corbett identified the most important parasitoid of *A. catoxantha* as *Bessa remota* (Diptera: Tachinidae) (Fig. 6.2). Since it parasitized several related species, it seemed possible that it might also attack *L. iridescens*. B.A.R. Gater had introduced this fly to an island that was a journey of 5 days from Malaya, but whether the flies could survive the longer trip to Fiji remained questionable.

Lea decided to attempt it if he could locate an '*Artona* outbreak', which was the only way to obtain large numbers of *B. remota*. Chasing reports of outbreaks up and down the Malay Archipelago, he finally arrived in Java in time to obtain large numbers of *B. remota*, and embarked for Fiji via commercial freighter, taking along small containerized coconut palms to maintain the caterpillar hosts of *B. remota* during the ocean voyage. Unfortunately, the parasitoids did not survive, but his idea of transporting the entire fly–caterpillar–coconut palm system was critical to successful efforts by later workers.

At the request of the Fijian government, the Imperial Bureaux of Entomology (IBE) in London seconded John Douglas Tothill to Fiji. A Canadian with a doctorate from Harvard, Tothill had worked as a US and then Canadian government entomologist, specializing in caterpillar pests of forest trees. He was given 2 years to solve the *Levuana* moth problem.

T.H.C. Taylor and Ronald W. Paine, young graduates of the Universities of London and Cambridge, respectively, were contracted to assist Tothill. *En route* to Fiji, their ship stopped at the Hawaiian Islands. On Tothill's instructions and with the help of sugar cane entomologists, they obtained a large number of parasitoids of various lepidopterous species and released them in Fiji. Few, if any, ever became established, but Tothill's chief objective was to put his assistants through a rehearsal of maintaining natural enemies of caterpillars on a long ocean voyage (Paine, 1994).

From our perspective three-quarters of a century later, the 'environmental friendliness' of some of their schemes would seem questionable. Pressured by the urgency of the problem, they considered the possibility of introducing from elsewhere in the Pacific the green tree ant, *Oecophylla smaragdina* (Fig. 2.8), as a possible predator of *L. iridescens*, judging that it was perhaps preferable that Fijians learn to tolerate its vicious bite, rather than endure the plunder of their coconut palms by *L. iridescens*. They were dissuaded from this venture only when, in a simple (and somewhat flawed) experiment, green tree ants confined with *L. iridescens* failed to prey on them.

An even more ill-considered scheme involved the introduction of insectivorous birds from the coconut-growing areas of India and Ceylon (now Sri Lanka). Birds were a curious choice, as it was known that zygaenids in general produced toxins (cyanogenic compounds) and thus birds avoided them. But, it was reasoned, *L. iridescens* might be an exception and, if not, perhaps the birds might prove useful as predators of other insect pests of coconuts. Potential effects of the birds on native insect or bird fauna seem not to have been considered. They engaged an Australian gentleman who had 'experience in travelling with insectivorous and other birds' to travel to India and Ceylon with a

Box 2.1. *continued*

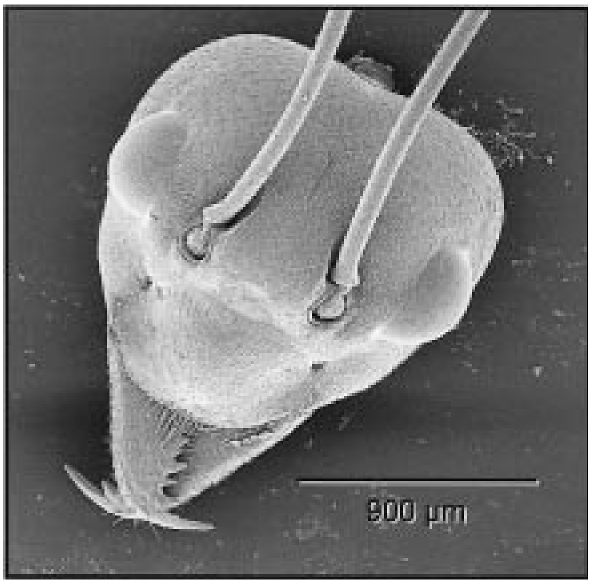


Fig. 2.8. *Oecophylla smaragdina* (Hymenoptera: Formicidae), head (SEM view). This ant is a voracious predator of caterpillars and other insects. Note the formidable mandibles with serrate cutting edges.

list of bird species and bring them to Fiji. White-vented drongos, magpie robins and toddy birds were thus imported, placed in an aviary and offered *L. iridescens* caterpillars, which they promptly demonstrated that they had no taste for. Nevertheless, Tothill still wanted to release them, at least for observation on a remote island, because they attacked several other coconut insects and also hornets. When the Director of the IBE back in London got wind of the scheme, however, he opposed it – not out of apprehensions about unknown environmental consequences, but because he thought that, if *L. iridescens* could be controlled by parasitoids, insectivorous birds might ruin things by preying selectively on parasitized caterpillars. Eventually, the imported-bird scheme was 'reluctantly abandoned'.

Tothill wanted one further search to be conducted in the areas that Simmonds and Lea had explored. They decided with a coin toss which assistant would get the task. Taylor won the toss and, after a sojourn in New Guinea, set off for Cochin China (then a republic on the Indochina peninsula). Several zygaenids that resembled *L. iridescens* were already known there and they felt that many species probably remained undiscovered. But something else about Cochin China intrigued Tothill. There had been a brisk trade in sandalwood between Fiji and southern China prior to the mid-1800s, when *L. iridescens* was first discovered in Fiji. The moth could have been introduced somehow with this traffic.

Taylor arrived in the Malay Peninsula in June, 6 months into the *Levuana* campaign; one-quarter of the period of their assignment had passed. So far, some species of zygaenid moths and their parasitoids had been collected in diverse localities of the Malay Archipelago and a flimsy connection had been built with sandalwood between Fiji and a possible native home of *L. iridescens* in Cochin China.

When Taylor arrived in Kuala Lumpur on his way to Cochin China, he met up with Simmonds, who had been dispatched there 3 months previously to 'wait for an *Artona* outbreak'. By chance, Corbett and Gater had just located an outbreak at Batu Gajah (Malay, Elephant Stone), a town about 175 km north of Kuala Lumpur. Both *B. remota* and *Apanteles* spp. were found parasitizing the larvae.

The task now was to collect the parasitoids and get them to Fiji. From Batu Gajah to the seaport of Singapore was a rail journey of about 500 km. More problematic was the fact that usually only one or two freighters per year sailed from Singapore to Suva, Fiji. It was a gamble that a port call of one of these would coincide with this *Artona* outbreak.

Luck was with them. A freighter called the *Clan Mackay* destined for Fiji via Australia would call at Singapore on 4 July.

Before Taylor's arrival in Kuala Lumpur, Simmonds had already had 100 young coconut palms potted in 'those useful articles ubiquitous in the tropics, the four-gallon kerosene or benzene tins'.

Box 2.1. *continued*

Seventeen carefully designed 1.5 m-tall cages were built, each to house four or five palms and their caterpillars. They were designed to allow free air movement and yet protect the contents from sea spray. The cages were equipped with removable poles so that each could be lifted by two men for loading.

Taylor, Simmonds and a crew of helpers collected tremendous numbers of caterpillars. It was easy to distinguish parasitized larvae, and these were placed in most of the cages. Early-instar larvae that were not parasitized were placed on other palms in separate cages, to serve as hosts for parasitoids that would emerge during the ocean voyage.

The arrival of the train in Singapore with Taylor and his cargo coincided with the arrival in that port of the *Clan Mackay*. The next leg of the trip would be even more difficult. Between Singapore and Fiji, one traversed six time zones, sailing over more than the equivalent of 20% of the earth's circumference at the equator. In 1925, the trip could be expected to take at least a couple of weeks.

The *Clan Mackay* left Singapore on 10 July and took the shipment as far as Surabaya, Java. Due to a fortuitous routing change, on the night of 12 July, Taylor was able to have the shipment transferred by small boat to another ship of the line, the *Clan Matheson*, which immediately put to sea, destined for Fiji.

Taylor and his cargo were now on the longest stretch of the journey. Surabaya to Fiji is about the same distance as North America to Africa. Although the route would seem to pass close by the continent of Australia and many island groups, things in the Pacific Ocean are far apart, as Charles Darwin (Darwin, 1834) recalled from his voyage on the *Beagle*:

> It is necessary to sail over this great ocean to comprehend its immensity. Moving quickly onwards for weeks together, we meet with nothing but the same blue, profoundly deep, ocean. Even within the archipelagos, the islands are mere specks, and far distant one from the other. Accustomed to look at maps drawn on a small scale, where dots, shading, and names are crowded together, we do not rightly judge how infinitely small the proportion of dry land is to water of this vast expanse.

More than a week out from Surabaya, halfway to Fiji, only a portion of the insects had survived, with more being lost each day. And, at that point, a shrill easterly wind impeded the ship's progress. The *Clan Matheson* swung south to avoid it, but this caused a delay of 2 days.

On 3 August, 26 days after loading the palms on the train at Batu Gajah, Taylor landed on Viti Levu with the cages containing potted palms, some live caterpillars and a total of 315 live *B. remota* imagos. Good entomology, teamwork, monumental determination and no small amount of luck had come together for Tothill and his assistants. But it was too early to celebrate. It remained to be proved that *B. remota* would attack and parasitize *L. iridescens*. If they did not, the gruelling voyage with the insects from Batu Gajah would have been wasted.

Before Taylor's arrival, an insectary had been set up containing *L. iridescens*. It was now time for the test. All 315 *B. remota* imagos were transferred to the insectary. The flies began ovipositing on the caterpillars. By the next day, 263 *L. iridescens* larvae had been parasitized by the tachinid flies. However, it was still too early for jubilation. The fact that the tachinid flies had oviposited on *L. iridescens* was no guarantee that they would complete their life cycle on this host. But, when several days later the first adult fly emerged from a pupa reared on *L. iridescens*, the entomologists could finally be more than cautiously optimistic.

Their next step would be to build up the colony of tachinid flies and cull any hyperparasitoids before releasing *B. remota* in the field. This was not as easy as they had expected. One morning several weeks later, they were appalled to find all the recently emerged flies dead or dying on the floor of the insectary. Some fly larvae survived, but the colony was almost reduced to the numbers that had survived the journey by sea. And this nerve-racking experience was repeated several weeks later. (Tothill then noticed that the flies often congregated in corners of the cage with intense sunlight, where the temperatures may have been lethal.) However, they overcame these set-backs and, by the end of November, almost 12,000 parasitized *L. iridescens* caterpillars had been released.

By January, *B. remota* was distributed wherever *L. iridescens* was known to infest coconut palms. Thirty-eight batches of *B. remota*, i.e. a total of 32,621 flies, had been liberated. The parasitism rate was high – over 90% in some cases. The *L. iridescens* population had been almost eliminated on some palms. The question now became whether the fly population would survive at a low density of *L. iridescens.*

The answer to this question came on the small island of Naigani, where there was an outbreak of *L. iridescens* in March 1926 and *B. remota* promptly attacked the caterpillars. As a result, *L. iridescens*

Box 2.1. *continued*

populations declined to the point where Tothill and his assistants could not find a single specimen. Were flies still present? To test for their presence, they released a small number of *L. iridescens*, nearly all of which quickly became parasitized by *B. remota*. By the end of 1926, *L. iridescens* became scarce in Viti Levu, Ovalau and the other nearby islands, where it had been a pest prior to the introduction of *B. remota*. Thus, the 2-year campaign was completed on time.

Two years later, Tothill and his assistants followed this remarkable achievement with a second stunningly successful biological control campaign against an entirely different kind of insect, the coconut scale, *Aspidiotus destructor* (Hemiptera: Diaspididae) (q.v.). Tothill left Fiji in 1927 to become Director of Agriculture of Uganda (he was eventually honoured as a Companion of St Michael and St George), but this did not break the momentum. Taylor and Paine continued the biological control efforts against coconut pests in Fiji, achieving complete control of the leaf-mining beetle, *Promecotheca coeruleipennis* (Coleoptera: Chrysomelidae) (q.v.).

The biological control campaigns against coconut pests in Fiji are reported in detail in the following publications: Tothill *et al.* (1930) on *L. iridescens*, Taylor (1935) on *A. destructor*, and Taylor (1937) on *P. coeruleipennis.* The first-named work is of additional interest for its detailed biological illustrations, prepared by Paine, exquisite paintings of insects, by Simmonds, and elegant botanical paintings, by Mr W.J. Belcher of Fiji. Paine's (1994) recollections of these events add an interesting perspective. Simmonds wrote a small book of reminiscences entitled *My Weapons have Wings*, but it was published privately (Paine, 1994) and is probably hard to come by.

In the decade following the introduction of the highly effective natural enemy from Malaysia, *L. iridescens* could not be found in Fiji, and the biological control programme with *B. remota* has sometimes been cited as an example of extinction of a species by a biological control agent. But there is a specimen of this moth collected in August 1941 in a government research-station collection in Fiji (Sands, 1997), and, while revisiting Fiji in 1956, Paine (1994) saw a coconut palm infested with *L. iridescens* caterpillars, and observed *B. remota* eggs on some of them. These records suggest that *L. iridescens* may survive as a rare insect in Fiji. But this question and that concerning the insect's origin remain unresolved.

In 1955, at a jubilee to review progress in biological control in the first half of the 20th century, Taylor, then Deputy-Director of the Anti-Locust Research Centre in London, reflected upon the successes in Fiji:

> In these cases, complete biological control was attained and it has stood the test of time; the results were so dramatically satisfactory that they caused entomologists and others of that period to regard the introduction of natural enemies as the simplest and most promising method of controlling insect pests in all parts of the world … It must be stressed, however, that the number of successes has been only a small proportion of the number of attempts made, and instances of complete, rapid and permanent results such as those obtained in Fiji and Hawaii many years ago must now be recognised as rare occurrences.

But perhaps it mattered that Tothill, Taylor and Paine were rare individuals.

the sea coast, from which the infestation sometimes spread inland. The insects appeared to attack younger palms only when they spread from densely infested adjacent older palms. Probably because the imagos of *H. catori* are poor fliers, palm plantings separated from infested plantings by natural barriers, e.g. lakes, swamps and forests, appeared to escape attack by this insect. The rainy season, from June to December, was favourable for the population development of this insect, while in December to April, i.e. the main part of the dry season, only low populations survived on palms in close proximity to the sea.

When the caterpillars are very numerous, they destroy almost all of the foliar surface except the midvein of the leaflet. Agronomists at the Marc Delorme research station in Port Bouët, Côte d'Ivoire, estimated that, in heavy infestations, attacks by *H. catori* can destroy up to 75% of the foliar surface of coconut palm, resulting in early shedding of fruits (Cachan, 1959).

Outbreaks of the pest have been attributed to reductions of natural enemies (parasitic Hymenoptera, Tachinidae and predacious Hemiptera) by insecticides applied against other pests (Genty, 1968). However, *Nomuraea* sp. (Deuteromycotina) has been considered to be the most important factor in regulating populations of *H. catori* (Genty, 1968; Mariau *et al.*, 1981).

Limacodidae

There are about 1000 described species of the family Limacodidae (Epstein, 1996). The family is represented in major zoogeographical regions, but concentrated in the tropics. Cock *et al.* (1987) published a comprehensive and well-illustrated review of the taxonomy, biology and control of Limacodidae of economic importance on palms in South-East Asia. Epstein (1996) published an excellent monograph on Limacodidae and related families of Zygaenoidea, which includes a taxonomic revision of these families, their bionomics and evolutionary studies. The moths are small to medium-sized, stout-bodied and covered with dense setae, giving them a woolly appearance (Colour Plate 4d). Their basic colour is most often brown, and the wings often have characteristic green patches. They are nocturnal, in contrast to the diurnal Zygaenidae, and have reduced but apparently functional mouth-parts (Epstein, 1996), while the Zygaenidae have a more developed proboscis. The antennae in most species are bipectinate, at least in the male. Females produce sex pheromones, as has been shown for *Setothosea asigna* (Sasaerila *et al.*, 1997). The flight of the moths is described as undulating and erratic. Outbreaks of limacodids tend to spread slowly, indicating low dispersal abilities (Godfray *et al.*, 1987).

Like the Zygaenidae, the caterpillars are sluglike, with the head retracted into the thorax. Thoracic legs are small. Suction discs are present ventrally on the abdomen, which in crawling are coordinated to produce a slow gliding motion. Species that bear tubercles with sharp urticating setae are referred to as nettle caterpillars (Colour Plates 4e, f, Figs 2.9 and 2.11) and some species that are smooth and appear to have a gelatinous consistency are referred to as slug caterpillars (Fig. 2.12), but there are no sharp dividing lines between these two

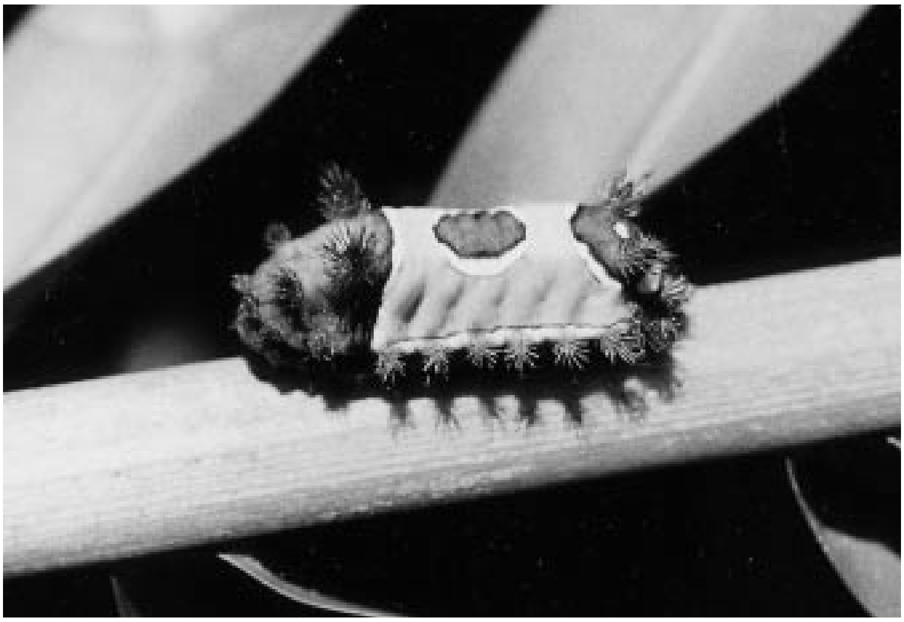


Fig. 2.9. *Acharia stimulea* (Lepidoptera: Limacodidae), saddleback caterpillar, a species common on palms in Florida.

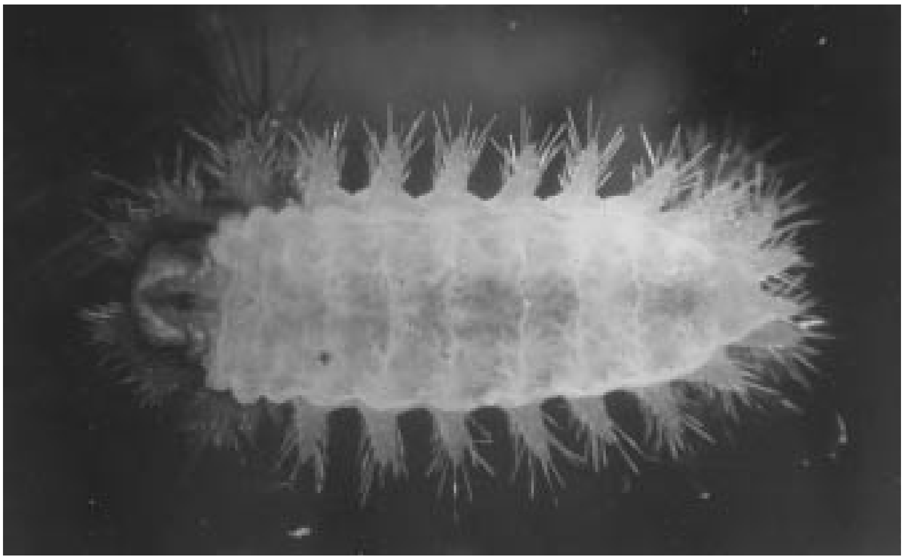


Fig. 2.10. *Acharia stimulea,* ventral surface of larva seen through a glass microscope slide on which it is crawling. With prolegs specialized as suction discs, limacodids are adapted to cling closely to the flat surfaces over which they move.

types. The pupae, usually thick and robust-looking, are enclosed in a hard, ovoid cocoon with a trapdoor exit. The dorsoventrally flattened eggs are laid singly or in overlapping clusters (Epstein, 1996, 1997).

Epstein (1988), noting Dyar's (1899) observation that limacodids are found more often on glabrous rather than rough or pubescent leaves, suggested that their method of locomotion via suction discs may be better adapted to the broad, smooth leaves of large monocotyledons, the usual hosts of this family (Fig. 2.10). In addition to palms, limacodids are among the most important defoliators of bananas and plantains (Ostmark, 1974; Stephens, 1975). Of the 92 Asian species discussed by Holloway *et al.* (1987) whose hosts were known, nearly one-third were reported from palms. Many were reported from palms and dicotyledons.

Although such observations indicate that limacodids prefer monocotyledons, many species are highly polyphagous (Aterrado and Abad, 1986; Epstein, 1996). In tropical countries, dicotyledonous host plants of limacodids include crop trees, such as citrus, coffee, cacao, guava and lychee. Limacodids of temperate regions are usually found on dicotyledonous trees and shrubs. They feed voraciously on foliage of oaks and other hardwood trees throughout the summer and early autumn, when tannins and other secondary plant substances are concentrated in leaves, and their diet may include old or tough leaves (Epstein, 1996).

Fig. 2.11. *Darna mindanensis* (Limacodidae), a limacodid distributed in the Philippines. Nettle caterpillars have tubercles and poisonous setae.

The Limacodidae appear to be best represented on palms in South-East Asia, and

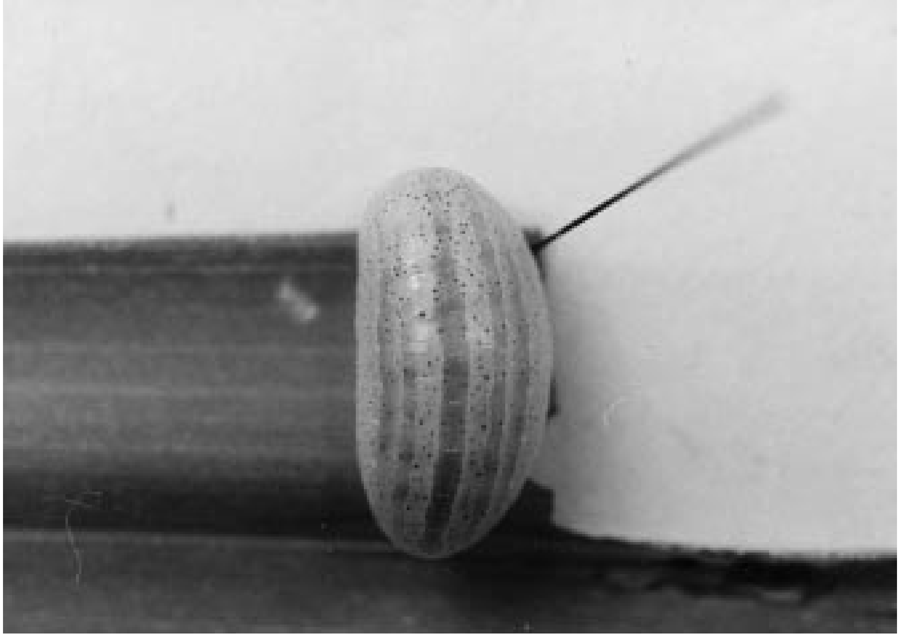


Fig. 2.12. *Chalcocelis albiguttatus* (Limacodidae), found on palms in the Philippines, an example of the 'slug' type of limacodid larva. Photo by A.A. Loyola.

are particularly well studied there (Cock *et al.*, 1987). Holloway *et al.* (1987) list 22 genera containing 64 species of limacodids known to utilize palms as hosts in South-East Asia. Many Asian species are known only from certain islands or restricted mainland localities, but about one-third of the species discussed by Holloway *et al.* (1987) are distributed in both insular and mainland South-East Asia. Fewer than ten species have been reported on palms in tropical America. In a list of limacodids reported to have reached outbreak levels on palms requiring artificial (i.e. chemical) control, Wood (1987) included nine genera and at least 13 species in Asia, one genus and two species in Africa and five genera and nine species in tropical America (Allen and Bull, 1954; Mariau, 1976a; Mariau *et al.*, 1981; Igbinosa, 1985b).

Limacodid caterpillars typically consume the equivalent of one or two leaflets per larva during their development. For example, a single larva of *Thosea vetusta*, a South-East Asian limacodid, is about 25 mm long at maturity and consumes 170–210 cm^2 of laminar area, i.e. the equivalent of two leaflets of African oil palm (Kimura, 1978). A larger South-East Asian limacodid (36 mm long at maturity), *Setothosea asigna*, consumes 300–500 cm^2 of leaf area, the equivalent of four to five leaflets, during development (Holloway *et al.*, 1987). Thus, 25 caterpillars of the latter species could consume up to 56.8% of the laminar tissue of one frond of African oil palm. Up to 2000 caterpillars per frond have been observed, e.g. for *Darna trima* during an outbreak (Holloway *et al.*, 1987).

While these observations illustrate the potential of limacodids to consume palm-leaf tissue, the effect of this loss on production of copra or other products has not been well defined under the total array of possible conditions. Without extensive research data, decisions on when to apply control measures must often be based on the intuitive judgement of experienced plantation managers or field entomologists. In general, the number of caterpillars per frond allowable (i.e. the treatment threshold) is inversely related to the area of laminar material consumed per larva, which, in turn, is often related to the size of the mature larva. Thus, treatment thresholds may be expected to vary from 10 to 20 caterpillars per frond for large species and from 30 to 80 caterpillars for small species (Wood, 1987). Indices have been recommended for many other species of limacodids (Mariau and Julia, 1973; Genty *et al.*, 1978; Mariau *et al.*, 1981; Holloway *et al.*, 1987).

Limacodid caterpillars tend to occupy fronds at mid-crown and, when two species occupy the same palm, they may be distributed on different fronds (Ang *et al.*, 1997). They usually feed on the abaxial surfaces. The caterpillars of early instars consume only the outer surfaces of leaf tissue, leaving the adaxial surface intact. This results in elongated parallel-sided window-like scars. Beginning with the fourth instar, the caterpillars may perforate these scars, so that the ultimate damage consists of holes all the way through the laminar tissue (Gallego *et al.*, 1983; Aterrado and Abad, 1986). More commonly, later instars feed on leaf margins, their heads retracted beneath the thorax, while clasping the margin with the outer edges of the thorax (Epstein, 1996). An exception to this behaviour was noted in caterpillars thought to be *Microthosea minima*. In this species, the early instars fed on the adaxial surface of palm fronds, migrating in the third instar to feed on the abaxial surface (Holloway *et al.*, 1987).

Feeding damage is often exacerbated by fungi, principally *Pestalotiopsis palmarum*, a pantropical species found on many species of palms, which may infect leaf tissue breached and damaged by early larval instars. This association has been reported with, for example, *Chalcocelis albiguttatus*, *Darna catenatus*, *D. trima*, *Parasa balitkae*, *Setora nitens* and *Thosea lutea* (Corbett, 1932; Holloway *et al.*, 1987).

A disproportionately high degree of damage caused by later- compared with earlier-instar limacodids provides an incentive to act against populations in early stages. An estimated 95% of the consumption of leaf tissue by limacodid caterpillars is by the three last larval instars (Mariau and Julia, 1973). Consumption of leaf tissue may be expected to increase linearly over time given a static population level of the pest, and exponentially if the pest's population level increases over several generations.

In addition to the damage that limacodids cause to plants by their feeding, their urticating setae can cause minor but painful injury to workers in plantations and nurseries. This is not only a problem during outbreaks, but also when populations are sparse and workers are consequently less alert to the occasional stinging caterpillar.

In the Philippines, nine genera and 22 species of coconut-feeding limacodids are known. Of these, species in five genera are consistently pests (Pacumbaba and Padua, 1988). Wood (1987) compiled a list of 25 species of limacodids reported to have reached economically significant outbreak levels in Asia, Africa or the Americas during the 20th century and rated them with respect to the frequency with which outbreaks had been reported. He rated four species, namely *Euprosterna eleasa* (syn. *Darna metaleuca*), *Parasa* sp., *S. nitens* and *Episibine intensa*, as frequently reported in outbreaks; others occurred in outbreaks less frequently to occasionally. Most of the pest species were reported on palms, with African oil palm the most frequently reported. Others were on coconut palm and two were on both of these species. Only three of the species were reported as pests of dicotyledonous species, including coffee, tea and cacao, respectively. In addition to species in Wood's list, many of the species included in the extensive reviews of Genty *et al.* (1978) and Holloway *et al.* (1987) have been serious pests in limited localities at one time or another.

Acharia stimulea, which is not a pest of crop palms, has been reported on more palm hosts than any other limacodid (Table 2.2), probably because it occurs in Florida, where an unusually high number of species of palms are grown as ornamental plants and where the Florida Department of Agriculture and Consumer Services has a highly effective plant inspection programme.

The best-known limacodids, of course, are species that have frequently undergone outbreaks and caused the greatest economic damage to economically important palms. Some significant limacodids of major regions are discussed below.

Table 2.2. Some important Limacodidae on palms, their host plants and their distribution.

Species	Pest of (palms)	Distribution	References
Acharia fusca	*Elaeis guineensis, Cocos nucifera*	Tropical South America	Genty and Mariau, 1975; Mariau, 1976a; Genty *et al.*, 1978
Acharia nesea	*E. guineensis*	Brazil, Argentina	Genty *et al.*, 1978
Acharia stimulea	Most frequent: *Adonidia merrillii* (syn. *Veitchia merrillii*), *Caryota mitis, Dypsis lutescens*. Additionally: *Archontophoenix alexandrae, Caryota* sp., *Chamaedorea* sp., *Cocos nucifera, Dictyosperma album, Nannorrhops ritchiana, Phoenix canariensis, Phoenix roebelenii, Washingtonia robusta*	South-eastern USA	Florida Department of Agriculture and Consumer Service, Division of Plant Industry (unpublished records)
Casphalia extranea	*E. guineensis, C. nucifera*	Côte d'Ivoire	Kouassi, 1993
Contheyla rotunda	*C. nucifera*	India	Mathewkutty and Subramanian, 1997
Darna catenatus	*C. nucifera, Metroxylon sagu*	Indonesia	Holloway *et al.*, 1987
Darna diducta	*Arenga* sp., *C. nucifera, E. guineensis, M. sagu, Roystonea* sp.	South-East Asia	Holloway *et al.*, 1987
Darna furva	*E. guineensis, C. nucifera, Salacca zalacca*	Thailand, north-eastern India, southern China, Taiwan	Holloway *et al.*, 1987; Zhang, 1994
Darna mindanensis	*C. nucifera*	Philippines	Holloway *et al.*, 1987
Darna nararia (syn. *Macroplectra nararia*)	*C. nucifera*	India, Sri Lanka	Zhang, 1994

Table 2.2. *continued*

Species	Pest of (palms)	Distribution	References
Darna sordida	*C. nucifera, E. guineensis*	Indonesia, Malaysia, Thailand	Holloway *et al.*, 1987
Darna trima	*C. nucifera, E. guineensis*	Malay Peninsula, Borneo, Sumatra, Java	Holloway *et al.*, 1987
Epsibine intensa	*E. guineensis*	Guyana, Colombia	Genty *et al.*, 1978
Epsibine sibinides	*E. guineensis*	Peru	Genty *et al.*, 1978
Euclea diversa	*E. guineensis*	Mexico to Peru	Genty *et al.*, 1978
Euprosterna eleasa (syn. *Darna metaleuca*)	*E. guineensis*	Mexico through tropical South America	Genty *et al.*, 1978
Natada subpectinata	*E. guineensis*	Trinidad, tropical South America	Genty *et al.*, 1978
Parasa darma	*C. nucifera*	Malaysia, Indonesia, Thailand, Philippines	Zhang, 1994
Parasa lepida	*C. nucifera, Nypa fruticans, Borassus flabellifer*	Asia	Holloway *et al.*, 1987
Parasa philepida	*C. nucifera*	Philippines	Holloway *et al.*, 1987
Parasa viridissima	*C. nucifera, E. guineensis*	Nigeria	Igbinosa 1985a, b, 1988
Pectinarosa alastor	*C. nucifera*	Indonesia	Holloway *et al.*, 1987
Penthocrates rufofascia	*C. nucifera*	Philippines	Holloway *et al.*, 1987
Penthocrates zelaznyi	*C. nucifera*	Philippines	Holloway *et al.*, 1987
Setora cupreiplaga	*C. nucifera, E. guineensis*	Borneo, Natuna Islands	Holloway *et al.*, 1987
Setora kelapa	*C. nucifera*	Indonesia	Soekarjoto *et al.*, 1980; Holloway *et al.*, 1987
Setora nitens	*C. nucifera, E. guineensis, M. sagu, N. fruticans*	Malay Peninsula, Indonesia	Zhang, 1994
Setothosea asigna	*C. nucifera, E. guineensis*	Indonesia, Malaysia, Philippines	Holloway *et al.*, 1987

Table 2.2. *continued*

Species	Pest of (palms)	Distribution	References
Thosea chrysoparala	*C. nucifera*	Ghana	Zhang, 1994
Thosea lutea	*C. nucifera,* *E. guineensis*	Malaysia, Indonesia	Holloway *et al.*, 1987; Zhang, 1994
Thosea monoloncha	*C. nucifera*	Indonesia, New Guinea	Zhang, 1994

Setora nitens is a major limacodid pest of palms in the Malay Peninsula, Java and Sumatra (Zhang, 1994). A highly polyphagous insect, its host plants include coconut palm, African oil palm, *M. sagu*, *N. fruticans*, bananas and diverse dicotyledonous trees, including cacao, cinchona, citrus, coffee, tea and others (Holloway *et al.*, 1987; Zhang, 1994).

The adult moth is brown, with dark reddish-brown bands on the wings, and has the typical woolly appearance of limacodids. The wing expanse of the female is 30–35 mm and that of the male about 15 mm. The eggs are oval, 2 mm × 3 mm. First-instar caterpillars are 3–4 mm long. Fifth-instar (i.e. mature) caterpillars are over 20 mm long, with large female mature instars up to 39 mm long. The caterpillars are typically green, but there are orange, red and other colour forms. Cocoons are spheroid, about 15 mm × 17 mm in females and 13 mm × 15 mm in males, smooth and light brown (Holloway *et al.*, 1987).

As is characteristic of limacodids, the moths are nocturnal. The females lay eggs in rows on the abaxial surfaces of the more mature fronds, often near the tips of leaflets (Holloway *et al.*, 1987). The eggs hatch in about a week. One female lays a total of about 250–350 eggs. The 3–4 mm long first-instar caterpillars feed only on the epidermis, forming translucent window-like areas, which may be invaded by *P. palmarum* or other fungi. Caterpillars of later instars feed from the margin of the lamina inward, leaving the midvein. As with many palmivorous caterpillars, *S. nitens* caterpillars attack the more mature fronds and, as population densities increase, move to ever younger fronds. Larval development takes 3–7 weeks (Wood, 1964, cited in Holloway *et al.*, 1987; Soekarjoto *et al.*, 1980). Caterpillars crawl down to the base of the trunk or among herbaceous vegetation to spin cocoons and pupate. The pupal stadium varies between 2½ and 4 weeks (Soekarjoto *et al.*, 1980; Holloway *et al.*, 1987).

Setora nitens, like many caterpillar pests of palms, may remain for long periods at low population levels, undergoing occasional devastating outbreaks. In north Sumatra, these tend to occur in the drier months of February and March, causing up to 60–90% defoliation. They are particularly severe pests of African oil palms of 2–8 years of age (Holloway *et al.*, 1987). Some caterpillars grow to be relatively large, and thus their consumption of foliage is correspondingly great (Wood, 1987). In addition to direct damage to palms, *S. nitens* is a nuisance in plantations because the venom of their urticating spines causes exceptionally painful reactions.

Natural enemies of many Limacodidae of South-East Asia are known, especially of the economically important species, such as *S. nitens* (Lay, 1996). Parasitoids of this species include one to a few species each of the families Braconidae, Eulophidae, Ichneumonidae, Sarcophagidae, Tachinidae and Trichogrammatidae. Predacious Hemiptera include a species of Pentatomidae and two species of Reduviidae. A virus and a fungus, *Cordyceps* sp., also attack *S. nitens* (Holloway *et al.*, 1987). Diagnostic tests using molecular technology have been developed for detecting viruses in *S. nitens* and *Acharia fusca* (q.v.). These can be used to monitor infection levels in the caterpillar populations (Philippe *et al.*, 1997). *Chaetoxorista javana* (Tachinidae) has been reported to be the most effective of the parasitoids (Corbett, 1932; Lever, 1979). Since the duration of its life cycle is about half of that of *S. nitens*, this fly species potentially multiplies rapidly compared with *S. nitens* (Lever, 1979).

Because *S. nitens* first attacks the older fronds, moving progressively to younger fronds, coconut farmers have sometimes removed the infested fronds, even when this means removing all opened fronds. Soekarjoto *et al.* (1980) investigated the effects of this practice, reporting that severe pruning resulted in a 76% reduction of fruits in the year following pruning. Palms that were severely infested with *S. nitens*, but not mechanically pruned, suffered a 14.3% reduction in fruits. The effects of severe pruning are thought to be due not only to the reduction of the palm's photosynthetic area, but also to damage to young fruits exposed to full sun. Thus, severe pruning to control these caterpillars does more damage than the caterpillars themselves.

In a study in Indonesia, *S. nitens* attacks were thought to cause more damage to young than to mature palms. The new fronds produced after an attack on young palms were stunted, but by the time they had produced eight new fronds the palms had appeared to recover and resumed production of normal fronds (Soekarjoto *et al.*, 1980).

Another form of mechanical control, which is particularly appropriate for nurseries and small landscape plantings, is manually removing the caterpillars from the palms. An old method described for control of *S. nitens* on tall palms consists of knocking the caterpillars off the foliage with a stiff brush of coconut fibre on a long pole (Miller, 1929).

Cultural practice may enhance biological control. Gabriel (1976) favoured maintaining a ground cover as habitat for natural enemies of limacodids.

Soekarjoto *et al.* (1980) observed that there were fewer caterpillars of *S. nitens* on fronds of tall varieties ('Bali', 'Palu' and 'Tenga') than on 'Nias Yellow Dwarf'. This difference apparently had no relation to the actual heights attained by the palms of the different varieties. The authors determined by electron-microscope examination that both stomata and trichomes on abaxial frond surfaces were denser on the dwarf variety than on the tall varieties. They noted that the head capsule of a recently eclosed larva of *S. nitens* is no larger than a trichome and suggested that the trichomes could serve as obstacles to the establishment of young caterpillars.

A substantial portion of outbreaks of *S. nitens* are thought to result indirectly from pesticide applications for various pests of coconut palm and African oil palm. Nevertheless, chemical control has been used effectively to interrupt severe outbreaks. Soekarjoto *et al.* (1980) found that certain insecticides sprayed on the foliage or fed into the palm's vascular system by 'root injection' were effective.

Parasa lepida (Colour Plate 4e) is a widespread Asian species, with three subspecies: *lepida* in India and adjacent areas, *lepidula* in China and Japan and *media* in mainland and insular South-East Asia as far east as Bali. The species is one of the most highly polyphagous limacodids, attacking monocotyledons and dicotyledons of diverse families. Palm hosts include coconut palm, *Borassus flabellifer* and *N. fruticans*, but not African oil palm (Holloway *et al.*, 1987).

The bionomics of *P. lepida* are similar to those described for *S. nitens*. The duration of the larval stage is about 4 to over 6 weeks (Desmier de Chenon, 1982). The caterpillars tend to aggregate while feeding and thus cause patchy damage to the palm. The pupae are often likewise aggregated in the crown of the palm, under the leaf bases or on the trunk. The pupal stage lasts about 20 days. The duration of the prepupa may be prolonged, probably through diapause, to over 100 days in the dry season. Pupation occurs at the beginning of the wet season (Holloway *et al.*, 1987; Marc E. Epstein, personal communication). It can be surmised that imagos are thus less likely to suffer desiccation or are timed to the leaf flush of important deciduous hosts. This contrasts with the general trend of limacodids to flourish in the dry season.

Desmier de Chenon (1982) observed a marked reduction in net production of coconut palm during the first 6 months following a severe defoliation by *P. lepida*. The palms produced no coconuts in the ensuing 18 months, and did not fully recover production until after 40 months following defoliation.

A natural-enemy complex similar to that described for *S. nitens* attacks *P. lepida*.

Mambarilla (syn. *Contheyla*) *rotunda* is a sporadic pest in Kerala State, the important coconut region on the south-west coast of India. The imagos are greyish-brown to dark grey moths. The wing-span is about 20 mm in the female and 16 mm in the male. The larvae are sluglike, with marginal tubercles bearing long spines and dorsal tubercles with short spines. They vary in colour from pale yellow, ash-grey, greyish brown to almost brick-red, with two narrow grey dorsal stripes. Cocoons are ovoid, about 8–15 mm long, spun of brown silk impregnated with a white powdery substance (Nirula *et al.*, 1954).

Their preferred host plant is coconut palm, relatively tall palms of this species being most frequently attacked. When high populations have developed on taller palms, the insects may attack younger palms and seedlings. In severe outbreaks, the insect attacks leaves of plantains. Additional hosts reported include *Curcuma angustifolia* (Zingiberaceae) and tea (Nirula *et al.*, 1954).

The slow, weak-flying imagos probably do not make extensive flights. They are often seen on coconut inflorescences. They have been observed to drink liquids (Marc E. Epstein, personal communication). Females mate in the morning and, during a period of about 2 days, lay a mean of 215 eggs in batches on the abaxial surfaces of fronds. The imago stage lasts only a few days. The mean larval period is 34 days. Cocoons are spun near the midvein of leaflets or other protected places on the palm. The pupal period is 10–14 days.

This limacodid does not usually occur at sufficient population levels to cause economically important damage, but is a devastating pest during outbreaks. The indirect effects of foliage consumption have resulted in up to 75% loss in coconut production. In an outbreak in 1936/37 in Edavanakad, all but the youngest fronds of 10,000 coconut palms were stripped, and the caterpillars even fed on surfaces of petioles (Nirula *et al.*, 1954).

Populations of *M. rotunda* are regulated by a complex of hymenopterous parasitoids of larvae and pupae in the families Braconidae, Chalcidae and Chrysididae.

The south-west coast of India has a monsoon climate (see Box 1.1), and heavy rains may cause catastrophic mortality to the weak, clumsy adult moths of *M. rotunda.*

Parasa (syn. *Latoia*) *viridissima* is a pest of coconut palms and African oil palms in Nigeria, West Africa. The moths are green, with brown markings. The caterpillars are green, with regularly spaced tufts of spines and two tufts of red-orange bristles posteriorly. The larval stage may last up to about 3 months. The spheroid cocoons are spun of whitish silk with incorporated spiny exuviae. During outbreaks, 90% of the palms in a plantation may be infested by *P. viridissima* (Mariau *et al.*, 1981; Igbinosa, 1988).

Natural enemies of *P. viridissima* are better known than most African caterpillars of palms. Two species of Braconidae, one of Eulophidae and a species of nematode, *Agamermis* sp. (Mermithidae), attack the caterpillars. Two species of Chalcidoidea, one of Ichneumonidae and one of Bombyliidae parasitize the pupae. A fly, *Palexorista* sp. (Diptera: Tachinidae), parasitizes both the caterpillars and the pupae and, in one study, was the most abundant in samples of parasitoids of this caterpillar. In that study, 17.8% of the caterpillars in 1980 and 11.1% in 1981 were parasitized, and each year most of the larvae were parasitized by the tachinid fly. Each of the other parasitic species was represented in samples by much smaller percentages. A virus, which may infect any larval stage, is a principal natural control agent (René Philippe, personal communication).

Spiders and mantids probably play additional roles in regulating populations of *L. viridissima* (Igbinosa, 1988).

By constructing a life-table for *L. viridissima* on African oil palm and coconut palm, Igbinosa (1985b) determined that the survival rate was optimal in the egg stage, and predation and microbial infection of the first two instars were the major factor that regulated generation-to-generation population growth.

Two additional important limacodids on coconut palm and, to a lesser extent, African oil palm in West Africa are *Parasa pallida* and *Casphalia extranea* (Mariau *et al.*, 1981). Their bionomics and control are similar to those of the above species. A densovirus that infects *C. extranea* has been investigated (Fediere *et al.*, 1990, 1991; Kouassi, 1993).

Acharia fusca (syn. *Sibine fusca*), a highly polyphagous caterpillar, is a pest of African oil palm and coconut palm distributed in northern South America (Genty *et al.*, 1978). Imagos have reddish-brown forewings and light brown hind-wings, with wing-spans of 48–54 mm in the female and 34–38 mm in the male. Caterpillars are pale green in early instars; after the fifth instar, the head and thorax are blue and the abdomen yellow (Genty *et al.*, 1978).

The larval stage of A. *fusca* consists of ten instars and lasts from about 6 to 9 weeks. In the first eight instars, the caterpillars live gregariously in colonies of ten to 60 individuals. They are more dispersed in the last two instars and then regroup at the leaf bases to form cocoons and pupate. Specialized deciduous spines are incorporated in the cocoon covering (Marc E. Epstein, personal communication). The pupal stage lasts about 4 to over 5 weeks (Genty and Mariau, 1975; Genty *et al.*, 1978).

Acharia fusca has a wide host range, including, in addition to palms, citrus and other dicotyledonous trees. Because *A. fusca* occurs gregariously and each caterpillar consumes the equivalent of 1.5 leaflets of a coconut palm, damage by this species can be severe.

Natural enemies include species of Braconidae, Chalcidae, Bombyliidae and Tachinidae. *Palpexorista coccyx* (Tachinidae) has been observed to parasitize 35–75% of the caterpillars of some populations. *Apanteles* sp. (*glomeratus* group) (Braconidae) parasitizes up to 30–35% of the caterpillars. *Systropus nitidus* (Bombyliidae) parasitize up to 65% of the cocoons (Genty, 1972; Mariau, 1976b).

Acharia fusca is susceptible to a densonucleosis viral disease, which causes a decrease in activity of the larvae within days after infection. The caterpillars lose their gregarious habit, become more dispersed and stop feeding. Symptoms of infection include buccal and anal secretions, softening of the larvae and a change in colour in young caterpillars from green to yellow and then brown. The disease sometimes decimates populations within about 2 weeks. Larger larvae drop to the ground, while younger larvae die stuck to the frond surfaces (Genty and Mariau, 1975).

The caterpillars can be controlled with an artificial application of this virus. To prepare this biological pesticide, caterpillars are collected while showing initial symptoms of the viral disease. These are ground up and liquefied in distilled water. Field trials were conducted in which solutions of the virus were applied to individual palms, using backpack sprayers, and to a 5 ha block by aerial application. It was found that a few grams of ground infected larvae per ha were sufficient to initiate an epizootic of the virus. The rapidity with which the virus spreads is greater with higher dosages and in populations consisting of earlier-instar larvae (Genty and Mariau, 1975). Also, it presumably spreads faster in dense populations. The virus apparently has the advantage of high specificity to *A. fusca*. The virus solution can be stored at 4°C for at least 2 years and be applied as needed (Genty and Mariau, 1975; Mariau, 1976b), including by aerial applications (Philippe *et al.*, 1997).

Acharia nesea is a pest of African oil palm and has been reported from dicotyledonous crop trees, such as cashew, mango and citrus. It is distributed in Brazil and Argentina. The highly gregarious colonies of 80–100 individuals can cause extensive defoliation (Genty *et al.*, 1978).

Pyraloidea

Several families of moths are grouped into the superfamily Pyraloidea because of common characteristics of the wing venation. A conspicuous morphological feature is a tendency for the labial palps to project forward, the basis for the term 'snout moths', which is sometimes applied to this group.

Pyralidae

Pyralidae is the largest family of Lepidoptera, with about 25,000 known species. Although species in this family vary greatly in size and appearance, typical pyralid moths are small and rather delicate, with dull-coloured bands or mottling on the wings. A characteristic of the family is a pair of tympanal organs on the first abdominal segment of the imagos. The caterpillars of most species are cryptophagous. Many are important pests of agriculture as fruit or stalk borers, miners or leaf tiers.

The subfamily Pyraustinae contains many species distributed throughout the world. Most of the species are native to the tropics. Two important species on palms are described below.

Omiodes blackburni (syn. *Hedylepta blackburni*), the coconut leaf-roller, attacks palms and other plants in the Hawaiian Islands and New Guinea (Zhang, 1994).

Imagos are basically brown. The forewing is brown, with two cream-coloured diagonal bands. The hind-wing is paler, with a single similar band. The wing-span of the female is about 30 mm. Caterpillars are up to 35 mm when fully developed, and dull green with two dorsal and two lateral whitish longitudinal stripes. Pupation takes place inside a thin cocoon constructed in the rolled leaflet (Lever, 1979).

The species is endemic to the Hawaiian Islands and is probably a natural associate of native palms, *Pritchardia* spp. Thirty-three of the 37 species of *Pritchardia* are native to the Hawaiian Islands. Most of these species occur on windward slopes in wet forests (Uhl and Dransfield, 1987). Several palm species and bananas are hosts. Coconut palm, probably introduced into the Hawaiian Islands by Polynesian colonists sometime after 400 CE, is a preferred host (Bess, 1974).

Female moths lay rows of about 40 eggs along the midveins on the abaxial surfaces of leaflets. The early-instar caterpillars spin a thin protective web and feed gregariously on the abaxial leaf epidermis. At a later stage, they disperse and form individual tubes by tying leaflets together. Sheltered in these tubes, a caterpillar feeds on the leaf margins until the leaflet is consumed to the midvein and then moves to a new leaflet and forms a new tube. The caterpillars are fully developed in about 4 weeks. The insect is present throughout the Hawaiian Islands, but most abundant and most likely to become a pest on windward sides of the islands. Palms in other areas of the islands that are exposed to winds are also susceptible to the pest, suggesting that windy conditions interfere with the pest's natural enemies (Bess, 1974).

Trathala flavoorbitalis (Ichneumonidae), which is native to the Hawaiian Islands, parasitizes up to 90% of the caterpillars of *O. blackburni*. Additional parasitoids of this species include species in the families Braconidae, Chalcidoidea, Trichogrammatidae and Tachinidae, some of which are native and some of which have been introduced from the continental USA and Japan. *Pheidole megacephala* (Formicidae) often destroys eggs and caterpillars (Illingworth, 1916; Lepesme, 1947; Lever, 1979).

Pimelephila ghesquierei is a pest of African oil palm in West Africa. Unlike most Lepidoptera considered in this chapter, *P. ghesquierei* does not consume laminar tissue of expanded fronds, but rather bores into the spear leaf to feed on young laminar tissue.

The moths are small (wing-span 25–35 mm) and dull-coloured, with olive-brown dark-mottled forewings, with scattered cinnamon-coloured spots, and paler hind-wings. The caterpillar is red in the first instar, becoming salmon-pink and lightly covered with setae in later instars, attaining a maximum length of 30–35 mm. The pupa is brown and enclosed in a cocoon of silk, with incorporated leaf-sheath fibres, and located on the adaxial surface of leaf bases of older fronds (Lever, 1979; Mariau *et al.*, 1981).

African oil palm is the main host plant. Additional hosts include coconut palm, (Lever, 1979) and *Raphia* spp. (Zhang, 1994). It has been reared on young seedlings of *Laccosperma* sp. (syn. *Ancistrophyllum* sp.) (Lepesme, 1947).

The caterpillars hatch from eggs laid at the base of the spear leaf and bore into it. The larval period lasts 4–8 weeks. Consumption of the tissue of the unfolded fronds becomes visible when these fronds open: they are perforated in a symmetrical configuration on both sides of the rachis. In young palms, the caterpillars may also damage the rachis, with a gummy exudate issuing from damaged areas. The fronds may break off where the rachis has been thus weakened. Damage by *P. ghesquierei* has the greatest potential impact on young palms in nurseries or in recent field plantings (Mariau *et al.*, 1981).

Pimelephila ghesquierei only occasionally reaches damaging population levels, being apparently regulated by parasitoids (Lever, 1979; Mariau *et al.*, 1981). Collection and destruction of pupae have been recommended to prevent population build-up in nurseries or young plantings (Lever, 1979), but Mariau *et al.* (1981) indicated that pupae, as well as the cryptophagous caterpillars, are difficult to find, and searching for them can damage young plants.

Damage to young palms by *P. ghesquierei* appears to be aggravated if the palms are growing under marginal conditions. Therefore, horticultural practices that promote vigorous growth may reduce damage by this insect. African oil palm grown in nurseries under shade are apparently more susceptible to attack than palms grown in full sun. Thus, planting young palms with sufficient spacing to allow maximum light and aeration has been recommended as a preventive against attacks by this pest.

Pimelephila ghesquierei can be controlled by chemicals in nurseries or young plantings. Mariau *et al.* (1981) suggested scouting every tenth row for damage. Treatments should be applied when 10% of the palms have at least one frond broken by *P. ghesquierei* damage.

Hesperioidea: Hesperiidae

Over 98% of the over 3000 described species of the superfamily Hesperioidea belong to the family Hesperiidae, known as skippers. Adult skippers are among the most familiar of insects. They are robust and relatively stout-bodied, with short, powerful wings. The head of skippers is distinctive among Lepidoptera: the frons and vertex are much wider than long. The head, including the compound eyes, is as wide or wider than the prothorax. The antennae, which arise far apart near the margins of the eyes, are clubbed apically; the club is usually curved backwards (Fig. 2.13).

The caterpillars of hesperiids are fusiform, clothed in a fine pile of short, secondary setae and lacking in longer primary setae. The head is typically wider than the prothorax and separated from the body by a constricted neck (Fig. 2.13). The prolegs bear crochets in a multiordinal circle. The caterpillars of skippers either fold and tie single leaves or tie several leaves together to form a shelter, leaving these at night to feed exposed on leaves. The pupal stage is a chrysalis. Many hesperiids feed on monocotyledons. Many of those that feed on dicotyledons prefer legumes.

Lepesme (1947) published an interesting illustration showing the striking similarities in the appearance of hesperiids associated with palms in various regions of the world. The following list, based on Lepesme's (1947) compilation, with other sources noted, shows that the known hesperiid fauna associated with palms is richer in

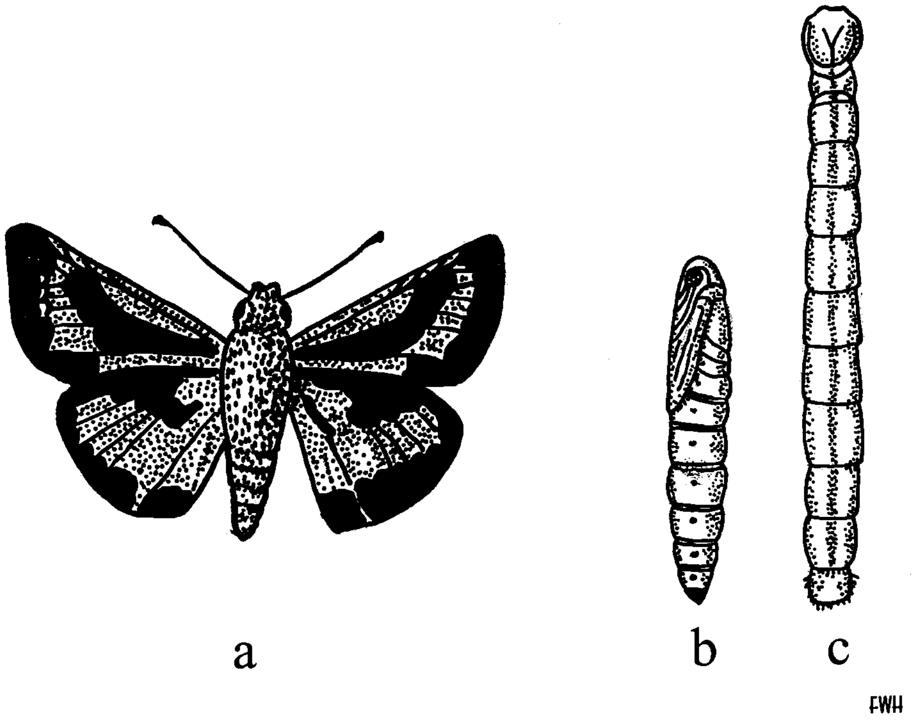


Fig. 2.13. *Cephrenes oceanica* (Lepidoptera: Hesperiidae). (a) Imago. (b) Pupa. (c) Larva. This skipper is distributed in tropical Asia. After Lepesme (1947).

Asia than in the Americas, with the fauna of Africa the poorest. Most are known from coconut palm and African oil palm and, in some cases, additional palms and monocotyledons. Steiner and Aminuddin (1997) reported on hesperiids on *Calamus*.

Asia:
- *Cephrenes oceanica*, India to the Malay Archipelago.
- *Cephrenes chrysozona* (syn. *Padraona chrysozona*), Malaysia and the Philippines (Wood, 1968; Zhang, 1994).
- *Erionota thrax*, South-East Asia.
- *Erionota torus*, Malay Peninsula.
- *Gangara thyrsis*, India to the Malay Archipelago.
- *Hidari irava*, South-East Asia.
- *Hyarotis adrastus*, China to the Malay Archipelago.
- *Lotongus calathus*, Malay Peninsula (Steiner and Aminuddin, 1997).
- *Paduca subfasciata*, Sri Lanka.
- *Plastingia tessellata*, the Malay Archipelago.
- *Quedara monteithi*, Malay Peninsula (Steiner and Aminuddin, 1997).
- *Salanoemia sala*, Malay Peninsula (Steiner and Aminuddin, 1997).
- *Suastus gremius*, India and Sri Lanka (Lepesme, 1947; Zhang, 1994).
- *Telicota ancilla* (syn. *Telicota bambusae*), New Guinea, the Solomon Islands and Queensland (Australia) (Lever, 1979; Zhang, 1994).

Africa:
- *Pteroteinon laufella*, West Africa.
- *Pyrrhochalcia iphis*, West Africa.
- *Rhopalocampta bixae*, West Africa.
- *Zophopetes cerymica*, West Africa.
- *Zophopetes dysmephila*, West Africa, Ethiopia, South Africa (Lever, 1979; Mariau *et al.*, 1981).

Americas:
- *Asbolis capucinus*, Florida and Cuba (Pyle, 1995).
- *Calpodes ethlius*, Brazil.
- *Euphyes arpa,* south-eastern USA (Pyle, 1995).
- *Perichares corydon*, Mexico to Brazil and the Antilles.
- *Perichares philetes*, Brazil (Pyle, 1995).
- *Synale hylaspes*, Brazil and Argentina.

Hidari irava, the coconut skipper, or coconut-leaf caterpillar, is occasionally a major pest of coconut palm in parts of mainland and insular South-East Asia. The imagos, with a wing-span of 42–54 mm, are brown, with four prominent golden-yellow spots and one to three translucent spots on each forewing. The caterpillars are greenish yellow, with a violet stripe on the abdomen, which broadens posteriorly. The dark brown head is broader than the thorax. Mature caterpillars are 46–53 mm long. The insects pupate in a pinkish-brown chrysalis, powdered with a white waxy material and typically suspended from leaflets and supported by a silken girdle (Lepesme, 1947; Baringbing and Bariya, 1977; Lever, 1979).

In addition to coconut palms, recorded palm hosts are African oil palm, *Areca catechu, Livistona chinensis*, *Metroxylon sagu* and *Arenga pinnata*. An additional host is bamboo (Baringbing and Bariya, 1977; Lever, 1979).

The imagos are active at dusk until dark, hiding in shade by day. The female lays eggs on palm fronds in chains or masses covered with scales. The caterpillar ties together the edges of leaflets to produce a tube within which it feeds, undergoing five instars during a period of about 5 weeks. The pupal stage lasts about 10 days. The total period from egg to emergence of the imago is about 50 days (Lever, 1979).

The caterpillars consume laminar tissue, leaving the midveins. In severe outbreaks, palms are almost defoliated, except for erect, i.e. younger, fronds (Richards, 1917). Damage has been especially severe in the Indonesian provinces of Central Java and Yogyakarta (Baringbing and Bariya, 1977).

In Malaysia, outbreaks of *H. irava* were limited to one generation, apparently by natural enemies (Richards, 1917). In Java, native parasitoids of *H. irava* include Braconidae, Ichneumonidae, Tachinidae, Scelionidae and Chalcidae (Lepesme, 1947; Baringbing and Bariya, 1977).

Natural enemies do not always adequately regulate populations of this insect; thus chemical treatments have been investigated. Foliar sprays of synthetic, organic, contact insecticides and trunk injections with monocrotophos, dicrotophos and phosphamidon were effective (Baringbing and Bariya, 1977).

Gangara thyrsis attacks various palm species in India, Sri Lanka, South-East Asia and the Philippines. The chocolate-brown imago is an unusually large skipper, with a wing-span of about 80 mm in the female imago. The forewing has two large, quadrangular, hyaline, golden spots in the centre and four smaller golden spots near the apex. The imagos are nocturnal. The caterpillar bears dense rows of white, waxy filaments.

Gangara thyrsis is a common pest of rattans (*Calamus* spp.) (Chung, 1995; Steiner and Aminuddin, 1997) and an occasional pest of coconut palms (Sathiamma and Abraham, 1998). Additional palm hosts include *A. catechu, Arenga*, *Livistona, M. sagu, N. fruticans* and *Roystonea regia.* The species also often attacks bananas. Like other species of skippers, the larvae are leaf-rollers (Lepesme, 1947; Zhang, 1994).

Cephrenes oceanica (syn. *Corone palmarum*, *Telicota palmarum*) is also widely distributed in Asia. The imagos are brown and yellow, with a wing-span of the female of about 40 mm. The dull-green caterpillars are 40 mm when fully grown (Fig. 2.13).

The caterpillar feeds on African oil palm, coconut palm, *A. catechu*, *Phoenix* sp. and *Calamus* sp. The insect is apparently most strongly attracted to *R. regia*, which is native to the Caribbean basin (Lepesme, 1947; Lever, 1979).

Erionota thrax (syn. *Pelopidas thrax*), a widely distributed skipper in Mauritius, the Malay Peninsula, the Malay Archipelago, China (Guangdong and Hong Kong), Japan and the Hawaiian Islands and mainly a pest of bananas, is sometimes found on coconut palm (Lever, 1979; Zhang, 1994).

Zophopetes cerymica is known from coconut palm and African oil palm in West Africa. The imagos are moderately large (wing-span 5–6 cm). They are basically brown, with four irregular, translucent, pale yellow patches on the forewings and violet spangles near the distal margins. The smooth yellow to green caterpillars are 50 mm long when fully developed and have yellow-ochre heads. The chrysalis is light brown.

The larvae feed inside a tube made by tying leaflets at the margins, as in other palmivorous hesperiids, development taking 5–6 weeks. The chrysalis remains inside the tube. The pupal stadium is about 1 month.

Unlike most other lepidopterous defoliators of palms, *Z. cerymica* prefers the highest fronds of palms of all ages. Infestations of plantations frequently start at the borders. Native hosts probably serve as reservoirs for infestation (Mariau *et al.*, 1981).

Pteroteinon laufella is a skipper that is often more damaging than *Z. cerymica* to young oil palms in West Africa. The imago is similar in size to that of *Z. cerymica*, but has blue-green wings. The head, bases of the wings and ventral surface of the tip of the abdomen are orange. The larvae of the two species are similar.

Synale hylaspes is a hesperiid associated with palms in Brazil and Argentina. The imago is a black skipper, with pale wing patches and a wing-spread of about 4.5 cm. Like other hesperiids, the green caterpillar ties a leaflet to form a tube, remaining in it by day and leaving it to feed by night. Coconut palm and *Livistona* spp. are recorded as hosts. It is an occasional pest in palm nurseries, where it may often be controlled by hand-collecting (Lepesme, 1947; Ferreira *et al.*, 1994).

Asbolis capucinus, a brown skipper, occurs in southern Florida and Cuba. Its larvae are leaf-rollers on palms of several species. The green-backed skipper, *Perichares philetes*, is widely distributed from southern Texas (USA) to Argentina. The larvae are usually found on large grasses, including sugar cane, but there is a record from *Desmoncus* sp. in Brazil (Pyle, 1995).

Paplionoidea

The butterflies *sensu stricto* belong to the superfamily Papilionoidea, which has about 14,500 known species. Butterflies (i.e. the imagos) are well known for their large, colourful wings, an apparent adaptation to their diurnal habits. The forewings are often rounded or triangular and the hind-wings 'tailed'. Most butterflies whose caterpillars feed on the foliage of palms are crepuscular or nocturnal, but their wings are also often large and colourful. The head of a butterfly is distinctive: the eyes are large in relation to the head and the proboscis is long and well developed. The antennae are clubbed. The thorax and abdomen are more slender in relation to breadth than in Hesperioidea.

The caterpillars are smooth, tuberculate or spiny, generally with a pile of fine secondary setae. The caterpillars feed externally on their host plants, almost always on the leaves. The crochets of prolegs occur in longitudinal rows. As in Hesperioidea, the pupa of butterflies is a chrysalis, i.e. it is exposed and suspended by a cremaster and often stabilized by a 'silken girdle'.

Nymphalidae

The Nymphalidae, the brush-footed butterflies, are one of the largest families of Lepidoptera and the largest family of Papilionoidea, comprising over 40% of the known species. The forelegs of nymphalids are reduced and not used in walking. The forewings are triangular and the hindwings are sometimes tailed. Typically, the upper surfaces of the wings have showy colours. However, they rest during the day, with wings extended dorsally, thus exposing the duller colours of the lower wing surfaces. Tricarinate antennae are a characteristic feature of this family.

The caterpillars of nymphalids usually fall into one of two general morphological types: (i) body fusiform with enlarged head bearing hornlike processes; or (ii) body cylindrical with median dorsal processes, the latter having spines.

AMATHUSIINAE. The subfamily Amathusiinae contains 80–100 species. The imagos are large, sturdy butterflies, which are often nocturnal, crepuscular or active in deep forest shade. The caterpillars are cylindrical and pubescent to hairy. Their hosts are monocotyledons, especially palms, bamboos, sugar cane and other grasses. This subfamily is distributed in tropical Australia and Asia in areas with the Aw or Af climate (see Box 1.1).

Amathusia phidippus is a common species on coconut palm and African oil palm in mainland South-East Asia and the Malay Archipelago. The caterpillars have also been collected on *Corypha* sp. (Zhang, 1994), bananas and *Agave* sp. (Gabriel, 1973). The imago, a large butterfly (wingspan of 85–105 mm), known as the palm king, is basically brown, with bands of various shades on the wings. The hind-wing bears two large eyelike spots and a smaller eyelike spot on the tail-like lobe (Colour Plate 5b).

The caterpillars are greenish grey to brown with longitudinal bands, with a thick pile of reddish-coloured setae, tufts of longer setae on the second and third abdominal segments, paired hornlike processes on the head and paired processes projecting from the anal segment. The earlier instars have three black dorsal spots (Lever, 1979). The chrysalis is light green.

The imago flies at dusk, resting by day in protected situations, such as the abaxial surfaces of palm fronds. Development from egg to imago takes about 2 months (Wood, 1968; Lever, 1979).

Lever (1979) rated it as more harmful to African oil palm than to coconut palms, but Wood (1968) indicated that, although the species is usually found on African oil palms, no severe outbreak has been recorded.

Three species of tachinid flies parasitize the caterpillars. Chalcidoid wasps also appear to be important parasitoids, as their populations appear to increase with those of *A. phidippus*.

BRASSOLINAE. The subfamily Brassolinae contains about 80 species. The imagos are large, often colourful, butterflies, with eyelike spots on the lower surfaces of the wings, which are easily observed when the butterfly is in its typical resting habit with the wings folded dorsally. The antennae are usually gradually dilated distally. The imagos are crepuscular and usually occupy forest habitats with the Aw or Af climate (see Box 1.1). The Brassolinae are widespread in tropical America and not represented in the eastern hemisphere.

Caterpillars of Brassolinae are unusually large at maturity. The head is large in relation to the thorax and fusiform body and at an oblique angle to them. Both the head and the terminal segment of the abdomen have a pair of long, posteriorly directed processes. The caterpillars feed on monocotyledons typical of forest habitats, i.e. certain non-gramineous plants, including palms. Caterpillars of palmivorous Brassolinae typically form tubes by tying together leaflets. The gregarious larvae remain in these tubes, venturing out at night to feed. Gregariousness is absent or reduced in some other Brassolinae, e.g. *Caligo* spp. These large insects seem well adapted to palms and other large plants. In some species, a protrusile glandular organ is present on the ventral side anterior to the prothoracic legs. The chrysalis is suspended on a cremaster.

Young (1980) suggested the general rule that butterfly species that utilize host plants that occur in large patches were more likely to be monophagous, as exemplified by palmivorous Brassolinae adapted to the forest understorey with a high proportion of palms.

Host data for most defoliators on palms consist of little more than listings of the palm species upon which they have been observed, sometimes with indications of apparent preferences for certain species. Link and Álvarez Filho (1979), in one of the few published studies comparing host-plant preferences of palmivorous Lepidoptera, compared the preferences of two Brassolinae, *Brassolis astyra* and *Opsiphanes invirae amplificatus* in a field survey of 14 species of palms in Santa María, Río Grande do Sul, Brazil, rating species of palms for severity of defoliation.

All species except *Dypsis lutescens* were attacked by one or both species of Brassolinae. Both species caused greatest damage to *Syagrus romanzoffiana*, which is native to that region. The authors suggested that it may be the natural host of these Brassolinae. Both species also caused severe defoliation to three species exotic to the region, including *Archontophoenix cunninghamiana*, *L. chinensis* and *Phoenix loureiri*. These species are not closely related within the palm family and are morphologically quite different.

Brassolis sophorae is generally distributed throughout much of the South American continent, from the Caribbean coast to Argentina, except for mountainous regions, and is found on Trinidad and Tobago. A large, robust, brown butterfly (wing-span of 60–100 mm), the upper surfaces of the forewings have diagonal yellow bands, which in the female are Y-shaped (Colour Plate 5d, Fig. 2.14). The hind-wing bears diagonal orange bands on the upper surface and three eyelike spots with heavy dark borders on the lower surface. Fully grown caterpillars are up to 80 mm long, i.e. about twice as long as most of the larger palmivorous caterpillars outside the subfamily Brassolinae. The early instars are yellow-brown; later instars are dark brownish red, with longitudinal lighter stripes. The large head capsule is red, with two black spots (Bondar, 1940; Lepesme, 1947; Genty *et al.*, 1978; Lever, 1979; Ferreira *et al.*, 1994).

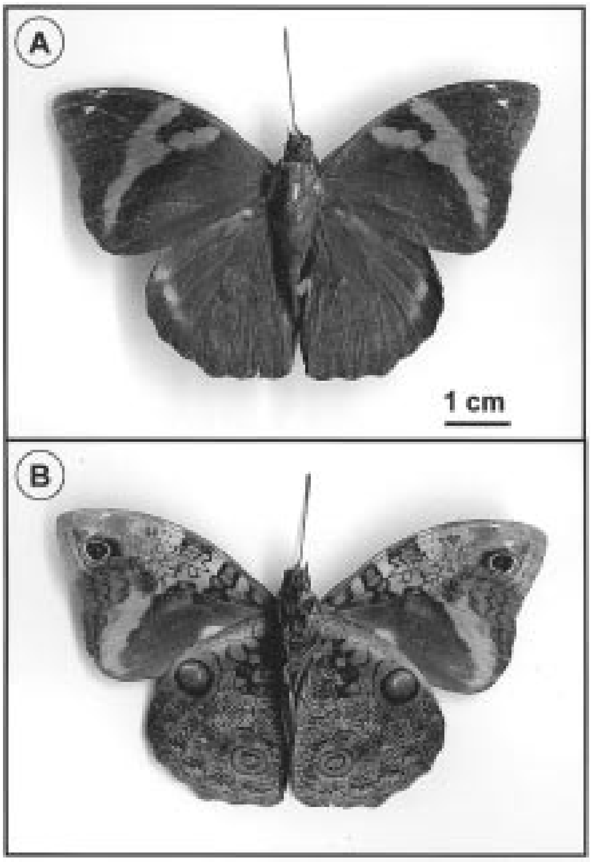


Fig. 2.14. *Brassolis sophorae* (Lepidoptera: Nymphalidae) imago, (A) dorsal, (B) ventral surface. Specimens from Colombia. The caterpillars of this brush-footed butterfly are important defoliators of palms in South America. Photo by Robin Giblin-Davis.

The species has a wide host range on palms, having been reported on African oil palm, coconut palm, date palm, *Acrocomia aculeata*, *Archontophoenix alexandrae, Archontophoenix cunninghamiana*, *S. romanzoffiana*, *Attalea* sp., *Bactris major*, *C. urens*, *Copernicia* sp., *Desmoncus major*, *Dypsis decaryi, D. lutescens*, *Euterpe* sp., *Hyophorbe lagenicaulis*, *Livistona* sp., *Mauritia flexuosa*, *Orbignya* sp., *P. canariensis*, *Phoenix reclinata*, *Pritchardia pacifica*, *Ptychosperma macarthurii*, *Roystonea oleracea*, *R. regia, Roystonea venezuelana, Sabal mauritiaeformis, Sabal umbraculifera, Scheelea macrocarpa* and *Washingtonia filifera*. The species also attacks other large monocotyledons, including bananas, *Ravenala madagascariensis* and *Strelitzia nicolae* (Cleare and Squire, 1934; Genty *et al.*, 1978; Stauffer *et al.*, 1993). This host list reveals no pattern in taxonomic affinities within the palm family. In a botanical park in Caracas, severe attacks were observed on more than 50% of each of the following species: *Acrocomia aculeata, A. alexandrae, B. major*, *D. lutescens* and *R. venezuelana*. This might suggest a preference for pinnate fronds, but severe infestations were also seen on 30% or more of some palm species with palmate fronds. *Caryota plumosa*, although in close proximity to infested *C. urens*, was not attacked (Stauffer *et al.*, 1993).

This conspicuous butterfly was apparently well known in colonial times. In 1705, more than half a century before the species was described by Linnaeus (1758), Maria Sybilla Merian published figures of the caterpillar and imago, with field notes on the insect's bionomics, in a book on insects of Suriname, cited in Cleare and Squire (1934). A.R. Wallace mentioned that *B. sophorae* fed on fronds of coconut palm 'and much disfigures them' (Wallace, 1853). But it was not until the late 1800s that outbreaks of the species on palms were first reported. Initially, these were mostly on 'cabbage palms' (probably *R. oleracea*), and less often on coconut palm and several other palm species. By the early 1900s, outbreaks on coconut palm had begun to occur annually in Guyana, shifting each year to different specific localities in that country. Since then, *B. sophorae* has become a pest of coconut palm and, to a lesser extent, African oil palm in many areas where these palms are grown in South America. It is also an important pest of landscape palms in some South American cities (Zenner de Polanía and Posada Flórez, 1992; Ruszczyk, 1996).

The imagos rest on the abaxial surfaces of palm foliage during the day 'in the gloomiest shades of the forest' (Wallace, 1853) and begin showing signs of activity in the very late afternoon as sunlight intensity decreases (Zanetti *et al.*, 1996). At dusk, they become fully active, during which period they mate. They are also active just before dawn (Wallace, 1853). During the period when an adult generation emerges, individual females vary in size and potential fecundity (i.e. the number of eggs produced prior to fertilization). Those that emerge toward the end of the period are relatively small and less fecund. Thus, there are greater and better mating opportunities for males that emerge during the median of the female emergence period (Carvalho *et al.*, 1998).

The flight of *B. sophorae* is described as 'feeble'. The females lay eggs in clusters of a few to over 200 eggs, presumably during hours of darkness, although this has not been observed. Oviposition is on diverse parts of the palm, including fronds, fibrous leaf bases, trunks and fruits, and sometimes on debris beneath palms. The eggs hatch in 20–25 days (Genty *et al.*, 1978).

The caterpillars consume the remains of the eggs from which they hatch and remain aggregated and inactive for about a day. In their first wanderings, often in single file, they select a feeding site on the palm frond. These earliest instars hide by day in protected situations afforded by the frond structure and feed on surface tissue by night. Later, the aggregated caterpillars tie a leaflet to form tubes, within which they hide by day. More advanced instars tie together several leaflets to form a 'nest', in which sometimes hundreds of caterpillars congregate. During a short period at night, the caterpillars proceed in single file to find feeding sites on the palm frond (Cleare and Squire, 1934). The larval stage takes 50–85 days. The chrysalis is fixed to petioles or the trunk or located on the ground beneath the palms. It lasts about 11–15 days (Ferreira *et al.*, 1994).

Individual consumption per caterpillar is relatively high, i.e. about 500–600 cm^2 of frond area (equivalent to about 2–2.5 leaflets of coconut palm) per caterpillar. This, combined with their gregarious habits, results in spectacular damage (Genty *et al.*, 1978; Ferreira *et al.*, 1994). They often consume up to 50% of the foliage of one coconut palm (Bastos *et al.*, 1979). The species undergoes one or two generations per year. In Aracajú, Brazil, a small population peak coincides with the wet season (June–August) and a greater peak coincides with the dry season (November–February) (Joana Maria Santos Ferreira, personal communication).

In the egg stage, *B. sophorae* may be attacked by species of Encyrtidae, Eulophidae and Scelionidae. The larval stage is attacked by Perilampidae, Tachinidae and Chalcidoidea. Species of Sarcophagidae and Chalcidae have been observed emerging from the pupae. Epizootics of the entomogenous fungus *B. bassiana* sometimes eliminate much of the larval population, and a second fungus, *Paecilomyces* spp. (Deuteromycotina) also attacks this species (Genty *et al.*, 1978; Pallazini *et al.*, 1988; Zenner de Polanía and Posada Flórez, 1992; Alves *et al.*, 1994; Duodu *et al.*, 1994). Application of a formulation of *Beauveria brongniarii* in coconut plantations has provided up to 90% control of *B. sophorae* in Brazil (Ferreira *et al.*, 1994).

The behavioural trait of aggregating in 'nests' has been successfully exploited to prevent population increases of this insect in plantations. Surveying periodically and collecting nests with the aid of pruning poles is an important control measure recommended for all areas where this species is present. Nests may be destroyed (Lever, 1979), but a better method is to hang them in cages in the area so that natural enemies may emerge from the caterpillars and attack caterpillars not found by the surveyors (Zenner de Polanía and Posada Flórez, 1992). Toxic baits, utilizing an aqueous solution of honey or rotted fruits, for control of the imagos are also used (Zenner de Polanía and Posada Flórez, 1992).

Brassolis astyra, like *B. sophorae*, has a wide distribution in South America (Genty *et al.*, 1978), but has not been reported from Trinidad (Lever, 1979). Based on a field survey in Rio Grande do Sul, Brazil, *B. astyra* attacked several different species of exotic palms but preferred and caused greatest damage to *S. romanzoffiana*, which is native to that region (Link and Álvarez Filho, 1979). The locality studied is at about 30°S latitude. *Brassolis astyra* is an occasional pest of coconut palm in the tropics (Genty *et al.*, 1978).

Opsiphanes quiteria is widespread in tropical America. A subspecies, *O. quiteria quirinus*, was studied in detail in Costa Rica (Young, 1977). The imagos were active just before dusk (1730–1800 h) under both clear and overcast skies and in both wet and dry conditions. Mating apparently takes place soon after eclosion from the pupal case. Females oviposit on trunks, fronds and fibrous leaf sheaths. On fronds, eggs are laid in rows, while on trunks they are clustered or single. On fibrous leaf sheaths, they are laid in a loose grouping. The females make short, rapid flights around the palms, landing occasionally to oviposit. About 60% of the 'ovipositional landings' occurred on the trunk and the others on fronds and associated fibrous sheaths. They thus laid proportionately more eggs on the trunk than on the fronds, compared with other Brassolinae. The caterpillars are large (105 mm long when fully developed) and gregarious, and they hide by day in the rolled leaf 'nest', venturing forth at night to feed, preferring the older fronds. Caterpillar populations were higher on the few coconut palms observed than on wild palms in the forest understorey observed over a 5-year period by Young. The relatively greater abundance of insect pests on economic plants in comparison with wild plants is usually attributed to the favourable conditions for insects provided by monocultures. However, in this case there was a maximum of ten coconut palms in the study locality. The author suggested that the destruction of the native habitat may have concentrated Brassolinae on coconut palms.

Opsiphanes cassina is found on African oil palm in Colombia, Ecuador and Peru (Genty *et al.*, 1978). The imagos are reddish brown, with orange-coloured transverse stripes on the forewings. The wing-span of the female is about 72 mm. The caterpillars are large – up to 90 mm when fully developed – and green with a yellow stripe. The chrysalis is light green (Genty *et al.*, 1978). An individual caterpillar may consume up to 800 cm^2 of foliar tissue of African oil palm, the equivalent of about three leaflets. Populations may increase rapidly, causing significant defoliation (Genty *et al.*, 1978).

A natural enemy complex of hymenopterous parasitoids and a nuclear polyhedrosis disease apparently regulates populations of *O. cassina*. Control measures may be occasionally necessary.

Bacillus thuringiensis may effectively control populations if applied while caterpillars are in early instars. Caterpillar populations have been controlled by applications of carbaryl. Control of imagos with insecticide-laced honey baits is said to effectively reduce populations (Genty *et al.*, 1978), but would appear to be hazardous to many kinds of non-target organisms.

The caterpillars of *Caligo* spp. feed mostly on Musaceae and Marantaceae, but are occasionally found on palm fronds in tropical South America. The caterpillars are large – up to 140 mm long. Although they are not gregarious, a single caterpillar may consume up to 1500 cm^2 of leaf tissue of African oil palm, the equivalent of about six leaflets. The imagos are relatively large, brown moths, some with metallic spangles, with up to 180 mm wing-spans. They are among the most spectacular butterflies of the American tropics (Lepesme, 1947).

SATYRINAE. The subfamily Satyrinae includes 3000 species distributed widely throughout the world. The adult butterflies are dull-coloured, usually brown or tan, with conspicuous eyelike spots on the lower wing surfaces. The eyes are more oval than that of most other nymphalids.

The fusiform caterpillars are clothed in a pile of short secondary setae. The head is large in relation to the thorax, often with dorsal processes bearing spines. The terminal abdominal segment is bifid. Food plants are monocotyledons, mostly grasses and sedges. Pupae are suspended by a cremaster or in a thin cocoon on the ground.

Elymnias hypermnestra is a palmivorous satyr known in the Malayan Peninsula and parts of Indonesia. The adult female butterfly is orange-brown, with irregular white markings at the wing borders and a wing-span of 55–75 mm. Males are slightly smaller, dark brown and with metallic blue markings on the margins of the forewings, and the hind-wings are reddish-brown to orange (Corbett, 1932; Lever, 1979).

The caterpillar (Colour Plate 5c), morphologically a typical satyr with a pair of dorsal processes bearing spines arising from the head and a bifid terminal abdominal segment, is green with four pairs of longitudinal yellowish stripes; the second pair from the meson is broadest and has red and blue spots. They are about 40 mm long when full-grown (Corbett, 1932; Lever, 1979). The chrysalis, pale green with yellow and red stripes, is attached to a palm frond (Corbett, 1932). Coconut palm, *A. catechu* and *Cyrtostachys lakka* have been listed as hosts but there are probably additional hosts.

Elymnias fraterna attacks fronds of coconut palm in Sri Lanka (Nirula, 1956). Several additional species of *Elymnias* are observed on palms in Asia. They are seldom, if ever, serious pests of coconut palm or other palms in commercial plantations (Lepesme, 1947). However, the feeding damage of a few of these caterpillars on a small ornamental palm may be sufficient to cause concern. Several additional species of this family are distributed from Asia to Oceania (Lepesme, 1947).

Melanitis leda is an additional satyrid reported on coconut palm from Africa to tropical Asia and Australia (Lepesme, 1947).

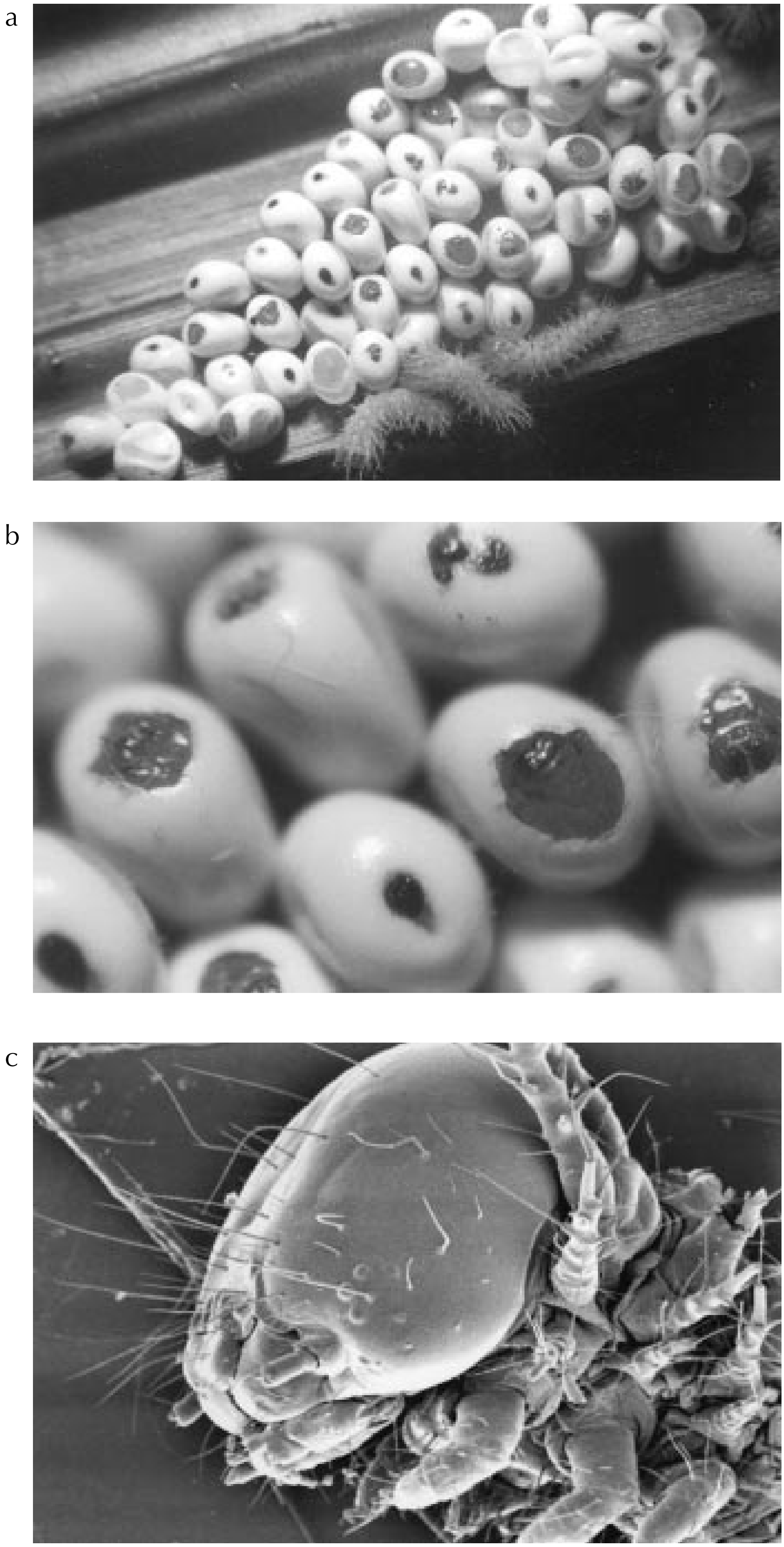
Bombycoidea: Saturniidae

The Saturniidae, the giant silk-moth family, comprises 1100 species worldwide. It is represented on palms by a few species native to the Americas.

The io moth caterpillar, *Automeris io*, is native to the eastern USA (Colour Plate 5f, g; Fig. 2.15). The adult moths are a burnt-orange colour, with conspicuous eyelike markings on the dorsal surface of the hind-wings (Colour Plate 5f). A highly polyphagous species, in southern Florida these colourful caterpillars are often found on palms. They are orange in the younger stages and bright yellow or greenish yellow in the mature stages, with a bold white lateral stripe with purplish-red borders (Colour Plate 5g). They feed on the leaf tissue of palms, growing from 1 mm to a length of 700 mm over a period of several weeks (Heppner, 1994; F.W. Howard, unpublished).

Automeris janis, *Automeris cinctistriga*, and *Automeris liberia* are similar species that attack palms and other plants in some parts of tropical America. Natural enemies, including Braconidae, Ichneumonidae and Tachinidae, usually control these species, but they are occasional pests on African oil palm and coconut palm (Genty *et al.*, 1978; Ferreira *et al.*, 1994; Zhang, 1994). *Periphoba hircia* is a saturniid recently reported from African oil palm in Peru (Couturier and Khan, 1993).

In their native habitats, giant silk moths are usually under natural control by parasitic wasps, but occasionally dense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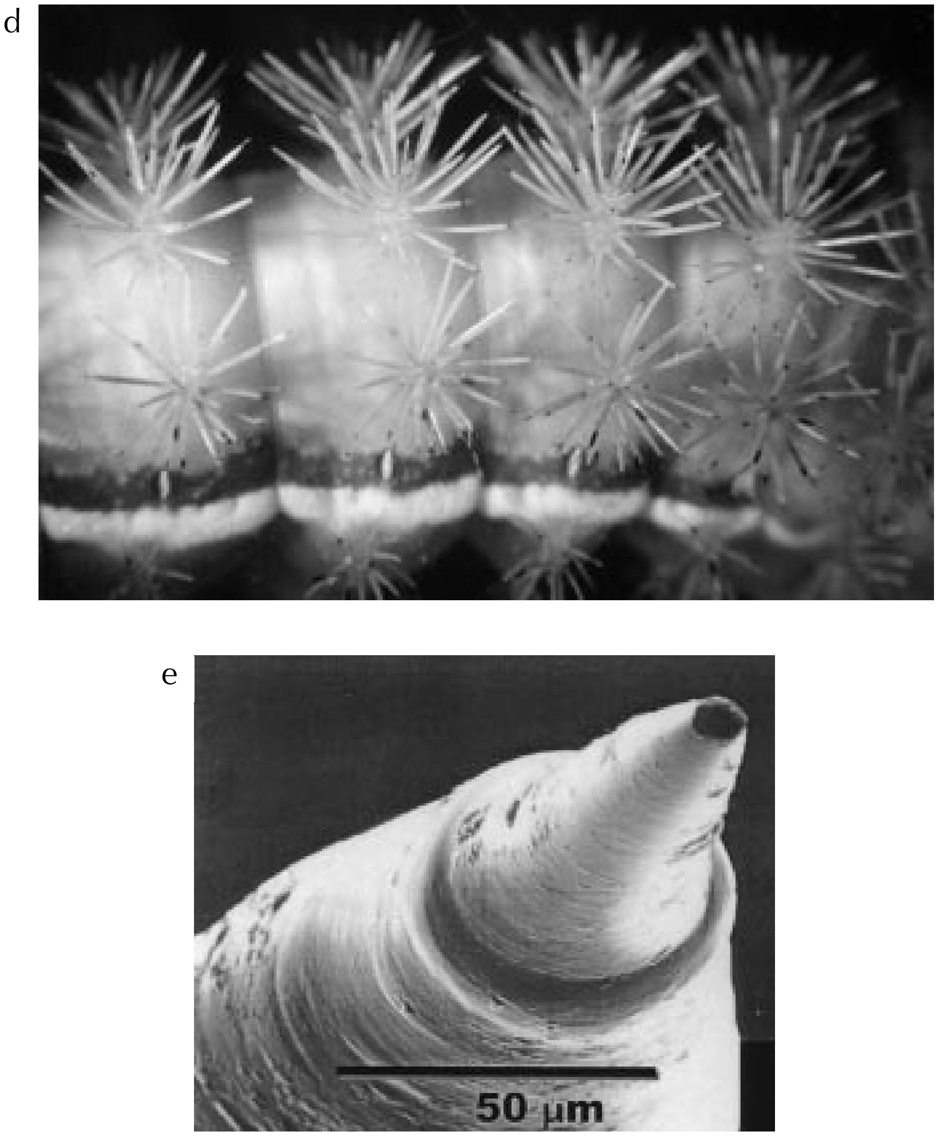


Fig. 2.15. (*and opposite*) *Automeris io* (Lepidoptera: Saturniidae), the larva of which attacks palms in Florida. (a) Egg cluster in various stages of hatching. (b) Detail showing hatching eggs. (c) Head of larva (SEM view). (d) Urticating setae of larva. (e) Tip of urticating seta magnified 1000 times by SEM view. Note orifice through which venom is injected, and constriction where seta probably breaks off, leaving venomous tip in victim.

populations cause considerable defoliation to palms (Fig. 2.16). Additionally, they are a hazard to nursery and landscape workers because of their stinging hairs (Fig. 2.15d, e; Heppner, 1994; Couppie *et al.*, 1998).

Coleoptera

Forrest W. Howard and
Reynaldo G. Abad

Second to Lepidoptera in importance as defoliators of palms on a worldwide basis and of equal or greater importance in particular localities are the beetles, order Coleoptera. Beetles are highly sclerotized, mandibulate, holometabolous insects, with forewings modified as leathery to rigid elytra, the latter serving the vital functions of protecting the hind-wings and abdomen and covering the abdominal spiracles to control water loss. The hind-wings are membranous, with reduced venation, longer than the elytra, and are the principal flight organs, although the elytra apparently contribute to lift or stability in flight.

Fig. 2.16. Defoliation of coconut palms by caterpillars. (a) Containerized palms defoliated by *Automeris io*, which left only the midribs of the fronds. (b) Egg mass, laid on a small portion of the lamina, which remained after feeding by previous generation.

Rigid or leathery forewings are known in groups other than Coleoptera, notably Orthoptera, Blattaria and Dermaptera, but their structure is different (Crowson, 1981; Lawrence and Britton, 1991).

Beetle larvae typically have sclerotized head capsules and soft thoracic and abdominal regions. In most beetle larvae, the thorax bears three pairs of five-segmented legs. However, leaf-mining larvae of the Hispinae, the subfamily containing most coleopterous defoliators of palms, are apodous (legless).

In most of the Coleoptera, the pupae are exarate, i.e. the appendages are free of the body rather than fused. Hispinae are again an exception. Their pupae are obtect, i.e. the appendages are fused to the body, as in many Lepidoptera.

With an estimated 300,000 described species, representing perhaps one-quarter of all species of known plants and animals, Coleoptera are the largest order of known species of organisms. Although it is sometimes suggested that the perceived predominance of beetles could reflect collecting biases and that some other taxon could eventually prove to be larger, there is no doubt that this order is a dominant form of life on this planet.

The Coleoptera are not basically a phytophagous order. Of the 171 families recognized by Crowson (1981), few are basically plant-feeders. The biology of many families is poorly known, but probably either the imagos or the larvae or both of somewhat more than half of the families of beetles are primarily associated with decaying organic matter, feeding on the decomposing matter itself or on fungal bodies, mycelia or spores (Lawrence, 1982). A small portion of beetle families are highly specialized, e.g. as parasites or inquilines of other insects. Slightly more than 10% of the families are basically predacious and about an equal portion contain significant numbers of species that feed on green algae, Bryophyta, Filicopsida and vascular plants, i.e. the classes Gymnospermae and Angiospermae. Almost every family of vascular plant contains species that are hosts of Coleoptera. Various species feed on diverse parts of vascular plants, including roots, main stems, shoots, buds, leaves, floral parts and pollen, as well as nectar and sap. Most species of beetles that feed on leaves of higher plants belong to either of the two largest families of beetles, Curculionidae and Chrysomelidae, both of which are entirely phytophagous. These two families constitute about 1% of the families but about one-third of the species of the Coleoptera. Most palmivorous Coleoptera are either curculionids or chrysomelids.

Some species of Curculionidae and Scarabaeidae are borers in palm buds, which results in damage to the fronds as they open. They are thus not defoliators as we define the term, and are treated in our chapter on borers (Chapter 5).

Chrysomelidae

Nearly all beetle defoliators of palms are species of the Chrysomelidae, or leaf beetles. This is one of the most important families of phytophagous insects and one of the largest families of beetles, with about 2500 genera and 35,000 known species in 15 subfamilies. Some of the most important pests of trees and crop plants are chrysomelids. Except for one subfamily, the Bruchidae, members of which feed internally in seeds, chrysomelids are defoliators, and the great majority of beetles found feeding on leaves of higher plants are chrysomelids. A morphological characteristic that distinguishes the Chrysomelidae is the structure of the tarsi. In most families of Coleoptera, there are five distinct tarsomeres. The tarsi of Chrysomelidae are often described as ‘apparently four-segmented’ or ‘pseudotetramerous’. There are actually five tarsomeres, but the fourth, or penultimate, tarsomere is usually greatly reduced and concealed in a notch of the third (Chen, 1973). In addition, the tarsomeres of Chrysomelidae are expanded and have adhesive lobes (a trait that is found in other groups that frequent aerial plant parts, e.g. Curculionidae).

In one grouping of the Chrysomelidae, the fourth segment is completely fused to the fifth and thus there are truly four tarsomeres. Most species of this grouping fall into one of two subgroups or branches, which are clearly distinguished by morphology and bionomics. These are the leaf-miner branch (hispines) and the tortoise beetle branch (cassidines). They are closely related, and are linked by intermediate forms. Systematists differ in their interpretations of the relationships bet-ween these two groups and they have been variously recognized as: a superfamily, the Cassidoidea, discrete but closely related to the Chrysomeloidea (Chen, 1973); two tribes, the Hispini and Cassidini, of the subfamily Hispinae of the Chrysomelidae (Lawrence and Britton, 1991); or the long-held concept of two closely related subfamilies, Hispinae and Cassidinae, of the Chrysomelidae (Crowson, 1981). Species of this group on palms are distinctly either hispines or cassidines, with no intermediate forms, and will be referred to as such in this review.

Morphological characteristics that hispines and cassidines share with Chrysomelidae in general are that the imagos are typically elongate, oval to orbicular insects, as seen from above, glabrous and often colourful, with filiform antennae (Fig. 2.17). The imagos of typical hispines are at least more than two times longer than wide, small, but more than 3 mm long. Some species are broadest posteriorly, giving them a slightly wedge-shaped appearance. The elytra typically have longitudinal ridges alternating with punctate rows (with minute pits). The antennae arise close together from the front of the head, the antennal sockets being subcontiguous. Their habit of carrying their filiform antennae in a V position is a good field identification character (Jones, 1913).

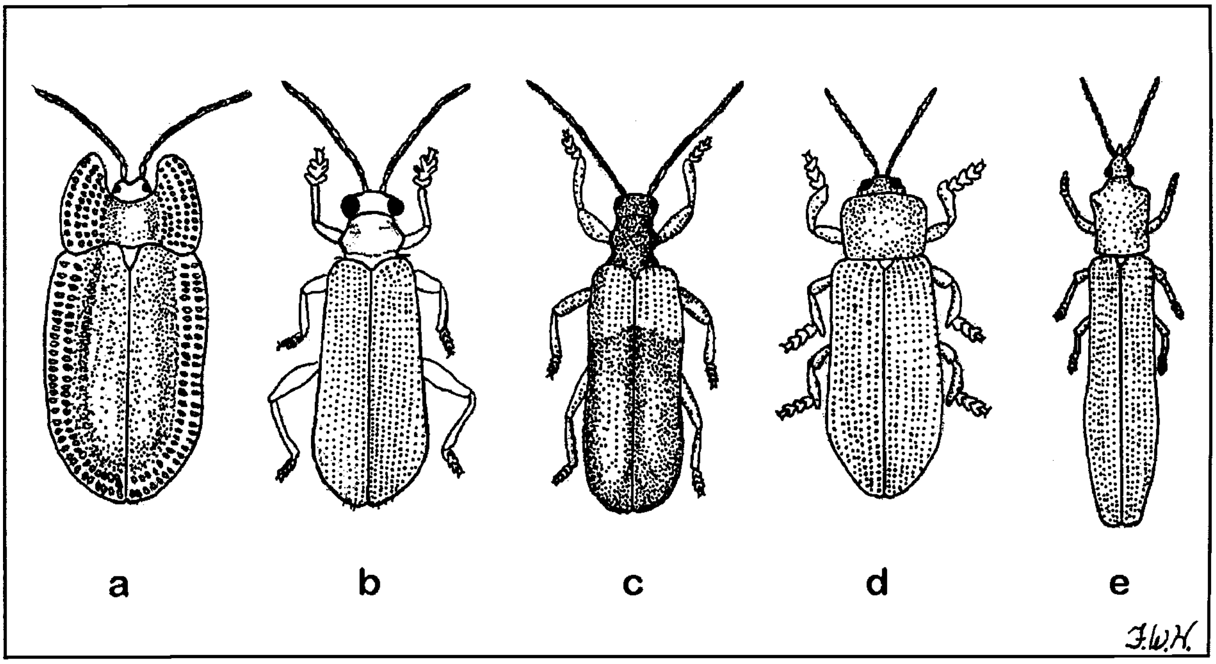


Fig. 2.17. Chrysomelidae (Coleoptera) associated with palms. Redrawn from sources indicated. (a) *Delocrania cossyphoides* (Cassidinae), South America (Bondar, 1940). (b) *Promecotheca guadala* (Hispinae), Solomon Islands (Gressitt, 1957). (c) *Promecotheca opacicola* (Hispinae), Vanuatu (Lepesme, 1947). (d) *Wallacea dactyliferae* (Hispinae), India (Maulik, 1919). (e) *Brontispa longissima* (Hispinae), Solomon Islands (Pagden and Lever, 1935).

The eyes are emarginate. An important characteristic that distinguishes the hispine–cassidine group from other Chrysomelidae is the relatively small mouth-parts in relation to the head. The mouth-parts are strongly hypognathous or opisthognathous and the frons of the head slopes posteriorly. The first three tarsomeres are expanded, with the third deeply bilobed, and the tarsomeres bear bifid adhesive setae.

Hispine and cassidine larvae are dorsoventrally flattened, with prognathous mouth-parts differing from the larvae of most chrysomelids, which are elongate and curved, with deflexed heads.

Typical hispine larvae feed between the abaxial and adaxial epidermis of the leaf. This activity results in a gallery, or leaf mine. A leaf mine is a feeding channel made by an insect larva or larvae in the parenchymal tissue of plants, in which the epidermis, or at least its outer wall, remains undamaged, thus shutting off the mining cavity from the outside. Leaf mines of hispines are visible externally, because only a thin layer of tissue is left above and below the mine, and this often changes colour due to necrosis. A leaf mine serves as both feeding and living quarters for a leaf-miner (Hering, 1951).

In some hispine species, each mine is constructed and occupied by an individual larva, while in others multiple larvae occupy the same mine. For example, in *Promecotheca guadala*, as many as five larvae may occur in a single mine (Gressitt, 1957). Hispine larvae penetrate the leaf soon after hatching and feed from side to side as they advance slowly forward. As a result, the mine is broader than the larva. Their adaptations for life in their mines include small size, dorsoventral flattening, the apodous condition and prognathous mouth-parts. Since they are adapted to feeding while moving forward, they never change mines naturally and, if removed from a mine and placed on the leaf surface, most species are unable to penetrate the leaf and initiate a new mine (O'Connor, 1940; Hering, 1951). While biting or tearing with the mandibles to form the mine, hispine larvae stabilize themselves by means of sclerotized toothlike projections on the abdomen, which grip the 'floor' of the mine. The ninth and terminal segment of some species is projected posteriorly in a bifurcate process (Fig. 2.18; Gressitt, 1957). Some species, e.g. *Brontispa* spp. on palms, feed between closely appressed leaflets of the unfolded youngest frond of a palm or have otherwise concealed habitats in leaves, but do not form true mines.

The leaf mine is an eminently favourable habitat for insect development. A rich food resource is constantly available and temperatures and humidity in mines tend to be higher and thus more favourable for insect development than in the surrounding air. Leaf-mining is relatively efficient, because the larva gains access to food resources with a minimum of motion. The tissue which they consume, the mesophyll, the major tissue between the abaxial and adaxial leaf epidermis, is composed of thin-walled cells that are rich in nutrients.

Because of their small size and high surface-to-volume ratio, one of the major hazards that insects contend with is desiccation, a problem especially for larvae, which have not developed the protection of a highly sclerotized exoskeleton. Leaf-mining larvae have expropriated the epidermis and cuticles of leaves and their moist internal environments for protection against direct sunlight and the drying effects of air movement, thus conserving water in their own tissues. Crowson (1981) suggested that the leaf-mining habit may avoid tannins, etc., which may be concentrated in the outer layers of leaf cells, and Hering (1951) suggested that a higher oxygen concentration within leaves by day may enhance the growth of the larvae.

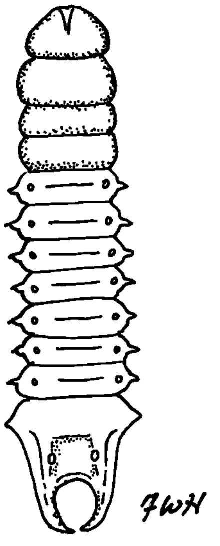


Fig. 2.18. *Brontispa longissima,* larva. After Froggatt and O'Connor (1941).

Protection from natural enemies is a secondary benefit, but, while the mine probably protects the larvae from a multitude of general predators, there are predators and parasitoids that transgress it. Various species of ants (Hymenoptera: Formicidae) are considered to be important natural enemies of many hispines (O'Connor, 1940; Froggatt and O'Connor, 1941; Hering, 1951; Gressitt, 1959), as are parasitic hymenopterous species.

The appearance of the mines of many species is quite distinct and, together with consideration of the host plant, is useful in identification of leaf-miners (Hering, 1951). Most leaf mines are blotch or linear mines. Some leaf-mining caterpillars eject frass from their mines, but most leaf-miners, including hispines, deposit it within the mine, where it accumulates in 'frass lines', which, in some cases, have diagnostic value. Miners avoid the larger and more fibrous leaf veins, which are an especially inefficient food source. Thus, linear mines wind through the net venation of leaves of dicotyledons (in many cases becoming serpentine mines), but in palms they are straight and parallel to the main veins (i.e. to the margins of leaflets or leaf segments).

Female hispines typically create a small cavity for the egg or egg clutch and cover their eggs with a cap or shield of faecal matter or plant fibres. This protective device, together with the cryptic habitat of the leaf-mining larvae, would seem to compensate for a relatively low reproductive rate in some species, e.g. 20 per female in *Promecotheca coeruleipennis.* Upon hatching, the larvae enter the leaf via the cavity that the female has made beneath the egg.

Hispine leaf-miners typically have three larval instars. Proportionally much larger volumes of tissue are consumed by the last instar compared with the first two instars. The obtect pupal stage is passed in the mine.

Palm leaf-miners other than Hispinae are rare, although four orders of insects contain leaf-miners of higher plants. Of these, Lepidoptera contain the greatest number of leaf-mining species, followed by Diptera, Coleoptera and Hymenoptera. The most important leaf-mining family in the tropics, Gracillariidae (Lepidoptera) (Hering, 1951), is not represented on palms. Buprestidae (Coleoptera) and Tineidae (Lepidoptera) are represented by a few species (Taylor, 1937; Bondar, 1940; Lepesme, 1947; Ferreira *et al.*, 1994).

Cassidines are called tortoise beetles because the form of the imagos suggests the highly convex carapace of those reptiles. The tortoise beetles are broadly oval or circular from above, with expanded lateral margins of the pronotum and elytra, so as to form a flange, which conceals the legs from above. The head, concealed from above by the anteriorly extended pronotum, appears to be withdrawn. Like their hispine relatives, their elytra characteristically have alternating longitudinal rows of ridges and punctations. Many species of tortoise beetles are showy, in some cases iridescent or with metallic colours. The larvae are elongate-oval and flat, with many spinelike tubercles, and with the thoracic and abdominal segments extended laterally to form a flange. They possess an anal tube, which excretes faeces, often combined with an adhesive substance. The larvae cover themselves with frass and discarded cuticles, which are added with each moult, and partially support this protective material by a caudal furcate process. Various authors have suggested that this serves as camouflage, for protection against desiccation or rain or for active defence. Eisner *et al.* (1967) observed that the shield of the larva of *Cassida rubiginosa* is highly manoeuvrable and is rotated in response to probing of the insect's body or tubercles with an instrument. The insects used the device effectively to shield themselves from predacious ants, which may be among their chief natural enemies.

An important difference between hispines and cassidines is bionomic: hispine larvae are leaf-miners or concealed feeders, while cassidine larvae are external plant-feeders. Additionally, the Hispinae have a strong proclivity for monocotyledonous hosts and the Cassidinae for dicotyledonous hosts. Hispines are most frequent on the monocotyledonous families Gramineae, Orchidaceae, Pandanaceae, Palmae and Zingiberaceae. In cassidines, only *Hemisphaerota* and a few related hispine-like genera utilize monocotyledonous hosts (Crowson, 1981).

No genera of the hispine–cassidine group are represented in the tropical regions of both the eastern and western hemispheres. Since the Eocene period (60 million years BP), these regions have been connected by land only through cooler regions, which acted as a barrier to these and many other basically tropical insect taxa (Crowson, 1981).

The hispine–cassidine group is basically tropical, with relatively few species found in temperate regions. It is very diverse in the Asia–Pacific region, with many species on mainland southern and south-eastern Asia, the Malay Archipelago and islands of the Indian and Pacific Oceans. In the Pacific, there are increasingly fewer species toward the eastern extensions of Melanesia and Micronesia, with no native hispine species in south-eastern Polynesia, New Zealand or the Hawaiian Islands (Gressitt, 1957).

Gressitt's (1957) review of the hispines of the South Pacific, concentrating on species east of the Philippines and the Lesser Sunda Islands, contains descriptions of 145 species and subspecies. Hosts were listed for less than half of these species; these were various monocotyledonous plants, many growing in forests. Hosts of 30 of the species were palms (Table 2.3).

Although species of hispines generally have very limited distributions, *Brontispa longissima* is an important introduced pest

Table 2.3. Geographical distributions and recorded host plants of palmivorous hispine beetles that occur in the South Pacific and some adjacent areas (some listed species extend their ranges beyond this region) (compiled from Gressitt, 1957, unless otherwise noted).

Hispine species	Geographical distribution	Host plants*
Aulostyrax heterospathi	Guadalcanal (Solomon Islands)	*Heterospathe* sp., *Clinostigma* sp.
Aulostyrax nuciferae incerta	Bougainville (Solomon Islands)	*Metroxylon* sp.
A. nuciferae nuciferae	Malaita (Solomon Islands)	*Cocos nucifera*
Brontispa balakae	Western Samoa	*Balaka*† *rechingeriana, Clinostigma oncorhyncha*
Brontispa castanea	Lord Howe Island	'on *Kentia*'‡
Brontispa linearis	Northern New Guinea	*Archontophoenix* sp.
Brontispa longissima	Sulawesi, New Guinea, Bismarck Archipelago, Solomon Islands, New Caledonia; introduced into Australia, Tahiti and Taiwan	*Areca catechu, Balaka*† sp., *Caryota* sp., *Clinostigma* sp., *C. nucifera, Metroxylon sagu*
Brontispa mariana	Caroline Islands, Mariana Islands	*C. nucifera*
Brontispa minor	Northern New Guinea	Unidentified palms, also *Alpinia* (Zingiberaceae)
Brontispa palauensis	Palau Islands	*C. nucifera*
Calamispa fasciata	Guadalcanal (Solomon Islands)	*Calamus* sp.
Callistola tripartita	Bismarck Archipelago	*Pandanus* sp. (Pandanaceae), rarely on *C. nucifera*
Enischnispa calamivora	Bismarck Archipelago	*Calamus* sp.
Isopedhispa cocotis	New Caledonia	*C. nucifera*
Octodonta subparallela	New Guinea, New Britain, New Ireland	*Calamus* sp.
Oxycephala cornigera	New Ireland (Bismarck Archipelago)	Adult and larval host: *Calamus* sp.; imagos on *C. nucifera; Heliconia* (Musaceae)
Oxycephala ruficollis	Admiralty Islands	*C. nucifera*
Plesispa reichei	Thailand (Anupap Thirakul, personal communication), Malay Peninsula and Archipelago, Philippines, New Guinea, Bismarck Archipelago (New Britain), Australia (CYP)	*Archontophoenix* sp., *A. catechu, Arenga pinnata,*§ *Calamus* spp., *C. nucifera, Cyrtostachys renda,*§ *M. sagu, Nypa fruticans, Roystonea regia, Flagellaria indica* (Flagellariaceae)
Promecotheca callosa	Southern New Guinea, Australia (CYP)	*C. nucifera,* unidentified native palms
Promecotheca coeruleipennis	Fiji, Samoa, Tonga	*C. nucifera, Livistona* sp., *Pritchardia pacifica*

Table 2.3. *continued*

Hispine species	Geographical distribution	Host plants*
Promecotheca cumingii	Sulawesi	*C. nucifera*
Promecotheca guadala	Guadalcanal (Solomon Islands)	*Balaka*† sp.
Promecotheca leveri bougainvilleana	Bougainville (Solomon Islands)	Adult hosts: *Areca* sp., *Balaka*†‖ sp.,*Calamus* sp.
Promecotheca leveri leveri	Ysabel Island (Solomon Islands)	Palms (unconfirmed)
Promecotheca opacicollis	Banks Islands, Vanuatu, Santa Cruz Islands	*C. nucifera*
Promecotheca papuana	North-east New Guinea, Bismarck Archipelago	*A. catechu, C. nucifera, Elaeis guineensis* (adult host), *M. sagu, N. fruticans*
Promecotheca ptychospermae	Ulawa Island (Solomon Islands)	*Balaka*† sp.
Promecotheca salomonina	Guadalcanal (Solomon Islands)	Adult hosts: *Balaka*† sp., *Calamus* sp.
Promecotheca soror	North Sulawesi, Moluccas	*C. nucifera*
Promecotheca varipes	Australia (Northern Territory)	*C. nucifera,*‖ *Pandanus* sp. (Pandanaceae)

[*] Palmae, unless otherwise indicated.

[†] *Balaka* and *Ptychosperma* were not distinguished in Gressitt's report.

[‡] Host data on label of holotype in collection of South Australian Museum (Eric Matthews, personal communication).

[§] Lange, 1950.

[‖] Gressitt (1959) implied that record should be confirmed.

CYP, Cape York Peninsula.

in several countries. *Promecotheca cumingii* (Colour Plate 6a) and *Plesispa reichei* also have relatively extensive geographical ranges. The fact that these three species are at times important pests of the ubiquitous coconut palm may have contributed in some way to their relatively extensive distribution. These and a few other species of *Promecotheca* and *Brontispa* that are pests of coconut are the hispines that are best known biologically.

The hispine genus *Promecotheca* has at least 35 species, distributed from mainland South-East Asia through the Malay Archipelago and as far east as Fiji. The larvae are leaf-miners of large monocotyledons including palms (Colour Plate 6b). Gressitt (1957) reviewed 22 species of this genus distributed in the South Pacific, reporting 12 as palmivorous (Table 2.3).

Adult beetles of most species of *Promecotheca* are very elongate insects, with a length of about a centimetre. Palmivorous species of *Promecotheca* native to South-East Asia and the Malay Archipelago are usually dull-coloured, while those native to localities east of there (New Guinea, north-eastern Australia, Fiji, etc.) tend to have showy colours (Taylor, 1937). For example, of the western group of species, *P. cumingii* is mostly brown ochre. In *Promecotheca opacicollis*, which is an example of the eastern group, the head is black, the anterior quarter of the elytron is orange and the posterior three-quarters brilliant bluish purple to metallic green (Risbec, 1937; Gressitt, 1957). Within species, there are colour variations on different islands or in different localities of larger islands (Froggatt, 1939; Gressitt, 1959). The larvae of *Promecotheca* species are about 1 cm long when fully developed.

Four species of *Promecotheca* are particularly well known because of their economic importance as pests of coconut palm: *P. coeruleipennis* (syn. *P. reichei*) distributed in Fiji, Tonga, Samoa, Wallis and Futuna Islands (Taylor, 1937); *P. papuana* (syn. *P. antiqua*) distributed in north-east New Guinea, New Britain and the Bismarck Archipelago (Froggatt and O'Connor, 1941; Baloch, 1972; Hassan, 1972); *P. opacicollis* (Risbec, 1937) in Vanuatu, Utupua and Vanikoro Island; and *P. cumingii* (syn. *P. nuciferae*) in the Malay Peninsula, the Philippines, the Moluccas, Sulawesi and Sri Lanka (Aldaba, 1930; Gabriel, 1976; Ming, 1977; Gallego *et al.*, 1983). In addition to coconut, these have been reported on *A. catechu*, *M. sagu*, *R. regia*, *L. chinensis* and *Pritchardia* spp. (Burkhill, 1918; Taylor, 1937; Lever, 1979), all of which are cultivated palms.

Promecotheca spp. are very scarce on native palms in natural habitats. Outbreaks are known only on palms grown in nurseries and monocultural plantations (Gressitt, 1959). African oil palm, although exotic to South-East Asia, is taxonomically related to coconut and is widely grown in the lowlands of South-East Asia, and therefore might be expected to serve as a host of species of *Promecotheca* that attack coconut palms. This is not the case, however. In fact, when *P. papuana* populations increased on coconut palm and females oviposited on adjacent African oil palms, the first instars did not survive on the latter palm for more than a day (Froggatt and O'Connor, 1941). Curiously, Gressitt (1959) observed a group of *A. catechu* heavily attacked by *P. papuana* near a planting of coconut palms that remained relatively free of the beetles.

The imagos of *Promecotheca* spp. feed on the abaxial surfaces of the distal portions of leaflets or leaf segments, leaving long, narrow fossae (Gressitt, 1959). The larvae are miners in the basal portions of leaflets (or leaf segments of palmate palms). When populations are light, particular leaflets may be damaged only on the distal or proximal portions by imagos or larvae, respectively. With denser populations, larvae and imagos may together damage entire leaflets (Colour Plate 6c). In addition to the direct damage caused by feeding, damaged leaf tissue may be invaded by fungi, e.g. *P. palmarum*.

The easiest way to detect the presence of *Promecotheca* spp. on a palm or in a plantation is by standing with one's back to the trunk and looking out at the abaxial leaflet surfaces, where the imagos feed. Of course, this method is not infallible, because in some cases only the less conspicuous larvae are present.

Promecotheca papuana attacks palms of any age from seedlings to palms 25 m or more in height, but seems to prefer tall palms (Froggatt, 1939; Gressitt, 1959). Adult *P. coeruleipennis* also often flies to tall, isolated palms (Taylor, 1937).

The adult beetles are quiescent for 2–3 days after emerging from the pupal case within the leaf mine. They then chew an oval opening in the upper wall of the mine. In at least *P. coeruleipennis*, they exit it during morning hours (Taylor, 1937). Imagos do not feed on the leaf upon which they developed as larvae, but fly to a younger leaf or to another palm.

During the first 2 weeks of adulthood, the beetles of *P. coeruleipennis* are gregarious. Groups of about 20 individuals, including males and females, cling to and feed on the abaxial surfaces of the distal third of the distal leaflets of younger fronds. One beetle makes several fossae per day. After this gregarious period, the males and females mate. The females then disperse, while the males remain on the same site. The females oviposit about 4 days later.

The adult beetles of *Promecotheca* spp. are active only during the day, especially during morning hours, remaining motionless on fronds at night. In their inverted position on the abaxial leaf surfaces, imagos crawl slowly and deliberately, clinging firmly even when strong winds buffet the fronds. The flight of *Promecotheca* spp. is slow and clumsy, probably never exceeding a distance of 100 m, and infestations tend to remain localized (Taylor, 1937; Froggatt, 1939; Gressitt, 1959).

Imagos of both sexes of *P. coeruleipennis* live and feed for about 1 month (Taylor, 1937). Froggatt (1939) observed that *P. papuana* lived for about 6 weeks on palms in cages and O'Connor (1940) reported that one female lived for 5 months in a cage. Taylor (1937) indicated that species of *Promecotheca* that attack palms in South-East Asia and the western Malay Archipelago usually have prolonged ovipositional periods, compared with those distributed east of there (New Guinea, northern Australia, Fiji, etc.). Consequently, in the Asian species, larvae of the same generation are usually in different instars. Taylor (1937) referred to this as the 'multiple-stage condition'. In contrast, the Pacific species, with their shorter oviposition periods, are prone to develop a 'one-stage condition', in which most of the larvae of a single generation are all in the same instar.

The females lay the eggs on abaxial leaf surfaces, usually on the proximal half of the leaflet, concealing each egg with a domelike covering of about 2.5–4 mm in diameter, composed of partially digested leaf fragments cemented together. Although small, the straw colour and convex shape of this covering makes it easily seen. The coverings cling to the leaflet surface up to 6 months after the eggs have hatched; thus their presence is not necessarily indicative of viable eggs. The somewhat oblong egg – about 1.5 mm long in *P. coeruleipennis* (Taylor, 1937), 2.5–3mm long in *P. papuana* (Froggatt and O'Connor, 1941) – is orientated with the long axis parallel to the major veins of the leaflet and with the ventral surface of the embryo toward the leaf surface and the cephalic end toward the leaflet tip, i.e. the direction in which the insect will feed and form its mine. *Promecotheca coeruleipennis* (Taylor, 1937) and *P. cumingii* (Jones, 1913; Gabriel, 1976) lay eggs singly. In contrast, *P. opacicollis* and *P. papuana* lay eggs in clusters of two to three and sometimes up to six, concealing the clusters with a single covering (Risbec, 1937; Froggatt, 1939; O'Connor, 1940; Froggatt and O'Connor, 1941; Gressitt, 1959). The female of *P. coeruleipennis* lays a total of 20 eggs (Taylor, 1937), while the female of *P. papuana* lays 80–100 eggs (O'Connor, 1940).

The eggs of *Promecotheca* spp. incubate for 2 to almost 3 weeks. Upon hatching, the first instar, which is about 1 mm long, penetrates directly below the egg into the leaf tissue and begins feeding, forming the mine normally in the direction of the leaflet tip, i.e. parallel to the major leaf veins. In *P. papuana* and *P. opacicollis*, larvae that hatch from the same egg cluster feed together in the same mine and even moult synchronously. There are three instars in *P. coeruleipennis* and *P. papuana* and four instars in *P. opacicollis* (Risbec, 1937; Taylor, 1937; Gressitt, 1959). The initial width of the mine is about 1 mm. During the first two instars, the mine extends to about half of its ultimate length and expands to a width of about 5 mm. The part of the mine made by the final instar is almost constant in width (Jones, 1913; Risbec, 1937; Taylor, 1937).

The leaf tissue above and below the mine remains green for 2 days after the mesophyll in that site has been eaten. During the period when each instar ceases feeding in order to moult, the tissue lining the mine turns brown, so that the part of the mine formed by each instar has a brown border, and a complete mine appears to consist of three chambers.

In species in which two or more larvae occur per mine, e.g. *P. papuana*, the larvae feed together in the same chamber, developing more or less simultaneously. The total length of the mines ranges from over 80 to nearly 400 mm (Pagden and Lever, 1935; Taylor, 1937; Gressitt, 1959; Lever, 1979). Mine lengths of different species have not been compared under identical conditions.

The mine is closer to, and creates a slight bulge in, the adaxial surface, and the larvae are seen most clearly by examining this surface (Taylor, 1937; Gressitt, 1959).

The duration of the larval stages of *Promecotheca* spp. ranges from a minimum of 17 days for *P. papuana* (Gressitt, 1959) and a maximum of 52 days for *P. coeruleipennis* in the relatively cool season in Fiji (Taylor, 1937). Larval development in the latter species was completed in 43 days in the warm season. In at least *P. papuana*, the first and second stadia last about a week or less each; the third stadium lasts a week or two (Gressitt, 1959). The instar of *P. coeruleipennis* and *P. cumingii* larvae may be determined easily: since only one larva occupies a mine, the number of head capsules in the mine indicates the number of times the insect has moulted. A second method is to count the number of chambers of the mine that have thus far been constructed, since each instar makes a separate chamber.

The pupal stage is passed in the mine. The duration of the pupal stage of *P. coeruleipennis* is 12 days in the warmer season and 18 in the cooler season (Taylor, 1937). That of *P. papuana* lasts from 12 to 24 days (Froggatt, 1939) and that of *P. cumingii* was reported to be 7.5 days (Jones, 1913).

An outbreak of *Promecotheca* spp. can result in extensive damage. Prior to establishing biological control for *P. coeruleipennis* in Fiji, the sequence of events in outbreaks was observed (Taylor, 1937). Populations of the beetles increased dramatically with successive generations on the same palms in a limited area, with little spread to other palms. After about 14 months, during which four generations had been completed, defoliation of the palms was at a maximum level. At this point, populations were so dense that there was little space left for oviposition and the beetles dispersed to fresh hosts.

Populations at the point of maximum defoliation were estimated at nearly 4000 beetles per palm. Their feeding caused a loss of about 12% of the functioning surface of younger fronds, and successively higher losses to a maximum of 90% of the surface of older fronds.

The populations that subsequently infested new hosts were denser than the incipient populations on the original hosts. Consequently, maximum defoliation and the next dispersal flight were reached more quickly, i.e. within two generations.

Outbreaks of *P. papuana* were similarly reported to begin as pronounced population increases on a few palms in close proximity before spreading more extensively. Infestations usually started near the seacoast and spread inland (Froggatt, 1939). Spectacular outbreaks of *P. papuana* have been observed, with estimated populations of 3000 beetles per frond and 35,000 per palm (Froggatt, 1939; O'Connor, 1940). A notable outbreak of *P. papuana* occurred months after a volcanic eruption in May 1937 in the Rabaul district of New Britain. Large quantities of ash fell on the plantations, followed by torrential rains. This may have decimated populations of natural enemies of the leaf-miner (O'Connor, 1940; Gressitt, 1959). Murray (1937) stated that, while walking through an infested plantation, he heard on all sides the continual drop of immature coconuts from palms that were unable to sustain them. Not a single inflorescence was developing in the entire plantation and a few hundred palms had died.

Outbreaks of *P. papuana* appear to be cyclical, occurring about every 10 to 15 years, often in the same localities. For example, based on trunk constrictions and on records, there were outbreaks in a plantation in New Britain in 1910, 1923, 1933–1935, 1940/41 and 1953–1955 (Gressitt, 1959). Outbreaks occur simultaneously in several localities. The insect is an especially serious pest in parts of New Guinea with an equatorial climate, i.e. where there is no definite dry season in normal years, but it seems possible that the outbreaks may be correlated with abnormal dry periods in this region, perhaps associated with the El Niño southern oscillation (ENSO) (see Box 1.1). *Promecotheca opacicollis* was reported to be most damaging in districts of Vanuatu with low rainfall or in drought years (Pagden and Lever, 1935).

Promecotheca cumingii was considered a minor pest of coconut palm in the Philippines during the early 1900s and during this period was introduced into the Malay Peninsula (Jones, 1913; Burkhill

1918). It has since been reported as a pest in the Philippines (Aldaba, 1931) and the Malay Peninsula (Ming, 1977). It was reported in Sri Lanka in 1970 and was a serious pest of coconut palm until brought under biological control by a single introduced species, *Sympiesis* (*Dimmockia*) *javanicus* (Fernando, 1972a, b; Delucchi, 1974; Dharmadhikari *et al.*, 1977; Perera, 1982).

Observations of damage by *P. coeruleipennis* indicated reduction in vigour of the palm and loss in production of coconuts. After severe defoliation, the rate of frond production remained as before (about one per month), but the fronds were smaller and weaker. Inflorescences failed to develop in the axils of highly damaged fronds, sometimes for several months. This, of course, represented a corresponding loss in harvestable coconuts. Defoliated palms also underwent premature shedding of coconuts, involving more late-stage coconuts and larger total numbers than normal. The mean reduction in coconut production in areas with maximum defoliation by *P. coeruleipennis* was estimated at 50% (Taylor, 1937).

On New Britain, Gressitt (1959) observed that, as damage increased, production of coconuts decreased until, with 80% of the fronds under attack, the palms produced no flowers or fruits. Losses of 30–50% in copra production have been reported on individual plantations. Severe outbreaks set back coconut production for 2 years. But Gressitt noted that premature shedding of coconuts caused by leaf-miners sometimes temporarily increased copra production, probably because the development of coconuts can be enhanced by thinning out the fruits.

The most important natural enemies of palmivorous *Promecotheca* spp. in general are ants and hymenopterous parasitoids (Heriot, 1934; O'Connor, 1940; Froggatt and O'Connor, 1941; Gressitt, 1959; Baloch, 1972; Delucchi, 1974).

Several ant species have been observed preying on eggs, larvae or pupae of *Promecotheca* spp. Since the eggs are protected by the covering placed by the female beetle and the larvae and pupae by the mine, they are not easy prey for ants. Those ants that penetrate these barriers are likely to be predacious species that occur in large colonies and that forage aggressively. In some cases, the ants enter through holes in the mines cut by earwigs (Dermaptera) (O'Connor, 1940; Gressitt, 1959). O'Connor (1940) reported that sometimes up to 50% of mines of *P. papuana* were occupied by ants. *Pheidole megacephala*, a species native to central Africa, which has been distributed widely by human activity (Lieberburg *et al.*, 1975), was observed to attack the eggs and larvae of *P. papuana*, and was considered to be the most important predacious ant of this species (O'Connor, 1940; Froggatt and O'Connor, 1941). However, Gressitt (1959) later reported that it was less frequent in palms than earlier reports would indicate. He rated *Technomyrmex albipes* as more important, and *Monomorium floricola*, *Camponotus papua* and *Polyrhachis* spp. as possibly important because they were frequently observed in coconut palms and, in some cases, had been observed to prey on *P. papuana* eggs or larvae.

Oecophylla smaragdina (Fig. 2.8) is a predacious ant that is widespread in Asia and the Pacific and was used as a biological control agent in ancient China (Caltagirone, 1981; Lokkers, 1986). Coconut growers in New Guinea considered it an important predator of *P. papuana*, but investigations by some researchers did not support this. In fact, populations of the leaf-miner sometimes flourished in the presence of abundant populations of *O. smaragdina* (Stanley, 1938; Froggatt, 1939; O'Connor, 1940; Froggatt and O'Connor, 1941). However, in other instances, *O. smaragdina* has been an effective predator of palm leaf-miners (Gressitt, 1959).

Gressitt suggested that earlier reports that *O. smaragdina* was not a significant predator of *P. papuana* may have been partly based on misleading observations. For example, he found that, since *O. smaragdina* could cross to adjacent palms wherever the fronds touched, the absence of these ants from the trunk of a palm, where field observations are often made, did not necessarily indicate their absence from the crown. Additionally, he suggested that, if observations were made during periods when the ants shifted their main activity to, for example, foraging, their role in predation would be underestimated.

Interspecific competition can be fierce among ants. Where two or more aggressive species occupy the same habitat, dominance may shift at times from one species to another, and predators may shift to whichever prey is most available.

Of the parasitoids that complement the role of ants and other predators in regulating populations of *P. papuana*, Gressitt (1959) considered three species as especially important. *Apleurotropis lalori* (Eulophidae) is endoparasitic in the larvae of *P. papuana* in New Guinea. After feeding in the beetle larva, the parasitoid chews its way out and pupates in the mine. The beetle larva remains distended, transparent and morbid. Upon emergence, the adult wasp cuts through the leaf tissue to exit the mine. *Eurytoma promecothecae* (Eurytomidae) is known only from New Britain and was apparently a major factor in controlling a serious outbreak of *P. papuana* on that island in 1937 (Gressitt, 1959). An ectoparasitic parasitoid, it attaches to a larva of *P. papuana*, sucking fluids until only the shrivelled carcass remains. The parasitoid then leaves the carcass and pupates in the mine. Imagos exit the mine by chewing through the leaf tissue. *Closterocerus splendens* (Eulophidae) is an egg parasite of *P. papuana* in the Bismarck Archipelago, but is a parasitoid of the larvae of *P. opacicollis* in Vanuatu. It was considered a major factor in breaking the overlapping of generations in *P. papuana* (Gressitt, 1959).

Promecotheca papuana normally occurs in a 'multiple-stage condition', i.e. so that generations overlap, and at any given time a population consists of individuals in various stages of development. In the 'one-stage condition', a population develops simultaneously from a synchronized egg hatch, so that all individuals of a population are in the same stage. This is characteristic of outbreaks of *Promecotheca* spp. and occurs occasionally as an aberration. Although it was shown that the 'one-stage condition' of *P. coeruleipennis* in Fiji was caused by the predatory activity of a mite, *Pyemotes ventricosus*, the factors that cause this in *P. papuana* are not known. They may involve a disruption of the natural enemies that normally regulate this species. Decimation of natural enemies during a prolonged drought is a possible factor. The 'one-stage' condition is typically protracted, sometimes for up to 2 years (Gressitt, 1959).

Oligosita utilis (*Coetosticha cratitia*) (Trichogrammatidae) parasitizes eggs of *P. opacicollis* and was found to be its most important natural enemy in the Solomon Islands (Pagden and Lever, 1935). Additional parasitoids, ants, fungi and birds were of lesser importance. Populations of the beetles declined after a heavy rain, but the actual mortality factor was not known, nor was it determined whether rains consistently affected populations (Risbec, 1937).

When it was discovered on coconut palm in the Philippines early in the 20th century, *P. cumingii* was considered to be of little, if any, economic significance. It was apparently controlled by natural enemies, predominantly chalcidoid parasitoids of the larvae and pupae (Jones, 1913). It is believed to have been introduced accidentally into the Malay Peninsula (Burkhill, 1918), where it apparently encountered natural enemies that controlled it, including *Pediobius parvulus* (Eulophidae) (Lever, 1979). A highly successful biological control campaign was conducted with this parasitoid against a pest in Fiji (Box 2.2).

Relationships between natural enemies and their hosts are generally known to vary considerably over time. Parasitization rates of a particular parasitoid–host association do not remain at fixed percentages, but in fact fluctuate, perhaps widely in some cases, and the ranking of species by dominance in the community may change over time. Thus, parasitization rates based on one-time sampling can be thought of as

Box 2.2. Right on target: classical biological control of a coconut leaf-miner in Fiji.

Promecotheca coeruleipennis is native to Fiji and nearby islands. Prior to the early 1930s, the beetle was confined to larger islands and was usually rare, with outbreaks being local and transitory. It was also present, but not a pest, on some of the 170 or so islands of Tonga (O'Connor, 1949). During this period, various natural enemies of the beetle were identified. *Oligosita utilis* (Hymenoptera: Chalcidoidea: Trichogrammatidae), a parasitoid of the egg, and *Elasmus hispidarum* (Hymenoptera: Chalcidoidea: Elasmidae), a parasitoid of the larva, were considered the most important in providing natural control of this beetle. *Elasmus hispidarum* is an ectoparasitoid, which attacks any larval instar, but not the pupae. The female *E. hispidarum* inserts its sting through the leaf tissue and into the leaf-miner larva, which causes it to become lethargic, and then oviposits in the mine. The larvae that hatch from these eggs attack *P. coeruleipennis* (Taylor, 1937). Early workers in Fiji found no internal parasites of *P. coeruleipennis* larvae or of the pupae.

In parts of Fiji, especially the Lau group of islands, *P. coeruleipennis* became a pest in the 1930s, because natural control of the species was disrupted by the inadvertent introduction of *Pyemotes ventricosus* (syn. *Pediculoides ventricosus*) (Acarina: Pyemotidae). The bionomics and relationships of this mite with *P. coeruleipennis*, explored in detail by Taylor (1937), are summarized here. Like all other members of the small family Pyemotidae, this mite is parasitic on immature stages of Lepidoptera, Coleoptera, Diptera and Hymenoptera. Largely because its hosts include pests of stored grain products, it has achieved a cosmopolitan distribution. It was probably introduced into Fiji early in the 20th century, and in 1921 was found there for the first time parasitizing *Levuana iridescens*. It soon occupied the mines in coconut fronds made by *P. coeruleipennis*. Penetrating these, the mites attacked larvae and pupae of this species, but only occasionally attacked the imagos.

Pyemotid mites are ectoparasites. *Pyemotes ventricosus* pierces the relatively soft integument of larvae of *P. coeruleipennis* and intersegmental membranes of pupae to suck haemolymph. Normally, a single *P. ventricosus* attacks one host larva or pupa, killing the host within 24 h, probably due to a toxin produced by the mite. The mites cannot usually reach the well-protected eggs of *P. coeruleipennis*, and usually do not effectively parasitize adult beetles, probably because of their harder integument and greater activity.

The mite was so destructive to the larvae of *P. coeruleipennis* that its initial effect was a dramatic reduction in the leaf-miner populations. It seemed that the leaf-miner problem was solved. But, unfortunately, populations of *E. hispidarum* and other natural parasitoids dependent on the beetle larvae now suffered a precipitous decline, while *P. coeruleipennis* eggs and imagos survived, because the mites rarely preyed on these stages. At the beginning of the next rainy season, adult beetles were in sufficient numbers to initiate a new generation. Rainy weather was highly adverse to the survival of the mites, hampering their movements on leaf surfaces or washing them off, and leaf mines often became filled with water, drowning the mites. However, as experiments showed, the leaf-miner larvae survived complete immersion in water for many hours. Thus, the leaf-miner entered the dry season free of the native parasitoids that had controlled it and free of the introduced parasitic mite. It quickly became a major pest of coconut palms in Fiji.

T.H.C. Taylor and R.W. Paine, who played major roles in the biological control campaign against *Levuana iridescens* in Fiji (Box. 2.1), recognized that, like other species of *Promecotheca* native to the Pacific region, *P. coeruleipennis* oviposits during a relatively short portion of the species' total life cycle. This behaviour would tend to synchronize the egg hatch, so that individuals of a small, incipient population would pass through the various development stages and reach maturity more or less simultaneously. In subsequent generations, populations would tend to be in the same stages at any given time. They referred to such populations as being in a 'one-stage condition'. However, because ovipositing females arrive on palms at different intervals and individual development rates differ due to genetic or microenvironmental factors, these beetles are usually in the 'multiple-stage condition'. The 'one-stage condition' was considered an aberration.

Due to the effects of *P. ventricosus*, the one-stage condition of *P. coeruleipennis* occurred more frequently than normal and was more prolonged. By eliminating eggs laid in the early portion of the oviposition period, *O. utilis* may have enhanced these effects. Consequently, there were long intervals during which *P. coeruleipennis* larvae were absent, which adversely affected survival of the parasitoids

Box 2.2. *continued*

dependent on this stage. The key to restoring natural control of *P. coeruleipennis* would be to limit the duration of the one-stage condition so that leaf-miner larvae would be continually available to support their natural enemies.

Taylor and Paine thought that this could be done by a carefully selected biological control agent, which could perhaps be found elsewhere in the Asia–Pacific region and introduced into Fiji, and which should meet as closely as possible certain criteria. Unlike the natural enemies of *P. coeruleipennis* in Fiji, which attacked the larvae and never the pupal stage of their host, it was desirable that the introduced parasitoid survive on any larval instar and also the pupa. It should have an adult life of at least 3 weeks, so that it could oviposit on different stages of the leaf-miner. Because outbreaks of *P. coeruleipennis* tended to spread after two generations, the species should be prolific enough to become as abundant as the leaf-miner within two generations of the latter. The parasitoid species should be active and capable of rapid spread and, of course, obtained from an area with an environment similar to that of Fiji. It was desirable that the parasitoid's host range be fairly narrow, so that its effect on non-target species would be minimal.

Parasitoids of *P. coeruleipennis*, which lived externally on this host, were themselves attacked by hyperparasitoids. An unknown risk was that these hyperparasitoids might attack introduced parasitoids. Taylor and Paine felt that this risk could be reduced by selecting a species that lived internally in its hosts. (However, it is now known that many species of hyperparasitoids can attack endoparasitic insects.)

The parasitoids of hispines are apparently attracted first to the host plants of the beetles and then search for the beetles themselves. Thus, the choice of parasitoids was narrowed to species that parasitized *Promecotheca* that attacked coconut, including *P. cumingii* in the Malay Peninsula and Malay Archipelago and *P. soror* in the Moluccas.

Of these, *P. cumingii* (referred to at that time as *P. nuciferae*) appeared to be the most promising source of parasitoids for the control of *P. coeruleipennis*. Its bionomics were very similar to those of the latter, but a notable difference was that it had a much higher reproductive potential. It was distributed throughout Java, but it was never a pest there. Therefore, its natural enemies were apparently highly effective in controlling its populations.

In Java, Paine collected six parasitoid species of *P. cumingii*, and found three that appeared to control outbreaks of the hispines by themselves. Of these, *Pediobius parvulus* (Eulophidae) appeared to be the most promising potential biological control agent for *P. coeruleipennis*. It was an internal parasitoid of all larval stages and also the pupae of its hosts, which included *P. cumingii* and a few other hispines. In the laboratory, the majority of adult females lived for 6 weeks and the females oviposited at irregular intervals almost throughout their adult life. In a laboratory with a mean temperature of 29.3°C, the period from oviposition to adult emergence was a mean of 19.5 days. The species had a satisfactorily high reproductive rate (mean of 77 eggs per 'larger' female). It was observed to be a strong, active flier. Its distribution was restricted to Java, but it appeared to be highly adaptable, occurring from the dry eastern end to the wet western end of the island and to about 1200 m. in elevation.

Transport of *P. parvulus* from Java to Fiji (and two less promising species, which did not become established) was an epic achievement, similar to that of transporting *Bessa remota* from Malaya to Fiji in the *Levuana* campaign in 1925 (Box 2.1). It was April 1933, and again a cargo of cages containing palms that supported parasitized larvae travelled under the watchful eye of Taylor. This time, the journey began at Buitenzorg (now Bogor). The infested palms were taken by lorry to Batavia (now Jakarta) and thence by steamer to New Caledonia. There they were transferred to another ship for Suva, Fiji. To prevent the introduction of *P. cumingii* to New Caledonia or Fiji, at an appropriate point while at sea, Taylor separated adult parasitoids and parasitized larvae and pupae of the leaf-miner and had the remainder of the material (palms infested with non-parasitized caterpillars, cages, etc.), thrown overboard. From Suva it was necessary to travel by motor launch to the Lau group of islands, a distance of about 300 km. The parasitoids arrived there 37 days after leaving Buitenzorg.

During the subsequent 12 months, about 26,000 *P. parvulus* were reared and liberated in about 50 localities in the Lau group of islands. The wasps spread through *P. coeruleipennis* populations on these islands and parasitized up to 100% of the larval and pupal stages. This insect was no longer considered a pest in Fiji by the end of the year, i.e. April 1934.

snapshots of a complex and ever mutable system.

Classical biological control of *P. coeruleipennis* in Fiji with *P. parvulus* was such an outstanding success that it became of interest for control of other species of *Promecotheca* in the Pacific. In 1937, M. Dupertuis introduced *P. parvulus* from Java into the New Hebrides (present-day Vanuatu) for control of *P. opacicollis*, which it controlled to some extent (Froggatt, 1939; Gressitt, 1959). In New Britain, where it was introduced from Fiji in 1938 for the control of *P. papuana*, it became established and sometimes abundant, but outbreaks of this beetle continued to occur (Gressitt, 1959).

A fungus, *Hirsutella jonesii*, has been isolated from field populations of *P. papuana* (Prior and Perry, 1980). It infects a small portion of the populations during damp weather, as does a bacterial disease (O'Connor, 1940). *Promecotheca* spp. can be controlled on seedlings in nurseries by crushing the immature stages manually (Froggatt, 1939).

An early method of controlling defoliators on palms was pruning and burning infested fronds. Pruning and destroying the seventh to tenth frond at early stages of an outbreak was recommended for control of *P. cumingii* when populations were at levels causing severe damage (Aldaba, 1931; Gabriel, 1976). Aldaba (1931) presented evidence that pruning these fronds when highly infested was no more detrimental to palms than severe damage due to *P. cumingii*.

A method described by Froggatt (1939) of destroying adult beetles was to stand fresh fronds of any attractive palm, e.g. *N. fruticans*, in rows between infested palms. The fronds could then be treated with insecticide or the beetles hand-collected from them. It is questionable, however, whether excised, upright fronds would attract a sufficiently large portion of the population of a relatively inactive beetle and, in any case, as fronds desiccated, they would often have to be replaced.

The genus *Brontispa* consists of at least a dozen species distributed on islands, mostly in the south-western Pacific and larger islands of the Malay Archipelago, but absent from mainland Asia (Gressitt, 1957). The westernmost species is *Brontispa limbata*, native to Mauritius and Rodríguez in the western Indian Ocean, and the species at the highest latitude is *B. castanea*, on Lord Howe Island (lat. 31° 30′ S).

Both the imagos and larvae of these beetles live between adjacent leaflets of unopened palm fronds and consume the epidermal tissue. Consequently, although they are concealed feeders, they feed on superficial leaf tissue rather than in the mesophyll and thus, unlike species of *Promecotheca*, they are not true leaf-miners.

Brontispa longissima (syn. *Brontispa froggatti*) attacks palms in Java, Sulawesi, Moluccas, New Guinea, the Bismarck Archipelago, the Solomons, Vanuatu and New Caledonia. It is an introduced species in Australia (Fenner, 1996), Tahiti (Cohic, 1961) and Taiwan (Liu, 1994). It is considered a recent introduction in Australia, but Gressitt (1957) examined some specimens from the Cape York Peninsula (Queensland) that may have been this species. It is one of the most widely distributed hispines in the Pacific region and the only one that we know has been introduced far outside its natural range, apparently by human activity.

The adult beetles are elongate, dorsoventrally flattened and 8–12 mm long. The colour of beetles from different localities varies greatly, from reddish brown to black, and some extreme colour forms were formerly recognized as distinct species (Gressitt, 1957; Lever, 1979).

It is principally a pest of young palms of less than 8 years of age (Lever, 1979). In addition to coconut palm, hosts include African oil palm, *A. catechu, Caryota* sp., *Clinostigma* sp., *Latania* sp., *M. sagu*, *Phoenix* sp. *Ptychosperma* sp. and *W. filifera* (Pagden and Lever, 1935; Lever, 1937, 1979; Froggatt and O'Connor, 1941; Gressitt, 1957).

The larvae and imagos feed on both surfaces of leaflets or leaf segments of the unopened leaf, stripping the tissue in narrow bands parallel to the midveins. When populations of the insects become dense, these bands merge to form extensive areas of necrotic tissue. This species usually attacks palms of 10 years or less in age, and is more likely to attack stressed than vigorous palms.

Imagos mate about 2 weeks after emerging from the pupal case. During the ovipositional period of several weeks, females lay about 120 brown, flat eggs, singly or in series of up to four eggs, surrounding these with a loosely arranged mass of debris and excrement. Eggs hatch in 3–4 days. The larvae have conspicuous cerci-like caudal processes, a feature often occurring in hispines. Larval development takes about 30–40 days. There are usually four instars, with up to six instars in rare cases. The pupa, which wiggles when disturbed, resides between appressed leaflets. The relatively short pupal period lasts 4–6 days (Pagden and Lever, 1935; Froggatt and O'Connor, 1941).

During the earlier part of the 20th century, *B. longissima* was considered a major pest of young coconut palms in nurseries and recent field plantings in Melanesia (Froggatt and O'Connor, 1941). The species usually attacked palms less than 10 years old (Pagden and Lever, 1935). In addition to the age of the palms, plant health and genetics appeared to influence the susceptibility of coconut palm to attack by these beetles. Less vigorous palms were considered more prone to attack (Pagden and Lever, 1935); thus palms grown on poorer sites and those neglected and overgrown with vines were said to be more susceptible than those on more fertile and more intensely managed sites (Froggatt and O'Connor, 1941). The greater vigour of coconut palms in Vanuatu was considered a factor in their greater resistance to these beetles compared with those grown in New Caledonia (Risbec, 1937). There were also varietal differences in susceptibility. *Brontispa longissima* preferred coconut palm of an unidentified variety introduced into the British Solomon Islands from the Malay Peninsula, compared with local varieties. The apparent resistance mechanism of the local variety was its more tightly compressed and adherent unopened leaflets, compared with the relatively loose leaflets of the Malayan variety (Pagden and Lever, 1935; Lever, 1937).

Chelisoches morio (Dermaptera) was considered to be an important predator of *B. longissima* in Vanuatu (Risbec, 1935, 1937). *Tetrastichodes brontispae* (Eulophidae), a parasitoid of *B. longissima* in Java, was introduced 'with some success' into Sulawesi for control of the 'local race' of this species (Pagden and Lever, 1935). This eulophid was introduced into the British Solomon Islands in 1936 in a venture typical of the period: the parasitoids were sent by airmail a distance of 5000 km from Java to Brisbane, Australia, and from there by sea an additional 2700 km to New Britain (Lever, 1937), where they were released.

Several isolates of *Metarhizium anisopliae* var. *anisopliae* (Deuteromycotina) were isolated from *B. longissima* in Taiwan. A fungicide-resistant isolate was obtained, and the insect was controlled by application of the fungus in small field trials (Liu *et al.*, 1989; Liu, 1994).

Brontispa mariana, discovered during an outbreak of the species on Saipan in 1931 (Esaki, 1940), is distributed on certain of the small islands of the Mariana and Caroline Islands (Micronesia). The glossy, dark brown, adult beetle is about 8.5–10.5 mm long. Mating is nocturnal, in contrast to some other brontispids, which mate during the day. There are indications that the females tend to oviposit more frequently on fronds already damaged by feeding, perhaps attracted to fermentation products or volatile plant substances. Imagos live for several months. The ovipositional period of one female is 60 days, during which it lays a total of 113 eggs. Eggs are usually laid singly or sometimes in groups of up to six. In a laboratory at about 30°C, eggs hatched in 5 or 6 days. The larva, yellowish white and with a forceps-like caudal process, is about 9–11 mm at maturity. The larvae often feed together in large masses between the unopened leaflets, undergoing four instars in about 23 days at about 30°C, with fresh leaf tissue supplied daily. The mean pupal period is about 5 days. The species was estimated to have three to nine generations per year (Lange, 1950).

Lange (1950) reported that coconut palms attacked by these beetles suffer a slow decline and loss of production. He reported that only about 30% of infested palms in Saipan in 1947 were bearing coconuts. Only one other insect, *Furcaspis oceanica* (Hemiptera: Diaspididae), infested coconut palm on that island, but it is not clear whether abiotic, horticultural and other factors may have contributed to the observed production loss.

The beetle caused such extensive damage to plantations of coconut palm on the small island of Saipan (about 180 km^2) in the Mariana group during the 1930s that, by 1936, about 70% of the plantations had been burned to control it (Lange, 1950). Plantations on Rota to the south were similarly affected.

Both of these small islands were devastated by the effects of the Second World War (W.H. Lange, personal communication). Surveys conducted in 1946 under US Navy administration as a part of economic rehabilitation efforts of the islands revealed that surviving coconut palms on Saipan and Rota were severely attacked by *B. mariana*. The earwig, *Chelisoches morio*, was the only natural enemy observed to affect *B. mariana*. Lange (1950) searched for more effective natural enemies in the Philippines, Malaysia and Java. He identified several species of parasitoids of brontispids of the Malay Archipelago as potentially effective natural enemies of *B. mariana* and attempted to introduce three of these into Saipan. He obtained parasitoids from both Malaysia and Java and made several introductions during the early months of 1948, either directly, by field release of imagos brought by air transport from Malaysia or Java, or by rearing them on *B. mariana* in a laboratory in Saipan before release. The two species that became established were: (i) *T. brontispae*, which parasitizes the larvae and pupae of *B. longissima*, *Plesispa reichei* and *Plesispa nipae*; and (ii) *Haeckeliana brontispae* (Trichogrammatidae), which parasitizes the eggs of these same species. A total of 5285 adult *T. brontispae* were liberated on Saipan and Rota. About 332 imagos of *H. brontispae*, most of which were brought from the Malay Peninsula, were released on Saipan and Rota. Both parasitoids became established. The parasitism rate of larvae and pupae of *B. mariana* by *T. brontispae* was 60% by the end of 1948.

At the western edge of the range of the genus, *Brontispa limbata* has been known since 1875 on Rodríguez and was found 80 years later on Mauritius. It is found most often on *Dictyosperma album* and *Acanthophoenix rubra*, both native palms which are largely extinct in the wild but are cultivated on those islands as ornamental plants and for their fruits. Additional hosts include *D. lutescens*, *Dictyosperma aureum*, *Hyophorbe vaughanii*, *Hyophorbe verschaffeltii* and *Rhapis* sp. It was reported on coconut palm on Mauritius, but Orian (1961) stated that this record was erroneous. The bionomics are similar to those described for *B. longissima* and *B. mariana*. They are pests of young palms. Serious damage due to this insect was reported in 1932, 1946 and 1960 (Orian, 1961).

Brontispa castanea, described in 1926 from specimens from Lord Howe Island and known only from there, represents the southern extension of this genus in this region. The holotype of *B. castanea* in the South Australian Museum was collected from *Kentia* (a synonym of *Howea*). The second specimen was collected from ‘thatch palm’ (Eric Matthews, personal communication), a local name for *Howea forsteriana*. The genus *Howea*, with two species, is endemic to Lord Howe Island. Although each species grows in dense, pure stands (Hutton, 1986), outbreaks of *B. castanea* have not been reported.

Oxycephala papuana is a hispine collected from coconut palm and *A. catechu* on Manus Island (New Guinea). The imagos, relatively large hispines, are more than 10 mm long. The elytra are deep black, the head and thorax yellow to orange-brown (Froggatt and O'Connor, 1941).

Plesispa reichei is a widely distributed hispine that has been collected from diverse palm species and a species of Flagellariaceae, a monocotyledonous family of the eastern hemisphere (Table 2.3). It is one of the major pests of coconut palm nurseries in the Philippines (Abad, 1983), Indonesia (Gressitt, 1957) and Thailand (Anupap Thirakul, personal communication). Adult females are about 10 mm long, with a brownish-orange head and thorax, and black elytra. Males are about 8.5 mm long. Imagos live 101–202 days, during which females lay 13–178 eggs. The species' bionomics is similar to that of species of *Brontispa*. Natural enemies include *Ooencyrtus podontieae*, *Ooencyrtus* sp. (Encyrtidae) and *Haeckeliona brontispa* (Trichogrammatidae), which attacks the egg (Gallego and Abad, 1985). Control in nurseries includes hand-collecting, when infestations are at low levels, and insecticide applications for more severe infestations (Loyola, 1994).

Plesispa nipae causes damage similar to that of *P. reichei* on *N. fruticans* in Malaysia (Corbett, 1932).

Several species of *Wallaceana* are known on palms in southern Asia (Gressitt, 1957). *Wallaceana palmarum* was reported from *A. catechu*, *Eugeissona triste*, *M. sagu* and *N. fruticans* in Malaysia. Although it occurs in association with *P. nipae* on *N. fruticans*, it apparently prefers *A. catechu*. *Wallaceana* sp. was reported from *Salacca conferta* in Malaysia (Lange, 1950). *Wallaceana dactyliferae* (Fig. 2.17d) attacks date palm in India (Maulik, 1919).

In West Africa, species of the genus *Coelaenomenodera* are important leaf-miners on palms. These have been referred to as *Coelaenomenodera elaeidis* and *Coelaenomenodera minuta*, but the taxonomy of these species needs clarification, and possibly additional species are involved (René Philippe, personal communications). These palm leaf-miners are considered the most important hispine pests of economic plants in West Africa (Wagner *et al.*, 1991). Larvae and imagos attack fronds of African oil palms above 3 years of age. In heavy infestations, leaflets of younger (central) fronds appear withered, grey-brown and with rolled edges. The necrotic areas eventually shatter, leaving only the midveins intact. Coconut palm, *Borassus* sp. and other palm species grown as ornamental plants are also attacked by one or more of these beetle species. The adult beetles feed on the abaxial surfaces of leaflets. Copulation takes place in the hottest part of day. Females lay eggs in clusters at the ends of adult feeding scars and cover them with regurgitated leaf fibre. The incubation period of the eggs is about a month. Up to five larvae may occupy one mine. The larval period is about 5 weeks, during which the larvae grow to a length of about 1 cm. The prepupae locate themselves in the middle of the mine. The pupal stage lasts about 2–3 weeks (Cotterell, 1925).

Although the adults are usually not very active, *Coelaenomenodera* spp. have been observed to migrate short distances in great numbers to find fresh host plants when their food source has become exhausted. Such flights have been observed in the middle of sunny days. Rain and overcast skies appeared to curtail this activity (Cotterell, 1925).

Heavy rains may reduce larval populations by flooding the galleries in leaves, while excessive heat may desiccate young larvae (Cotterell, 1925; Mariau and Morin, 1974). Several species of Eulophidae parasitize the eggs and others parasitize the larvae of *Coelaenomenodera* sp., and these parasitoids may be attacked by hyperparasitic Eulophidae (Mariau, 1999a). In observations in Ghana in the 1920s, up to about 90% of these beetles were normally parasitized (Cotterell, 1925). As has been mentioned elsewhere in this book, ground cover in palm plantations is often beneficial in providing nectaries for natural enemies of palm pests. An unusual benefit of *Pueraria phaseoloides* as a ground cover under African oil palms in Ghana was that it supported a hispine leaf-miner, *Platypria coronata*, which served as an alternate host for four of the eulophid parasitoids of *Coelaenomenodera* sp. (Bernon and Graves, 1979). Ants, which scrape open the galleries and prey on the larvae, are also important in regulating the populations of *Coelaenomenodera* sp. (Mariau and Morin, 1974; Mariau, 1999a).

Cotterell (1925) observed that imagos of *Coelaenomenodera* sp. were commonly attacked by entomogenous fungi, a factor undoubtedly related to the high humidity of their habitat, but doubted that this effectively reduced their populations.

Cotterell (1925) reported that *Coelaenomenodera* sp. was usually a minor pest, but there was an outbreak of *Coelaenomenodera* sp. in Nigeria in 1923, which he suggested was brought on by an unusual storm, which may have decimated parasitoid populations. In recent times, damage to African oil palms in West Africa by these beetles has been widespread and outbreaks are not uncommon (Bernon and Graves, 1979). Natural control is most effective when the generations of the pest overlap. During an outbreak, the generations become more sharply defined, with the numbers of eggs, larvae and pupae peaking more or less simultaneously. Under such conditions, the reproduction rate of natural enemies is not sufficient to control the respective stages (Mariau and Morin, 1972).

The American oil palm, *Elaeis oleifera*, is resistant to *Coelaenomenodera* spp., but is susceptible to a fungus disease in West Africa and is less productive in oil than *Elaeis guineensis*. A hybrid (*E. guineensis* × *E. oleifera*) proved to be highly resistant to the leaf-miners (Philippe, 1977; Mariau, 1999b). Hybrids between the American and African oil palms show resistance to several pests, but may be less productive than the African oil palm. Further research is expected to result in improved oil palm hybrids (Meunier *et al.*, 1976).

Pruning of infested fronds may reduce populations of *Coelaenomenodera* sp., with less disruption of the natural-enemy complex than would be experienced with chemical control. Removal of all fronds with leaf-miner damage (seven to eight fronds per palm) reduced larval and adult populations by 75–100% at two locations in Nigeria. A one-time pruning of up to 30% of the fronds may have little effect on oil production over the next several years (Calvez, 1976). However, more information is needed on pruning as a routine or long-term control method.

Additional species of *Coelaenomenodera* are pests of coconut palm in Madagascar (Mariau, 1975).

Gyllenhalius palmarum, a cassidine, is an additional chrysomelid found on African oil palms in Nigeria. Natural control of this insect is usually effective. *Cassida* sp. is a pest of *Raphia* spp. in nurseries in Nigeria. *Chiridopsis quadriplagiata* and *Phygasia helvola* attack *Raphia* in forests in that country (D.A. Enobakhare, personal communication).

Several genera and species of hispine–cassidine beetles are found on palms in tropical America.

Alurnus humeralis is known on African oil palm in Colombia and Ecuador. One of the largest of chrysomelid beetles, the imagos are 15 mm wide × 35 mm long, with a black head, red prothorax and yellow-green elytra, with a black dot on each elytron. The light brown larvae are 43 mm at maturity. This insect attacks spear leaves and young opened leaves. The incubation period of the egg is 29–43 days. The larvae undergo eight instars during 221–254 days, a prepupal stage of 3–17 days and pupal stage of 26–37 days (Genty *et al.*, 1978).

Cephaloleia vagelineata attacks African oil palm and has been observed on wild unidentified palms from Mexico to tropical South America. The flat, black adult beetles are about 1.3 mm wide × 5.0 mm long. The elytra each have a clavate-shaped mark. The eggs are inserted singly into the rachis of young fronds. The flat, oval, white larvae are about 5 mm long at maturity.

Feeding of the larvae on the surfaces of the rachis of spear leaves and young fronds causes necrotic areas. The imagos feed on young fronds before they are fully unfolded, forming fossae parallel to major veins. Dense populations have been observed to diminish after heavy rains (Genty *et al.*, 1978). This or a closely related species was reported attacking African oil palms and *Elaeis oleifera* in Colombia, and may play a role in introducing an infectious agent that causes a bud rot. Various chemicals have been tested for its control (Urueta-Sandino 1972, 1974, 1975).

Coraliomela brunnea (Fig. 2.19) is one of the eight most important arthropod pests of coconut palm in Brazil. It is distributed from Argentina and Paraguay to throughout most of Brazil. The imagos are about 10 mm long, with red elytra, black thorax and head and yellow legs. The females oviposit on the adaxial or abaxial surfaces of younger foliage, and eggs incubate for about 19 days. Upon hatching, the yellowish-cream-coloured larvae move to and penetrate the spear leaf and feed in the tender unopened leaflets. As the spear leaf unfolds, the larvae move to still unopened leaflets. The feeding of the larvae results in perforations of the leaflets, this damage being visible when the spear leaf unfolds. The period of the larval stage – 180 days – is unusually long, even for a palm defoliator. Mature larvae are about 30 mm long. These attach themselves with a secretion to petioles of older fronds and pupate, the pupae hanging head down from the petiole. The prepupal period is about 11 days and the pupal period 20 days. Host plants in addition to coconut palm include *Allagoptera arenaria, Polyandrococos caudescens, Syagrus coronata, S. romanzoffiana, Syagrus schizophylla* and *Syagrus vagans*, all native to Brazil (Bondar, 1940; Ferreira *et al.*, 1994). Dense populations may destroy the youngest fronds of young palms and thus undoubtedly retard their growth. Serious attacks of this beetle have not been observed on mature palms. Species of Eulophidae are important egg parasitoids of *C. brunnea*. Chemical control of the pest has been studied (Ferreira *et al.*, 1994).

Fig. 2.19. *Coraliomela brunnea* (Hispinae) larva and its damage on coconut seedling, Sergipe, Brazil. Photo by Dalva Luiz de Queiroz Santana.

Mecistomela marginata is a chrysomelid pest of coconut palm in Brazil, which does damage similar to that of *C. brunnea*, but is less important (Ferreira *et al.*, 1994).

One species of *Tetrastichus* and two species of *Closterocerus* (Eulophidae) have been identified as parasitoids of *C. brunnea* (Ferreira and Morin, 1984). Manual collecting of imagos has been suggested as an effective way to reduce populations in plantations.

Hispoleptis subfasciata is a pest of African oil palm in the llanos of Colombia and in Brazil. The imagos and mature larvae are about 8.5 mm long. The imagos are shiny and pale yellow, with black markings on the thorax and elytra. The larvae are yellow, with the head retracted into the thorax.

The basic life history of *H. subfasciata* is typical of hispine leaf-miners of palms. The female beetle forms small depressions in the abaxial frond surface, where it lays eggs in pairs. The larvae are true leaf-miners and the pupae remain in the mine. Recently emerged imagos remain in the tunnel a few days before cutting an exit hole and leaving the mine (Genty *et al.*, 1978).

Additional species of *Hispoleptis* include *H. elaeidis* (south-western Colombia and western Ecuador), *H. ollagnieri* (northern Colombia) and *H. diluta* (north-eastern Brazil, the Guianas, south-eastern Colombia). These are found on wild palms and apparently prefer coconut palm.

Delocrania cossyphoides, a tortoise beetle, attacks African oil palm and coconut palm in tropical South America to Panama. The imagos are about 2.5 mm wide, 7–8 mm long and light brown in colour, with punctations densely distributed in the cuticle. The larva has a dark brown head and yellowish-white body, with 12 pairs of lateral spines (Bondar, 1940; Ferreira *et al.*, 1994).

The larvae and adult beetles occur together, usually on young foliage. They feed on the abaxial epidermis of palm leaflets, starting near the midvein and extending their activity laterally. The eggs are laid on the abaxial surface, single file, in groups of five or six, along the midvein (Bondar, 1940; Ferreira *et al.*, 1994).

Host plants additional to the above include *Attalea funifera, P. caudescens* and *S. coronata* (Lepesme, 1947).

Delocrania cossyphoides is usually under effective natural control. Species of Eulophidae and Ichneumonidae associated with it are thought to be its major natural enemies (Genty *et al.*, 1978).

Within the natural range of the beetle, frequent inspection of the abaxial frond surface of young palms for the damage of this beetle, with spot treatments with insecticides, is recommended (Ferreira *et al.*, 1994).

At least seven species of *Hemisphaerota* are found in tropical America. *Hemisphaerota tristis* (syn. *Spaethiella tristis*), a tortoise beetle, is found on African oil palm and coconut palm in Colombia, Suriname and Brazil (Genty *et al.*, 1978). The adult beetle is hemispherical, dark blue in colour, 3.3 mm wide × 3.9 mm long and 2 mm thick. The elytra are highly sculptured, with longitudinal ridges interspersed with punctate rows. The larvae, yellowish white and more elongate than the imago, discharge faecal material through the anal tube, forming a mass of filaments. The larvae moult and pass through successive instars and finally the pupal stage protected by this structure.

The imagos feed on adaxial and abaxial surfaces of leaflets, forming narrow necrotic areas parallel with the leaflet margins. The adult female beetle scrapes a cavity in the abaxial frond surface, places an egg in it and covers this with a viscous substance with incorporated frass. The larva, which bears a shell-like mass of strands, feeds only on abaxial frond surfaces (Genty *et al.*, 1978; Ferreira *et al.*, 1994). Reported host plants include coconut palm, African oil palm, *A. funifera*, *S. coronata* and other *Syagrus* spp. The insect completes its life cycle in about 56 days (Garcia *et al.*, 1996).

Genty *et al.* (1978) reported that feeding often damages 30% of leaflet surfaces. However, Ferreira *et al.* (1994) considered the insect to be of little, if any, economic importance in Brazil. Species of Ichneumonidae and Eulophidae attack the last larval instar and pupae, respectively, and entomogenous fungi infect larvae and imagos (Genty *et al.*, 1978; Garcia *et al.*, 1996).

Hemisphaerota cyanea (Fig. 2.20) was described in 1823 by Thomas Say, who stated that this tortoise beetle was common on the sea islands of Georgia and on the Florida peninsula. The adult beetles are about 6 mm long, dark blue to purple and metallic, with the elytra having longitudinal ridges interspersed with punctations. The antennae have a black basal segment and a yellow flagellum of ten segments. The larvae produce a mass of faecal strands, which resemble plant fibres, similar to that of the previous species (Fig. 2.21).

Hemisphaerota cyanea is common on *S. palmetto* and *S. repens*, which are ubiquitous native palms of the coastal regions of the south-eastern USA, including the Florida peninsula. *Acoelorraphe wrighti*, native to the extreme southern portion of

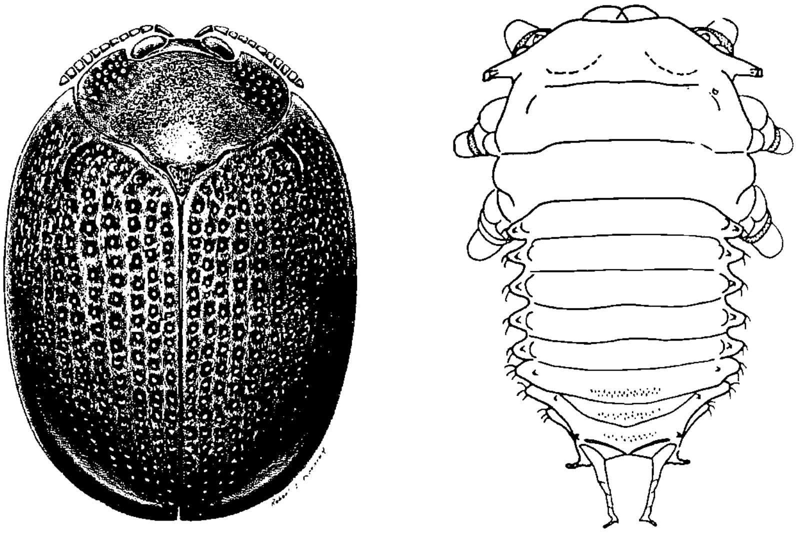
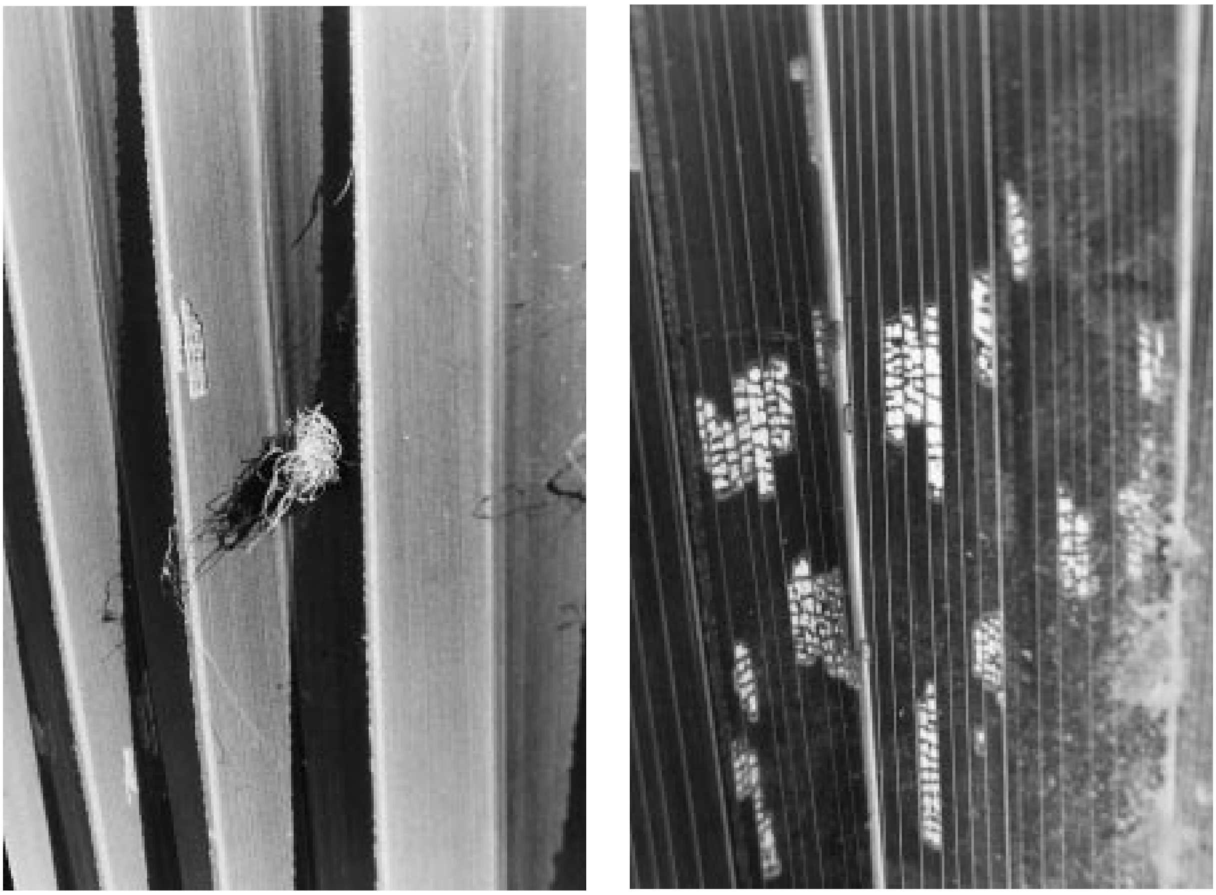


Fig. 2.20. *Hemisphaerota cyanea* (Coleoptera: Cassidinae), imago and larva. This tortoise beetle is common on *Sabal palmetto* in the south-eastern USA. Courtesy of Robert Woodruff.



a b

Fig. 2.21. *Hemisphaerota cyanea.* (a) Pupal cocoon on frond of *Sabal palmetto.* (b) Feeding damage. Florida Everglades.

Florida, *Sabal minor* and *Sabal etonia* are also hosts. It has also been collected on species of exotic palms grown in Florida, including coconut palm, *S. romanzoffiana*, *Chamaerops humilis* and *Washingtonia robusta*. We have usually found it on palmate- rather than pinnate-leaf palms. *Hemisphaerota palmarum* is a similar species found in Hispaniola (West Indies) (Blackwelder, 1946).

Spaethiella costipennis is a tortoise beetle known on African oil palm in northern Colombia. The imago is red and slightly larger than that of *H. tristis* (Genty *et al.*, 1978).

Additional families of Coleoptera

Scarabaeidae

A few scarab beetles are defoliators of palms. These include *Scapanes* spp., reported on coconut palms in New Guinea and the Solomon Islands; imagos of *Xylotrupes gideon*, which eat foliage of coconut palm, African oil palm and cashew (*Anacardium occidentale*) in South-East Asia; and *Papuana laevipennis*, which is a pest of *Colocasia esculenta* (Araceae), but also consumes foliage of coconut palm in the Moluccas (Hill, 1987).

Buprestidae

Taphrocerus cocois, a beetle native to Brazil, is a leaf-miner of coconut palms, African oil palms, *Attalea*, *Polyandrococos* and *Syagrus*. The larvae make mines in the fronds similar to those of hispine leaf-miners. Hymenopterous parasitoids maintain these beetles at very low population levels (Ferreira *et al.*, 1994).

Orthoptera

Dave Moore and Forrest W. Howard

The families of Orthoptera of greatest importance on palms are the short-horned grasshoppers (Acrididae) and the long-horned grasshoppers (Tettigoniidae). A related order, Phasmida, formerly considered a family of Orthoptera, is also of importance on palms.

Acrididae

Short-horned grasshoppers typically occupy open areas, where they are generalist feeders on low vegetation. Some species occasionally attack palm seedlings and, less frequently, mature palms.

Aularches miliaris, the spotted locust or coffee locust, a widespread acridid and a pest of numerous crops in South-East and southern Asia, is a pest of coconut palm in Sri Lanka and Thailand (Priyanthie Fernando and Anupap Thirakul, personal communications). It is a large grasshopper with green-brown wings with yellow spots. Coconut plantations near dense forest are those most likely to be attacked by large numbers of these grasshoppers (Mahindapala and Pinto, 1991). Hand-collecting the larvae and imagos and ploughing the soil have been effective in reducing their populations in some crops (Joseph, 1986).

Tropidacris cristata is an extremely large grasshopper (Fig. 2.22). This and a few other species of this genus attack palms and tree crops in South America. It is not often reported on palms (Lever, 1979). *Nomadacris setemfasciata* is a grasshopper pest of palms and crop trees in Asia and Africa (Lever, 1979; Mahindapala and Pinto, 1991).

Microtylopteryx hebardi was observed in a rainforest habitat in Costa Rica, where *Chamaedorea* spp. in the understorey were among its host plants (Braker, 1989).

In Asia, Africa and some parts of South America, waves of locusts (*Schistocerca* spp. and *Locusta migratoria*) periodically migrate and attack large areas of crops, including coconut palm plantations.

Tettigoniidae

Tettigoniidae are distinguished from other Orthoptera by their long, slender antennae of over 30 segments, which are often longer

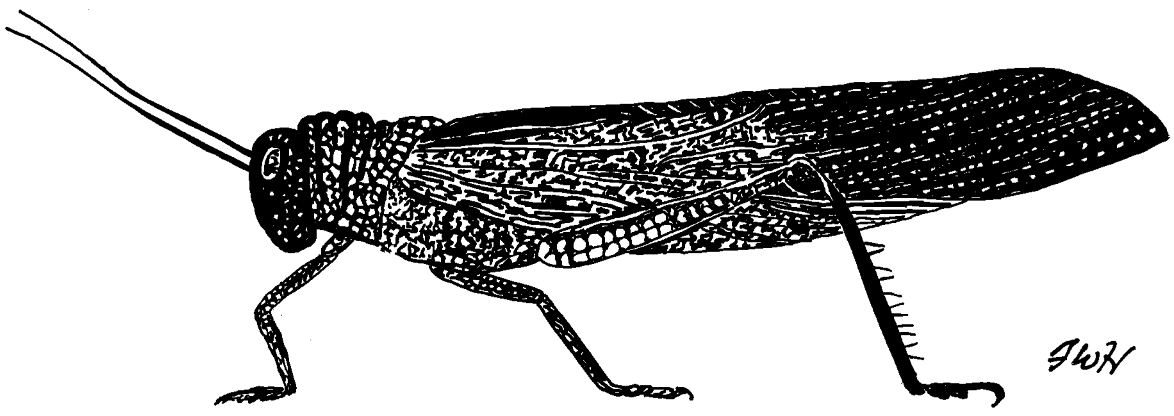


Fig. 2.22. *Tropidacris cristata*, a grasshopper (Orthoptera) of tropical America, which occasionally defoliates palms.

than the insect's body. They are known as bush crickets, long-horned grasshoppers or katydids.

There are over 5000 described species of tettigoniids (Rentz, 1996; Nickle and Naskrecki, 1997). They seem to excite fierce loyalty from the scientists that study them, and are interesting in many aspects, perhaps most especially in their mate attraction by complex song (Bailey and Rentz, 1990). They may be valuable components of the diets of many vertebrate predators (Belwood, 1990), some of which may be attracted by the serenading of the male.

They are found in such diverse habitats as tropical forests and Austrian mountainsides (Belwood, 1990; Illich and Haslett, 1994; Ito *et al.*, 1995) and may be predators or herbivores.

A coconut feeder, *Sexava femorata*, exhibits a stridulatory mechanism in defence.

Genera with species of palm pests include *Eumossula*, *Pseudoniscara*, *Segestes* (Colour Plate 6d), *Segestidea* and *Sexava*. *Sexava* is probably the most commonly cited, including *S. nubila, S. karnyi* and *S. coriacea*. Collectively, tettigoniids are the most important pests of African oil palm in Papua New Guinea (Bob Prior, personal communication). *Segestidea novaeguineae, Segestidea defoliaria* and *Segestes decoratus* are pests of African oil palm in Papua New Guinea, where they are the subject of a research programme to develop integrated management (Kathirithamby *et al.*, 1998). Strepsiptera are being investigated as natural enemies for their control (Solulu *et al.*, 1998). Young (1985) lists other tettigoniids that attack palms in Papua New Guinea.

Adult female tettigoniids lay the majority of their 20–40 slender, curved eggs (9–13 mm long) into soil around the base of palms, using the large, scimitar-shaped ovipositor to reach a depth of 10–15 mm. Eggs are also laid in the roots of trunk epiphytes and on the leaf bases of necrotic palm fronds (Young, 1985). Oviposition occurs at night and emergence may be between 40 and 100 days later. After hatching, the dark green, first-instar nymphs, with antennae which may be many times the body length, seek out a palm and crawl to the crown, where they complete their development over 20–26 weeks.

During the day, they hide deep in the crown at the leaf bases. Their secretive manner, green coloration, stillness and habit of arranging themselves on a leaflet so that their ridged dorsal surface appears to be a continuation of the midvein of the leaflet make them difficult to see. Often, their damage is noticed before the insects themselves are seen. They often attack the younger fronds first, but dense populations of *Sexava* can effectively defoliate the entire palm. They have powerful jaws, capable of drawing a drop of blood when handled.

Their natural enemies add to the diversity of the arthropod life of palms. Egg parasitoids, such as *Doirania leefmansi* (Trichogrammatidae) and *Leefmansia bicolor* (Encyrtidae), have been used in biological control programmes of doubtful value. The parasitoids preferentially attack eggs exposed on the soil surface and hence miss the vast majority. Other egg parasitoids include *Triteleia atrella* (Scelionidae), Mymaridae, such as *Anneckia oophaga* and *Platypatasson fransseni*, and Eulophidae. Imagos appear to be relatively free of hymenopterous parasitoids, but they may be attacked by *Exorista notabilis* (Diptera: Tachinidae) (Prior, 1988).

Stichotrema dallatorreanum (Strepsiptera) is parasitic on tettigoniids. Strepsiptera are parasites of insects in six orders, are of widespread distribution and have extreme sexual dimorphism and an unusual life cycle. Males are short-lived and free-living, while females are permanently endoparasitic. *Stichotrema dallatorreanum* belongs to the family Myrmecolacidae, males of which parasitize a host (thought to be the ant *Camponotus papua*) different from that of the female. High levels of parasitism of *Segestidea novaeguineae* by *S. dallatorreanum* are thought to keep populations under control. When a *Sexava* host is parasitized, its digestive and reproductive systems are pushed against the body wall by the parasite, which occupies the whole abdomen. The life cycle of the female of *S. dallatorreanum* is about 90 days and she may produce 750,000–1,000,000 young and so, theoretically, can reproduce much faster than the host. However, the free-living first-instar larvae must suffer very high losses (Solulu *et al.*, 1998).

The *Sexava* species are known mainly as foliar feeders, but probably consume some inflorescence material. Recent work has implicated tettigoniids as important herbivores of inflorescences and fruits of *Calyptrogyne ghiesbreghtiana*, an understorey palm found in Central America (Cunningham, 1997).

Phasmida and Hymenoptera

Forrest W. Howard

Phasmida

The Phasmida are a small order of insects referred to as stick insects and leaf insects because of their resemblance to these plant structures (Colour Plate 6e; Fig. 2.23). This adaptation is perceived as a form of camouflage that protects these insects from birds and other vertebrate predators, which are abundant in the arboreal habitats that

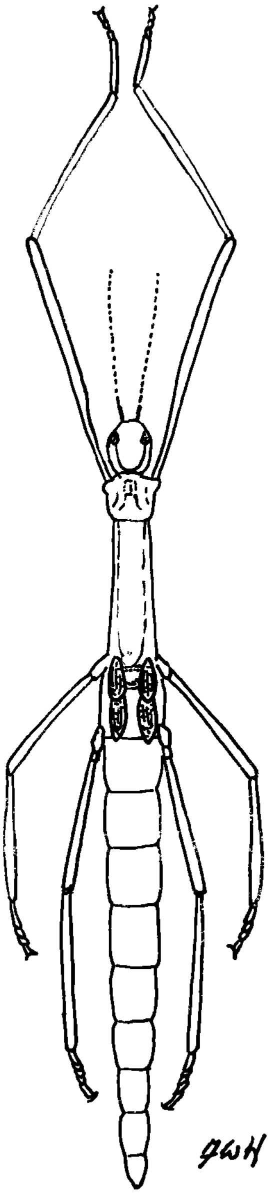


Fig. 2.23. *Graeffea crouani*, a stick insect (Phasmida), which is a pest of palms in Oceania. Redrawn from Lepesme (1947).

phasmids occupy. Until recently, they were placed in Orthoptera and, like a large proportion of that order, they are chewing insects that feed on diverse plants.

Stick insects have been recorded as pests of coconut palms since the early 1800s (Lepesme, 1947). These include several species in the subfamily Platycraninae, including *Graeffea crouani*, *Graeffea seychellensis*, *Graeffea lifuensis*, *Ophicrania leveri* and *Megacrania phelaus*. All are endemic to particular island groups of the Pacific, except for *G. seychellensis*, which is endemic to the Seychelles (Lever, 1979).

Female stick insects lay eggs while in the crowns of trees and palms. The method of oviposition of many of the species is primitive: they do not glue their eggs to plant parts, as do most higher insects, but simply allow them to drop. Some eggs fall into leaf axils, but probably more fall to the ground.

The eggs may incubate for as long as 100 days before hatching (Lever, 1979), during which period they may be subject to intense predation by insects, lizards, rodents and other predators (Dharmaraju, 1978; Rapp, 1995). In some species of stick insects the eggs have a capitulum (caplike structure), which induces ants to carry the eggs to their nests. There they eat the capitulum and then discard the egg in a refuse pile in their nest. The eggs are thus protected during their long incubation period. This interesting example of mutualism has not been reported in stick insects that attack palms and, in fact, ants are regarded as important predators of the eggs of palmivorous stick insects.

After hatching, the larvae climb the palm trunks and feed on the foliage. The entire larval stage may last 100 days or longer, so that the period from egg to imago is about 6 months (O'Connor, 1949). The imagos, typically over 100 mm long, secrete an acrid white liquid from thoracic pores when disturbed. The chemical has been studied in *G. crouani* (Smith *et al.*, 1979).

Although they are usually under natural control, stick insects become major pests under some conditions. They seem to be especially abundant on small islands (Lever, 1979; Dharmaraju, 1980b).

Ground-cover management to reduce the suitability of the habitat for larvae may help control these insects (Gutiérrez, 1981; Anon., 1983). Sticky bands or other barriers on palm trunks may prevent them from reaching the foliage (Lever, 1979). Trunk injections of insecticides have been effective for control of stick insects on palms (Dharmaraju, 1977).

Hymenoptera

The order Hymenoptera includes bees, wasps, ants and sawflies. Most hymenopterans are moderately sized to minute insects, with chewing or chewing–lapping mouth-parts, filiform antennae typically with a conspicuous bend, elongate wings, with simple venation, and the ovipositor often prolonged as a sting, saw or drill. Bees, wasps and ants belong to one of two suborders, the Apocrita. A characteristic of the Apocrita is that the first abdominal segment is fused to the metathorax and the second abdominal segment is narrowed so as to form an apparent constriction ('waist', or petiole) between abdomen and thorax. Apocrita contain many species of importance as predators and parasitoids of insects and as pollinators of entomophilous plants, including palms.

Formicidae

Ants (Formicidae) are generally predatory insects or scavengers, but some species damage plants through their feeding or indirectly in nest-making or tending honeydew-producers. The most important ants that defoliate palms are leaf-cutting ants (Myrmicinae: Attini), of which there are about 200 species distributed in tropical America. *Atta cephalotes*, *Atta laevigata* and *Atta sexdens sexdens* are the species most often reported as pests.

Biologists find leaf-cutting ants, with their highly evolved social structure, to be particularly fascinating denizens of tropical forests (Wilson, 1971; North *et al.*, 1999; Wetterer, 1999). They are also of interest to economic entomologists in the American tropics as pests of coffee, citrus, cacao and other crop trees, and sometimes palms, including coconut palms and African oil palms.

The large nests of leaf-cutting ants consist of a mound of loose soil with air vents and many galleries extending deep below the soil surface. A colony may consist of millions of workers. Ant trails of up to 100 m or more radiate from the nest into trees. The ants cut small pieces of leaf tissue and take them to their nests. On palms, the damage is visible as semicircular pieces cut from margins of pinnae. The ants do not consume this plant material, however, but deposit it in the nest as a substrate for a fungus, which is their actual food source.

Atta spp. are attacked by many kinds of natural enemies. The young queen ant, before burrowing into the soil, is highly vulnerable to vertebrate and insect predators (Entwistle, 1977). Certain species of ants (e.g. *Azteca* spp.) are especially effective against the young queens, and conserving them in plantations may reduce attacks on palms by *Atta* spp. It is sometimes necessary to destroy ant nests or apply insecticides to protect palm plantations from leaf-cutting ants (Zenner de Polanía and Posada Flórez, 1992; Ferreira *et al.*, 1994). Some advances have been made in research on microbial control of leaf-cutting ants (Jaccoud *et al.*, 1999).

Leaf-cutting bees (Apoidea: Megachilidae) are similar to leaf-cutting ants in that they remove foliar tissue without consuming it as food. They notch the margins of leaves and use the small disc-shaped pieces of tissue to line their nests. *Megachile palmarum* notch leaves of palms in Hawaii and attach their nests to the abaxial surface of fronds (Lepesme, 1947). The damage is not significant.

In sawflies (Symphyta), the second suborder of Hymenoptera, there is no apparent constriction. The larvae of Symphyta are very similar in appearance to the caterpillars of Lepidoptera and, like them, are usually defoliators and, to a lesser extent, borers, leaf-miners and gall-makers. Sawflies attack a wide variety of dicotyledons and conifers, but are virtually unknown on palms.

3

Sap-feeders on Palms

Forrest W. Howard

> The piercing–sucking mouth parts take the most valuable liquids in the world – the sap of growing plants and the blood of living animals.
>
> (C.L. Metcalf and W.P. Flint, American entomologists, *Destructive and Useful Insects, Their Habits and Control.* McGraw-Hill, 1939)

About half of the species of exopterygote insects are characterized by a relatively long proboscis (beak), formed by a modified, grooved labium (rostrum), together with enclosed stylets (e.g. Figs 3.1, 3.8 and 3.11). In feeding, the stylets pierce deeply into tissue to feed on liquids. Most are phytophagous. A minority are predators of insects and other invertebrates, and an even smaller minority are haematophagous on vertebrate animals or are mycetophagous. With probably more than 85,000 known species, the Hemiptera are the fifth largest order, surpassed only by the four major endopterygote orders, i.e. Coleoptera, Diptera, Hymenoptera and Lepidoptera.

We consider most of the species in this chapter to be primarily associated with the foliage of palms. However, many hemipterans, especially Sternorrhyncha, are typically eurymerous, i.e. they may infest foliage, stems or fruits (Beardsley and Gonzalez, 1975). The apparent preference of some species for foliar tissue may be largely a reflection of the large surface area and long-term availability of green tissue here. Some scale insects treated in this chapter, including Phoenicococcidae and Halimococcidae, are primarily on stems, but may be found on fronds. Hemipterans that are basically frugivorous are discussed in Chapter 4.

A long-held concept of the order Hemiptera was that it comprised two suborders,

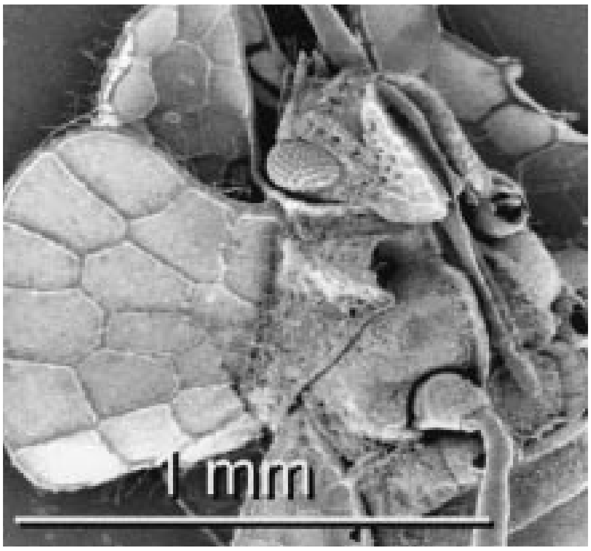


Fig. 3.1. Head and thorax of *Stephanitis typica* (Tingidae) (SEM ventral view) showing the typical proboscis of suborder Heteroptera. Specimen obtained from the Philippines.

namely Heteroptera (true bugs) and Homoptera (cicadas, leafhoppers *sensu lato*, aphids, whiteflies, scale insects, etc.). Another concept was that these insects constituted two orders, namely Hemiptera (corresponding to the Heteroptera) and Homoptera. In both classifications, the Homoptera were divided into two groupings, the Auchenorrhyncha (cicadas, and leafhoppers *sensu lato*) and the Sternorrhyncha (aphids, scale insects, etc.). A more recent concept, which we adopt in this work, includes all of these forms in a single order, the Hemiptera, with four suborders: Coleorrhyncha, Heteroptera, Auchenorrhyncha and Sternorrhyncha (Dolling, 1991). Since the latter two suborders share some important characteristics (e.g. production of honeydew and wax), we sometimes discuss them together, using the old name, Homoptera. The concept of the order Hemiptera that we follow is diagrammed in Fig. 3.2.

Coleorrhyncha, comprising about 20 species found among mosses and liverworts in cool regions of the southern hemisphere, are considered the most primitive Hemiptera. They have heteropteran and homopteran characteristics and are considered a suborder by Dolling (1991). They are not associated with palms.

Hemiptera associated with palms include species of the suborders Heteroptera, Auchenorrhyncha and Sternorrhyncha. The Heteroptera, known as the true bugs, are characterized by a prognathous proboscis, i.e. the proboscis arises from far forward on the head. The proximal portion of the forewing is coriaceous and opaque, while the distal portion is membranous. Wings with this structure, called hemelytra, are unique to Heteroptera and are the basis for the names Hemiptera and Heteroptera. The hind-wings are entirely membranous. The wings lie flattened over the abdomen when at rest (Fig. 3.3). The majority of true bugs share this basic design. About 33,000 living species classified into 76 families of Heteroptera are known. About 88% of the species are terrestrial and almost 70% of these feed on plant sap. A minority of terrestrial Heteroptera are predacious, mycetophagous or haematophagous on vertebrate animals (Dolling, 1991).

The two remaining suborders of Hemiptera are the Auchenorrhyncha and the Sternorrhyncha. The main criterion separating them from the Heteroptera is the placement of the proboscis. The proboscis of the Auchenorrhyncha arises farther back on the ventral area of the head than in

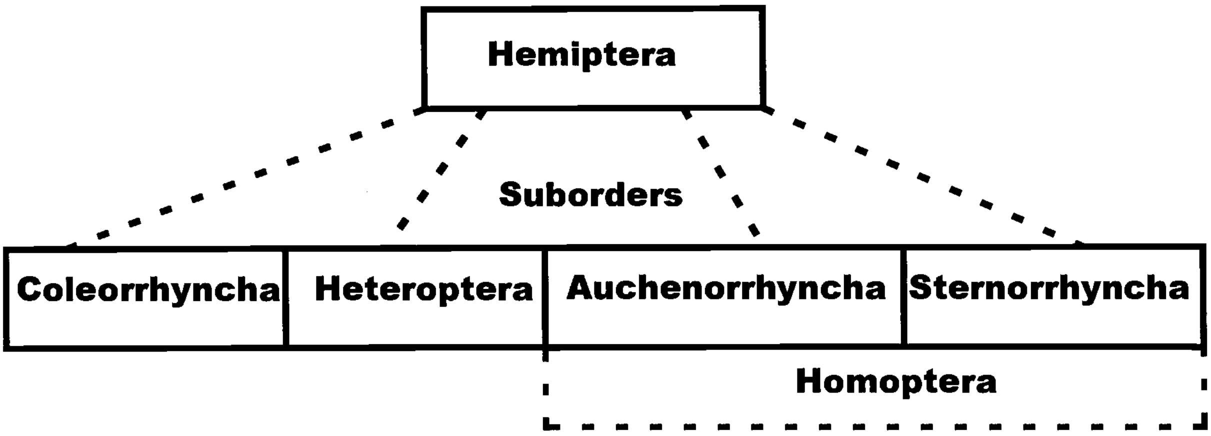


Fig. 3.2. Relationships between taxa of Hemiptera. The order Hemiptera includes four suborders as shown. The formerly recognized order Homoptera currently has no taxonomic status, but the term is still useful because the suborders Auchenorrhyncha and Sternorrhyncha have some characteristics in common.

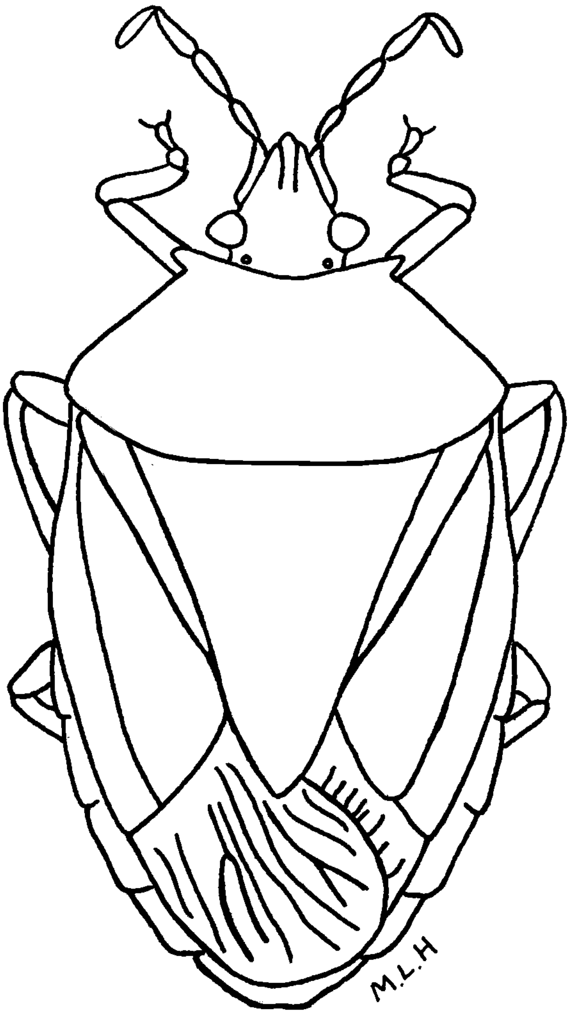


Fig. 3.3. *Lincus spurcus* (Pentatomidae). Redrawn by Martha Howard from Cassier *et al.* (1994).

Heteroptera (Fig. 3.8). In the Sternorrhyncha, the proboscis articulates even further back from between the forecoxae (Fig. 3.20b).

In the suborder Auchenorrhyncha, the texture of the forewings is usually thin and membranous to parchment-like throughout, the uniform texture being reflected in the name Homoptera. Their forewings are often thicker than the hind-wings and may be highly coloured and patterned. A quite consistent character is the manner in which the wings are held at rest: they typically slope on either side in a tectiform (rooflike) manner (Colour Plate 8, Fig. 3.9). A large portion of the suborder consists of highly active insects with an elongated, streamlined form, e.g. leafhoppers (Cicadellidae) and planthoppers (Fulgoroidea). Other taxa are morphologically adapted to a more sedentary life, e.g. Membracidae and Flatidae.

The antennae, positioned ventral to the eyes, have an enlarged, often bulbous, pedicel, with dense sensilla and a setaceous flagellum, known as an arista (Figs 3.8 and 3.11d). The ovipositors of the females are shaped like cutlasses and used to insert the eggs into plant tissue (Fig. 3.11c). Their hindlegs are saltatorial and typically have conspicuous spines. Intraspecific communication is often acoustic (Tishechkin, 1997). About 37,000 species in 28 families of this suborder have been described (Dolling, 1991).

The Sternorrhyncha are a more diverse suborder, which includes soft-bodied insects with moderately active immature and mature stages (Aphididae) and forms with sessile immature but active adult stages (Psyllidae, Aleyrodidae, Adelgidae and Phylloxeridae), as well as the sluggish mealybugs and sessile scale insects (Coccoidea). About 15,000 species in 41 families of Sternorrhyncha have been described (Dolling, 1991). Almost all Auchenorrhyncha and Sternorrhyncha are phytophagous.

The hemipteran proboscis, the defining characteristic of this order, is formed by a pair of stylets, derived from ancestral mandibles, which are closely appressed and lateral to a second pair of stylets, derived from maxillae. The inner surfaces of the stylet sheath (i.e. maxillary stylets) are grooved, forming an anterior canal, down which saliva issues when feeding, and a posterior canal, larger in diameter, through which liquid food is drawn up into the pharynx. In most Heteroptera and Auchenorrhyncha, the labium is modified as a rostrum, with a groove that holds the stylets when the insect is at rest. The rostrum bends while guiding the stylets when they are extended to probe or penetrate tissue. The labrum is merely a small triangular structure that covers the bases of the stylets. In Coccoidea and some others, the stylets are long and coiled and held in an invagination in the integument when not feeding.

The mechanism that draws sap through the stylets and into the alimentary tract acts similarly to a suction bulb. Muscles in the head contract to dilate the cibarium, which is a part of the pharynx.

Hemipterans are attracted to plants by colour (often in the yellow part of the spectrum) and, at least in some cases, by volatile compounds, which the insects associate with a particular host plant. Most Heteroptera have a ‘lacerate-and-flush’ method of feeding, slashing the tissue and mixing it with saliva and then imbibing the mixture (Miles, 1972). They feed mostly on mesophyll, although *Stephanitis typica* (q.v.), at least, may feed in the phloem as well as other tissues. Generally, in Auchenorrhyncha and Sternorrhyncha, feeding is more precise. In Auchenorrhyncha, species of Fulgoroidea are predominantly phloem feeders, while the superfamilies Cicadoidea, Cicadelloidea and Cercopoidea predominantly feed in xylem (Carver *et al.*, 1991). Sternorrhyncha insert their stylets very slowly and tend to feed on phloem, but also mesophyll.

Auchenorrhyncha and active Sternorrhyncha may explore the surface of the plants with the end of the labium to find preferred sites, indicated by textural differences. As the plant surface is pressed with the labium, a seal is formed with a small amount of saliva. This salivary deposit remains and can be stained to serve as a record of the number of probes per unit area or time period (Waters, 1976). As the stylets penetrate leaf tissue, salivary components form a gelatinous tubelike lining of the puncture hole. This stylet sheath acts as a support for stylet penetration. It remains after feeding. The stylets initially penetrate peripheral parenchyma, and are retracted unless they take up some substance that stimulates the insect to probe more deeply. Sucking of sap is stimulated by sucrose and certain amino acids. Homopterans, which are notably persistent feeders, may feed at the same site for hours.

The tissues in which hemipterans feed can be determined by sectioning fronds and following the course of the stylet sheaths. Some sheaths are branched, perhaps reflecting partial withdrawal of the flexible stylets and then insertion in a different direction.

Studies in which planthoppers were caged on coconut-leaf tissue, which was then sectioned and the stylet tracks traced, revealed that the stylets of a planthopper, *Myndus crudus* (Cixiidae), penetrated the leaf tissue, terminating in the phloem and more rarely in xylem (Waters, 1976; Fisher and Tsai, 1978; Tsai and Fisher, 1993). However, some insect species that penetrated coconut-leaf tissue in these studies are rarely found on palms in nature.

Feeding behaviour of aphids may exemplify that of Sternorrhyncha in general (Dixon, 1985). Aphids, which are weak fliers, depend heavily on air currents to be dispersed to or in the vicinity of plants. Like Auchenorrhyncha, aphids in general are attracted over short distances to electromagnetic waves in the yellow portion of the spectrum, i.e. yellow colour. Once on the plant, they explore its physical and chemical properties, using their antennae for detecting superficial properties and their stylets for probing internal characteristics. The insects can usually determine in a minute or less if the plant is a suitable host.

If the plant is accepted as a host, the aphid probes more deeply and feeds, usually in the phloem. It may take more than half an hour for the stylets to reach this tissue. Phloem sap is under sufficient pressure to force it through the fine food canal in the aphid’s stylets, but experiments indicate that they actively take up fluids through the stylets by the action of the cibarial pump (Dixon, 1985).

Hemipterans generally have symbiotic microorganisms in the alimentary system, which aid in digestion.

Many species of Heteroptera and Auchenorrhyncha have been described without host data, while host data may be routinely included in the taxonomic descriptions of Sternorrhyncha. Similarly, as the biology of a species becomes known, it may be easier to accumulate data on the host ranges of Sternorrhyncha than of the other suborders of Hemiptera. This is because the mere presence of a mature scale insect, mealybug, etc. on a plant indicates that it developed on this host. In contrast, the highly mobile Heteroptera and Auchenorrhyncha may alight on many different plants that are not their hosts.

Phloem sap is rich in sugars and poor in amino acids; thus Fulgoroidea and phloem-feeding Sternorrhyncha have to ingest large amounts of phloem sap to acquire amino acids for growth (Dixon, 1985). Many Sternorrhyncha and Auchenorrhyncha have an alimentary filter system, in which there is a broad loop in the midgut that forms a junction between the anterior and posterior parts. This allows excess sugars and water to pass quickly into the hindgut, leaving nutrients such as amino acids to pass into the main digestive system.

Some Hemiptera that feed in phloem release a watery substance, known as honeydew, from the anus (reviewed by Malumphy, 1997). Honeydew consists largely of water, with about 2–5% sugars (usually fructose, glucose, melezitose and sucrose) and a smaller percentage of amino acids. The amount produced per day varies with the species and many other factors, but that produced by aphids has been measured as ranging from nearly twice the aphid's body weight to many times this per hour (Wilson, 1971). Honeydew differs from plant sap and floral and extrafloral nectars, principally in its osmotic potential and in the composition of sugars (Buckley, 1987; Dolling, 1991). Some variability has been found in honeydew produced by different species of hemipterans, or the same species of hemipteran on different species of plants. Many insects, predominantly Diptera and Hymenoptera, that feed opportunistically on free liquids are attracted to honeydew, which is considered an important food source for them.

Hemipterans that produce honeydew are almost always associated with ants (Formicidae). Darwin (1859) wrote of this relationship: 'One of the strongest instances of an animal apparently performing an action for the sole good of another, with which I am acquainted, is that of aphides voluntarily yielding their sweet excretion to ants'. The modern view is that the relationship is an example of mutualism, in which ants palpitate hemipterans with their antennae, soliciting them to release honeydew, and in turn protect them from their natural enemies. This relationship is the subject of three fascinating reviews: Wilson (1971), Buckley (1987) and Gullan (1997).

Most ants associated with hemipterans are in the families Dolichoderinae, Formicinae or Myrmicinae. Ants transport honeydew-producing hemipterans to fresh feeding sites, on either the same or different plants, and some species harbour eggs of their symbionts in their nests during adverse periods. The mutualism between ants and hemipterans has long been compared to the relationship between herdsmen and their herds. That the ants often thin out their 'herds' by consuming some individuals completes the analogy. When disturbed, aphids produce an alarm pheromone. Some ant species respond to this chemical by an increased aggressiveness against intruders. One suspects that Coccoidea associated with ants may also produce such pheromones, but this has not been studied.

Hemipterans that are manipulated by ants release their honeydew in droplets, which the ants imbibe. Unattended, the hemipterans typically expel honeydew forcibly in order to rid themselves of it. Honeydew thus accumulates on the plant surfaces as a sticky coating, serving as a food source for many kinds of insects. These may include ants not involved mutualistically with the scale insects, Hymenoptera other than Formicidae and Diptera.

Honeydew supports the growth of microfungi, especially dark-coloured Ascomycetes of the order Dothideales (reviewed by Mibey, 1997). The mycelium of these fungi forms a dense, black, mat of the consistency of charred paper on plant surfaces. This substance, known as sooty mould, is detrimental to plant growth, because it blocks sunlight from reaching photosynthetic tissue. On ornamental plants, the mere presence of sooty mould constitutes aesthetic damage.

Honeydew may even play an indirect role in dispersal of some insects that produce it, for it attracts insects and birds that may sometimes inadvertently spread immature scale insects, etc., which cling to their legs and bodies (Williams, 1984).

Honeydew is produced in some auchenorrhynchous families, including Cicadellidae, Cercopidae, Membracidae, Issidae and Tropiduchidae (Wilson, 1971; Buckley, 1987), and in the sternorrhynchous Psyllidae, Aleyrodidae, Aphidoidea and ten families of Coccoidea (q.v.).

Particular ant and hemipteran species sharing a mutualistic relationship have not necessarily co-evolved. For example, in southern Florida, palm aphids (*Cerataphis* spp.), which are of Asian origin, are tended by various species of ants, one of the most frequent being *Solenopsis invicta*, which was introduced from South America (Colour Plate 10b). This symbiotic relationship seems especially paradoxical when the aphid is infesting *Washingtonia robusta*, an exotic palm in Florida, which is native to the south-western USA and Mexico!

In some situations, controlling ant populations helps control honeydew-producing Hempitera. Conversely, Rudolf Scheffrahn (personal communications) is investigating situations in Florida in which controlling honeydew-producing Hemiptera on palms and other plants near houses may help to control household ants.

Feeding by Hemiptera drains energy from plants. This is influenced by such factors as the sizes of the insects, their feeding behaviour and their abundance. Additionally, Hemiptera are the vectors of the majority of insect-transmitted microbial plant pathogens. These are concentrated in Homoptera, including, in their order of importance, Aphididae, Cicadellidae, Fulgoroidea, Aleyrodidae and Pseudococcidae.

Many Homoptera have glands that produce wax. In the Auchenorrhyncha, females of some Fulgoroidea produce wax to cover eggs, and the immature stages of many fulgoroids produce flocculent waxy threads. In *M. crudus*, the wax threads encase their excrement and are probably the insect's way of isolating toxic wastes (Pope, 1985). In the Sternorrhyncha, wax production is developed to an extraordinary degree. Waxy coatings, flocculent waxy threads and other such products are produced by psyllids, whiteflies, Hormaphidinae, mealybugs, etc., suggesting an evolutionary step leading to the distinct architecture of the highly protective waxy scale of the armoured scale insects (Diaspididae).

As exopterygote insects, Hemiptera in general develop from egg to imago by hemimetabolous, or gradual, metamorphosis, and their immature forms typically occupy the same hosts as the imagos.

In some Hemiptera and other exopterygotes, metamorphosis could not be described as 'gradual', because the immature stages differ markedly from the imago. Between the larval and adult stage of Aleyrodidae and of male Coccoidea is an intermediate stage. Many recent authors refer to this as the pupal stage. In at least some species, this stage feeds from the plant for a time, and probably differs in many other respects from the pupal stage of endopterygote insects. Coccoidea, Aleyrodidae and Thysanoptera are the only taxa in the hemimetabolous branch of Insecta with quiescent immature stages.

Heteroptera that attack the foliage of particular palm species are present in some localities, but in general the suborder is not well represented on palm foliage. A few species each in the families Tingidae and Thaumastocoridae are strongly associated with palms and one to a few species in other families, e.g. Pentatomidae, Pyrrhocoridae, include palms in their host range.

A search of palms in any tropical locality is likely to reveal species of Auchenorrhyncha. Most species are in one of 13 families; most are in the superfamily Fulgoroidea.

Some palmivorous Heteroptera and

Auchenorrhyncha transmit lethal diseases of palms. The families Aphididae, Aleyrodidae and Cicadellidae are the most important hemipterous families in regard to vectors of diseases of crop plants, but of these, only a species of cicadellid is a vector of a disease of palms. Several species distributed in the families Tingidae, Pentatomidae and Cixiidae are considered to be important vectors of palm diseases.

Sternorrhyncha are the most amply represented hemipterous suborder on palm fronds. Palm growers are accustomed to contending with sternorrhynchous insects as a matter of course. Among the insects consistently found on palms are species of whiteflies (Aleyrodidae), soft scale insects (Coccidae) and armoured scale insects (Diaspididae).

The imagos of sternorrhynchous insects are flightless or weak fliers at best, and their immature stages are sessile or relatively inactive. They may move to nearby new hosts under their own power or may be carried by ants, but depend on air currents and chance for long-distance dispersal. With relatively meagre dispersal powers, they are best adapted to stable food sources. Armoured scale insects, the most advanced Sternorrhyncha, primarily infest woody plants, which offer a more stable food source than herbaceous plants. Some species are restricted to stems. Many species infest the leaves of deciduous trees and shrubs. These most often survive the winter (or dry season) by moving to the bark each year prior to leaf-fall. Often the forms on bark are morphological variants of the leaf-inhabiting forms of the same species. This expense of energy is unnecessary for insects that infest fronds of palms and other 'evergreen trees'.

Palms grown in monocultures in nurseries or groves would offer especially favourable conditions for such insects. The species of palms that tend to grow together in grovelike stands (e.g. *Sabal palmetto* or *Nypa fruticans* (Colour Plate 1e, f)) or in extensive areas in the forest understorey (e.g. *Licuala* spp. (Fig. 1.3d)) would be easily colonized by Sternorrhyncha.

Hemiptera: Heteroptera

Forrest W. Howard

Heteroptera that attack fronds of particular palm species are present in some localities, but, in general, the suborder is not well represented on palm foliage. Large, basically phytophagous, families of Heteroptera, including the Miridae (10,000 species) and Coreidae (2000 species), contain few species that feed on palm fronds, although Coreidae are represented on palms by frugivorous species (Chapter 4). A few species each in the families Tingidae and Thaumastocoridae are strongly associated with palms. Families of Heteroptera with significant representation on palm foliage include the following:

Heteroptera
  Miridae
  Pentatomidae
  Tingidae
  Thaumastocoridae

Miridae

The Miridae are the largest family of Heteroptera, with about 10,000 described species. Known as plant bugs, they are small and delicate. They are predominantly phytophagous and some species are important pests, but only two species are significant on palms.

Carvalhoia arecae (Bryocorinae) is a major pest of *Areca catechu* in Kerala and Karnataka States, India. Known as spindle bugs, these insects occupy the leaf axils of the youngest fronds and attack the spear leaf, locally called the spindle. The feeding damage to the spear leaf appears as chlorotic streaks in the newly unfolded frond. The activity of this bug peaks in November (Radha and Rawther, 1976; Koya *et al.*, 1979; Davasahayam and Nair, 1982). A method of control was reported in which a specially designed applicator was used to apply a granulated insecticide into the two youngest leaf axils (Abraham, 1976). *Carvalhoia arecae* is also a pest of young oil palms in nurseries (Dhileepan, 1991).

Parasthenaridea arecae (Phylinae) has a similar biology on palms in Malaysia (Lepesme, 1947).

Pentatomidae

Imagos of Pentatomidae are usually between about 1 and 2 cm long. Their large pronotum and scutellum and broad shieldlike shape are distinctive. Highly developed dorsal abdominal and metathoracic glands emit volatile chemicals with a repellent odour in some species, for which characteristic they are called 'stink bugs'. These substances probably provide protection and may function in sex attraction and aggregation, but their roles in Pentatomidae have not been fully elucidated (Aldrich, 1988). The vast majority are phytophagous, but members of the subfamily Asopinae are predacious, especially on caterpillars, e.g. *Cantheconidea furcellata*, which attacks larvae of the coconut pest *Artona catoxantha* in Asia. The barrel-shaped eggs of pentatomids are laid in compact masses. The larvae are orbicular in outline, dorsoventrally compressed and often colourful and different in colour from that of the imago. There is a total of 5000 known species (Dolling, 1991).

Lincus (Pentatomidae: Discocephalinae) is a genus with more than 30 species distributed in tropical South America, 11 of which have been collected on palms. These bugs are about 10 mm long and drably coloured. A typical, but not omnipresent, characteristic of the genus is an elongated lobe at each anterolateral angle of the pronotum (Fig. 3.3). An obscure genus, most species were not known until described by Rolston (1983, 1989) from specimens in remote localities more than 100 years after the genus was defined by Stål. The few species that have been studied biologically include *Lincus spathuliger*, thought to be a vector of coffee phloem necrosis, and several palmivorous species suspected to be vectors of severe palm diseases associated with protozoa, namely, hart-rot of coconut palm and sudden wilt of African oil palm. These and other names of palm diseases are explained in Box 3.1.

Box 3.1. How palm diseases are named.

The names of plant diseases are not scientific names governed by an international code. They could be considered as vernacular names (although perhaps most of them have been coined by plant pathologists rather than farmers). The names are typically meant to be descriptive of the causal organism or principal symptom (e.g. blast, blight, blister, canker, dieback, gummosis, leaf spot, mildew, mosaic, mould, rot, rust, smut, wart, wilt, etc.); however, they are not consistent in this regard. The term 'rust' is almost invariably applied to diseases caused by species of a particular family of fungi, but 'blight' in a name may denote a virus, bacterium or fungus. Names often indicate a plant part or tissue affected (as in leaf blight, phloem necrosis, stem bleeding), but sometimes, after a name becomes accepted, it is found that the infection is elsewhere in the plant. An example is 'root wilt' (discussed below). Place-names indicating where the disease was first discovered are sometimes attached (e.g. Cape St Paul wilt), but commonly the disease is, or becomes, more widely distributed. Other words attempt to describe colours, textures, the general condition of the plant (e.g. tristeza, citrus stubborn) and many other factors.

In naming palm diseases, the difficulty is partly due to the limited array of visible effects (symptoms) of systemic diseases that palms display. Typically, the fronds turn yellow and then brown and desiccated, or in some palm species they turn brown without a yellow phase. The leaflets often wilt, i.e. fold and droop. This effect usually proceeds from older to younger fronds. The tissues of the inflorescence typically darken and the fruits abort. The ultimate stage of any lethal disease of palms is the rotting of the meristematic bud (sc. heart), accompanied by a putrid odour.

What variability there is in these symptoms is mostly in the rapidity with which they are expressed and, to a lesser extent, in the sequence of fruit dehiscence. These may be highly variable in the same disease, thus obscuring slight but consistent differences between different diseases. They are so similar that such terms as bud rot, hart-rot and lethal yellowing of coconut palm could be considered descriptive of virtually any systemic disease of palms.

Box 3.1. *continued*

Long after lethal yellowing had become widely recognized as the name for a disease of coconut palms, the disease was found to attack many other species of palms. In some of these – for example, the date palm – the fronds turn brown without a yellow phase. Thus, lethal yellowing of date palms and several other affected species is not characterized by the yellowing of the fronds or any other tissue!

Systemic palm diseases are generally accompanied by leaf wilt. One way to distinguish different 'wilts' is to attach a place name. Thus, the names Coronie wilt, from a district of that name in Suriname, and Cedros wilt, from the peninsula of that name in Trinidad, would have been useful for distinguishing two different wilt diseases. In this case, it became unnecessary. These were early names for what is now considered to be a single disease, hart-rot.

A disease of coconuts in southern India referred to as coconut root (wilt) disease is a phytoplasma-associated disease. A wilt has been said to affect the fronds, but this may be questioned (P. Jones, personal communication). In this book, the disease is referred to as Kerala coconut decline.

Sudden wilt of African oil palm is one of the more appropriate names for a lethal disease of palms, because the characteristic wilt condition indeed appears quite precipitately. 'Sudden wither' (Turner, 1981) conveys the idea better, but has not caught on. The disease is known in South and Central America; thus the name *marchitez sorpresiva*, Spanish for sudden wilt, has been adopted by some authors writing in English or French (e.g. Perthuis *et al.*, 1985; Couturier and Kahn, 1989). The shortened version used by some authors, *marchitez* (which means 'wilt'), may be a bit too brief.

One of the most appropriate names for a systemic palm disease is red ring, which refers to the disease's defining symptom, a circular band of reddish tissue seen in cross-sections of the stem (Colour Plate 14d). It is perhaps captious to point out that the reddish zone is not annular. In fact, the affected tissues form a hollow conical frustum (see Box 5.2).

Changes over time in the names of a disease, while perhaps inevitable, may cause confusion to those who later attempt to retrieve information. Witness the tortuous nomenclatural history of lethal yellowing. In the late 1800s, a disease that was thought to occur only in western Jamaica was named west end bud rot (Ashby, 1921). Later researchers concluded that this same disease was also present elsewhere in the West Indies, renaming it unknown disease (Martyn, 1949), thus dropping the restrictive 'west end' appellation in favour of a name that reflected the elusiveness of its aetiology. This name was soon replaced by the less enigmatic lethal yellowing (Nutman and Roberts, 1955). But in some reports the disease was called bronze leaf wilt, because it was thought to be the same as another disease of coconut palms by that name in northern South America, which is currently considered to be caused by abiotic factors.

Names for lethal yellowing in languages other than English went their own way. Generally, diseases of coconut palm, including lethal yellowing, were known as *pudrición del cogollo* in Spanish and *pourriture de coeur* in French (bud rot and hart-rot, respectively). *Pudrición del cogollo de Cuba* was thought to be unique; it is now considered synonymous with lethal yellowing.

In the Caribbean, lethal yellowing was known only on coconut palms, but, when it invaded Florida, additional palm species began to die of apparently the same disease. A definite link was established when it was shown that these were all associated with phytoplasmas (Thomas, 1974, 1979). But, because there was no means to determine whether or not the causal phytoplasmas belonged to the same species, the conservative approach was to refer to the phytoplasma diseases of the palms other than coconut as lethal declines (Thomas, 1979; Howard and Thomas, 1980; McCoy *et al.*, 1980a). Researchers spoke of a lethal decline of date palms, of *Adonidia* (as *Veitchia*) *merrillii* and of some 30 additional species, even while tacitly acknowledging that these were all probably identical to lethal yellowing of coconut palms.

It did not simplify matters that the name lethal decline was to be put into further service. In the 1930s–1970s, researchers in Africa reported Cape St Paul wilt, Kribi disease, Kaincopé disease and Awka wilt as separate diseases of coconut palms, the place names being the localities where they were initially reported. But, by the 1970s, their symptoms and epidemiology were better known and they were all shown to be associated with phytoplasmas (except Awka wilt, which was not investigated). They were thus considered to be a single disease, which was called lethal yellowing, because of its similarities to the Caribbean phytoplasma-associated palm disease. But there were nagging differences between lethal yellowing of the Caribbean and what was called lethal yellowing in West Africa. In the late 1980s, new technology made identification of different kinds of phytoplasmas possible

Box 3.1. *continued*

(Harrison *et al.*, 1994). It is now known that the phytoplasmas associated with similar lethal palm diseases in East and West Africa and the Caribbean are three different entities. The outcome: the name 'lethal yellowing' has been retained for the Caribbean disease, and the African diseases are now called 'lethal declines'.

Meanwhile, the diseases of palms other than coconut in Florida that had been referred to as 'lethal decline' were shown to be caused by the same phytoplasma as coconut lethal yellowing (Harrison *et al.*, 1994). At that point, the name 'lethal yellowing' was extended to include the additional palm species (including species, such as date palm, which are susceptible to the disease but do not undergo the yellowing symptom).

Borrowing a foreign word is a way of coining a unique name in a particular language. For example, gadan-gadan, a Bicolano name for a debilitating and ultimately lethal disease of coconut palms in the Philippines, was adopted into English as cadang-cadang, presumably partly for its uniqueness, and has become the internationally accepted name for the disease. Loosely translated, it means 'dying'; thus, in Bicolano, it is hardly a unique name for a lethal disease.

We could devise names such as Caribbean coconut palm phytoplasmiasis and South American coconut palm phytomoniasis, for lethal yellowing and hart-rot, respectively, that is, names based on the exact cause and its host(s), and defined more precisely by the disease's original distribution. Why not?

Perhaps some contemporary or future Linnaeus will devise a consistent nomenclatural system for plant diseases. Only one result of such an event may be safely predicted: a great deal of resistance to change.

Although there are pronounced differences in oviposition behaviour, the females of the known palmivorous species generally lay their eggs in lines of several each on petioles beneath the fibrous sheaths, and the insects complete their life cycle in this area. The oviposition rate is highest during the rainy season (Llosa *et al.*, 1990). The development period, consisting of five larval instars, lasts 2 months in *Lincus lethifer* and more than 5 months in *Lincus tumidifrons* (Alvañil Álvarez, 1993). The imago of *L. lethifer* lives a little more than a month (Desmier de Chenon, 1984). The insects commonly occur in mixed aggregations of imagos and immature forms. The morphology of the scent glands of *Lincus spurcus* has been studied in detail (Cassier *et al.*, 1994). Whether they release an aggregation pheromone or defensive chemicals is not yet known (reviewed by Aldrich, 1988). Louise *et al.* (1986) collected over 300 imagos and > 1800 larvae of *Lincus bipunctata* (syn. *Lincus croupius* (Anon., 1993)) from one palm by removing the fronds. They reported that this insect is crepuscular and avoids light, sheltering in the organic debris that collects in leaf axils.

That *Lincus lobuliger* feeds on palms was shown by a study in which a systemic insecticide, monocrotophos, fed into the roots of coconut palms was effective in controlling the insect (Moura and De Resende, 1995).

Several species of *Lincus* were collected from *Astrocaryum* spp., a cocosoid genus, in seasonally flooded forests of Peruvian Amazonia. Up to 60 bugs per palm were found inside the fibrous sheaths at the bases of petioles (Couturier and Kahn, 1989).

Lincus bipunctata has been collected from Orchidaceae growing on coconut palms (Michel Dollet, personal communication). In the laboratory, imagos of *L. tumidifrons* survived for > 100–300 days on pieces of fruits and stems of Zingiberaceae, beets and corn-cob (Alvañil Álvarez, 1993). *Lincus spathuliger*, which was collected in unspecified palm plantations (Louise *et al.*, 1986), is best known on coffee (Stahel, 1954).

Hart-rot of coconut palm and sudden wilt of African oil palm are both diseases associated with organisms traditionally referred to as protozoa (Parthasarathy *et al.*, 1976; Parthasarathy and van Slobbe, 1978; van Slobbe *et al.*, 1978; Waters, 1978). Coconut hart-rot killed 15,000 coconut palms during a 2-year period in Trinidad (Waters, 1978) and is currently widely distributed in the tropics of South America and as far north as Nicaragua in Central America. Sudden wilt of African oil palm, reported widely in the same region, is presumably caused by the same disease organism (Dollet, 1984; Muller *et al.*, 1994, 1995).

The taxonomy of the Protozoa has been undergoing intense revision in the last two decades, and further changes may be anticipated (Corliss, 1994). The causal organism of hart-rot and sudden wilt is a protozoan in the family Trypanosomatidae. Provisionally, the Protozoa include unicellular eukaryotes with membrane-bound organelles, such as nuclei. They are thus more advanced than bacteria and blue-green algae (prokaryotic organisms), which lack organelles; protozoa are linked to all higher plants and animals. Trypanosomes constitute one order of free-swimming flagellated Protozoa. Most trypanosomes are parasitic in animals, and some cause serious human diseases, such as American and African trypanosomiasis (Chagas' disease and African sleeping sickness, respectively). A few trypanosomes live in plants. All are presumably transmitted by insects. Several different species are believed to be involved. For convenience, they are placed in a single genus, *Phytomonas*, a name referring to their endophytic habitat.

Species of *Phytomonas* are not identifiable by appearance. A single strain can have different morphological forms in different plant species (Dollet, 1984). Researchers have made progress towards developing molecular methods of distinguishing them (Menara *et al.*, 1988; Ahomadegbe *et al.*, 1992; Marché *et al.*, 1993, 1995; Dollet, 1994; Muller *et al.*, 1994, 1995).

Species of eight families of plants are known to harbour *Phytomonas* spp. Most are species in the lactiferous families Euphorbiaceae and Asclepiadaceae. Because their effects on these hosts are generally benign, they were largely ignored by plant pathologists until they were found to be associated with diseases of non-lactiferous host plants, notably coffee and the two economically important palms mentioned. Their pathogenicity to the latter plants may be related to invasion of the phloem; in the lactiferous plants, they are concentrated in latex cells, which are excretory structures (Parthasarathy *et al.*, 1976). Also, RNA virus-like particles were found in phytomonads associated with hart-rot and sudden wilt of African oil palm (Marché *et al.*, 1993, 1995), but not in phytomonads from lactiferous plants. The nature of the pathogenicity of phytomonads remains under investigation.

Several species of insects in the families Lygaeidae and Coreidae have been implicated as vectors of phytomonads to lactiferous plants (Dollet, 1984). Heteroptera are probably more apt to transmit phytomonads than, for example, aphids and other small Sternorrhyncha, whose stylets would generally be too fine for these organisms to pass through. These trypanosomes may be primarily parasitic in insects, with a portion of the species adapted to the plants upon which the insects feed (reviewed by Leach, 1940).

The vectors of the lethal phytomonad-associated diseases of non-lactiferous plants, i.e. phloem necrosis of coffee (Stahel, 1954) and the two palm species mentioned, are believed to be bugs of the genera *Lincus* and *Ochlerus.* Species studied as possible vectors include, of hart-rot of coconut palm, *Lincus apollo*, *L. bipunctata, Lincus dentiger* and *L. lobuliger* and, of sudden wilt of African oil palm, *Ochlerus* sp., *L. lethifer* and *L. tumidifrons* (Desmier de Chenon, 1984; Perthuis *et al.*, 1985; Louise *et al.*, 1986; Dollet *et al.*, 1993, 1997; Moura and De Resende, 1995; Alvañil Álvarez, 1993). It may be anticipated that evidence incriminating these and perhaps additional species of *Lincus* will be substantiated in the future by controlled, replicated experiments.

Phytomonad-associated palm diseases seem to have spread from north-central South America to other parts of tropical America, as increasing areas were planted to coconut palms and African oil palms. Hart-rot has been considered a major deterrent to coconut-growing in Suriname since the 19th century (Maas, 1971). It was much later that hart-rot was reported in Brazil

(Bezerra and de Figueredo, 1982) and sudden wilt of African oil palm in Colombia (McCoy and Martínez-López, 1982; Alvañil Álvarez, 1993), Peru (Dollet *et al.*, 1977), Ecuador (van Slobbe *et al.*, 1978) and Costa Rica (McCoy *et al.*, 1984). Palms in the wild have been found to have trypanosomes in their phloem tissue, including *Maximiliana maripa*, in Suriname (van Slobbe *et al.*, 1978), and *Attalea funifera*, in Brazil.

The symptoms of hart-rot, described by Parthasarathy and van Slobbe (1978) and Waters (1978), are very similar to those of lethal yellowing, but some differences have been noted. Parthasarathy reported that hart-rot progresses more rapidly, killing the palm within 4–6 weeks after the appearance of symptoms. Other authors indicated that this period may vary considerably (e.g. 8–12 weeks (Waters, 1978) and 6 months (Mena *et al.*, 1975)), so as to overlap with that of lethal yellowing. In hart-rot-affected coconut palms, the intermediate or mature fruits may be more persistent, although Waters (1978) reported that, in the final stages of the disease, all fruits are usually shed. The 'flag leaf' associated with lethal yellowing has not been observed in palms affected with hart-rot, but, in any case, it is an undependable symptom of the former.

A clear difference between lethal yellowing and hart-rot has to do with varietal resistance. Malayan dwarf coconut palm varieties are resistant to lethal yellowing but highly susceptible to hart-rot. However, this characteristic does not distinguish hart-rot from red ring, for which there is no known varietal resistance. Hartrot of coconut palm and sudden wilt of African oil palm are apparently caused by the same kind of protozoan (Dollet, 1984). The red-ring nematode also affects both of these palms. In contrast, lethal yellowing affects coconut and more than 30 additional palm species, but does not affect African oil palm.

Symptoms of sudden wilt are described by van Slobbe *et al.* (1978). Several similar diseases of African oil palm have been reported in South America, but the symptoms of most are inadequately known. Van Slobbe *et al.* (1978) concluded that a disease called 'vascular wilt' of African oil palm is different from sudden wilt. This is now known to be caused by *Fusarium* sp. (Michel Dollet, personal communication). Coconut and African oil palms of 2–5 years old are most susceptible to phytomonad-associated diseases, but palms up to 20 years old may contract the disease (Alvañil Álvarez, 1993).

A species of Encyrtidae (Hymenoptera) parasitizes *Lincus malevolus*, causing an atrophying of gonads (Rasplus *et al.*, 1990). *Telenomus* sp. (Hymenoptera: Scelionidae) parasitizes eggs of *Lincus* sp., probably *L. bipunctata* (Louise *et al.*, 1986). In the early 1900s, A.W. Drost (cited by Segeren and Alexander, 1984) observed in Suriname that coconut plantations where weed control was not practised seemed to have the greatest incidence of hart-rot, and recommended weed control, along with removal and burning of symptomatic palms, as a method of controlling this disease. Many lactiferous plants growing in coconut plantations harbour phytomonads (Kastelein *et al.*, 1984), although these are probably not the same species as those involved in hart-rot. Replicated studies by Segeren and Alexander (1984) confirmed that hart-rot can be curtailed by keeping coconut plantations free of weeds. They suggested that certain weeds may serve either as reservoirs for the phytomonads or as hosts of the insect vectors. Further studies of the possible role of weeds in the disease cycle of phytomonad-associated disease may result in techniques useful in integrated control.

Insecticides have been found to reduce populations of *Lincus* spp. on palms and perhaps could be used to interrupt an epidemic of hart-rot or sudden wilt (Louise *et al.*, 1986; Moura and De Resende, 1995).

Thaumastocoridae

The Thaumastocoridae are a family of minute, flat bugs, typically about 2.5 mm in length (an unusually large species, *Discocoris imperialis*, is 4.6 mm long), with the head as broad as the thorax and with a pair of structures called ‘mandibular plates’ often projecting forward from the head. A notable feature is their asymmetrical male genitalia (lacking one or both parameres). In male Thaumastocoridae, bilateral asymmetry may be either dextral or sinistral, depending on the species, or may vary intraspecifically among individuals (Drake and Slater, 1957).

Worldwide, the family consists of six genera and 18 species. In the eastern hemisphere, there are 11 species endemic to Australia and Tasmania, and a single species in southern India. These species of the eastern hemisphere are found on *Acacia*, *Eucalyptus, Melaleuca* and other dicotyledonous trees. The thaumastocorids found in the western hemisphere are associated with palms. *Xylastodoris luteolus*, a monotypic species of Cuba and Florida, feeds on the newly developing fronds of its palm host, and at least four of the five species of the South American genus *Discocoris* feed on the infructescences of palms (Slater and Schuh, 1990).

The family has long intrigued hemipterists because of its disjunct distribution (which suggests that it is a relict of a widely distributed ancestral family) and its recondite relationships with other Hemiptera. The western hemisphere species of this family, contained in the monotypic genus *Xylastodoris* and *Discocoris* (with five species), comprise a subfamily, Xylastodorinae (Slater and Brailovsky, 1983; Schuh and Stys, 1991; Couturier *et al.*, 1998a). Some authors consider the xylastodorids to be a separate family (Viana and Carpintero, 1981; Dolling, 1991). A thaumastocorid, *Paleodoris lattini*, known from fossils in Dominican amber (about 20–40 million years old), is taxonomically near *X. luteolus*, and is thought to have lived between palm pinnae (Poinar and Santiago Blay, 1997).

With their flat bodies and short legs, xylastodorine bugs are closely appressed to the surfaces of their palm hosts. Schuh (1975) mentioned that *Discocoris drakei* clung to surfaces so tenaciously that it was almost impossible to pick one of the insects up with a common insect aspirator. In collecting them, he found it necessary to strike an infested inflorescence against a hard surface to knock them loose.

Xylastodoris luteolus attacks young fronds of *Roystonea regia* in Cuba and Florida (Colour Plate 7b). It is known on no other host. Because the insect, known as the royal palm bug, is a common pest of a popular ornamental palm in Florida, and is more easily accessible than the species of Xylastodorinae found in remote localities of South America, it is the best known of this group. But, because it prefers relatively tall palms and does not survive in laboratory colonies or other small systems, even this species is difficult to study. Most of our information on the insect’s bionomics is from Baranowski (1958).

The imagos are elongate, 2–2.5 mm long, and of a pale yellow-green colour, from which is derived the specific name, *luteolus*. We have seen no colour change in the bright red eyes of this insect in response to light and darkness, as in some Heteroptera observed previously (Howard, 1989b). The larvae are slightly paler and bear two yellow-orange dorsal abdominal scent glands; imagos bear one of these.

The bugs attack fronds just as they are unfolding. This results in small, yellow spots scattered on the abaxial frond surfaces. More advanced damage consists of yellow streaks, which turn brown (Colour Plate 7c, d). A highly infested frond turns grey-brown and then a lighter grey colour as it becomes bleached in the sunlight. The desiccated tissue becomes tattered, due to wind action, giving the frond a frizzled appearance.

In southern Florida, dense populations of *X. luteolus* occur on fronds from about mid-March to early July. We have observed up to 300 bugs per leaflet during this period. As each new frond is produced monthly, the bugs attack it, so that four or five fronds may be damaged by early summer. About that time, the bug populations diminish, so that the fronds produced the rest of the year remain green. By autumn, the fronds that were damaged the previous spring are midway in the otherwise green crown. By the following spring, the previous year's damaged fronds are the lowest in the crown and these may persist on the palm at the same time that new fronds become damaged (Baranowski, 1958; Howard and Stopek, 1998).

Damage to fronds by frosts, storms, salt spray and even nutritional deficiencies may sometimes be confused with that of royal palm bugs, especially if it occurs in late winter or spring. Since the damage is restricted to tall palms, it may be difficult to diagnose. But, by working in the tops of palms (e.g. from a bucket truck (Fig. 8.2)) and closely examining damage associated with dense populations of royal palm bugs and then observing this damage from the ground, one learns to recognize it.

Xylastodoris luteolus was first collected in Cuba in 1918 from *R. regia* (Barber, 1920) and found shortly thereafter in Florida (Moznette, 1921). It is currently distributed throughout southern Florida on *R. regia* (Baranowski, 1958) and presumably throughout most of Cuba on the same host.

Roystonea regia is native to Florida, Cuba, the Cayman Islands and Yucatán, Mexico (McCurrach, 1960; Meerow, 1992; Quero, 1992). It has been planted as an ornamental palm throughout the tropics. Whether *X. luteolus* is associated with it outside Cuba and Florida or with any of the other 15 species of *Roystonea* in the Caribbean region (Uhl and Dransfield, 1987) has not been investigated.

Mature royal palms were abundant as ornamental plants in Miami at the beginning of the 20th century (Griffing, 1912). Earlier plantings may have been propagated from native royal palms, which grow on a few hummocks and were formerly considered to be an endemic species, *Roystonea elata*. Royal palms introduced from Cuba were considered to be a separate species (*R. regia*) and, until recently, were said to be more abundant in ornamental plantings in Florida than the native *Roystonea*. The two species are now considered conspecific, with *R. elata* as a junior synonym of *R. regia* (Scott Zona, personal communication). Both the bug and its palm host are relatively recent arrivals in southern Florida, since that area was submerged 6000 years ago (Myers, 1984).

Baranowski (1958) reported that *X. luteolus* tended to infest taller royal palms and was scarce or absent from palms of this species less than about 4 m tall. He studied *X. luteolus* by caging the insects on fronds in the field. His attempts to study them in the laboratory were frustrated because larvae did not survive more than a few days on excised frond material, even though it was changed daily.

The egg is pale amber in colour, elongate, 0.5 mm long and capped at one end by a white operculum. Females usually lay single eggs in the fibrous tufts that occur along the leaflet midvein on the abaxial surface, averaging one egg per day over a 15-day period (Fig. 3.4). The eggs hatch in about 8 days. There are five larval instars, each of which lasts several days, so that the insects develop from egg to imago in 23–37 days. The generation time thus approximates the period between the production of each new frond (Baranowski, 1958).

The male genitalia of *X. luteolus* are asymmetrical, orientated towards the right in about half of the males and towards the left in the other half. The bugs have been observed to mate while in the confined habitat of the folded leaflet, the females lining up along the midvein and orientated distally or proximally so as to expose only one side. The presence of males with left- and right-orientated genitalia appears to be an adaptation to ensure that some will mate regardless of the orientation of the female (Baranowski, 1958).

In palms that the bugs attack in early April, up to five fronds (i.e. about a third of the crown) may be necrotic by August (Colour Plate 7c). The impact of this damage on the vigour of the palms has not been measured, but may be presumed to be significant. Additionally, the damage to the aesthetic quality of these palms is obvious. In Florida, outbreaks of *X. luteolus* have occurred at intervals of several years. Damage was reported to have been unusually intense in 1921 (the year that *X. luteolus* was first reported), 1957 and 1975

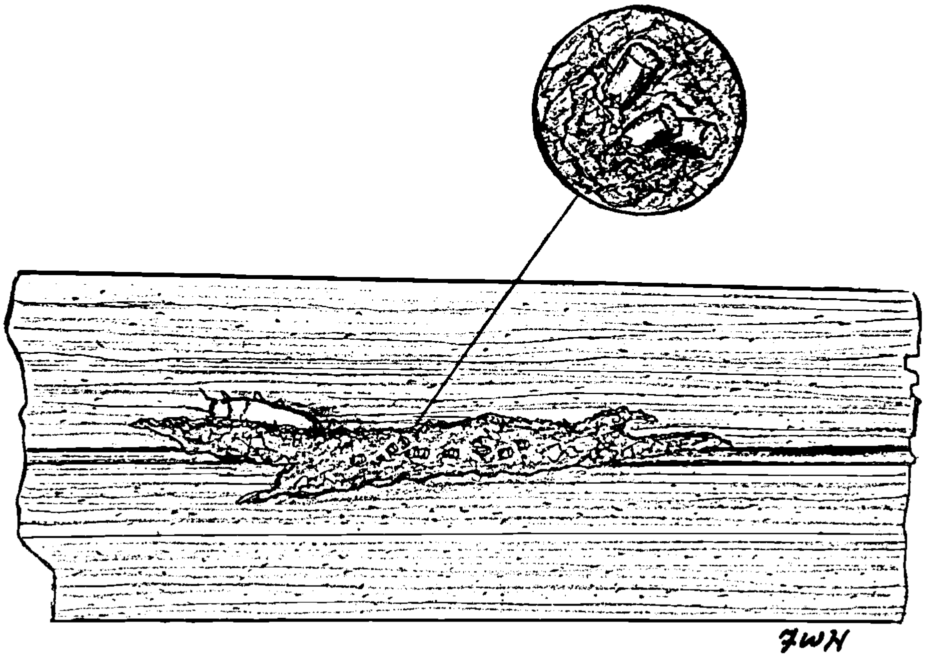


Fig. 3.4. *Xylastodoris luteolus* (Thaumastocoridae), imago partially hidden and eggs inserted in fibrous tufts on pinna midvein. Known in Florida and Cuba.

(Reinert, 1975). Because these reports were based on opportunistic observations by different people, they may be biased and inaccurate, but most observers would agree that royal palm-bug damage is more intense in some years than in others. During the 1990s, widespread damage was observed annually. Because of its attractiveness in avenue plantings and new landscaped urban developments requiring large palms and its apparent immunity to lethal yellowing, Cuban royal palm has become more abundant in southern Florida than at any time in the region's history. This may have contributed to an increase in the bug's populations. Perhaps more importantly, during the 1990s there were no extensive severe frosts in southern Florida.

No significant predators or parasitoids of this insect are known in Florida. Natural enemies may have been left behind when the bug invaded from Cuba. Cuba and perhaps other islands of the West Indies should be explored for natural enemies of royal palm bug.

The damage to royal palms is sometimes severe enough in Florida for insecticides to be applied to control the bugs (Reinert, 1975), but chemical control is difficult because of the height of the infested palms. Drift from insecticides sprayed into the crowns of these palms is particularly undesirable in cities. Trunk injections of insecticides are inappropriate for royal palms because the smooth, columnar trunks are part of their aesthetic appeal. Recently, a root drench with the chloronicotinyl insecticide, imidacloprid, was found to be highly effective. This compound was selected because it is a systemic insecticide, is relatively safe and was known to be effective against lace bugs (Tingidae), which are closely related to Thaumastocoridae. A single treatment applied in the late winter protected large Cuban royal palms from damage by *X. luteolus* during the spring season that followed (Howard and Stopek, 1998, 1999) and, since damaging populations are confined to the spring, no further treatment was necessary that year. Surprisingly, the treated palms remained free for a second season (F.W. Howard, unpublished). The effectiveness of imidacloprid against royal palm bug may be partly due to its tendency to accumulate in younger plant tissue. Since it is taken up slowly by plants, it is generally applied as a preventive treatment before the season when the target insects cause damage. Thus, the pest status of the royal palm bug must be predicted prior to the spring season. A rough prediction may be based on the insect's abundance and the extent of damage the previous year, together with an assessment of the weather conditions likely to influence population development (e.g. absence of frosts, relatively high mean temperatures).

Discocoris vianai was the second species of Thaumastocoridae discovered in the western hemisphere (Fig. 3.5). It was described from Argentina on *Euterpe edulis* (Kormilev, 1955). It is about the size of *X. luteolus*, with a testaceous colour and fine, shallow punctations on the pronotum and scutellum.

Discocoris drakei, an ovate, flat bug, was first collected near the Pacific coast of Colombia (Slater and Ashlock, 1959) and subsequently from inflorescences of *Phytelephas* sp. at 800 m altitude in Peru (Schuh, 1975). The bugs conceal themselves around the bases of maturing and mature fruits or in the concave peduncle scars left on the inflorescence after fruits are shed. The hemelytra are strikingly asymmetrical. The left forewing is a normal hemelytron, with a coriaceous basal part and a distal membranous area, while the right forewing is entirely coriaceous without a distal membranous area. Because the right wing overlaps the left when the wings are at rest, the dorsal surface of the insect is completely covered by sclerotized surfaces. Presumably this is an adaptation for an insect that manoeuvres in tight places (Schuh, 1975).

Discocoris imperialis was collected on the infructescence of *Socratea montana* at 1150 m altitude in Colombia. The imagos of this species, the largest known thaumastocorid, are broadly ovate and 4.6 mm long. Their general colour is light tan (Slater and Schuh, 1990).

Discocoris kormilevi was described from Argentina. It was found on a cocosoid palm, *Butia yatay* (Viana and Carpintero, 1981).

Discocoris fernandezi is broadly ovate and of an almost uniform light tan colour, with densely spaced, coarse, puncta on the pronotum and scutellum and with bright red eyes. The type specimens of the species were collected in northern Venezuela at 1100 m and from near the Venezuela–Guyana–Brazil border at 1800 m. The host was not known, but, because all other known species of Xylastodorinae are associated with palms, Slater and Brailovsky (1983) suggested that *D. fernandezi* is also palmivorous.

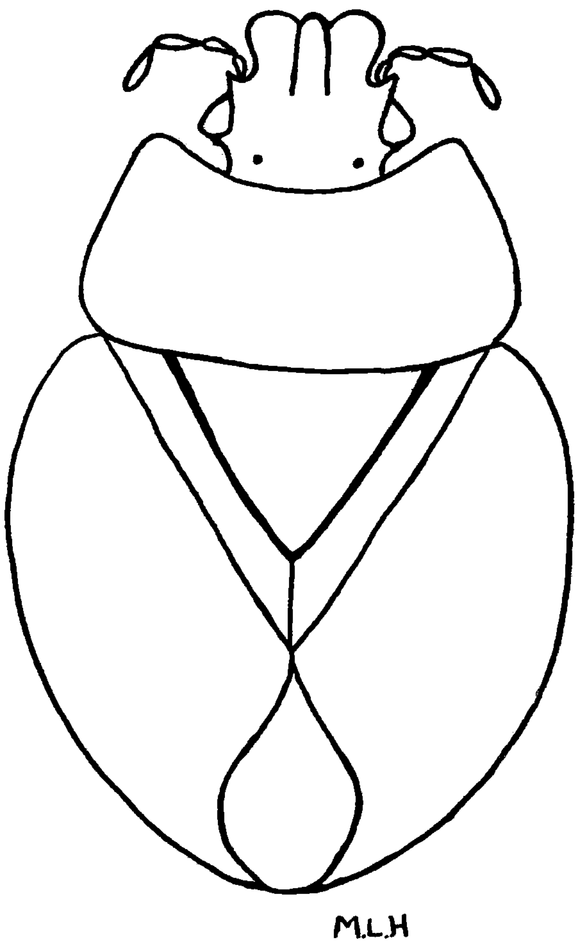


Fig. 3.5. *Discocoris vianai* (Thaumastocoridae), known only from *Euterpe edulis* in Argentina. Redrawn by Martha Howard from Kormilev (1955).

Tingidae

Species of Tingidae are, like the Thaumastocoridae, mostly small bugs of 2–8 mm or less. Called lace bugs, the veins of the forewings are in a delicate reticulated pattern, which extends over the pronotum. The pronotum of many species has a bizarre shape, some being extended laterally, others very spinose or with crestlike outgrowths. Their tarsi are two-segmented, while those of thaumastocorids are three-segmented. The larvae lack the elaborate lacelike ornamentation that defines the family, but typically bear numerous spine-like tubercles and glandular setae (Livingston, 1978). There are about 1820 species in 250 genera in the world (Drake and Ruhoff, 1965; Arnett, 1985; Dolling, 1991; Schuh and Slater, 1995). Most species feed on trees or woody shrubs. Overall, Tingidae inflict more damage on ornamental trees and shrubs than any other family of Heteroptera (Johnson and Lyon, 1991). They generally feed on palisade and other mesophyll cells, typically causing the fronds to acquire a speckled appearance. The females often insert their eggs into the plant tissue near leaf veins and cover them with a brown viscid substance, which solidifies to a conelike structure on the surface of the frond (Bourgoing, 1991; Johnson and Lyon, 1991). The largest of three subfamilies, Tinginae, contains all of the important economic pests (Schuh and Slater, 1995), including those discussed here.

Stephanitis typica, known by the names coconut lace bug and banana lace bug, is the best-known tingid associated with palms (Colour Plate 7a, Figs 3.1 and 3.6). This is the only lace bug commonly reported on coconut palms in tropical Asia, where it is widely disseminated. It occurs as far east as New Guinea (Corbett, 1932; Lever, 1979; Zelazny and Pacumbaba, 1982; Mathen *et al.*, 1990; Bourgoing, 1991). The genus *Stephanitis* includes over 60 other species, including some well-known pests of temperate-zone fruit and ornamental trees and shrubs.

The head, pronotum and hemelytra are of a whitish colour, but the latter structure is pale and hyaline, so that the blackish abdomen shows through it. The length from the tip of the projection on the head to the posterior margins of the forewing is about 4 mm (Distant, 1903).

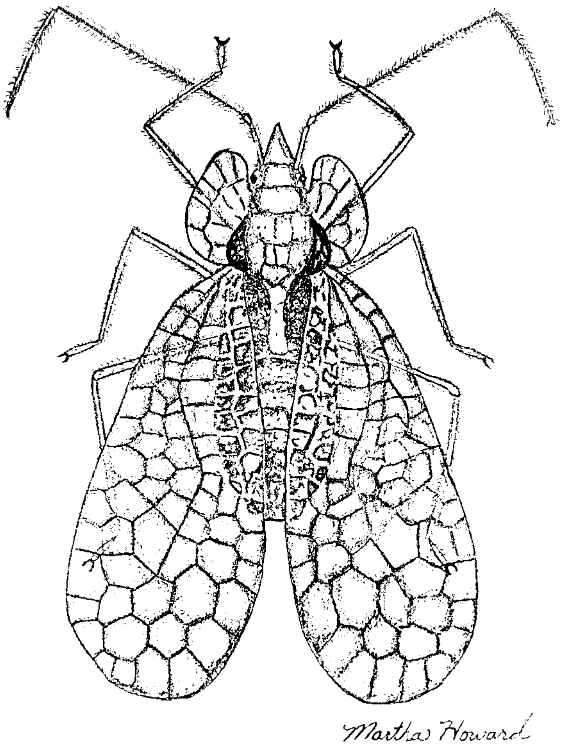


Fig. 3.6. *Stephanitis typica* (Tingidae). Drawn by Martha Howard from photographs and specimens from the Philippines.

The life stages were described in detail by Mathen (1960). The insect completes its life cycle from egg to imago on foliage of monocotyledons and dicotyledons, seeming to prefer the former, including African oil palm, coconut palm and species of Musaceae and Zingiberaceae (Mathen and Kurian, 1980; J.J. Solomon, personal communication). Imagos and larvae feed in the same sites. The larvae aggregate, a trait more pronounced in early instars. A female typically lays about 30 eggs, concealing them by inserting them deep in the abaxial surfaces of fronds and covering them with a lipid material, as do Tingidae in general (Bourgoing, 1991). These hatch after about 12 days. The larval stage lasts about 13 days and consists of five instars. Imagos live up to 25 days in the laboratory (Mathen and Kurian, 1980). In southern India, *S. typica* populations tend to increase during dry periods and decrease during wet periods (Mathen and Kurian, 1968).

The bugs insert their stylets through the stomata, which are abundantly distributed on the abaxial frond surface (Mathen *et al.*, 1988). This feeding behaviour would seem to be especially advantageous for penetrating the tough surface of palm fronds, but *Stephanitis rhododendri* also penetrates the stomata of its *Rhododendron* spp. hosts (Johnson, 1937). Imagos feed for 10–30 min at a time and at 80 or more sites during a 24 h period (Mathen and Kurian, 1980). The stylets can penetrate a maximum of 600 μm and, since the maximum thickness of the lamina is about 400 μm, the insect is capable of reaching tissue throughout the interior of the lamina. Although *S. typica* feeds on palisade cells, the stylets of this bug apparently also penetrate frequently into the phloem (Mathen *et al.*, 1988).

Feeding sites become marked by minute chlorotic flecks on the adaxial surface (Colour Plate 7a) (Mathen and Kurian, 1980). The feeding damage may be conspicuous, but mature palms seem to tolerate populations of up to 500 imagos and larvae without detectable economic damage (J.J. Solomon, personal communication).

The major impact on palms of *S. typica* is as a vector of Kerala coconut decline (syn., coconut root (wilt) disease), a non-lethal debilitating disease of coconut palms in Kerala and Tamil Nadu States, India. The disease, discovered in the 1870s, is associated with a phytoplasma (Solomon *et al.*, 1983; Solomon, 1991, 1997). It affects growth and production of palms and increases their susceptibility to leaf fungus diseases. A survey in 1984/85 revealed that it was prevalent in different degrees of intensity over an area of 410,000 ha, causing an annual loss of 968 million coconuts (Solomon *et al.*, 1983; Solomon, 1997).

A series of studies to identify a vector of Kerala coconut decline were similar to those undertaken to implicate a vector of lethal yellowing. It was found to be the most abundant hemipteran on coconut palms in Kerala (Nagaraj and Menon, 1956). Experiments were conducted in which *S. typica* was caged to healthy palms in the field. Nearby palms without these insects caged to them served as controls. Higher percentages of the palms with caged *S. typica* contracted Kerala coconut decline compared with the controls (Nagaraj and Menon, 1956; Shanta *et al.*, 1960). Thus, further scrutiny of this insect as a possible vector was encouraged. One out of six coconut seedlings exposed to *S. typica* in an insect-proof house contracted the disease (Shanta *et al.*, 1964). Palms that were highly infested with the lace bug tended to be the first to contract the disease. In one study (Mathen, 1982), there were four times as many *S. typica* on diseased compared with healthy palms. This was followed by a study that showed that a high percentage of the palms that contracted Kerala coconut decline were those that had high numbers of *S. typica* the previous year (Mathen, 1985). The salivary glands of *S. typica* were described anatomically (Mathen *et al.*, 1987a) and *S. typica* that had fed on a coconut palm infected with the phytoplasmas and given an incubation period of 13–18 days harboured phytoplasmas in the salivary glands and supra-oesophageal ganglia (Mathen *et al.*, 1987b). Finally, a transmission experiment, basically similar in design to the experiment that implicated *M. crudus* as a vector of lethal yellowing (Howard *et al.*, 1983), was conducted. It involved the continual introduction of *S. typica* into large screen cages erected over field tanks made of bricks, plastered with cement and filled with sterilized soil (Fig. 3.7). The palms placed in the cages were brought from a disease-free area. Over 1000 bugs were introduced into each cage over 17 months before the first of four of the test plants developed symptoms of Kerala coconut decline (Mathen *et al.*, 1990). The sum of this evidence is convincing that *S. typica* is a vector of this disease.

Other putative vectors are *Sophonia greeni* (Cicadellidae: Nirvaninae) and *Proutista moesta* (Derbidae) (Rajan and Mathen, 1984, 1985; Solomon, 1997).

The insect can be controlled by insecticides in nurseries. A species of mirid is a predator of *S. typica* (Mathen and Kurian, 1972). Species of Trichogrammatidae parasitize the eggs (Livingston and Yacoob, 1986). Management methods for Kerala coconut decline have not yet been developed. Host-plant resistance to the disease

Fig. 3.7. Cages for testing *Stephanitis typica* as a vector of Kerala coconut decline in Kerala, India. Photo by Mr E.R. Asokan.

is under investigation. Although an imidacloprid treatment for *Xylastodoris luteolus* (Howard and Stopek, 1998, 1999) might be effective against *S. typica*, chemical control is not a promising approach for controlling this insect in plantations. Perhaps with more knowledge of this species, a cultural control method could be developed to reduce vector populations (Solomon, 1997).

Leptopharsa gibbicarina is a pest of African oil palm in Colombia. It also attacks coconut palms, *Aiphanes* sp., *Bactris* sp. and *Elaeis oleifera* (Zenner de Polanía and Posada Flórez, 1992). The imagos are 2.6–2.9 mm long and generally whitish in colouring, with the typical lace-like wings of tingids. A distinctive characteristic of the wings at rest is that their costal margins are coarctate, i.e. curved inward, giving the appearance of a constriction (Froeschner, 1976). The females insert their eggs into leaf tissue along a major vein of the abaxial surface, usually covering them with excrement. Upon hatching, larvae mingle with the imagos, maturing in 6 weeks. The imagos live for more than a month. The insects are generally most abundant on lower fronds and attain greater population densities in extensive African oil palm plantations, compared with sparse plantings. They are relatively more abundant in the dry season (Zenner de Polanía and Posada Flórez, 1992). Feeding behaviour is similar to that of *S. typica*. The bugs prefer upper and middle fronds, seldom infesting the older fronds. Dense populations of *L. gibbicarina* cause considerable damage, and leaf surfaces injured by lace bug feeding may be invaded by fungi, such as *Pestalotiopsis* spp., which causes further damage.

Leptopharsa gibbicarina is attacked by a large complex of natural enemies, which includes predacious Neuroptera, ants (especially *Crematogaster* spp.) and *Beauveria* sp. (Aldana de la Torre *et al.*, 1995). When these are not effective in maintaining low populations of the lace bug, an option is to treat the palm with a systemic insecticide, such as monocrotophos, applied by a root-absorption method. In this method, the insecticide is fed into the roots from a small bag. This method is preferable to trunk infections in zones where red ring could be transmitted by contaminated equipment (Zenner de Polanía and Posada Flórez, 1992).

Pleseobirsa bicinta is a second lace bug pest of African oil palm in South America, with a wider distribution, which includes the Amazon regions of Colombia, Ecuador and Peru. This species can be distinguished from *L. gibbicarina* by the lack of a 'constriction' in the wings at rest and the general outline of the body: *P. bicinta* is almost square, rather than oblong.

The two species tend to occupy different portions of the frond. *Leptopharsa gibbicarina* is often distributed on most of the pinnae of a frond, while *P. bicinta* is likely to be concentrated on the pinnae close to the petiole.

In infested plantations, populations of *L. gibbicarina* tend to be spread rather uniformly on palms over many hectares; in contrast, populations of *P. bicinta* vary greatly from one palm to the next, a characteristic that Mariau (1994) attributed to low dispersal capabilities.

Because of its more extensive distribution on fronds and more uniform populations in plantations, *L. gibbicarina* is considered the more damaging of these two lace bugs (Mariau, 1994).

Corythucha gossypii is a polyphagous lace bug widely distributed in tropical America and extreme southern parts of the USA. A large portion of its recorded hosts consists of tropical fruit and ornamental trees and two palms, namely African oil palm and *R. regia*, in Colombia (Drake and Ruhoff, 1965; Froeschner, 1976).

Allotingis binotata was described from specimens collected on *Thrinax wendlandiana*, a native palm in Cuba, but is not a pest and has not been studied biologically (Drake and Ruhoff, 1965).

Acysta interrupta is a common tingid in African oil palm plantations in Costa Rica. It causes indirect damage by spreading *Pestalotiopsis* sp. (Carlos Chinchilla, personal communication).

Hemiptera: Auchenorrhyncha

Forrest W. Howard and Michael R. Wilson

Auchenorrhyncha associated with palms are generally inconspicuous insects. With some exceptions, they occur in light to moderate populations and rarely cause material damage to palms through their feeding. Nearly all of them have the habit of remaining motionless for long periods while feeding on the abaxial leaf surfaces, often next to a midvein or in the shelter formed where the leaflet joins the rachis. Some complete their life cycle on palms, but most feed on palms only as imagos, passing their larval stage on another host.

Sometimes many palms must be examined to find just one or a few of these insects. They went largely unnoticed by earlier economic entomologists, who were more concerned with insects that caused obvious and direct damage to palms.

In recent decades, much has been learned concerning the Auchenorrhyncha on palms in several regions. The main impetus for these studies has been to identify potential vectors of palm diseases. Prior to the 1970s, lethal yellowing of the Caribbean region was thought to be caused by a virus or similar microbial pathogen transmitted by insects (Bruner and Boucle, 1943). Thus, in the 1960s, surveys were conducted to identify the Hemiptera associated with coconut palms in Jamaica (Grylls and Hunt, 1971; Farr, 1985). Following the discovery in the early 1970s that lethal yellowing was associated with a phytoplasma (referred to until recently as a mycoplasma-like organism), researchers began to focus attention on the suborder Auchenorrhyncha, which by then was known to contain most vectors of phytoplasmas (the exceptions are some species of Psyllidae, which are Sternorrhyncha closely related to Auchenorrhyncha). Surveys of Auchenorrhyncha on palms have since been conducted as part of research on several palm diseases in different regions (Table 3.1).

Most species of Auchenorrhyncha of importance on palms are in the superfamily Fulgoroidea, and these are mostly members of the families Cixiidae and Derbidae. One to several important palm-associated species are also in the additional fulgoroid families listed below. Cicadellidae and Membracidae are not of widespread importance on palms, but are represented in some localities. The topic of Auchenorrhyncha on palms has been reviewed previously (Wilson, 1987b, 1988b, 1997).

Table 3.1. Surveys conducted to identify Auchenorrhyncha as potential vectors of palm diseases.

Region	Palm species	Disease	Pathogen	References
Jamaica	Coconut	Lethal yellowing (LY)	Phytoplasma	Grylls and Hunt, 1971; Schuiling, 1976; Eskafi, 1982; Farr, 1985
Florida, USA	Many species	LY	Phytoplasma	Woodiel, 1976; Howard and Mead, 1980
Dominican Republic	Many species	LY	Phytoplasma	Howard *et al.*, 1981
Mexico	Coconut	LY	Phytoplasma	Can Itzá, 1996
Texas, USA	*Phoenix* spp.	Similar or identical to LY	Phytoplasma	Meyerdirk and Hart, 1982
India	Coconut	Kerala coconut decline	Phytoplasma	Rajan and Mathen, 1985
Philippines*	Coconut	Cadang-cadang	Viroid	Zelazny and Pacumbaba, 1982
West Africa	Coconut	LY-like disease	Phytoplasma	Wilson, 1987a, b, 1988b, 1997
East Africa	Coconut	LY-like disease	Phytoplasma	Wilson 1987a, b, 1988b, 1997

*Survey included all phytophagous insects on coconut palm.

Families of Auchenorrhyncha of significance on palm foliage include the following:

- Auchenorrhyncha
  - Fulgoroidea
    - Cixiidae
    - Delphacidae
    - Derbidae
    - Achilidae
    - Tropiduchidae
    - Issidae
    - Lophopidae
    - Ricaniidae
    - Flatidae
    - Meenoplidae
  - Cicadoidea
    - Cicadidae
  - Cicadelloidea
    - Cicadellidae
    - Membracidae

Fulgoroidea

The superfamily Fulgoroidea (planthoppers) includes 20 families and over 8000 species (Dolling, 1991). Morphologically, planthoppers resemble cicadellids, but are distinguished from them by their tibial spines, which occur in clusters or whorls, not in rows. Their antennae are positioned ventrally to the eyes and have an enlarged, often bulbous, pedicel with dense sensilla and an arista (Figs 3.8, 3.11d and 3.15d). The larvae have abundant sensory pits and those of many species produce wax filaments (Fig. 3.17b). Most species are phloem-feeders and most are not highly host-specific (Wilson, 1997).

Cixiidae

The Cixiidae is a large cosmopolitan family of the superfamily Fulgoroidea, with more than 1000 described species (Dolling, 1991). Structural details that separate cixiids from other fulgoroids include characteristics of wing venation and prominent setae on the veins of the forewings. Strongly developed carinae on the head are useful field characters for identifying different species of cixiids, as are the three to five longitudinal carinae of the mesonotum. In the few species that are well known biologically, the larvae are primarily root-feeders, often of herbaceous plants, and the imagos live on the above-ground portions of the same or different plants. Several species of the cixiid genus

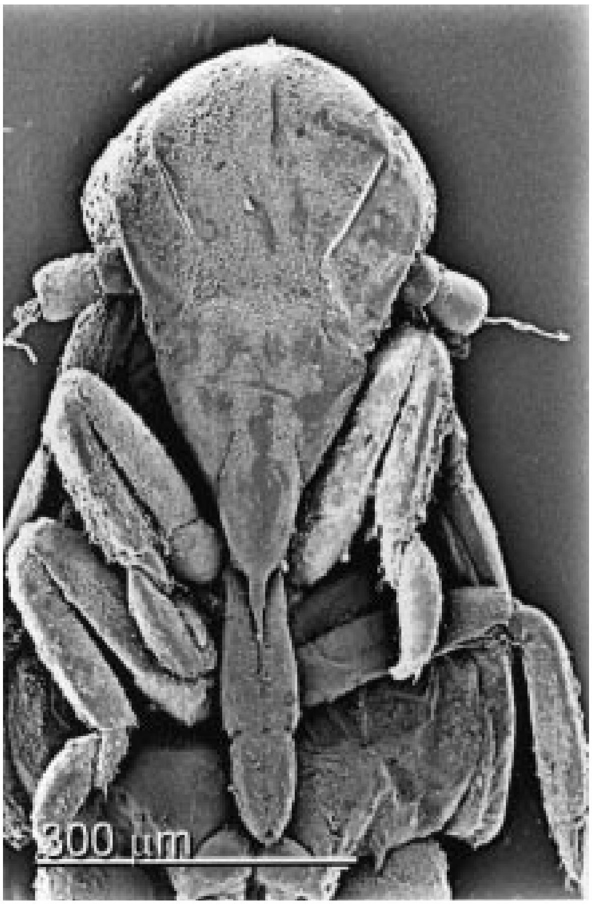


Fig. 3.8. Head of *Ormenaria rufifascia* (Flatidae) (SEM view), a planthopper common on *Sabal palmetto* in Florida. The proboscis, orientated posteriorly, is typical of Auchenorrhyncha.

Fig. 3.9. *Myndus crudus* (Fulgoroidea: Cixiidae) imago, a planthopper distributed widely in tropical America and southern Florida.

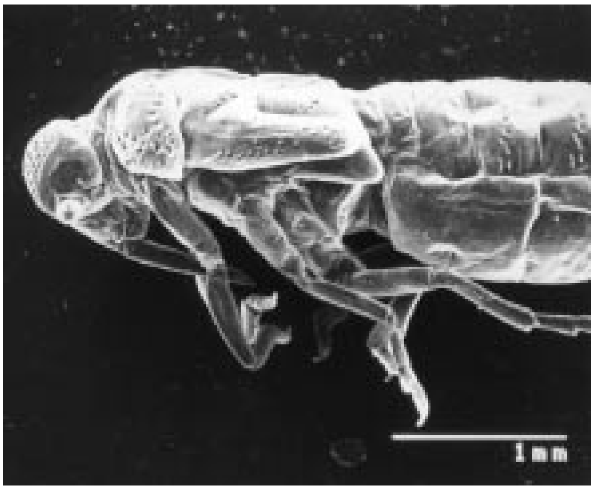


Fig. 3.10. *Myndus crudus* larva, SEM view. The larva lives on roots of grasses; the forelegs are apparently modified for digging.

Myndus are significant associates of palms in the eastern and western hemispheres.

Myndus crudus (syn. *Haplaxius crudus*, *Haplaxius pallidus*, *Paramyndus cocois*) (Colour Plate 8d, Figs 3.9–3.11) is better known than other palm-associated cixiids because it is considered to be the principal vector of lethal yellowing in Florida

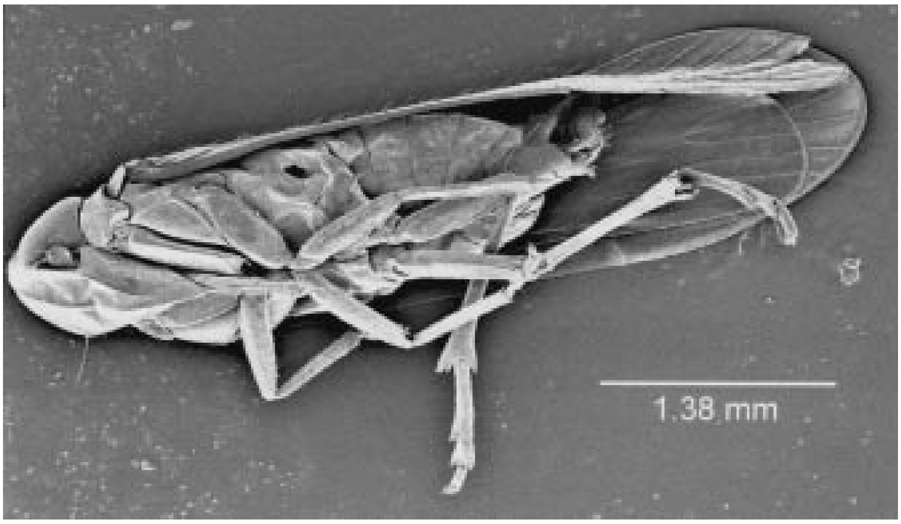
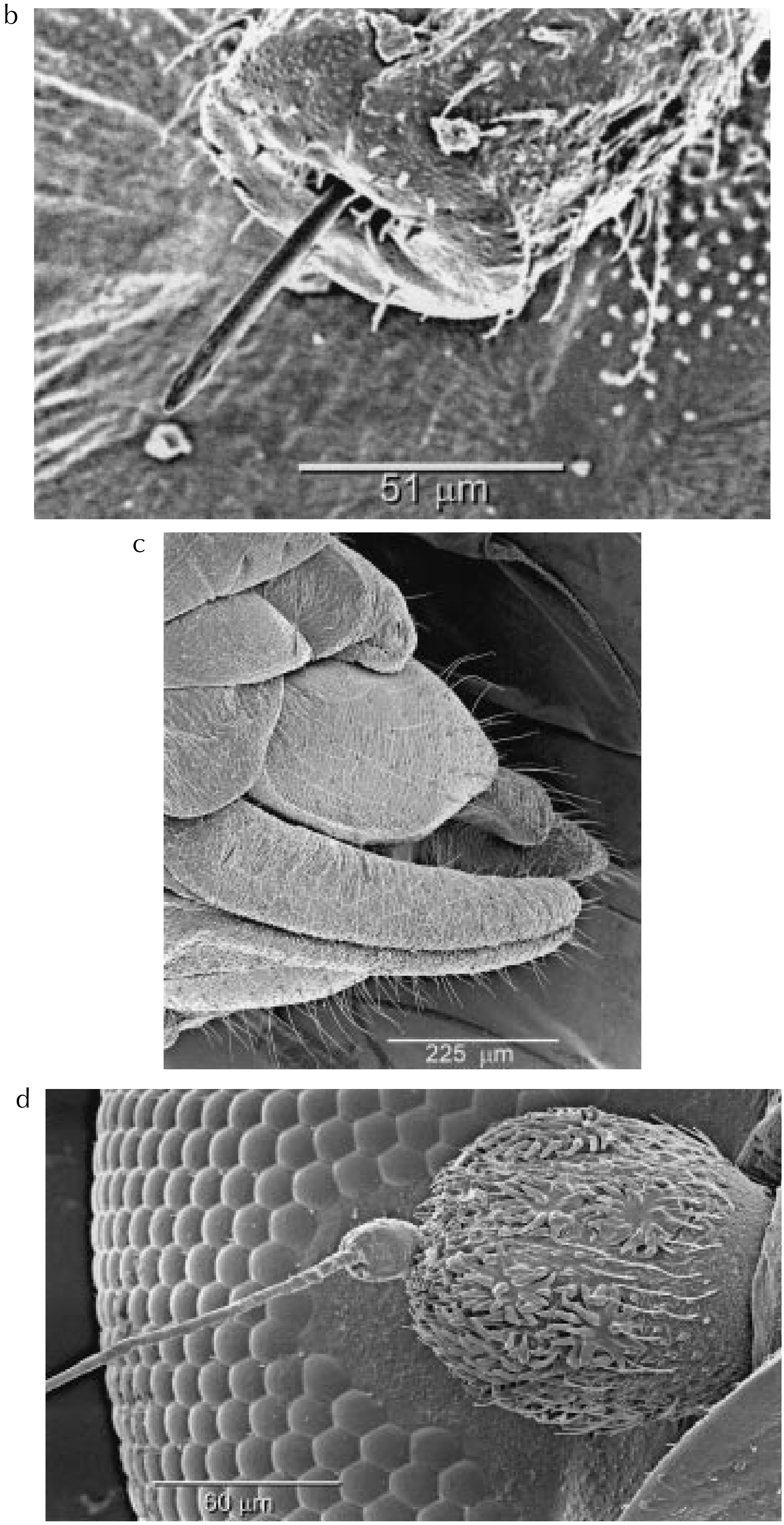


Fig. 3.11. (*and opposite*) *Myndus crudus*, SEM views. (a) Male. (b) Proboscis with stylets. (c) Ovipositor of female, adapted to inserting eggs into plant tissue. (d) Antenna of male.


b
51 µm
c
225 µm
d
60 µm

(Howard and Thomas, 1980; Howard *et al.*, 1983, 1984b; Howard, 1987, 1995a, 1997) and may be assumed to play a similar role in other lethal yellowing-affected areas of the Americas. Virtually all recent studies of this insect have been conducted in relation to its association with lethal yellowing.

The larvae of *M. crudus* develop in the root zone of grasses. The imagos fly to palms. In southern Florida, where many species of palms are grown as ornamental plants, *M. crudus* imagos were observed on 26 species of palms, including native and exotic species (Howard and Mead, 1980). They were reported on 11 of 25 palm species native to Yucatán, Mexico (Carrillo Ramírez and Piña Razo, 1990).

Myndus crudus has been reported from Trinidad, Venezuela, Colombia, Central America, Mexico, Cuba, the Cayman Islands, Jamaica and Florida (Kramer, 1979). Given the close geographical proximity and biogeographical affinities between Florida and the Bahamas, *M. crudus* is probably present in at least some of the Bahama Islands. The sparse populations of this insect in southern Texas (Meyerdirk and Hart, 1982) may consist of seasonal migrants from further south.

In a survey of Auchenorrhyncha associated with palms in the Dominican Republic, *M. crudus* was not found but an almost identical species was collected on coconut palm. Specimens were deposited in the collection of the US National Museum, but have not been described (Howard *et al.*, 1981). *Myndus crudus* has not been reported in Puerto Rico, the auchenorrhynchous fauna of which is quite well known, or on other islands of the eastern Caribbean north of Trinidad (Howard, 1991).

Female imagos are about 5 mm long, from the vertex of the head to the distal end of the wing, and of varying shades of a greyish-brown colour. Their prominent cutlass-shaped ovipositor (Fig. 3.11c) easily distinguishes them from males, which are slightly smaller and have a more sharply attenuated abdomen. The males are of a pale straw colour, which grades into vivid green toward the end of the abdomen. The imagos blend well with the various colours of palm foliage. In both sexes, the wings are hyaline, with brownish veins. Conspicuous but sparse setae can be observed along the veins under magnification. As in other species of *Myndus*, in a facial view the carinae at the margins of the frons are very prominent. An ocellus is present medially. The eyes are light- and dark-adapted. Due to the distal–medial movement of internal pigments, the eyes of *M. crudus* observed during the daylight hours are usually straw-coloured and those collected after dusk are maroon-coloured. The imagos are apparently active day and night (Howard, 1981). Eyes of dried specimens are maroon.

In testing coloured sticky traps to develop a standardized trap for *M. crudus*, higher numbers of imagos were trapped on blue and white compared with several other colours, including yellow, which has long been recognized as the colour most attractive to Hemiptera in general (Cherry and Howard, 1984). According to the paint manufacturer, the blue and white paints had higher concentrations of titanium dioxide than the other paints. This compound is mixed with some paints to ‘brighten’ the colour, i.e. make it more reflective of ultraviolet light. It thus appears that this factor, rather than colour *per se*, was most important in attracting this insect (R.H. Cherry and F.W. Howard, unpublished).

The larvae are grey to tan. The eyes are dark maroon and do not appear to change in response to light conditions, as is the case with the imagos. There is a faint red blush on the front of the head and rostrum and around the eyes; this colouring is also on the legs, where it grades to a bright red distally. There are numerous pits on the head, notum and abdomen, and a thin wax bloom over all surfaces. The foretibia are flattened and slightly dilated, possibly a modification for digging or shaping soil (Fig. 3.10). There is a toothlike projection ventrally on each femur (Wilson and Tsai, 1982), the function of which is unknown.

Studies of stylet tracks of *M. crudus* revealed that they penetrated tissue of fronds of coconut palm, in many cases ending in the smallest veins, which contained mostly or only phloem tissue. Those that ended in a few larger veins terminated in the phloem region, either bypassing or traversing the xylem. Multiple feeding tracks often extended from a single epidermal puncture. In some cases, a track went all the way through to the opposite surface of the frond (Waters, 1976; Fisher and Tsai, 1978; Tsai and Fisher, 1993). Sites on leaf tissue probed by *M. crudus* were located by a technique in which the labial imprints were stained (Waters, 1977). Radioisotopes were detected in *M. crudus* captured near coconut palms that had been tagged with them (Eskafi, 1982), proving that they had fed on the palms and indicating that they fed for longer periods than, for example, cicadellids. Molecular techniques have also shown that *M. crudus* feeds on palms (Harrison and Oropeza, 1997).

Myndus crudus adults have been observed to visit monocotyledons additional to palms and grasses, including *Pandanus utilis* in Florida (F.W. Howard, unpublished) and *Heliconia bihai* in Mexico (Carrillo Ramírez and Piña Razo, 1990).

Before it was established that palms were the principal hosts of the imagos, they were occasionally reported on various dicotyledonous shrubs in Cuba (Myers, 1926). But, on the rare occasions when we have observed *M. crudus* on dicotyledonous trees or shrubs, they were apparently vagrants from nearby *M. crudus*-infested palms (F.W. Howard, unpublished).

Knowledge of preferences of the adults for species or selections of palms is very preliminary. In Florida during periods when *M. crudus* was abundant, we frequently observed hundreds of *M. crudus* on coconut palm, *W. robusta* and *Adonidia merrillii*, while on some nearby palms, e.g. *Dypsis lutescens*, *R. regia* and *Syagrus romanzoffiana*, this insect was absent or rare (F.W. Howard, unpublished). Results of a study of Auchenorrhyncha on coconut and date palms agreed with our general observations – that these insects rarely visit young date palms. However, their numbers were about equal on mature coconut and date palms (Howard, 1980a).

There appears to be no relationship between attractiveness of palm species to *M. crudus* and susceptibility to lethal yellowing. Large numbers of *M. crudus* can often be observed on non-susceptible palm species (Howard and Mead, 1980; F.W. Howard, unpublished). Preliminary observations suggested that ‘Malayan Dwarf’ (lethal yellowing-resistant) palms may be more attractive to *M. crudus* than ‘Jamaica Tall’ (lethal yellowing-susceptible) palms (Tsai and Kirsch, 1978). In any case, differences in numbers of imagos on a plant do not necessarily translate to feeding preferences and, for that matter, feeding preferences are only one factor in transmission of disease agents.

Whether *M. crudus* can sustain field populations in the absence of palms is not known. They occur in scattered, sparse populations in sugar cane, presumably far from palms (Hall, 1988). Woodiel and Tsai (1978) observed that, when coconut palms at a golf-course were eliminated by lethal yellowing, the numbers of *M. crudus* captured in rotary traps remained about the same. There is no mention of other palms that may have been in the vicinity, however. Laboratory colonies of *M. crudus* have been maintained on grasses alone (Simon Eden-Green, personal communication).

Myndus crudus males and females have been observed mating while on palms, but it is not known whether they also mate while on grasses or elsewhere. The female inserts eggs into above-ground portions of grasses, 1–2 cm from the root collar, often beneath the sheaths of lower leaves that are desiccated and beginning to deteriorate. Eggs are laid singly or in rows of up to five eggs. The white, spindle-shaped eggs are inserted so that the cephalic end of the embryo is exposed, facilitating hatching (Zenner de Polanía and Lopez, 1977). Upon hatching, larvae immediately move down to the soil surface (Zenner de Polanía and Lopez, 1977). Wilson and Tsai (1982) published detailed morphological descriptions of the five instars and reported larval lengths as increasing from 0.64 mm (first instar) to 2.68 mm (fifth instar). The mean development period of the larval stage was 80.8 days at 24°C and 52.6 days at 30°C (Tsai and Kirsch, 1978).

At least during the day, larvae usually remain on the soil surface beneath bits of palm fibre and other detritus. When disturbed, they become active, usually running a short distance until they find the next shelter. When walking, they may traverse about three body lengths per second. When disturbed, they jumped about 5–10 cm (about 19–37 body lengths), although the femora are only moderately developed (F.W. Howard, unpublished). The last three preanal abdominal segments have wax-moulding devices, which secrete hollow filaments of wax, at least some of which encase their excretions. The larvae line depressions and spaces in the soil with this waxy, flocculent material. Perhaps this adaptation insulates the larvae from the toxic substances in their excrement, facilitating life in a confined habitat (Pope, 1985).

Van Duzee (1907) described *M. crudus* from specimens of imagos collected in Jamaica without host data. The larvae were unknown for many years. In Cuba, imagos were occasionally found on sugar cane and other grasses (Myers, 1926; van Dine, 1926). Stephen Cole Bruner, who as Chief of the Estación Experimental Agronómica in Cuba from 1919 to 1953 reported many pioneering entomological observations, suspected that the larval stage developed on small grasses (Bruner, 1922). This was questioned (Myers, 1926) but confirmed about 50 years later (Zenner de Polanía and Lopez, 1977; Eden-Green, 1978).

By searching the root zones of plants in the field in Colombia (Zenner de Polanía and Lopez, 1977), Florida (Tsai and Kirsch, 1978) and Mexico (Villanueva Barradas *et al.*, 1987; Carrillo Ramírez and Piña Razo, 1990; Piña Quijano, 1993), a total of at least 20 species of grasses (Gramineae) and a few species of sedges (Cyperaceae) have been identified as *M. crudus* larval hosts.

In rearing larvae of *M. crudus* for study, *Stenotaphrum secundatum* was found empirically to be one of the best hosts (Tsai *et al.*, 1976; Eden-Green, 1978). *Stenotaphrum secundatum* has been the most widely planted grass in the urban areas of south-eastern Florida for many years and would appear to have been an important factor influencing the high population levels of *M. crudus* observed in this area at the time of a major lethal yellowing epidemic in the 1970s and early 1980s (Howard, 1980b; Howard and Barrant, 1989). It was the only herbaceous plant species common to several isolated areas in Florida where both lethal yellowing and *M. crudus* were present (Howard *et al.*, 1984a). Five selections of *S. secundatum* were tested and found to be highly favourable hosts of the larvae (Howard, 1990a). Unfortunately, the other grass species common as turf in Florida, namely *Paspalum notatum*, *Cynodon dactylon* and *Zoisia* sp., are also good hosts of *M. crudus* larvae (Reinert, 1980; Howard, 1990b).

Additional grasses that proved to be highly suitable hosts were *Cenchrus cilaris*, *Cynodon nlemfluensis nlemfluensis* cv. 'Puerto Rico Star Grass', *Digitaria eriantha* and *Panicum purpurescens* (Howard, 1989a, 1990a, b). 'Puerto Rico Star Grass' is one of the most common introduced grasses in Puerto Rico; thus *M. crudus* might find that island a highly acceptable habitat were it ever introduced there.

Panicum maximum was considered to be the principal host of *M. crudus* in African oil palm plantations in Colombia (Zenner de Polanía and Lopez, 1977). In tests in Florida, this grass was 'moderately favourable' as a host; the mean number of *M. crudus* that developed on *P. maximum* was about 60% of the number that developed on the highly favourable host, *S. secundatum* (Howard, 1989a). This is one of the most common grasses in coconut palm plantations in Jamaica (Basil Been, personal communication) and may have been a factor in the lethal yellowing epidemic on that island in the 1950s–1970s.

In Qintana Roo (eastern Yucatán Peninsula), Mexico, *Chloris inflata*, *Chloris petraea*, *Fimbristylis spathaceae* and *Andropogon bicornis* were observed to be highly favourable larval hosts of *M. crudus*. Of these, *A. bicornis* was considered to be the most preferred larval host of *M. crudus* (Carrillo Ramírez and Piña Razo, 1990). This native grass is abundant in that area and distributed widely from Mexico to Brazil and in the West Indies (Sauget and Liogier, 1974). On the north coast of Yucatán, *Distichlis spicata* was observed to be a preferred larval host of *M. crudus* (Patricia Piña Quijano, personal communication), although in the study area it was sparse in relation to other grasses. This grass is common on the Pacific and Atlantic coasts of North America, extending to the Pacific coast of South America (Hitchcock, 1950).

Several factors that influence larval populations, additional to the availability of host plants are at least partly understood. The height of a preferred grass host appears to influence the numbers of *M. crudus* that develop on it. In samples at the soil surface, larvae were slightly to 25% more frequent in unmown than in mown grass. In tests with containerized grasses, there were about twice as many larvae in unclipped compared with clipped grass (Howard and Villanueva-Barradas, 1994).

In a field study in Florida, over 50% of the *M. crudus* larvae were on the soil surface; the rest were below the surface, to a maximum depth of 3 cm (Howard and Villanueva-Barradas, 1994). Zenner de Polanía and Lopez (1977) reported that in Colombia larvae were found in the soil to a maximum depth of 20 cm. Larvae of *M. crudus* that infest containerized grasses are frequently observed on the soil surface and at depths of up to 10 cm or more in the relatively accessible and well-aerated spaces between the soil and container sides, but never more than a few centimetres from the soil surface (F.W. Howard, unpublished).

The larvae prefer resting sites beneath leaf litter and other organic matter. Where pieces of bark, coconut fibre and similar material were scattered on the ground, higher numbers of imagos developed than in plots without such materials (Howard and Oropeza, 1998).

In Cuba, *M. crudus* was most commonly encountered on grasses in damp hollows and at the edges of ponds and creeks (Myers, 1926). In Mexico and Central America, this insect was more abundant in areas of human population (Villanueva Barradas, 1991). Villanueva Barradas (1991) suggested that this might have been due to irrigation of lawns and gardens. In Florida, they tend to be most abundant on the moister sites, but this has not been investigated experimentally (F.W. Howard, unpublished).

Lethal Yellowing: Nature, Impact and Distribution

Lethal yellowing is one of the most important plant diseases affecting tropical agriculture (Colour Plate 9). Known only in parts of the Americas, it is one of several diseases of palms associated with phytoplasmas. Similar phytoplasma-associated diseases of palms are known in West and East Africa and Asia. Much detailed information on the history, economic impact, biology and management of these diseases may be found in McCoy *et al.* (1983), Robert and Zizumbo (1990), Eden-Green (1991, 1995, 1997a), Oropeza *et al.* (1995) and Eden-Green and Ofori (1997). The Centre for Information on Coconut Lethal Yellowing, an Internet site, is also a valuable source of information on this subject.

Lethal yellowing is thought to have killed coconut palms in Cuba, the Cayman Islands, Hispaniola (Haiti and the Dominican Republic) and Jamaica at least as early as the 1800s (Fig. 3.12; Howard, 1983). During this early period, the disease was perhaps most widespread in Cuba (Bruner and Boucle, 1943). In Jamaica, lethal yellowing was present only in the western areas until the 1950s, when it suddenly began spreading eastward and eventually devastated coconut plantations throughout the island, killing an estimated 4–5 million coconut palms in 20 years (Eden-Green 1979, 1991). The disease was present on New Providence Island (Bahamas) by the 1920s (Leach, 1946) and Key West, Florida, perhaps as early as the 1930s and definitely by the 1950s. It appeared on Key Largo in 1969 and on the Florida mainland in Miami in 1971. By 1973, it had spread north along the east coast to Palm Beach county, and had killed an estimated 100,000 coconut palms and thousands of palms of other species by 1983 (Howard, 1983). Lethal yellowing was epidemic in south-eastern Florida from 1971 to the mid-1980s and appeared on Florida's west coast in the late 1980s.

Lethal yellowing was diagnosed for the first time in Mexico in 1982, near Cancún on the north-eastern tip of the Yucatán Peninsula (McCoy *et al.*, 1982) and became highly epidemic. By 1987, an estimated 200,000 coconut palms had been killed in the Yucatán Peninsula (Villanueva Barradas *et al.*, 1987). Lethal yellowing had spread to Tabasco State, about 900 km from Cancún, by 1995 (Arellano and Oropeza, 1995; Escamilla *et al.*, 1995) and as far west in Tabasco as the coastal town of Paraiso by 1999 (700 km from Cancún) (Oropeza and Córdova, 1998; Carlos Oropeza, personal communication). It spread south to Belize in 1992 and was reported on Roatán of the Bay Islands of Honduras (800 km from Cancún) in 1996 (Ashburner *et al.*, 1996). It has since spread to the mainland of Honduras.

Currently, lethal yellowing persists at a low level in southern Florida and in areas of Mexico, where the disease had been epidemic years ago. Cases of the disease are seen there only occasionally. The absence of palms or their replacement by resistant palms has probably prevented a resurgence of the disease over most of these areas. The situation was similar in Jamaica; however, by the late 1990s there had been a resurgence of lethal yellowing in that country (Hugh Harries, personal communication).

Fig. 3.12. Coconut plantation affected by lethal yellowing, Jamaica.

SUSCEPTIBLE PALM SPECIES. Lethal yellowing was first recognized in the western Caribbean as a disease exclusively of coconut palms, and is still approached largely as a disease of that economically important palm species. However, when the disease invaded Florida, it entered a new arena. The diversity of ornamental palms was greater in the urban areas of southern Florida than in any Caribbean country. It was under these circumstances that susceptible palm species additional to coconut were discovered.

The susceptibility of species has been determined mostly by opportunistic observations on palm species that were common in the landscape in southern Florida, especially during the lethal-yellowing epidemic of the 1970s and early 1980s. To date, 38 species of palms have been shown to be susceptible to lethal yellowing (Table 3.2). Our susceptibility ratings of 'low', 'moderate' and 'high' are subjective and should be interpreted only as general guidelines. Data are available to rate only the more common species. It has been shown that the susceptibility of coconut palms of different cultivars varies according to site (Ashburner and Been, 1997) and this may also be true of other species of palms.

Lethal-yellowing susceptibility is distributed among diverse subfamilies and genera of palms (Thomas, 1974, 1979; Thomas and Norris, 1981). Only seven genera have more than one susceptible species (*Nannorrhops* is monotypic). *Pritchardia* is regarded as a highly susceptible genus, based on observations of four species, although there are 29 additional species for which susceptibility data are lacking. In other genera, e.g. *Veitchia* and *Phoenix*, susceptibility varies among different species (Howard, 1992; Howard and Harrison, 1997). One species outside Palmae is known to be susceptible: *P. utilis* (Pandanaceae) (Fig. 1.16b; Thomas and Donselman, 1979; Harrison and Oropeza, 1997).

Lethal-yellowing susceptibility does not appear to be related to any obvious botanical feature, such as phenology of flowering, leaf morphology, plant architecture, etc., or to the ecological conditions to which palms are adapted. For example, susceptible palms include tender and cold-hardy species, species native to both arid and humid regions, etc.

The only trends seem to be in geographical relationships: proportionally more species of palms of eastern-hemisphere origin are susceptible than palms native to the western hemisphere. No palms native to Jamaica, Cuba, Hispaniola, Florida or Yucatán are known to have contracted lethal yellowing, even though some species are ubiquitous and have been exposed for many years to lethal yellowing. As of July 2000, six species of American origin, compared with 32 species of eastern-hemisphere origin, were known to be susceptible. The most highly susceptible palms, i.e. coconut palm and *Pritchardia* spp., are native to Oceania. A relatively high proportion (16.2%) of susceptible palms are native to one island, Madagascar (Table 3.2; Howard, 1983; Nigel Harrison, personal communication).

Differences in susceptibility at the subspecific level are known only for the economically important coconut palm (see 'Disease management').

Many cultivars of date palm are known, some of which have been grown for centuries (Box 1.2). Efforts to determine whether there are varietal differences in susceptibility to lethal yellowing in date palm have not gone beyond a preliminary test (Howard *et al.*, 1985; Howard, 1992).

SYMPTOMS. The symptoms of lethal yellowing in bearing 'Jamaica Tall' coconut palms include premature shedding of fruits of all sizes. The inflorescence develops into a blackened, gnarled structure. Next, the fronds turn yellow, beginning with the older ones and advancing toward the younger ones near the centre of the crown. Sometimes a younger frond will turn yellow early in this sequence. This is commonly called a 'flag leaf' (a term borrowed from the plant pathology of bananas) and is a significant symptom for diagnosing lethal yellowing, but is not consistently present. Fronds that have turned yellow desiccate and turn light brown and hang from the

Table 3.2. Palm species that are susceptible to lethal yellowing in Florida.

Scientific name	Region of origin	Frequency in Florida landscape	Relative LY susceptibility
Adonidia merrillii	Philippines	Common	Moderate to high
Aiphanes lindeniana	Caribbean	Rare	Unknown
Allagoptera arenaria	Brazil	Rare	Unknown
Arenga engleri	South-East Asia	Rare	Unknown
Borassus flabellifer	India	Rare	Moderate
Caryota mitis	South-East Asia	Common	Moderate to high
Caryota rumphiana	South-East Asia	Rare	Unknown
Chelyocarpus chuco	South America	Rare	Unknown
Cocos nucifera	Melanesia	Common	High to low, depending on cultivar or hybrid
Corypha elata	India	Rare	Unknown
Cryosophila warscewiczii	Central America	Rare	Unknown
Cyphophoenix nucele	Lifou (Loyalty Islands)	Rare	Unknown
Dictyosperma album	Madagascar	Common	Moderate
Dypsis cabadae	Madagascar	Rare	Unknown
Dypsis decaryi	Madagascar	Common	Slight
Gaussia attenuata	Puerto Rico	Rare	Unknown
Howea belmoreana	Lord Howe Island	Rare	Unknown
Howea forsteriana	Lord Howe Island	Rare	Unknown
Hyophorbe verschaffeltii	Madagascar	Common	Slight to moderate
Latania lontaroides	Madagascar	Common	Moderate
Livistona chinensis	China	Common	Moderate
Livistona rotundifolia	South-East Asia	Rare	Unknown
Nannorrhops ritchiana	Middle East to India	Rare	Unknown
Phoenix canariensis	Canary Islands	Common	Moderate
Phoenix dactylifera	North Africa to Middle East	Common, formerly rare	Moderate to high
Phoenix reclinata	Africa	Common	Low
Phoenix rupicola	India	Rare	Unknown
Phoenix sylvestris	India	Rare	Unknown
Pritchardia affinis	Hawaii	Rare	Probably high
Pritchardia pacifica	Tonga (South Pacific)	Rare; formerly common	High
Pritchardia remota	Hawaiian Islands	Rare	High
Pritchardia thurstonii	Fiji	Rare; formerly common	High
Ravenea hildebrandtii	Madagascar	Rare	Unknown
Syagrus schizophylla	Brazil	Uncommon	Moderate
Trachycarpus fortunei	China	Uncommon	Moderate
Veitchia arecina	New Caledonia	Rare	Unknown

palms. The final stage is the death of the bud, causing the youngest unfolded leaf (the spear leaf) to collapse. The entire bud may rot within days. The entire sequence of symptoms from initial fruit drop to death of the bud usually takes from 3 to 6 months.

Field diagnosis of lethal yellowing can be difficult. Non-bearing palms do not express some of the clearest symptoms, i.e. those of the inflorescence and fruits. Symptoms differ slightly according to coconut variety, and pronouncedly in different species of palms. Diseases other than lethal yellowing in tropical America may easily be confused for symptoms of lethal yellowing, including hart-rot, red ring and *Phytophthora* bud rot. Field diagnoses are adequate for routine work in a locality where the identity of the disease has been confirmed by laboratory diagnostic techniques (Box 3.2).

Box 3.2. Probing the unseen world: how phytoplasmas are detected in plants.

Phytoplasmas are too small to be seen under a light microscope and cannot be cultured and subjected to diagnostic tests, as is done with bacteria. Therefore, during the 1970s and most of the 1980s, the transmission electron microscope (TEM) was the essential laboratory instrument for studying phytoplasmas and for confirming diagnoses of diseases associated with them. The standard practice in diagnosing lethal yellowing in research projects was to carefully examine the palm for symptoms (i.e. make a field diagnosis) and, if the palm had symptoms of lethal yellowing, cut down the palm, extract the bud, preserve it, take it to the laboratory and embed a small sample in plastic. A special microtome was employed to slice tissue of palms into ultrathin sections, which were then prepared for TEM examination. The apical meristem and adjacent tissues were preferred, because phytoplasmas were most readily found there. In transmission experiments, it was deemed important to verify field diagnoses by TEM examination (Howard *et al.*, 1983), but field diagnoses alone sufficed for large field experiments involving many palms (Howard, 1979). The TEM procedure had the disadvantages that the preparation of samples was time-consuming and necessitated the sacrifice of the palm (Norris and McCoy, 1982). Furthermore, different species or genetic strains of phytoplasmas could not be identified, since all phytoplasmas look alike under the TEM. That is why the lethal yellowing-like diseases of Africa were tentatively considered synonymous with Caribbean lethal yellowing.

The DAPI fluorescence test has had some application for detecting phytoplasmas in plants, including palms. Phytoplasma infections result in the accumulation of deoxyribonucleic acid (DNA) in phloem sieve elements, which can be detected by bathing samples in 4′, 6′-diamidino-2-phenylindole (DAPI), a reagent that binds to DNA and fluoresces under UV radiation.

Since the early 1990s, TEM and DAPI diagnostic techniques for lethal yellowing and similar palm diseases have been largely replaced by molecular techniques (Harrison *et al.*, 1994), the basic principles of which are explained below:

DNA molecules, located in chromosomes and the source of the cell's genetic information, are unique for each organism. DNA molecules are normally paired strands. But DNA can be isolated from a particular organism, and the two strands separated by heating or application of certain chemicals. DNA separated into two strands per molecule is described as 'denatured'. A segment of a single strand of DNA from a particular organism (e.g. from the phytoplasma that causes Caribbean lethal yellowing, or the one that causes lethal disease of coconut palms in East Africa) can be used as a 'DNA probe'.

To use the probe to test for the presence of the lethal-yellowing phytoplasma in tissues (e.g. of a palm or an insect suspected to harbour the phytoplasma), DNA from the presumed infected tissues is purified, denatured and then transferred on to a membrane and fixed on it. The probe is then introduced on to the membrane. A single strand of DNA will bind only to its other half, i.e. its complementary strand. Therefore, the probe for lethal yellowing will 'hybridize with' (bind with) only DNA of the lethal-yellowing phytoplasma.

The membrane is then washed, so that only strands that have hybridized with the probe are left. Two steps in the procedure facilitate finding the hybridized probes on the membrane:

1. The DNA segments are sorted by size by electrophoresis. This is a method that utilizes the principle that, when DNA molecules in solution are subjected to an electric field, they migrate at different rates according to size.

2. The probe is tagged, e.g. with a radioactive isotope. Thus, if X-ray film is exposed to the membrane, any hybridized DNA molecules will show up on the film and it will indicate that the palm had lethal yellowing. If no molecules show up on the film, the palm tissue that was sampled does not harbour the phytoplasma.

In cases in which extremely small quantities of DNA are to be analysed, the polymerase chain reaction (PCR) is employed. In this technique, a small quantity of DNA can be extended by cycles of heating and cooling, which alternately denatures the DNA and then, through the action of an enzyme (polymerase), duplicates it. This allows detection of extremely small quantities of DNA in tissues.

Molecular techniques are more rapid than TEM examinations for lethal-yellowing diagnoses, and allow detection of extremely small populations of phytoplasmas in plant tissue. Without sacrificing the palm, leaf tissue of suspected lethal-yellowing cases can be sampled in the field, brought or mailed to a laboratory and tested for the presence of phytoplasmas.

CAUSAL ORGANISM. Researchers of several institutions have concurred that lethal yellowing appears to be caused by phytoplasmas. One line of evidence is that phytoplasmas have been observed in phloem sieve tubes of palms with lethal-yellowing symptoms, but not in symptomless palms (Beakbane *et al.*, 1972; Heinze *et al.*, 1972a, b; Plavsic-Banjac *et al.*, 1972; Parthasarathy, 1974; Thomas, 1974, 1979; Thomas and Donselman, 1979; Thomas and Norris, 1981; Howard *et al.*, 1983).

Evidence was also obtained by injecting palms with various therapeutic materials. Penicillin, which kills bacteria by interfering with cell-wall synthesis, has no effect on lethal yellowing. However, tetracycline antibiotics, which are effective against other phytoplasmas associated with other plant diseases, retard or prevent the development of symptoms of lethal yellowing (McCoy, 1972; Hunt *et al.*, 1974; McCoy and Gwin, 1977).

Phytoplasmas and mycoplasmas are classified in the Mollicutes, the smallest and simplest organisms known. Until recently, phytoplasmas were known as 'mycoplasma-like organisms'. Investigators have been attempting to elucidate the relationships between different strains or species of phytoplasmas (Seemüller *et al.*, 1998). More than 300 diseases of tropical plants are caused by phytoplasmas (Dollet, 1999).

MODE OF SPREAD. Many kinds of organisms, especially insects, have been suspected and some of them studied and tested as potential vectors of lethal yellowing. Earlier work was reviewed by Johnson and Eden-Green (1978) and McCoy *et al.* (1983).

Once a phytoplasma had been implicated as the causal agent, the search for vectors focused on species of Auchenorrhyncha, as indicated previously. Field surveys in lethal yellowing-affected areas of Jamaica (Schuiling, 1976) and Florida (Woodiel, 1976) revealed that *M. crudus* was the only species of Auchenorrhyncha common on palms in both localities. When lethal yellowing was observed to attack palms additional to coconut palm in Florida, *M. crudus* was found consistently on almost all palm species then known to be susceptible. Exceptions were palms too rare in Florida for adequate sampling (Howard and Mead, 1980). The geographical distribution of lethal yellowing in Florida coincided with high population levels of *M. crudus* on palms (Howard, 1980b). Suppression of populations of *M. crudus* with insecticides coincided with a reduction in the spread of lethal yellowing (Howard and McCoy, 1980). These observations provided the incentive to conduct a series of transmission experiments, in which a total of 20 unequivocal lethal-yellowing transmissions took place inside cages into which *M. crudus* captured from lethal yellowing-affected areas were introduced (reviewed by Howard, 1987, 1995a).

Harrison and Oropeza (1997) found further evidence that *M. crudus* is a vector. Phytoplasmas were detected in 7.9% of 1321 *M. crudus* adults captured from coconut palms with lethal-yellowing symptoms, using a molecular assay that was not sensitive enough to detect phytoplasmas unless they had multiplied in the insect.

Some insect-borne diseases are known to be transmitted by only one vector species. In diseases that are transmitted by more than one species, the vector species are usually closely related taxonomically. Since no other cixiid is common on palms in lethal yellowing-affected areas, no species is suspected on the basis of its affinity to *M. crudus*.

It may be conjectured that populations of *M. crudus* could harbour the lethal-yellowing phytoplasmas indefinitely, passing them to successive generations. This would be possible if transovarial transmission of phytoplasmas occurred in *M. crudus*, a phenomenon that was shown for *Hishimonoides sellatiformis* (Cicadellidae: Deltocephalinae: Opsiini) (Kawakita *et al.*, 2000).

DISEASE MANAGEMENT. An antibiotic treatment using oxytetracycline injected into the trunk of coconut and other palms prevents lethal yellowing or keeps it in remission.

Injections are effective if repeated every 3 months. Several communities in Florida maintained injection programmes during the lethal-yellowing epidemic, but eventually adopted the planting of resistant palms as their principal method of managing the disease.

For the foreseeable future, resistant palms will be the principal method of preventing or managing lethal yellowing. Many species of palms that were growing in the areas where lethal yellowing has been epidemic have been unaffected by the disease (Howard and Collins, 1978; Howard *et al.*, 1979). Most species native to Florida and the western Caribbean, especially ubiquitous palms, such as *Acoelorrhaphe wrightii*, *Coccothrinax* spp. *Copernicia* spp., *Roystonea* spp. and *Sabal* spp., can be said to have been adequately tested against lethal yellowing, without any cases having been reported. Several species of Australian origin are among the most popular ornamental palms in southern Florida and none of them is susceptible. These include *Archontophoenix alexandrae, Carpentaria acuminata, Ptychosperma elegans* and *Wodyetia bifurcata*. Other ubiquitous ornamental palms exotic to Florida that are apparently not susceptible to lethal yellowing include *Dypsis lutescens, Phoenix roebelenii, Ptychosperma macarthurii, W. robusta* and *S. romanzoffiana*. Such palms are good choices for landscaping in areas threatened or affected by lethal yellowing.

Many selections of coconut palm were tested for resistance to lethal yellowing by the Coconut Industry Board in Jamaica (Been, 1981). Three highly resistant selections that have been planted extensively to replace coconut palms lost to lethal yellowing and to prevent future loss are ‘Malayan Green Dwarf’, ‘Malayan Yellow Dwarf’ and ‘Malayan Golden Dwarf’ (syn. ‘Malayan Red Dwarf’) (Nutman and Roberts, 1955; Whitehead, 1966; Harries *et al.*, 1970/71; Harries, 1971, 1973; Been, 1981, 1995b).

The ‘Malayan Dwarf’ selections have been extensively planted in Jamaica since the 1960s. Many were planted in Key West, Florida, in response to the earlier epidemic there in the 1950s–1960s. Replicated trials in the 1960s in Jamaica revealed that ‘Malayan Dwarf’ palms were 96% resistance, i.e. if exposed to lethal yellowing, 96 of 100 could be expected to survive (Been 1981). More extensive observations have shown that the resistance of these palms varies with site (Ashburner and Been, 1997). On most sites observed in Florida, Jamaica and Mexico, the resistance of ‘Malayan Dwarf’ selections under lethal-yellowing epidemic conditions has approached 90% or more, but, on occasional sites, losses have been higher, to a maximum of 50% (Howard *et al.*, 1987).

The ‘Panama Tall’ (syn. ‘Pacific Tall’), a cultivar that is relatively resistant to lethal yellowing, is the most common cultivar on the western coasts of tropical America (Harries, 1971; Zizumbo Villarreal *et al.*, 1993). ‘Malayan Dwarf’ selections may be crossed with the ‘Pacific Tall’ to produce ‘Maypan’ hybrids, so as to combine the higher resistance of the dwarf selections with the larger size and adaptability of the tall type, with the further advantage of hybrid vigour (Harries and Romney, 1974; Been, 1995b). By 1989, the Coconut Industry Board had distributed a total of 10 million resistant coconut palms (‘Malayan Dwarf’ selections and ‘Maypans’) in Jamaica, and it was largely this programme that allowed the coconut industry of that country to rebound from the lethal-yellowing epidemic of the previous decades (Been, 1995a). Several selections additional to those mentioned above have shown a high degree of resistance in trials in Jamaica, but have not been planted extensively (Been, 1995a).

PEST MANAGEMENT PROSPECTS FOR *M. CRUDUS*. Reduction of vector populations could be combined with use of resistant palms to further reduce loss of palms and to reduce disease pressure that could ultimately overcome resistance mechanisms.

Adult *M. crudus* are sometimes seen infected with fungi, identified in Florida as *Hirsutella citriformis*. A similar or identical fungus was observed on *M. crudus* in

Trinidad (Fennah, 1945). Up to 58% of the imagos were infected with a *Hirsutella* fungus in Chetumal, Mexico. An unidentified parasitic wasp attacks *M. crudus* in Mexico and Central America, but has not been observed in Florida (Villanueva Barradas *et al.*, 1985, 1987). Parasitic mites (Erythraeidae) have been observed infrequently on *M. crudus* in Mexico and in Florida (Howard, 1987). Spiders, including Theridiidae, are predators of *M. crudus* (Howard and Edwards, 1984). In fact, examination of spider-webs on fronds is a good method for detecting the presence of this and other flying insects in palms. Ants, lizards and tree frogs also prey on these planthoppers. All of these natural enemies were observed in areas where lethal yellowing was epidemic, suggesting prima facie that natural control of the vector is not effective enough to prevent the spread of lethal yellowing.

Although experimental suppression of populations of *M. crudus* with insecticides applied to palms resulted in a slight reduction in the spread of lethal yellowing (Howard and McCoy, 1980), chemical control of vectors on a broad scale would be too costly, environmentally deleterious and unsafe and would eventually result in insecticide-resistant vectors.

Identification of the hosts that support the development of the larvae of *M. crudus* has practical significance, because of the potential for controlling vector populations (Howard, 1985). A reduction in *M. crudus* was observed in an African oil palm plantation where known hosts of this insect were eliminated (Mena *et al.*, 1975). Ground covers are maintained in palm plantations for preventing soil erosion, adding organic matter, reducing competition of noxious weeds and providing forage for livestock (Shelton, 1991a, b; Shelton and Stür, 1991).

Grasses that were poor hosts of the larvae of *M. crudus* included *Brachiaria brizantha, Brachiaria dictyoneura, Brachiaria humidicola, Chloris gayana, Hemarthria altissima, Hyparrhenia rufa, Pennisetum purpureum* and a selection of sugar cane (Howard, 1989a, 1990a, b, 1995b).

The differences in productivity of *M. crudus* of the different grasses observed in these tests may have been due to ovipositional preferences, different survival rates of larvae or to a combination of these. Host-plant preferences of this insect may also be influenced by environmental conditions. The tests were designed to provide ovipositing females with a choice between *S. secundatum* and other grasses. It is possible that, if a poor host were the only grass available, *M. crudus* might colonize it at higher population levels.

Since *M. crudus* could adapt to different monocotyledons, herbaceous dicotyledons used as ground cover in palm plantations might be more effective than grasses for reducing the suitability of the habitat for this insect. In addition to the usual benefits of ground cover, leguminous species increase the availability of nitrogen in the soil (Michaud *et al.*, 1989; Mannetje, 1997). Additionally, dicotyledons generally have nectariferous flowers and many have extrafloral nectaries, and thus are more likely than grasses to support the adults of hymenopterous parasitoids of caterpillars and other pests.

Legumes tested as hosts of *M. crudus* supported few, if any, larvae of this insect (Howard, 1999a). *Arachis pintoi* and *Pueraria phaseoloides* did not serve as larval hosts, and are particularly suitable for use as ground cover. *Pueraria phaseoloides* (tropical kudzu) is widely known as a ground cover in plantations of coconut, African oil palm and other crops in many tropical countries (Hartley, 1988; Bourgoing, 1991; Yuhaeni and Ivory, 1994; Figs 3.13a and 3.14). *Arachis pintoi* forms a dense, low, ground cover (Fig. 3.13b). A highly palatable and nutritious forage, it is grown in many tropical countries (Menéndez and Matheu, 1995). It was found to be highly persistent under coconut palms in Indonesia (Mullen *et al.*, 1997). With its attractive, intense green foliage and continually blooming yellow flowers, it may also find use as an ornamental ground cover. Maintaining a ground cover of plants that are poor hosts of *M. crudus*, such as *A. pintoi* or *P. phaseoloides*, may help reduce

Fig. 3.13. Leguminous ground covers. Because they do not support the larval development of *Myndus crudus*, they are advantageous for use in coconut plantations in lethal yellowing-affected areas. (a) Tropical kudzu, *Pueraria phaseoloides*. (b) *Arachis pintoi*.

vector pressure in plantations or landscape areas. Combining this with the use of resistant palms might minimize losses to lethal yellowing. Tests of this integrated management method should be conducted under farm conditions. A disadvantage of leguminous ground covers is that they are generally not as persistent as grasses (Shelton, 1991b), but agronomic research on these plants may eventually solve this problem.

Myndus crudus, perhaps infected with phytoplasmas, could be spread accidentally via unregulated movement of living hosts of *M. crudus*, such as sugar cane cuttings or turf grasses for landscaping. Recommendations for safe movement of coconut germ-plasm are outlined in Frison et al. (1993). These methods could be modified for other palm species.

Additional Cixiidae of interest

Myndus skarphion is a relatively unknown cixiid (Kramer, 1979). The host plants are not known, but some specimens were

Fig. 3.14. Ground-cover management: passing a roller over tropical kudzu to encourage lateral spreading and formation of dense growth. Costa Rica. Photo by Richard Illingworth.

found in a ship's hold with bananas from Central America. It is distributed from Mexico through Panama (Kramer, 1979). It was collected by W.G. van Slobbe (identified by Lois B. O'Brien, personal communication) from African oil palms in Nicaragua in 1988, and thus is of interest because it could easily be confused with *M. crudus* in the field. The imagos are about the same size and colour as *M. crudus*; however, the species can be distinguished from the latter under a hand-lens by an orange stripe on each side of the frons.

Myndus taffini is a planthopper native to Vanuatu. The imagos superficially resemble those of *M. crudus* of the American tropics. Like the latter species, they occupy the abaxial surfaces of leaflets of coconut palms, where mating takes place. In coconut plantations, they are more abundant near borders with forest areas than in the interior of plantations. The larvae have been found in rotting wood permeated with roots of bourao, *Hibiscus tiliaceus* (Malvaceae) (Julia, 1982).

In observations to identify potential vectors of coconut foliar decay of coconut palms on the island of Santo, Vanuatu, *M. taffini* became the principal suspect, because population abundance of the species was correlated with high disease incidence in plantations. The species was then tested as a vector in numerous transmission experiments. Seedlings or palms up to 3 years old of the 'Malayan Red Dwarf' coconut palm were grown in polybags. Some of the palms in cages into which *M. taffini* were released contracted coconut foliar decay, while palms remained symptomless in cages into which other kinds of insects or no insects were introduced. This evidence is consistent with the hypothesis that *M. taffini* transmits the disease agent. DNA of the virus that causes foliar decay has been detected in *M. taffini*, providing further evidence that the insect transmits this disease (Randles, 1997), although this may merely indicate that the insect accumulates the virus while feeding, without necessarily transmitting it to palms (John Randles, personal communication).

In coconut palms attacked by foliar decay, fronds of position 7–11 become yellow, turn necrotic and then collapse, so that dead fronds hang through green lower fronds. Inflorescences subtended by necrotic fronds may become necrotic or produce fewer coconuts than normal. The disease is lethal within 1–2 years (Randles, 1997).

The tall coconut palms of local origin in Vanuatu ('Vanuatu Tall') tolerate infection, while some introduced varieties are susceptible. The susceptibility of 'Malayan Red Dwarf' is especially high. Hybrids between 'Vanuatu Tall' and some other varieties show mild symptoms when infected (Calvez *et al.*, 1980).

After much arduous investigation using complicated technology, the causal organism of foliar decay was identified as a unique virus of a new taxonomic group (Randles, 1997). The virus has not been found in *H. tiliaceus*, the apparent developmental host of *M. taffini*. Randles (1997) suggested that the larvae of *M. taffini* living on roots of the latter host could possibly acquire the virus from roots of coconut palm growing in close proximity.

Myndus adiopodoumeensis has been studied in Ghana as a suspected vector of Cape St Paul wilt, a disease of coconut palm thought to be identical to lethal yellowing-like diseases reported elsewhere in the coconut-growing areas of West Africa.

The biology of *M. adiopodoumeensis* resembles that of *M. crudus*. The imagos are found on palm foliage, usually the middle portions of the canopy. They prefer coconut palm to African oil palm. The larvae develop in the root zone of *P. maximum* and other grasses. They were also reported among roots of some Asteraceae, but it is unclear whether they developed on these plants or moved there from nearby grasses, and their frequency on asters in comparison with grasses has not been reported. The populations are denser and oviposition is more active during the rainy season, but larvae may be found in the root zones of grasses all year.

The planthopper was tested rigorously as a possible vector of the agent that causes Cape St Paul wilt, but results were inconclusive (Dery *et al.*, 1996, 1997).

Prior to the intensive studies of Auchenorrhyncha on palms stimulated by research on lethal yellowing beginning in the 1950s, *Oliarus cocosivora* seems to have been practically the only cixiid mentioned on palms (Muir, 1929; Lepesme, 1947). In Malaysia, young coconut seedlings were sometimes heavily infested with this planthopper and Corbett (1932) considered it important enough to include a drawing of it in his *Insects of Coconuts in Malaya*. In recent times, *O. cocosivora* has not been considered a pest.

Species of *Myndus* additional to *M. taffini* known from coconut palms in Oceania include *M. maculosus* in the Philippines (Zelazny and Pacumbaba, 1982), *M. mavors* in the Solomon Islands, *M. macfarlanei* in the Santa Cruz Islands and *M. chazeaui* in New Caledonia (Wilson, 1988a; Bourgoin and Wilson, 1992).

Delphacidae

The family Delphacidae can be distinguished from other auchenorrhynchous families by the presence of a conspicuous movable spur at the distal end of the tibia, a structure present in both imagos and larvae. The family is mostly associated with Gramineae, and some species are well-known vectors of virus diseases of maize and sugar cane. There are 1100 described species in the family.

A few polyphagous species of Delphacidae have been collected from palms in various localities, including the Hawaiian Islands, the Seychelles and Mauritius (Lepesme, 1947; Wilson, 1987a, 1997). *Nesodryas antiope*, known previously in Mauritius and the Seychelles, was found to be quite common on coconut palms in Tanzania (Wilson, 1987a).

In Côte d'Ivoire, two species that are cosmopolitan grass-infesting species, *Sogatella kolophon* and *Tagosodes cubanus*, apparently transmit an unknown agent (presumably a virus) that causes dry bud rot of young coconut palms (*pourriture sèche du coeur du cocotier*) from the seedling stage up to the second year of planting. The disease affects African oil palms to a lesser extent. It has been observed in Asia and Africa (Julia, 1979b; Julia and Mariau, 1982; Mariau, 1999c).

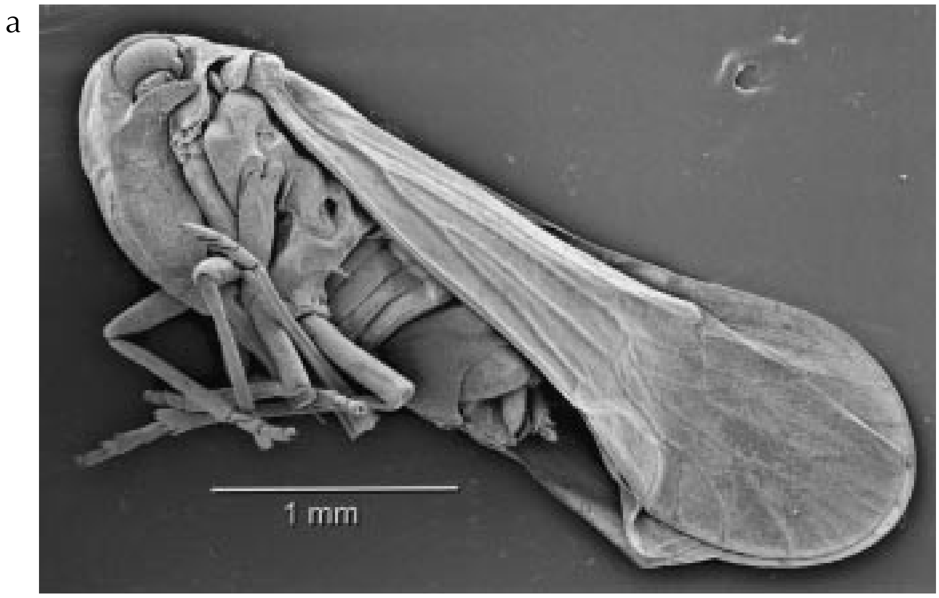
The imagos of *S. kolophon* are about 3–4 mm long and yellowish. Those of *T. cubanus* are about the same size but darker.

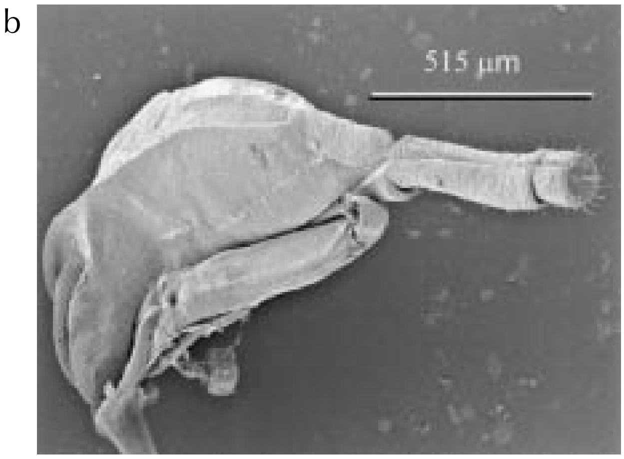
The planthoppers are abundant only in the wet season. They prefer open sites and tend not to infest young palms in the shade. Grasses are the primary hosts of the delphacids, and elimination of them from nurseries or in a circle around field-planted palms reduces the incidence of the disease (Mariau *et al.*, 1981). *Sogatella kolophon* is present in Florida but rare on mature palms (Howard and Mead, 1980).

Derbidae

Derbidae are a large family of planthoppers with more than 1000 species (Wilson, 1987a; Fig. 3.15). Muir (1917), who described a large portion of the known derbids, felt that the family reached its highest diversity in the Philippines and Malay Archipelago, and noted that a large portion of the species there were endemic. About 20% of the known species are in Africa south of the Sahara (Wilson, 1987a). In the Americas, fewer species are known.

The family is well represented on palms and other monocotyledons. For example, in Lepesme's (1947) compilation of records of insects of palms, Derbidae are represented by 52 species. In contrast, Lepesme listed no more than four species for any of the other auchenorrhynchous families that he discussed. Twenty-nine species of Derbidae listed by Lepesme were from coconut palm and/or African oil palm in





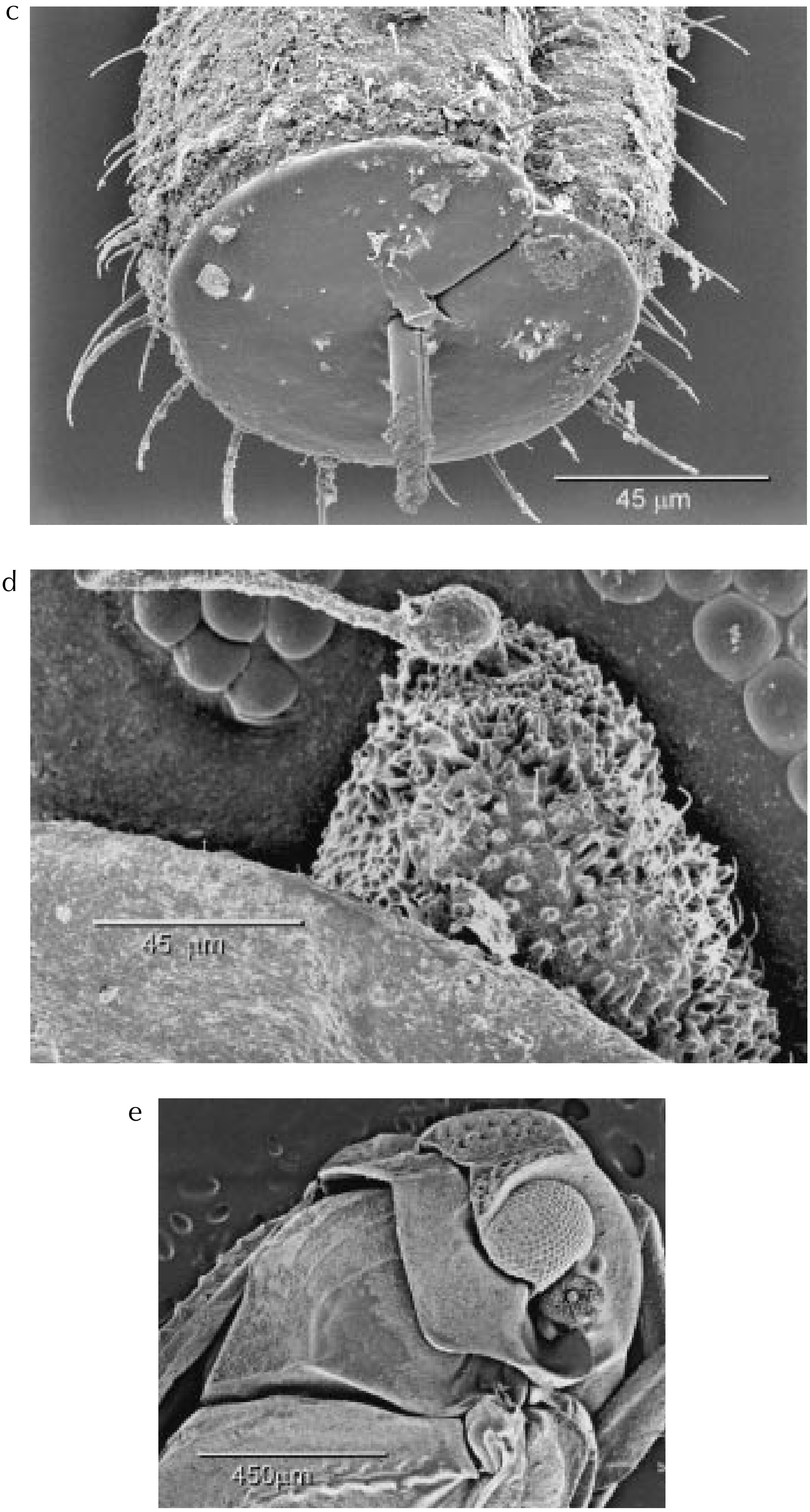


Fig. 3.15. (*and opposite*) Derbidae of palms of tropical America (SEM views). (a) Male imago of *Cedusa inflata*. (b) Head. (c) Stylets. (d) Antenna. (e) Head and pronotum of *Omolicna cubana*.

Africa, 22 species mostly from unspecified palms in Asia and one from palms in Puerto Rico. Sixteen species known from palms in the Philippines at that time (Muir, 1917) were omitted from Lepesme's review.

One to a few species of derbids have been collected in surveys of Auchenorrhyncha on palms in each of the following countries or areas: the Dominican Republic (Howard *et al.*, 1981), Jamaica (Schuiling, 1976; Eskafi, 1982), Yucatán, Mexico (Can Itzá, 1996), Florida (Howard and Mead, 1980) and Tanzania (Wilson, 1987a). In a survey on coconut palms in the Philippines, 16 species of derbids were collected (Zelazny and Pacumbaba, 1982), supporting Muir's (1917) concept that the family is unusually diverse there.

The host plants of the adults of many species of Derbidae are not known, but at least 92 species have been reported from palms (Table 3.3). The consistency with which they are found on palms indicates that they are attracted to them and thus probably feed on them. Most of what meagre knowledge we have of this large family has been published by a handful of entomologists interested in this group. Both the number of species associated with palms and the number of palm species that derbids visit may be much greater than our compilation indicates.

In a study using tagging with radioactive isotopes, it was shown that six species of Derbidae, namely *Cedusa wolcotti*, *Cedusa* sp., *Dawnaria sordidulum*, *Omolicna cubana*, *Omolicna* sp. and *Neocenchrea* sp., fed on a palm for relatively long periods (Eskafi, 1982). In coconut plantations in tropical America, the greyish imagos of *Omolicna* spp. are among the most consistently found Auchenorrhyncha on palm foliage, but they are seldom, if ever, abundant.

The larvae of Derbidae are often found in rotting wood debris and are thought to feed on fungi in such habitats (Flynn and Kramer, 1983; Carver *et al.*, 1991; Wilson *et al.*, 1994). Imagos of *Heronax maculipennis* were reared from larvae taken from stumps of buri palm, *Corypha elata*, in the Philippines (Muir, 1917). Larvae of the derbid *O. cubana* were reared on an *in vitro* culture of the fungus *Rhizoctonia solani* (Eden-Green, 1973).

Because *Cedusa inflata* (Colour Plate 8e) was one of the Auchenorrhyncha on palms in areas affected by lethal yellowing in Jamaica and Florida, observations were made to learn some aspects of its biology and to assess its potential role as a vector. The genus was reviewed by Flynn and Kramer (1983) and Kramer (1986). *Cedusa inflata* was described from Hispaniola and

Table 3.3. Species of Derbidae reported on palms.

Species of Derbidae	Palm hosts	Locality	Reference
Acanthocerana puncifrons	*Cocos nucifera*	Luzon (Philippines)	Zelazny and Pacumbaba, 1982
Cedusa aziza	*C. nucifera*	Mexico	Kramer, 1986
Cedusa inflata	21 species	Cuba, Florida, Hispaniola, Puerto Rico	Howard and Mead, 1980; Flynn and Kramer, 1983
Cedusa wolcotti	*C. nucifera* and unidentified	Puerto Rico, Jamaica	Wolcott, 1937*; Eskafi, 1982
Dawnaria sordidulum	*C. nucifera*	Jamaica	Eskafi, 1982
Decora pavo	Unidentified	Java	Muir, 1915*
Devadanda leefmansi	Unidentified	Java	Muir, 1915*
Devadanda perplexa	Unidentified	Java	Muir, 1915*
Diostrombus abdominalis	*C. nucifera*	Tanzania, South Africa	Harris, 1934*; Wilson, 1987a
Diostrombus cocos	*C. nucifera*, *Elaeis guineensis*	Sierra Leone	Hargreaves, 1927*

Table 3.3. *continued*

Species of Derbidae	Palm hosts	Locality	Reference
Diostrombus dilatatus	*C. nucifera,* *E. guineensis,* *Sabal* sp.	Sierra Leone	Hargreaves, 1927*
Diostrombus luteus	*E. guineensis*	Sierra Leone	Hargreaves, 1927*
Diostrombus mkurangai	*C. nucifera*	Tanzania	Wilson, 1987a
Diostrombus nitidus	*C. nucifera,* *E. guineensis,* *Sabal* sp.	Sierra Leone	Hargreaves, 1927*
Diostrombus schuilingi	*C. nucifera*	Tanzania	Wilson, 1987a
Distantinia nigrocacuminis	Unidentified	Luzon	Muir, 1917
Eosaccharissa ouwensii	Unidentified	Java	Muir, 1915*
Eosaccharissa pulchra	*C. nucifera*	Luzon	Muir, 1917
Helcita occidentalis	*E. guineensis*	Sierra Leone	Hargreaves, 1927*
Helcita wahlbergi	*E. guineensis*	Sierra Leone	Hargreaves, 1927*
Herpis flavescens	*C. nucifera*	Luzon (Philippines)	Zelazny and Pacumbaba, 1982
Kamendaka albomaculata	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1927*
Kamendaka ukutu	*C. nucifera*	Tanzania	Wilson, 1987a
Kamendaka sp.	*C. nucifera*	Luzon (Philippines)	Zelazny and Pacumbaba, 1982
Lamenia albipennis	Unidentified	Java	Muir, 1915*
Lamenia sp.	*C. nucifera*	Luzon (Philippines)	Zelazny and Pacumbaba, 1982
Leomelicharia delicata	Unidentified	Luzon	Muir, 1917
Leomelicharia delicatissima	Unidentified	Luzon	Muir, 1917
Leomelicharia nigrovittata	Unidentified	Luzon	Muir, 1917
Leomelicharia pulchra	Unidentified	Luzon	Muir, 1917
Leptaleocera coccinella	Unidentified	Java	Muir, 1915*
Levu africana	*E. guineensis*	Sierra Leone	Hargreaves, 1937*
Levu irrorata	Unidentified	Luzon, Mindanao	Muir, 1917
Lydda annetti	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1937*
Lydda cocos	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1927*
Lydda hargreavesi	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1937*
Lydda lineatipes	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1937*
Malenia aburiensis	*E. guineensis*	Sierra Leone	Hargreaves, 1937*
Malenia nigripes	*Raphia vinifera*	Sierra Leone	Hargreaves, 1937*
Mecynorhynchus fuscus	Unidentified	Java	Muir, 1915*
Mecynorhynchus hyalinus	Unidentified	Java	Muir, 1915*
Mecynorhynchus obscurus	Unidentified	Java	Muir, 1915*
Mecynorhynchus stramineus	Unidentified	Java	Muir, 1915*
Megatropis obliquefasciata	*C. nucifera*	Luzon (Philippines)	Zelazny and Pacumbaba, 1982
Muiria iridescens	Unidentified	Luzon	Muir, 1917
Mysidioides africana	*E. guineensis*	Sierra Leone	Hargreaves, 1937*
Mysidioides jacobsoni	Unidentified	Java	Muir, 1915*
Mysidioides sp.	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Neocenchrea sp.	*Adonidia* (*syn. Veitchia*) *merrillii,* *C. nucifera, Sabal*	Jamaica, Dominican Republic	Howard *et al*., 1981; Eskafi, 1982
Nesokaha lineata	*C. nucifera*	Luzon	Muir, 1917
Nesokaha nigropunctata	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Nesokaha philippina	*C. nucifera*	Luzon	Muir, 1917

Table 3.3. *continued*

Species of Derbidae	Palm hosts	Locality	Reference
Nesokaha rubrinervis	*C. nucifera*	Luzon	Muir, 1917
Nesorhamma badia	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Omolicna cubana and other *Omolicna* spp.	*C. nucifera,* *Pritchardia*	Tropical America	Howard and Mead, 1980; Howard *et al.*, 1981; Eskafi, 1982; F.W. Howard, unpublished
Pamendanga fuscipennis	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Paraphenice mawae	*C. nucifera*	Tanzania	Wilson, 1987a
Paraphenice sierraleonensis	*C. nucifera,* *E. guineensis*	Sierra Leone	Hargreaves, 1937*
Paraproutista albicosta	Unidentified	Java	Muir, 1915*
Paraproutista brunnia	Unidentified	Sulawesi	Muir, 1915*
Patara chambeziensis	*C. nucifera*	Tanzania	Wilson, 1987a
Patara elaeidis	*E. guineensis*	Sierra Leone	Muir, 1930*
Patara hargreavesi	*E. guineensis*	Sierra Leone	Muir, 1930*
Patara minazi	*C. nucifera*	Tanzania	Wilson, 1987a
Peggiopsis javana	Unidentified	Java	Muir, 1915*
Peggiopsis nigrovenosa	Unidentified	Java	Muir, 1915*
Phaciocephala pseudobadia	*Nypa fruticans*	Mindanao (Philippines)	Muir, 1917
Phenice pongwei	*C. nucifera*	Tanzania	Wilson, 1987a
Phenice stellulata	*E. guineensis*	Sierra Leone	Hargreaves, 1937*
Proutista dolosa	Unidentified	Java	Muir, 1915*
Proutista fritillaris	*C. nucifera,* *E. guineensis,* *Sabal* sp.	Equatorial Africa	Hargreaves, 1937*; Wilson, 1987a
Proutista moesta	*C. nucifera,* *E. guineensis*	Widespread in Asia, introduced in Tanzania	Muir, 1917; Corbett, 1932*; Miller, 1932*; Vesey-FitzGerald, 1941*; Wilson, 1987a
Proutista pseudomoesta	Unidentified	Java	Muir, 1915*
Pyrrhoneura maculata	*C. nucifera*	Luzon	Muir, 1917
Rhotana sp.	*E. guineensis*	Malaysia	Corbett, 1934*
Robigus magawai	*C. nucifera*	Tanzania to South Africa	Wilson, 1987a
Saccharodite sp.	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Sikaiana makii	Unidentified	Luzon and Taiwan	Muir, 1917
Sikaiana vitriceps	Unidentified	Luzon	Muir, 1917
Sumangala sp.	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Swezeyia vandergooti	Unidentified	Java	Muir, 1915*
Vekunta pseudobadia	Unidentified	Java	Muir, 1915*
Vekunta sp.	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Zeugma javana	Unidentified	Java	Muir, 1915*
Zeugma valdezi	*C. nucifera*	Luzon	Zelazny and Pacumbaba, 1982
Zorabana vipaku	*C. nucifera*	Tanzania	Wilson, 1987a
Zoraida bohemani	*E. guineensis*	Sierra Leone	Hargreaves, 1937*
Zoraida maculicosta	*Sabal* sp.	Sierra Leone	Hargreaves, 1937*
Zoraida sinuosa	*E. guineensis*	Sierra Leone	Hargreaves, 1937*

*Cited by Lepesme, 1947.

is reported from Puerto Rico, Cuba and Florida (Flynn and Kramer, 1983).

The imagos (Colour Plate 8e, Fig. 3.15) have a short abdomen but long wings, so as to appear similar in size to the imagos of *M. crudus* (4–5 mm long), which often occupy foliage of the same palms. However, the general colour of *C. inflata* is a glaucous grey which, in the larger surface areas, grades into a purplish colour. Also, the experienced eye discerns slight differences in the outlines of the two species (e.g. from above, *C. inflata* appears as slightly spindle-shaped, compared with *M. crudus*, which is more cylindrical). The larvae are reddish purple in the early instars. Later instars are a dark, dull purple and about 1.8–2.0 mm long (Fig. 3.16).

In a survey of Auchenorrhyncha on palms grown as ornamental plants in mostly urban areas of southern Florida, *C. inflata* was found on 21 species of palms, second in number of 'apparent palm hosts' only to *M. crudus* (Cixiidae), which was found on 26 species of palms (Howard and Mead, 1980). However, while *M. crudus* was abundant and widespread on palms, *C. inflata* was found in lower numbers and only at six of the 112 sites where auchenorrhynchous insects were sampled (F.W. Howard, unpublished). The presence of this insect on diverse palm species reflected the diversity of the palms themselves at some of these sites, which included a large collection of living palms at Fairchild Tropical Garden in Miami and two additional sites with unusually diverse palm collections. A notable feature of the palm collections was that they were under particularly conscientious horticultural maintenance, which included frequent irrigation and the use of wood chips and other organic debris as a mulch around the base of each palm. We hypothesized that the constantly moist wood chips served as a habitat for the larvae of *C. inflata* (Howard *et al.*, 2000).

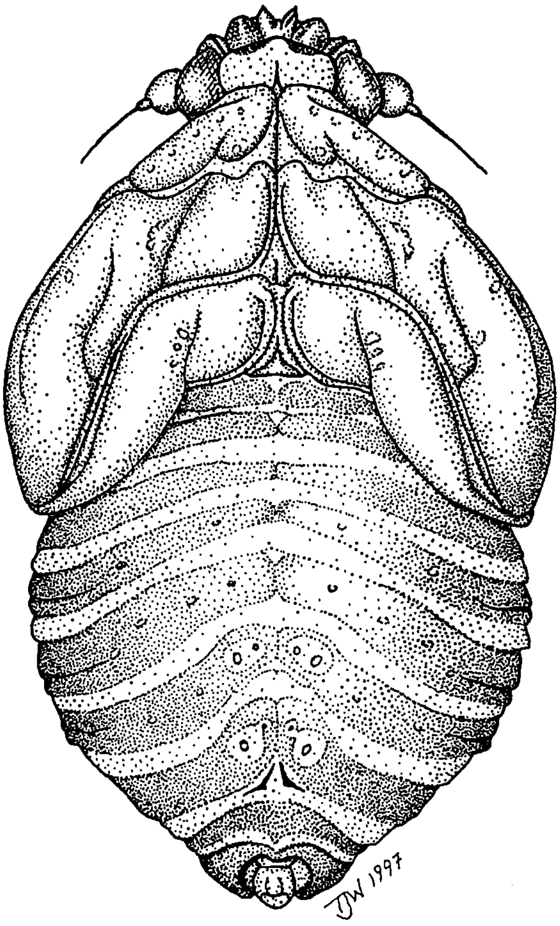


Fig. 3.16. *Cedusa inflata* (Derbidae), larva. Drawn by Thomas Weissling.

In Jamaica, *C. inflata* adults have a similarly patchy distribution in coconut plantations (Schuiling, 1976). In the Dominican Republic, one or two imagos per palm were observed in five widely separated localities (Howard *et al.*, 1981). However, other derbids, especially *Omolicna* spp., which are rare on palms in Florida (Howard and Mead, 1980), are among the most consistently found Auchenorrhyncha on fronds in coconut plantations in the Caribbean and elsewhere in the American tropics. In Jamaica, debris in leaf axils was searched exhaustively without finding derbid larvae (Wilson, 1997). Fungi, ferns and seed plants, e.g. *Ficus* spp., commonly grow in debris in leaf axils, implying that moisture levels are fairly stable there. However, debris on the ground in plantations is undoubtedly much more abundant and may be the principal habitat of *Omolicna* larvae.

When *C. inflata* imagos were consistently observed on a coconut palm, wood chips beneath it were searched, and purplish derbid larvae were collected and reared to imagos of *C. inflata.* An experiment was then conducted in which dead fronds, inflorescences and other debris from palms were placed in piles in coconut plantings. A mean of 56.1 larvae of *C. inflata* were found in all ten of the piles. A mean of 6.1 adult *C. inflata* were present on palms near debris piles, but they were virtually absent from palms > 15 m away from piles. Apparently, they do not readily disperse from the vicinity of their larval habitat.

Derbids are not pests of palms, but some African derbids have been occasionally abundant enough on palms to cause slight leaf chlorosis (Wilson, 1987a). No species of Derbidae is known to transmit plant pathogens. *Cedusa* spp. were too rare and spotty in Jamaica and Florida during lethal yellowing epidemics to be suspected as vectors of the disease (Howard and Mead, 1980; S.J. Eden-Green, personal communication). *Diostrombus mkurangai* (Derbidae) was reported as abundant on coconut palms in Tanzania, and thus is suspected as a possible vector of a lethal yellowing-like disease in that country (Mpunami *et al.*, 1997).

Proutista moesta, a bluish-black planthopper of 3.5 mm in length, is widespread on coconut palms, rice, maize and sugar cane in tropical Asia (Lepesme, 1947). Its larvae develop in rotting wood. Because the species was consistently found on coconut foliage in areas affected by Kerala coconut decline disease (q.v.) in India, it has been suspected as a vector of that disease (Rajan and Mathen, 1985). Phytoplasmas were detected in the salivary glands of this species more than 37 days after feeding on the foliage of a palm with this disease. Work is planned or in progress to investigate this suspected vector (Solomon, 1997). This insect is apparently a vector of yellowleaf disease in *Areca catechu* (Ponnamma and Solomon, 1998).

Achilidae

Achilidae are usually dull-tan or brown planthoppers. There are about 350 species, in some of which the wings are held flat, instead of tectiform, like most Auchenorrhyncha. As in many Derbidae, the larvae live beneath loose bark of trees or in decaying debris (Carver *et al.*, 1991; Dolling, 1991).

The one species associated with palms, *Synedoche helenae*, has been observed on *Washingtonia filifera* in desert areas of southern California, where this palm is native. The imagos are believed to feed on foliage nocturnally and shelter among persistent dead leaves by day. The larvae are presumed to live in decaying debris in leaf axils (O'Brien, 1971; Wilson, 1987b).

Tropiduchidae

The Tropiduchidae are a small family with about 330 species, distributed mostly in tropical regions (Carver *et al.*, 1991; Dolling, 1991). Characteristics of the thoracic segments, and the greater development of venation in the apical compared with the distal portion of the wing are important in distinguishing them from related groups. Most species are 5–7 mm long, with greenish, yellowish to brownish bodies and clear forewings, which are longer than the body. They are common on undergrowth of tropical forests (Kosztarab, 1982; Carver *et al.*, 1991).

Ommatissus is a genus of the Tropiduchidae distributed in the eastern hemisphere. Several species of this genus are unusual among palmivorous Auchenorrhyncha for four reasons:

1. Most Auchenorrhyncha on palms develop as larvae on some other plant and as adults attack palms. In contrast, *Ommatissus* spp. complete their life cycle on palms.

2. Most Auchenorrhyncha on palms occur in light populations, causing negligible direct damage. The few species of importance are vectors or putative vectors of palm diseases. In contrast, *Ommatissus lybicus* and *Ommatissus binotatus* cause significant direct damage to palms through feeding, honeydew production or damage associated with oviposition.

3. *Ommatissus* spp. produce honeydew more abundantly than most Auchenorrhyncha associated with palms.

4. While palmivorous species of Auchenorrhyncha are generally associated with multiple species of palms, *Ommatissus* spp. seem to be more restrictive in their host ranges. (This may be illusory: a single palm species predominates in each of the natural habitats of the species discussed below.)

Ommatissus lybicus was referred to in earlier literature as the 'lybicus' variety of *O. binotatus.* It was raised to species status by Asche and Wilson (1989). The species is one of the major pests of date palms in the Middle East and North Africa, and is apparently restricted to this host species. It is known as the 'Old World date bug', and as the 'dubas bug' (Colour Plate 8a, b, c). The insect is notable for its copious honeydew production (Dowson, 1936) and the latter name (actually written in English–Arabic dictionaries as 'dibs') is Arabic for various syrupy liquids.

The adult female is yellowish brown, varying to greenish, 5–6 mm long, with pairs of black dots at the base of the frons, laterally on the pronotum and often on the vertex of the head and on the seventh and eighth abdominal segments. The wings are clear, with the venation concentrated at the apices, as is typical for this family. The male is slightly smaller, with a greater wing length in proportion to body length, has a more tapered abdomen and always lacks the pairs of spots on the abdomen (Hussain, 1963a; Talhouk, 1977; Klein and Venezian, 1985; Asche and Wilson, 1989).

The females use their cutlass-like ovipositor to partially insert about 100–130 eggs singly in rows into any green tissue of the date palms except the fruits, but most often along the midveins on the adaxial surfaces of pinnae of younger fronds. Eggs hatch during summer in 18–21 days and after more than 170 days in winter (Dowson, 1936; Hussain, 1963a; Klein and Venezian, 1985; Al-Abbasi, 1988).

The youngest instars are basically pale grey. Later instars are yellowish brown, with distinct brown lines and with red eyes. They bear a cluster of waxy caudal filaments, the number of which can be used to determine the larval stage (Al-Abbasi, 1988). In the spring generation, the eggs hatch in April or May and the insect develops through five larval instars to imago in about 4–8 weeks, imagos emerging in June. This generation coincides with the period when fruits are forming (Alfieri, 1934). There are about equal numbers of females and males. Mating takes place on palm fronds, and oviposition is completed in June. The eggs of this generation aestivate over the hot summer, hatching towards the end of August. This second generation develops to imagos by the end of September. Imagos of the autumn generation may disperse to new palms, mate and oviposit. The insect overwinters in the egg stage.

The larvae and imagos feed in the shelter of the adaxial surfaces of reduplicate pinnae (Klein and Venezian, 1985). The insect's preference for oviposition and development on the 'upper' surfaces of the pinnae is consistent with that shown by other small insects that feed on date palm fronds (e.g. *Parlatoria blanchardi* (q.v.)).

When disturbed, the imagos jump to distances of 12 times their length and may fly a short distance. The anatomy of the organs involved in jumping in this species has been studied (Al-Abbasi, 1987). The larvae may jump short distances when disturbed.

Ommatissus lybicus is distributed in North Africa, from Algeria to Egypt, and in Iraq and the countries of the Arabian Peninsula (Waller and Bridge, 1978; El-Haidari, 1982). It apparently originated in the Tigris–Euphrates River valley, from which it has spread in recent decades. Dowson (1936) reported that, in the 1930s, few of the 7 million date palms in the Basrah area of Iraq were free of the bugs. Talhouk (1977) considered it to be especially serious in the Basrah area and some oases of Egypt and Libya. In the 1980s, it was reported for the first time in Sudan (El-Haidari, 1982) and in Israel (Klein and Venezian, 1985).

One of the earlier outbreaks noted by entomologists was in the extensive date palm groves of the large Oasis of Siwa in Egypt (Alfieri, 1934), an inland location so remote in the desert that the inhabitants speak a unique language, Siwa. The spread of the insect to such locations has apparently been by transport of offshoots with eggs.

Ommatissus lybicus was observed more often on mature than on young date palms, possibly because the larger palms offer greater protection (Klein and Venezian, 1985). In heavy infestations, there are thousands of the bugs per frond (Dowson, 1936). Relatively high humidity, dense plant spacing and shading seem to promote population growth of this insect. For example, in Iraq, high populations were observed most often in date palm groves that were either near rivers, were densely planted with palms or were interplanted with fruit-trees (Hussain, 1974). Yet the insect survives dust-storms and persists on large date palms during extremely hot, dry periods. The imagos can survive mild winters in the Middle East, but did not survive the 1982/83 winter in Israel, when there were many nights with freezing temperatures. The eggs are apparently slightly more able to survive cold periods (Klein and Venezian, 1985).

Ommatissus lybicus apparently prefers particular cultivars of date palm. In Israel, 'Medjhool' palms were more highly infested than nearby 'Deglet Noor' palms, possibly because in the former cultivar the whorls of fronds tended to be relatively closed (Klein and Venezian, 1985).

Dense populations of this insect undoubtedly weaken their palm hosts by draining sap. The bugs produce extremely large quantities of honeydew, which supports sooty mould in some localities. However, sooty mould was not observed on palms infested with *O. lybicus* in the Arava Valley, Israel (Klein and Venezian, 1985). Under some conditions, when honeydew is abundant, it ferments and a vinegar smell is said to permeate the surrounding area (Dowson, 1936). In the usually rainless conditions where date palms grow (desert climate (BW) (see Box 1.1)), a thick layer of dust may accumulate on honeydew-coated surfaces. Following months of bug infestation, the frond surfaces tend to become chlorotic. Collapsed spathes of young inflorescences have been observed on heavily infested palms, possibly due to invasion of fungi in feeding sites. Extremely heavy populations are thought to have caused the death of some palms (Dowson, 1936). Dates of infested palms are reported to be smaller and to ripen more slowly, with a high percentage of reducing sugars and low percentage of sucrose (Hussain, 1974). In Iraq, losses of 50% of the date crop have been attributed to this insect (Talhouk, 1977). However, in Israel, no loss in production was detected in palms that had been heavily infested for 2 years (Klein and Venezian, 1985).

Cultural practices that promote the health of palms are said to reduce damage by *O. lybicus* (Talhouk, 1977).

The insect is probably under natural control in some parts of the Middle East, but little is known regarding relationships between *O. lybicus* and natural enemies. Hussein (1974) listed several natural enemies of *O. lybicus*, including a species of Chalcidoidea, a predacious neuropteran and coccinellid beetles. These obviously do not provide adequate natural control everywhere the bug occurs, and it is questionable whether coccinellids, in particular, are adapted to prey on this auchenorrhynchous insect or its well-protected eggs. In the Arava Valley, Israel, where *O. lybicus* was introduced relatively recently, no natural enemies of the insect were observed (Klein and Venezian, 1985).

Various chemical treatments have been applied to control the bugs, including aerial applications (El-Haidari *et al.*, 1968; Talhouk, 1977). A rather unusual problem is that the insects, because they frequent the adaxial surfaces, are protected from contact sprays applied from below (Dowson, 1936). Use of chemicals may have undesirable effects, such as upsetting the balance between mites (Acari) that infest date palms and their natural enemies (Klein and Venezian, 1985). In Israel, experiments were conducted in the mid-1980s to test aldicarb and its isomer butocarboxim by soil application for control of *O. lybicus*. The excellent control obtained in preliminary experiments became widely known, and farmers began using the method before researchers had a chance to refine it. As a result, *O. lybicus* seems to have been eliminated from date groves in Israel, as it has not been found there since widespread treatments of date palms with butocarboxim in 1986 (Meir Klein, personal communication).

Ommatissus binotatus is distributed in the southern Iberian Peninsula and Sicily and has recently been reported in Montpellier in southern France (Labonne and Bonfils, 1998). The insect completes its life cycle on *Chamaerops humilis*, the European fan palm of the Mediterranean region. It is not known from other hosts.

Guglielmino (1997a, b) reported on the natural history of this insect, with detailed descriptions of the morphology of immature stages, including the ultrastructure of the eggshell. The biology of *O. binotatus* is similar to that of *O. lybicus*; however, there are some interesting contrasts. *Ommatissus binotatus* is a univoltine species, overwintering in the egg stage. Thus, the insects are active during the hot, dry Mediterranean summer and inactive during the relatively cool, wet winter months (Mediterranean climate (Cs): see Box 1.1).

A second difference is that *O. binotatus* infests the abaxial surfaces of fronds, rather than the adaxial surfaces as does *O. lybicus*. Thus, the bug that attacks the palmate fronds of *Chamaerops* conforms to the general tendency of leaf-feeding insects, while the behaviour of *O. lybicus* is more specialized, as is that of *Parlatoria blanchardi* and other insects that visit the induplicate leaflets of *Phoenix*.

Females insert their eggs into the tissue of the abaxial frond surfaces, causing damage thought to be more important than that caused directly by their feeding. The deleterious effects of sooty mould, which may be extensive if dense populations produce copious honeydew, may be even more important. However, Guglielmino (1997a) reported that, at least in Sicily, palms are not usually highly infested by this insect, notwithstanding that she observed no evidence of its regulation by natural enemies.

Chamaerops humilis (Colour Plate 2f) is grown as an ornamental plant throughout the Mediterranean region and other areas of the world, especially those with a Cs climate, e.g. California. The only palm species native to Europe, *C. humilis* is a typical component of Mediterranean woodland, especially on rocky, arid sites, in the coastal areas west of Malta, in both North Africa and southern Europe (Uhl and Dransfield, 1987). Lepesme (1947) listed 28 species of insects associated with this palm. *Ommatissus binotatus* is not known throughout the entire range of *C. humilis*.

In Morocco, *Ommatissus magribus* apparently occupies the niche of *O. binotatus* and is thought to be distributed on *C. humilis* throughout North Africa (Asche and Wilson, 1989). *Ommatissus tumidulus* feeds on *Phoenix* sp. in Sudan. A key to the species of this genus was published by Asche and Wilson (1989).

In Luzon, Philippines, *Kallitaxila apicalis* is a tropiduchid that completes its life cycle on coconut palm (Zelazny and Pacumbaba, 1982). *Tambinia verticalis* fills a similar niche in Zanzibar and Tanzania. It was originally known from dicotyledonous trees in India (Wilson, 1986). *Athestia chariclo* was intercepted in the USA on fronds of *Chamaedorea* from Mexico, suggesting that the family is represented on palms in wild areas in the American tropics (Wilson, 1987b).

Issidae

The family Issidae is widely distributed, with 1000 species (Dolling, 1991). The imagos are dull-coloured, with wings that are broad in relation to their length and sometimes highly convex, giving them a short, stout appearance compared with most Auchenorrhyncha.

Asarcopus palmarum is a reddish-brown planthopper that infests date palm in its native home in North Africa and the Middle East. It was introduced into California, probably before the 1920s, where it attacks young palms of the several species of *Phoenix* grown there. The planthoppers feed on inflorescence stalks, tender growth of the newest frond and the lighter-coloured tissue at the base of petioles, causing irregular brown areas. Occasionally, populations become dense and produce excessive honeydew, which attracts ants (Carpenter and Elmer, 1978).

Colpoptera spp. feed on coconut palms in Jamaica, but are not common on this host (Eskafi, 1982; Wilson, 1987b).

Lophopidae

Lophopidae are planthoppers that may be recognized by the prominent carinae of the frons. There are 120 species, most of which are distributed in Asia (Dolling, 1991). There is extensive literature only for *Pyrilla perpusilla*, a pest of sugar cane in southern Asia. Three species native to Oceania are important on palms (Wilson, 1987b).

Zophiuma lobulata feeds on coconut palm, *A. catechu* and *Pandanus* in New Guinea. It has also been reported on *Passiflora quadrangularis.*

The imagos are 16–18 mm long, i.e. large relative to other Auchenorrhyncha. They are brown, with two red horizontal bands on the frons. A conspicuous field character is a black, tear-drop-shaped spot, with a smaller, subcentral, white spot on the distal end of each forewing.

Zophiuma lobulata is unusual in that it pierces and feeds in the tough tissue of the petiole, midveins and leaf veins, rather than in the lamina, as do most Auchenorrhyncha. Both larvae and imagos feed on older fronds, moving to younger fronds as the latter become necrotic. The larval stage is of relatively long duration for Auchenorrhyncha, i.e. 82–85 days.

An outbreak of this planthopper occurred near a settlement called Finschhafen on the Huon Peninsula in eastern Papua New Guinea during the 1960s. Up to 1000 planthoppers per frond were observed. Infested coconut palms developed a condition characterized by yellowing, followed by bronzing of the fronds, reduced fruit production, stunting of growth and death of some young palms. Suspected to be caused by a microbial pathogen transmitted by the planthopper, researchers named it Finschhafen coconut disorder. However, through well-designed research, Smith (1980) obtained convincing evidence that it was caused directly by the insect’s feeding over a 7–15-month period. Young palms with the disorder recovered when planted in areas relatively free of the insect.

Populations of *Z. lobulata* are usually at low levels, presumably due to natural control agents, including an encyrtid egg parasitoid and entomogenous fungi (Smith, 1980).

Painella simmondsi is associated with a condition similar to Finschhafen disorder in the Solomon Islands (Stapley, 1976, cited in Wilson, 1987b). *Virgilia luzonensis* completes its life cycle on coconut palm in Luzon, Philippines (Zelazny and Pacumbaba, 1982).

Ricaniidae

The Ricaniidae, like the Flatidae, resemble small moths, because of their triangular and steeply tectiform wings when at rest. They are medium-to-large planthoppers. There are 380 species, all but a few of which are found in the eastern hemisphere (Kosztarab, 1982; Dolling, 1991). *Ricania speculum* in Malaysia and *Pochasia fasciata* in West Africa have been reported on palms (Wilson, 1987b).

Flatidae

The imagos of Flatidae are recognized by their broad, triangular forewings, which are steeply tectiform, giving the insect a laterally flattened appearance. Most species are green, with colourful patterns. The larvae occupy the same host plant as the imagos, are dorsoventrally flattened and produce long wax filaments. There are about 1000 species, distributed mostly in the tropics (Dolling, 1991).

Ormenaria rufifascia is a flatid planthopper commonly found on *S. palmetto* in Florida to south-eastern Georgia (Figs 3.8 and 3.17). In Cuba, it was collected from *Colpothrinax wrightii* (Metcalf and Bruner, 1948). Although it has been collected on 20 diverse species of palms and a few other plants (Wilson and Tsai, 1984), it seems to be most abundant on palms with palmate fronds. The adult is 11 mm long and of a pale blue-green ground colour, with reddish stripes on the thorax and two orange patches on the head. In southern Florida, the larvae, pale green with fine orange stripes, are present on fronds in April and May, and imagos are present through July (Mead, 1965).

Psenoflata brevis can apparently complete its life cycle on coconut palm and *Coccoloba uvifera* (Polygonaceae) in Jamaica (Eden-Green, 1973; Schuiling, 1976; Schuiling *et al.*, 1976). A few additional species of Flatidae on palms have been reported from localities in Asia, Africa and the Americas, but probably none of them are common and they may be primarily associated with plants other than palms (Lepesme, 1947; Howard *et al.*, 1981; Wilson, 1997).

Meenoplidae

The family Meenoplidae contains about 100 species, distributed only in the eastern hemisphere. Meenoplid planthoppers are small and inconspicuous. The larvae of some species are root-feeders (Carver *et al.*, 1991). *Meenoplus* spp. have been reported from palms in Africa (Lepesme, 1947; Wilson, 1997).

Cicadidae

Cicadidae, with 2000 species (Dolling, 1991), are generally the largest in size of the Auchenorrhyncha. The song of cicadas in the treetops on warm days is a familiar sound in many regions. The imagos feed on aerial parts of plants and the larvae on roots. Their representation on palms is meagre.

Lepesme (1947) listed two species of *Dendubia* that attack palms and other plants in Malaysia, and *Mogannia insignis* from African oil palm in West Africa.

Oviposition into foliar and fruit tissue by *Diceroprocta apache*, a cicada of the deserts of the south-western USA, sometimes causes damage to date palms (Carpenter and Elmer, 1978).

In Jamaica, *Proarna hilaris* feeds on coconut palms and inserts eggs into petiole tissue, and the larvae feed on roots. It is one of many insect species tested as a vector of lethal yellowing, with negative results (Eden-Green and Schuiling, 1978).

Cicadelloidea: Cicadellidae

The Cicadellidae (leafhoppers) is the largest family of Auchenorrhyncha, with 20,000 species (Dolling, 1991). Leafhoppers are small insects, usually less than 10 mm long, with cylindrical, streamlined bodies. The spines on their hind tibia are in rows,

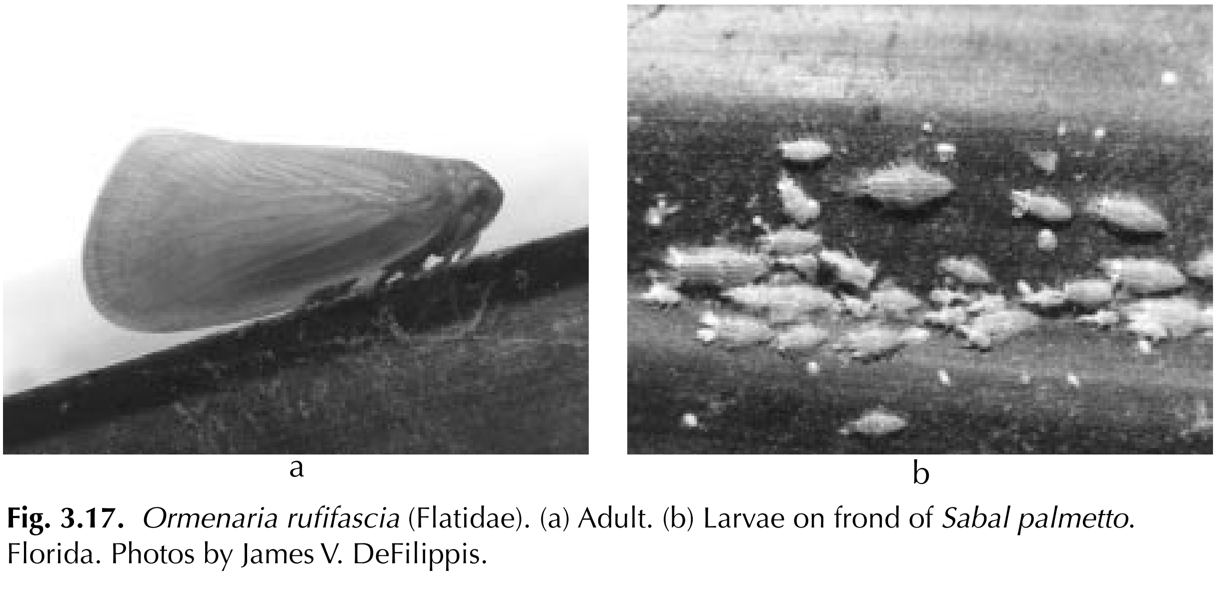


Fig. 3.17. *Ormenaria rufifascia* (Flatidae). (a) Adult. (b) Larvae on frond of *Sabal palmetto.* Florida. Photos by James V. DeFilippis.

rather than whorls. This character is useful for distinguishing them from insects of related auchenorrhynchous taxa (e.g. Fulgoroidea, Membracidae, Cercopidae). Leafhoppers seem to be especially diverse and abundant in meadows and other open habitats. However, some studies indicate that the family may also be very diverse in tree canopies. For example, based on sampling in tropical-forest canopies in Panama, the number of species of Cicadellidae surpassed that of all other auchenorrhynchous families and, in some sites, was about equal to or exceeded the superfamily Fulgoroidea (Wolda, 1979). The family was predominant among hemipterous taxa in tropical rainforests studied in Sulawesi (Casson and Hodkinson, 1991). Most Cicadellidae are phloem-feeders. Species of the subfamily Cicadellinae are xylem-feeders, while the tiny leafhoppers of the subfamily Typhlocybinae are mostly mesophyll-feeders (Wilson, 1997).

In Florida and the Caribbean region, leafhoppers are seldom found in the foliage of tall palms, but are occasionally found on low-growing palms near grasses and other herbaceous plants, which probably serve as their principal hosts (Howard and Mead, 1980; Howard *et al.*, 1981). Fifteen species of Cicadellidae were found, by radioactive tagging, to feed on coconut palm foliage in Jamaica. *Empoasca* sp. (Typhlocybinae), an unusually small leafhopper, was the most frequent leafhopper in the samples. However, radiographic counts indicated that fewer of the cicadellid species had fed on palm foliage, compared with *M. crudus* and several species of Derbidae, and they tended to feed for shorter periods than the other taxa (Eskafi, 1982).

The fact that collectors often concentrate on palm foliage that is easily reached from the ground probably often biases surveys of palm insects for Cicadellidae, which are often very diverse in nearby undergrowth. For example, 27 species of Cicadellidae were captured in a survey of phytophagous palm insects in Luzon, Philippines (Zelazny and Pacumbaba, 1982). That almost 94% of the palms examined were less than 5 years old may have biased these results for cicadellids. They reported only one species, *Tettigoniella makilingiensis*, on older palms. Similarly, in a survey on *Phoenix* in Texas, in which some of the palms were less than 2 m in trunk height, Cicadellidae were predominantly represented in samples, with a total of 24 species (Meyerdirk and Hart, 1982). In a survey of Auchenorrhyncha on palms in the Dominican Republic, specimens were collected entirely from small palms to minimize the equipment needed and to cover more territory during a short period. Thus, the survey was probably biased for cicadellids. Five cicadellids were collected. These were cosmopolitan species primarily associated with herbaceous plants (Howard *et al.*, 1981). They are seldom observed on larger palms in Florida or the West Indies.

Recilia mica (Euscelinae) is a leafhopper reported as a vector of blast disease of young African oil palm and coconut palm in Côte d'Ivoire (Desmier de Chenon, 1979; Julia, 1979b; Renard *et al.*, 1982). The causal organism of the disease is believed to be a phytoplasma (Dollet, 1980). The problem has been severe enough for insecticide treatments to be tested against it (de Franqueville *et al.*, 1991). The leafhoppers were primarily associated with grasses (*Paspalum* and *Pennisetum*). When these grasses were removed from the nursery, the incidence of blast diminished (Desmier de Chenon, 1979; Renard and de Franqueville, 1989). Rice is another host of the leafhopper, and growing it near coconut palms may increase the incidence of blast (Zakra *et al.*, 1986). Shading the palm seedlings helps prevent attack by these leafhoppers (Eden-Green, 1997b). *Recilia mica* was also thought to spread the fungus *Cercospora elaedis*, which causes a leaf spot of African oil palm (Renard and Quillec, 1979). Neither of these two diseases has had a serious impact on palm culture.

An undescribed minute leafhopper, *Nzinga* sp. (Cicadellidae: Typhlocybinae), was suspected on the basis of its abundance in coconut palms to be a vector of lethal yellowing-like diseases of coconut palm in West Africa (Dery *et al.*, 1997).

However, typhlocybines feed in mesophyll (Wilson, 1997), making it less likely that they transmit phloem-inhabiting phytoplasmas.

Sophonia greeni (Cicadellidae: Nirvaninae) was consistently present on coconut foliage in areas affected by Kerala coconut decline (Rajan and Mathen, 1984; Solomon, 1997).

Membracidae

The family Membracidae, known as tree hoppers, is characterized by an unusually pronounced pronotum, which is often of a peculiar shape and projected posteriorly. With their bizarre forms, often colourful patterns and a degree of social development, they are among the most intriguing insects to tropical biologists. Woody dicotyledons are the hosts of most species, and they are more likely to feed on twigs and thin stems, rather than leaves. The family contains 2400 species, most of which are in tropical America (Carver *et al.*, 1991; Dolling, 1991).

Only one species of Membracidae is known to have an important association with palms (Wilson, 1987b). *Idioderma virescens* has been collected in Florida on native *Serenoa repens* and on seven taxonomically diverse exotic species (Howard and Mead, 1980). It is distributed throughout the Florida peninsula (Kopp and Tsai, 1983). Records in the Dominican Republic were from coconut palm and *A. merrillii*, both exotic palms there (Howard *et al.*, 1981). It is known, without host data, from near Brownsville, Texas (Kopp and Tsai, 1983), Cuba (Metcalf and Bruner, 1925) and Bimini, Bahamas (Metcalf, 1954). In Jamaica, Eskafi (1982) reported evidence from radiological techniques that *I. virescens* (as *Idiodema varia*) fed on coconut palm foliage. Larval development of this species has been observed on *S. repens* and *Phoenix roebelenii* (Kopp and Tsai, 1983).

The adult tree hoppers are about 4 mm in length, highly convex and with the lateral margins pointed. Females are deep green in colour. There are green and brown male morphs. The females insert the eggs in rows in the inflorescence stalks, and the larvae develop on these structures, but the insects are also often seen on fronds. The larval stage takes about 3 weeks and the imagos live up to about 2 months. As in other membracids, adult females occupy colonies with their larvae. They are never abundant insects, but are most numerous in the summer (Kopp and Tsai, 1983). They produce honeydew and are often tended by ants (Colour Plate 8f).

Idioderma virescens is not common or abundant enough to be considered a pest, but is one of many insects that, at one time or another, have been suspected as possible vectors of lethal yellowing (Tsai, 1980). However, membracids are not known to transmit phytoplasmas and, since, during the lethal yellowing epidemic in Florida, *I. virescens* was only occasionally observed on coconut and other lethal yellowing-susceptible palms, it was not seriously suspected as a vector (Howard and Mead, 1980). It is not suspected as a vector of lethal yellowing in Jamaica, Mexico or Central America.

Additional palm diseases thought to be transmitted by Auchenorrhyncha

Cadang-cadang is a disease of coconut palms distributed in parts of the Philippines. It is associated with a viroid, referred to as coconut cadang-cadang viroid (CCCvd) (Hanold and Randles, 1991). On the assumption that cadang-cadang may be transmitted by an insect, an extensive survey of phytophagous insects associated with coconut palms was conducted in the Philippines (Table 3.1). Sixty-three insect species were identified, 81% of which were Auchenorrhyncha (Zelazny and Pacumbaba, 1982). Most of the species were represented by few specimens, and the sampling did not generate data that would indicate any particular species as a potential vector.

In 1980, lethal yellowing was reported in the Rio Grande Valley of southern Texas, where it destroyed large numbers of

Phoenix canariensis, a common palm in that area, and *Phoenix dactylifera*, which was less common. The symptoms were the same as those of lethal yellowing of *Phoenix* spp. in Florida, and phytoplasmas were observed by electron-microscope (EM) examination of tissue samples from the palms. As with lethal yellowing in Florida, *Washingtonia* spp. were not affected (McCoy *et al.*, 1980a, b). This was the first time that lethal yellowing had been reported outside the range of coconut palms. In Florida, this added credence to an earlier popular prediction that lethal yellowing would eventually invade the central and northern parts of the peninsula, where, as in southern Texas, *P. canariensis* and other cold-hardy palms were common, but where winters were too cold for coconut palms. However, lethal yellowing has not spread beyond the range of coconut palms during the period of almost three decades that it has been active in southern Florida.

DNA probe technology developed in the 1990s (see Box 3.2) would provide a means of determining whether the disease in Texas was caused by a phytoplasma identical to that which causes lethal yellowing in Florida. However, this question cannot be answered; virtually all of the *Phoenix* palms that survived the disease in Texas were later killed in a hard frost in 1989, and the disease is no longer present there.

During the period when the disease in Texas was still active, a survey of Auchenorrhyncha associated with palms was conducted to determine potential vectors (Meyerdirk and Hart, 1982). Comparative population data were not reported, but *Oliarus acicus* (Cixiidae) was the most abundant insect sampled. *Myndus crudus* was also collected, but in much smaller numbers. These were the only species that appeared to feed on palms. Twenty-six additional species were collected, most of which were Cicadellidae. Since collections included specimens collected from palms of 0.6–2.0 m in trunk height, many of the species, especially cicadellids, were probably associated with grasses and other small plants.

Phytoplasma-associated diseases of coconut palms occur in Africa that are very similar to lethal yellowing of the Americas. Until recently, it was unclear whether they were a single disease, which varied in certain characteristics depending on the locality, or indeed different diseases, i.e. caused by different strains of phytoplasma (Whitehead, 1966; Howard, 1983). Recent studies with molecular methods have revealed three distinct diseases: the phytoplasma-associated palm disease in the Americas, which continues to be referred to as lethal yellowing, and distinct diseases of East and West Africa, respectively, each associated with a different strain of phytoplasma. The American strain seems to be more closely related to the East African than to the West African strain. The disease of Kenya, Tanzania and Mozambique (East Africa) has recently been referred to as ‘lethal disease’. In West Africa, Cape St Paul wilt in Ghana, Kaincopé disease in Togo, Awka wilt in Nigeria and Kribi disease in Cameroon are all presumably the same disease, but so far their respective local names continue to be used (Jones *et al.*, 1995; Eden-Green, 1997a; Harrison and Oropeza, 1997; Tymon and Jones, 1997). No insect vectors have been incriminated for the African lethal yellowing-like diseases, but *Myndus adiopodoumeensis* was frequently found associated with coconut palms in some parts of Ghana and has been studied as a suspected vector (Dery *et al.*, 1997; Wilson, 1997). A leafhopper, *Nzinga* sp. (Cicadellidae: Typhlocybinae) (q.v.) is an additional suspected vector (Dery *et al.*, 1997). The latter two species, as well as unidentified Derbidae and other insects, were screened for phytoplasmas associated with the West African lethal-yellowing strain, without finding evidence of these pathogens (Offei *et al.*, 1997). *Diostrombus mkurangai* (Derbidae) has been suspected as the vector of the disease in Tanzania because of its abundance on coconut palms (Mpunami *et al.*, 1997).

Marchitez sorpresiva and hart-rot (q.v.) are diseases of African oil palm and coconut palm, respectively, in South America associated with protozoans and thought to be transmitted by pentatomid bugs. However, Zenner de Polanía and Posada Flórez (1992) recognized a second disease in Colombia under the same name. It affected African oil palms on about 2000 ha in the Zulia River valley. The causal agent was not determined, but, because *M. crudus* was abundant on the foliage of the palms, it was suspected as the vector. Zenner de Polanía and Lopez (1977) therefore conducted a study of the bionomics of *M. crudus*, which we view as one of the most valuable contributions to basic knowledge of this insect. In additional studies on *M. crudus* in Colombia, populations of the insect were reduced by converting the ground cover in the plantation from grasses to legumes. This was followed by a reduction in the disease. Palms in a grove were exposed to *M. crudus* adults by bagging them on individual pinnae. There were more cases of marchitez sorpresiva in bagged than in unbagged palms (Mena and Martínez-López, 1977), but, because all palms were also exposed to free insects and the pattern of disease spread observed could have occurred independently of the experimental treatments, there is some uncertainty regarding these results.

With the efficiency of new diagnostic techniques, palm diseases associated with phytoplasmas have been reported with increasing frequency. In addition to those mentioned, these include a disease of coconut palms found recently in Oaxaca, Mexico (Oropeza and Córdova, 1998). A disease of a close relative of palms, *Carludovica* sp. (Cyclanthaceae), is associated with phytoplasmas and was initially suspected to be identical to lethal yellowing, since it was discovered in an area where lethal yellowing was epidemic on coconut palms in Campeche, Mexico. However, with molecular techniques the apparent pathogen was found to be a phytoplasma of a different strain (Oropeza and Córdova, 1998). A disease called white-tip dieback of date palms in northern Sudan was recently reported to be associated with phytoplasmas (Cronjé *et al.*, 2000). Diseases of coconut palm that have some similarities to lethal yellowing but for which the pathogens are not known include leaf-scorch decline in Sri Lanka, Malaysia wilt in Malaysia, Socorro wilt in the Philippines, Natuna wilt in the Natuna Islands, Indonesia, and several similar diseases in other islands of Indonesia (Eden-Green, 1997b). Tatipaka disease in Andhra Pradesh, India, is thought to be caused by a virus (Solomon *et al.*, 1998). Insect vectors are not known for any of these diseases.

Hemiptera: Sternorrhyncha

Forrest W. Howard

Sternorrhyncha are the suborder of Hemiptera best represented on palms. Most species on palms thrive on the foliage, but these basically eurymerous insects may be found on stems, fruits and, more rarely, roots. Families of the suborder Sternorrhyncha of significance on palms include the following:

- Sternorrhyncha
    - Aphididae
        - Hormaphidinae
    - Aleyrodidae
    - Coccoidea
        - Margarodidae
        - Pseudococcidae
        - Eriococcidae
        - Coccidae
        - Conchaspididae
        - Asterolecaniidae
        - Diaspididae
        - Phoenicococcidae
        - Halimococcidae
        - Beesoniidae
        - Genus *Comstockiella* (family uncertain)

Aphididae

Aphids (Aphididae) are soft-bodied insects, usually less than a few millimetres long. Most species have a globular body, with spindly legs, a relatively long proboscis and membranous wings with simple venation. Aphid species are polymorphic, and morphs include alate (winged) and apterous (wingless) imagos. A pterostigma on the costal margin of the forewings of alates is a good field identification character for the family. A pair of tubular structures, the siphunculi, present on the dorsum of the fifth abdominal segment, functions in releasing intraspecific chemicals, particularly alarm pheromones. Aphids tend to live in dense aggregations. Although some well-known aphids are pests of annual crop plants, most species are associated with arborescent rather than with herbaceous plants. This may be due to the greater architectural complexity of arborescent forms, as explained by Dixon (1985).

Aphids are phloem-feeders, and they are the major insect family with species that transmit plant-pathogenic viruses. About 200 of 4000 known species are vectors (Heathcote, 1976). Palms are affected by very few virus diseases (Plumb *et al.*, 1978), a fact that may be related to the paucity of aphid species associated with palms (Nigel Harrison, personal communication).

Aphids are more diverse in temperate than in tropical regions. Even in the temperate zone, they are less diverse at lower latitudes and where floral diversity is relatively high. These trends are contrary to the general trends in biodiversity (Dixon, 1985).

The largest subfamily is Aphidinae, with more than 2000 known species, i.e. more than half of the known species of the family (Dolling, 1991). Most of the familiar aphid pests of farm and garden belong to this family; however, species of Aphidinae occur only occasionally and transitorily on palms.

The only important aphids on palms are in the genus *Cerataphis* (Hormaphidinae), which is native to Asia. Aphids of this genus form galls in dicotyledonous primary host plants and infest monocotyledons, including bamboos, *Pandanus*, Orchidaceae and palms, as alternate host plants (Blackman and Eastop, 1984).

The apterous forms of *Cerataphis* spp. on monocotyledonous hosts are usually not recognized as aphids by the casual observer. That they remain motionless for long periods is typical of aphids in general, but, because their legs are short and hidden beneath the body, they appear to be legless and sessile. They are strikingly similar to certain aleyrodids, sharing with them a circular, slightly convex shape, the division of the body into cephalothorax and abdomen, the blackish colour of the imagos, a fringe of white waxy filaments that circumscribes the body, and simple rather than compound eyes. Siphunculi, a key aphid character, are present, but are reduced to inconspicuous shallow rings.

Based on recent taxonomic research, two species of *Cerataphis* infest palms: *C. brasiliensis* (syn. *C. palmae*, *C. variabilis* and *C. fransseni*) and *C. lataniae* (Russell, 1996; Colour Plate 10a, b, Figs 3.18–3.20). *Cerataphis formosana* is considered a synonym of *C. lataniae* (Tao, 1999). The two species on palms are currently separated on the basis of 'dagger-like' setae on the

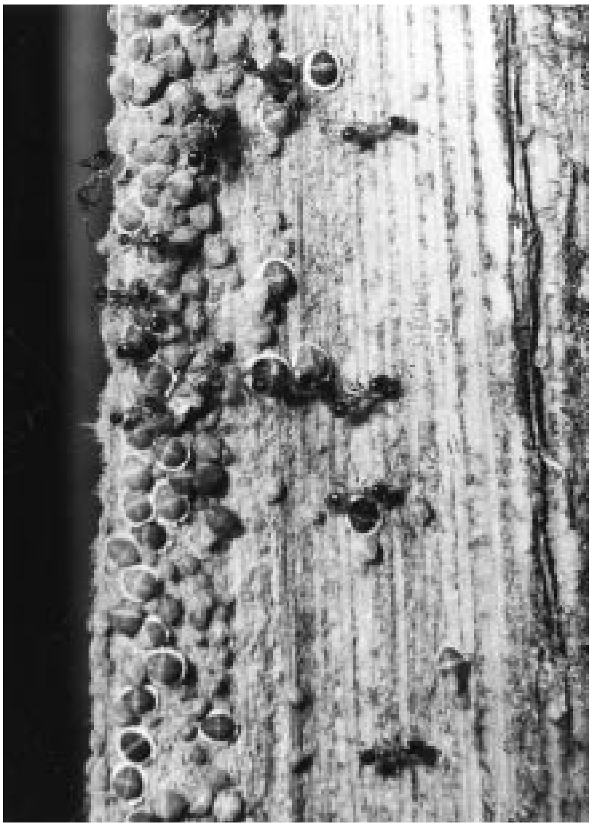


Fig. 3.18. *Cerataphis brasiliensis* (Aphididae: Hormaphidinae) infestation on coconut spear leaf. Photo by James V. DeFilippis.

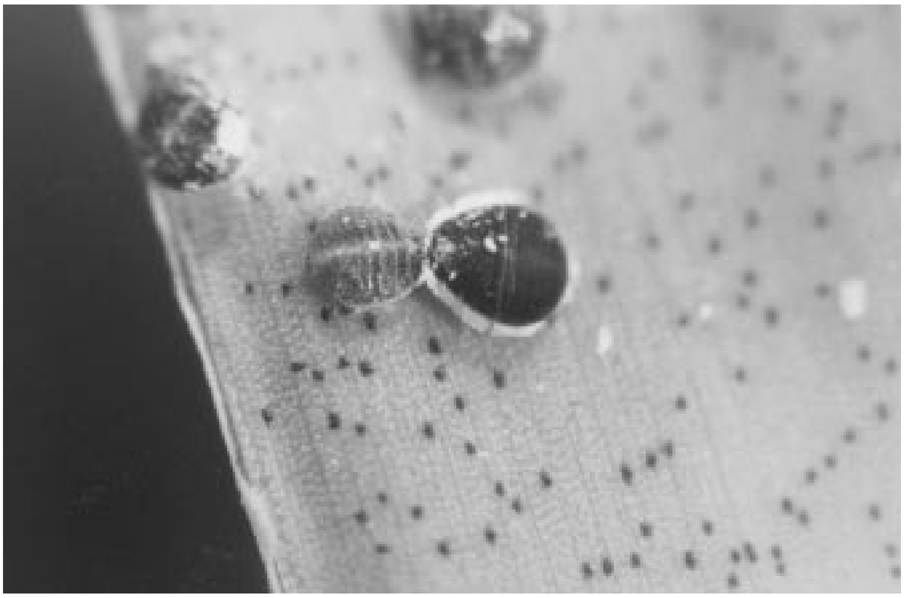


Fig. 3.19. *Cerataphis brasiliensis*, altercation between two individuals. Photo by Robin Giblin-Davis.

head of *C. brasiliensis*, which are lacking in *C. lataniae* (Russell, 1996). However, since this character is quite variable in the form identified as *C. brasiliensis*, some taxonomists question whether these are really distinct species (Susan Halbert and Georges Remaudière, personal communication). If indeed they are separate species, they have probably often been confused with each other and sometimes even with *Cerataphis orchidearum*, which infests orchids.

Cerataphis brasiliensis and *C. lataniae* have been widely disseminated and are now common on palms throughout the humid tropical regions of the world. Some of this dissemination took place early in the 20th century, as they were known in Puerto Rico by 1924 (Wolcott, 1936). They were apparently spread by movement of living palms, since there is no significant international commerce in *Styrax* plants, their alternate host. In contrast, many of the whiteflies, mealybugs and scale insects

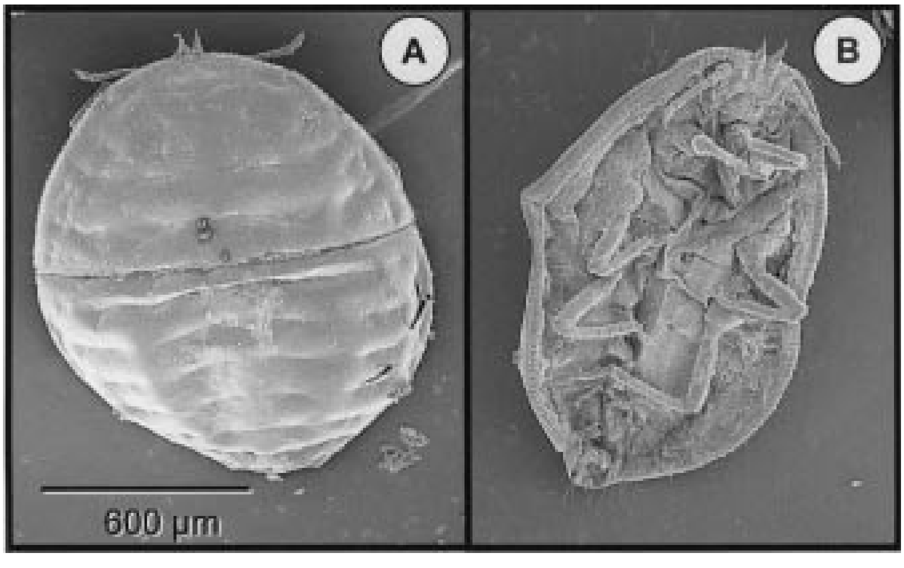


Fig. 3.20. *Cerataphis brasiliensis* adult, SEM views. (A) Dorsal view. (B) Ventral view. Note frontal horns.

that have achieved pantropical distribution on palms are highly polyphagous and may have been spread on other plants.

They apparently require a tropical climate, for they are common in southern Florida, but rare north of Lake Okeechobee (see Box 1.1). (Admittedly, fewer of their host-plant species grow in northern Florida, but *W. robusta*, a very suitable host, is common there.)

Stern *et al.* (1995) published details of the life history of *C. brasiliensis (*as *C. fransseni)* in its region of origin (Fig. 3.21). *Cerataphis brasiliensis* is native to tropical South-East Asia, where its primary host is *Styrax benzoin* (Styracaceae), a tree that occurs in humid, shady forests and is also cultivated (Backer and Bakhuizen van den Brink, 1965). Like many aphids, *C. brasiliensis* is polymorphic and alternates between hosts. Various species of palms are the alternate hosts. A specialized stage, the sexupara, migrates from palms to the primary host and produces males and oviparous (egg-laying) females, which then mate. The female is thought to lay a single egg, from which hatches an apterous form, which reproduces asexually and viviparously, i.e. by depositing live larvae rather than eggs. This form, referred to by aphid specialists as a fundatrix (i.e. the founder of the aphid colony), induces the formation of a gall in an axillary bud of *S. benzoin*, which becomes the home of the offspring that it produces.

The several generations produced within the gall develop into three forms: (i) apterous adults with highly sclerotized heads, which bear strong spinelike setae; (ii) similarly armed 'soldiers', which are second-instar sterile larvae, which fulfil the roles of cleaning excrement and exuviae from the interior of the gall and protecting the colony from certain intruders; and (iii) alates, which migrate and establish colonies on palms.

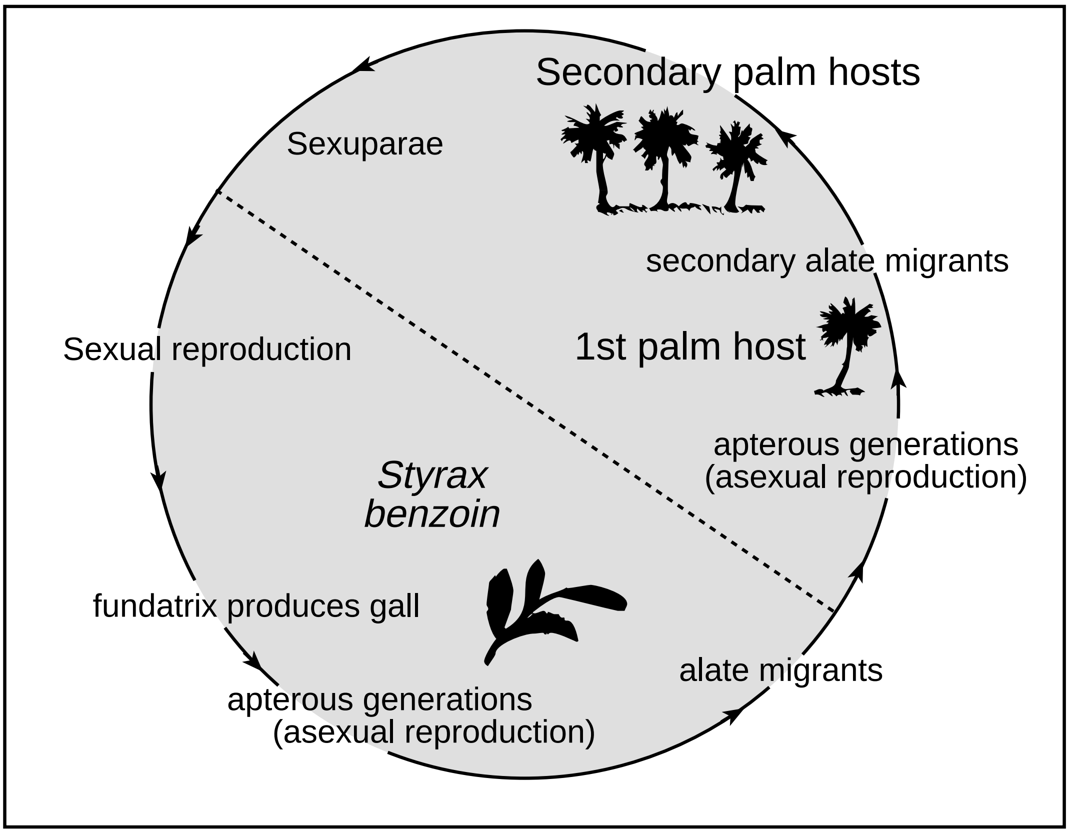


Fig. 3.21. Life cycle of *Cerataphis brasiliensis* in its native region in tropical Asia. The generations alternate between a dicotyledonous host (*Styrax benzoin*) and palm hosts.

The colonies on palms consist of blackish imagos and olive-coloured immature forms, of which there are three instars (Denmark, 1965). The colony that infests palms produces one to several generations of apterous individuals, but, at some point, some of the aphids develop into two kinds of alate migrants: some that fly to new palms to establish colonies there, and the sexuparae, which migrate back to *S. benzoin*.

In tropical countries where *C. brasiliensis* is present but *S. benzoin* is absent, *C. brasiliensis* apparently lives entirely on palms. The alates are rarely seen. Palm aphids of all stages on palms in Florida were observed to engage in 'duels', apparently for feeding sites (Howard *et al.*, 1998).

Aphids in general migrate when the quality of their host plant deteriorates or when their own populations become extremely dense. In some species, aphid colonies respond to increased mutual contact due to increasing population density by producing alates (Dixon, 1985). Over short distances, aphids fly randomly to plants, probe them and quickly leave those that do not have chemical and physical cues that they associate with their host plant (Dixon, 1985). In some cases, aphids may be passively dispersed for long distances by air currents (Hardy and Cheng, 1986).

Aphids have a formidable ability to rapidly expand their populations once they have become established on a host plant. Aphid reproduction usually involves parthenogenesis, viviparity and 'telescoping of generations' (i.e. the development within a parthenogenetic female of parthenogenetic larvae, which in turn contain developing embryos), a combination that results in extremely rapid development of colonies from solitary females that successfully find host plants (Dixon, 1985). In studies in a glasshouse in the Philippines, *Cerataphis* sp. developed from first instar to imago in 6–11 days and produced 91 young per female during a reproductive period of abut 23 days. No males were observed (Sumalde and Calilung, 1982).

Cerataphis spp. form dense aggregations on the unopened and younger fronds of palms and sometimes the inflorescence. Their gregarious habit is typical of myrmecophilous (ant-associated) aphids, a habit that probably facilitates honeydew collecting and protection by ants (Colour Plate 10b). In Tanzania, relatively high numbers of *C. brasiliensis* (as *C. variabilis*) and of a pugnacious ant, *Anoplolepis custodiens*, on coconut palms were positively correlated (Lohr, 1992), and similar relationships between palm aphids and ants are probably universal. In Florida, various species of ants tend palm aphids. An aggressive exotic ant, *Solenopsis invicta*, is particularly effective in protecting them from coccinellid predators (F.W. Howard, unpublished observations). Although these relationships have not been studied in detail in palm aphids, myrmecophilous aphid species in general respond to palpitation by ants by increasing their intake of phloem sap and excreting more honeydew. Under these conditions, the aphids develop more rapidly, produce more larvae and migrate less. However, in some cases, ants prey on the aphids that they tend, in effect culling them and regulating their population so as to conserve the host plant. When disturbed by an intruder, aphids emit an alarm pheromone. Ants that are symbiotic with the aphids may respond to this volatile chemical by becoming more active and thus protective of the aphids (Buckley, 1987).

Planting density and the bionomics of the ant species associated with the different populations of *C. brasiliensis* are probably major factors influencing the population densities of this species. Enobakhare (1994) reported that, in Nigeria, *C. brasiliensis* prefers younger to older palms.

Since aphids are prone to build up extremely dense populations, their effects on plants may be considerable. In addition to damage caused by feeding, aphids affect plants by producing honeydew, which supports sooty mould (Colour Plate 10a). Infested young palms in nurseries and seed-beds often become stunted. Dense populations on mature palms cause extensive necrosis on the younger fronds where the aphids tend to aggregate.

In southern Florida, diverse exotic palm species native to various regions are hosts of *C. brasiliensis*, e.g. coconut palms, *C. humilis, Cryosophila warscewiczii, Livistona chinensis, P. elegans* and *W. robusta*, but this aphid has not been observed on, for example, *A. merrillii, D. lutescens, Phoenix* spp. or *S. romanzoffiana*, all of which are common in the region. The aphid is not known to infest palms native to Florida (F.W. Howard, unpublished). They seem to prefer selections of 'Malayan Dwarf' coconut palms over the 'Jamaica Tall' variety (Reinert and Woodiel, 1974; Mariau, 1999b). In Nigeria, *Cerataphis* sp. is a pest of coconut palm, *Raphia hookeri* and *Raphia vinifera* and is less common on African oil palm. As a pest of coconut palm in Nigeria, it is rated as more serious than the armoured scale insect, *Aspidiotus destructor* (Hemiptera: Diaspididae) (Enobakhare, 1994).

Palm aphids have limited mobility on plants and thus are easy targets for even sluggish predators, such as syrphid and coccinellid larvae, which are among their principal natural enemies (Sumalde and Calilung, 1982). In Florida and elsewhere in the Americas, common native coccinellids, such as *Cycloneda sanguinea* and *Hippodamia convergens*, prey on palm aphids (Colour Plate 16d; F.W. Howard, unpublished). Many aphid species are attacked by parasitoid wasps, but this has not been reported in palm-infesting *Cerataphis* species. Ants associated with aphids are generally protective of them, but may regulate their populations, as discussed above. Ants that benefit aphid populations may otherwise be beneficial as predators of more severe palm pests, as was the case in Tanzania, where *A. custodiens* benefited palm-aphid populations, but reduced populations of *Pseudotheraptus wayi* and the damage it caused to coconuts. In this case, production of coconuts was not affected by the aphid infestations; thus the overall effect of the ant was beneficial (Lohr, 1992).

Several chemicals have been tested for control of palm aphids, and chemical control may sometimes be an option, especially in nurseries (Reinert and Woodiel, 1974; Jalaluddin and Mohanasundaram, 1990b).

Aleyrodidae

As Sternorrhyncha with alate males and females, the Aleyrodidae, or whiteflies, seem closely related to Psyllidae and Aphididae. But they share larval characteristics with the more advanced Coccoidea: their first instars are mobile 'crawlers' and subsequent instars are sessile. In contrast to aphids, which attain their greatest diversity in cooler regions, whiteflies are more diverse in the tropics. Opportunistic and transient, whiteflies may be considered as the tropical counterpart of aphids (Mound and Halsey, 1978). Perhaps whiteflies have thus had more opportunities than the latter group to adapt to palms.

There are about 1270 described species of this family (Martin, 1996). Most species of whiteflies are in the subfamily Aleyrodinae, which is widespread throughout the tropics and warm areas of the world. A second subfamily, the Aleurodicinae, contains only about 100 species, most of which are of neotropical origin. There are less than a dozen species of Aleurodicinae native to the eastern hemisphere, mostly endemic to Asia (Martin, 1996). The imagos of Aleurodicinae tend to be larger than those of Aleyrodinae, with greater development of wing veins and a more complex structure of fourth instars (Mound and Halsey, 1978).

The imagos of Aleyrodidae are soft, fragile insects, 1–3 mm long. The broad forewings and hind-wings are similar in length and are held tectiform when at rest. The integument, variously coloured in different species, is coated with white powdery wax, secreted from abdominal glands. Females, which are very similar in appearance to the males, typically lay eggs in circles, spirals or, in some species, loose clumps, depositing flocculent or dustlike wax particles on the oviposition site. The mobile first-instar crawlers wander a few millimetres from where they hatch before settling. The remaining immature instars are sessile, with vestigial legs. In the fourth instar a drastic transformation takes place, after which the insect moults to the alate male or female adult stage. The fourth instar of aleyrodids is often referred to as a pupal stage, because it is transitional between the highly dissimilar larval and adult stages. However, because the fourth instar feeds initially, it is unlike the pupal stage of endopterygote insects (Mound and Halsey, 1978; Gill, 1990b; Dolling, 1991).

Because species may be distinguished by the arrangement of pores and other minute structures of the fourth instar and this stage is easier to collect than the more transitory imagos, it has long been the stage used for identification of aleyrodids. Specimens at this stage are mounted on microscope slides, using techniques similar to those used for Coccoidea (Martin, 1987).

The immature stages produce waxy secretions. Those of the fourth instar are elaborate and often distinctive for each species. Most have a marginal fringe of wax filaments, which may be tubular, attenuated to points, ribbon-like, etc., and many species also secrete dorsal filaments. The appearance of the fourth instar may vary in response to the texture of the substrate.

Aleyrodid imagos and immature forms each have a distinctive structure on the last abdominal segment, called the *vasiform orifice*, which bears the anus and a flap. Its unique morphology is useful for distinguishing immature whiteflies from Coccoidea. The adult emerges through a T-shaped exit slit in the exuviae of the fourth instar. This is easily distinguished from the small, rough-edged, circular exit holes of parasitoids.

The insects of this family are predominantly associated with dicotyledonous woody perennial plants. Whiteflies feed mostly on phloem sap, so far as is known (Dolling, 1991). Aleyrodidae are one of the families of Hemiptera known to transmit plant pathogens. About 70 virus diseases are transmitted by whiteflies, but only a few species of this family have been incriminated as vectors (Heathcote, 1976; Cohen, 1990). Most of these virus diseases affect annual crop plants. Very few whitefly-borne viral diseases are known in woody perennials (Byrne *et al.*, 1990) and none are known to affect palms. Thus, whiteflies may affect palms directly, through feeding, and indirectly, by producing honeydew, which supports sooty mould, but are not known to affect palms indirectly via disease transmission.

Because whitefly identification is based on the sessile fourth instar, host data for species are relatively complete and reliable, as is the case with the Coccoidea. Plant species upon which whiteflies have laid eggs have sometimes been recorded as hosts. This leads to errors, because whitefly imagos sometimes visit and even oviposit on plant species that do not support their larval development (Howard and Neel, 1977). However, aleyrodids that attain the fourth instar on a plant may be expected to complete development to the adult stage.

High host specificity is characteristic of Aleyrodidae: more than 85% of the known species have five or fewer hosts (Mound and Halsey, 1978; Byrne *et al.*, 1990). But aleyrodid pests of agricultural crops are usually highly polyphagous, and a good portion of aleyrodids on palms come from their ranks. Most of the species that infest palms also infest dicotyledonous hosts, and are probably primarily adapted to them.

Forty-three species of Aleyrodidae (i.e. about 3.8% of the known species) were listed on palms by Mound and Halsey (1978). These were almost equally divided between Aleyrodinae and Aleurodicinae. Since Aleyrodinae have about 12 times more species than Aleurodicinae, the latter family is proportionally far better represented on palms. About 80% of the whiteflies reported on palms were on coconut palm (Table 3.4). Because this palm species is ubiquitous in the tropics and is grown in extensive monocultures, it is an easy target for whiteflies. Additionally, coconut palms are examined for pests far more often than most palm species.

Table 3.4. Species of Aleyrodidae reported on palm hosts (compiled from records in Mound and Halsey, 1978, unless otherwise noted).

Species of Aleyrodidae	Palm hosts	Other hosts	Distribution
Aleyrodinae			
Acutaleyrodes palmae	*Acanthophoenix rubra*	nr	Réunion
Aleurocanthus bambusae	*Phoenix dactylifera*	M*	India
Aleurocanthus cocois	*Cocos nucifera*	D*	India, South-East Asia
Aleurocanthus dissimilis	*C. nucifera*	nr	Myanmar
Aleurocanthus gateri	*C. nucifera*	nr	South-East Asia
Aleurocanthus nubilans	*Areca catechu*	D*	India
Aleurocanthus palauensis	*C. nucifera*	nr	Palau Islands
Aleurocanthus woglumi	*Elaeis oleifera*	M* D***	Pantropical
Aleurocanthus yusopei	*C. nucifera*	nr	Malaysia
Aleuroglandulus magnus	*Chamaedorea wendlandiana, Synechanthus warscewiczianus*	nr	Panama
Aleuroglandulus subtilis	*C. wendlandiana, S. warscewiczianus*	D*	Brazil, Panama
Aleuroplatus andropogoni	*Adonidia merrillii, C. nucifera, Elaeis guineensis*	D**	West Africa
Aleuroplatus cococolus	*C. nucifera*	D*	West Indies, Brazil
Aleurotrachelus atratus	*C. nucifera*	nr	Tropical America
Aleurotrachelus serratus	Wild unidentified palm	nr	Riau Archipelago (Indonesia)
Aleurotrachelus stellatus	*C. nucifera*	D*	Brazil
Anomaleyrodes palmae	Unidentified palm	nr	Madagascar
Dialeurodes citri	*Sabal megacarpa*	D***	Cosmopolitan
Dialeurodes simmondsi	*C. nucifera*	nr	Malaysia
Dialeuropora papillata	*E. guineensis*	D**	West Africa, Chad
Tetraleurodes palmae	*E. guineensis*	nr	Sudan
Aleurodicinae			
Aleurodicus antillensis	*C. nucifera*	D*	Puerto Rico
Aleurodicus coccolobae	*C. nucifera*	D**	Tropical America
Aleurodicus cocois	*C. nucifera, Washingtonia robusta*	D***	Tropical America
Aleurodicus destructor	*C. nucifera*	D**	Australia, Oceania, South-East Asia
Aleurodicus dispersus	*A. merrillii, Caryota mitis, Chamaedorea* spp., *Coccothrinax argentata, C. nucifera, Dypsis lutescens, Scheelea leandroana, Washingtonia* spp. plus others	D***	Pantropical
Aleurodicus flavus	*C. nucifera*	D*	Brazil
Aleurodicus jamaicensis	*C. nucifera*	D*	Jamaica
Aleurodicus neglectus	*C. nucifera*	D**	Southern Caribbean, South America
Aleurodicus ornatus	*C. nucifera*	D*	Jamaica
Aleurodicus pulvinatus	*C. nucifera*	M* D**	Brazil, Guyana, Trinidad
Aleurodicus trinidadensis	*C. nucifera*	D*	Trinidad
Aleuronudus bahiensis	*C. nucifera*	D*	Brazil
Aleuronudus induratus (syn. *Petaleurodicus induratus*)	*C. nucifera*	nr	Brazil

Table 3.4. *continued*

Species of Aleyrodidae	Palm hosts	Other hosts	Distribution
Ceraleurodicus assymmetricus	*C. nucifera*	nr	Brazil, Trinidad
Ceraleurodicus moreirai	Unidentified palm	D*	Brazil
Ceraleurodicus splendidus	*C. nucifera*	nr	Brazil
Lecanoideus floccissimus	*C. nucifera, Howea forsteriana, P. dactylifera, Washingtonia filifera, W. robusta* plus others (Carnero *et al.*, 1999)		Ecuador, Canary Islands
Nipaleyrodes elongata	*Nypa fruticans*	nr	Malaysia
Octaleurodicus nitidus	*C. nucifera*	nr	Brazil
Octaleurodicus pulcherrimus	*C. nucifera*	nr	Trinidad
Paraleyrodes crateraformans	*C. nucifera*	D*	Brazil
Paraleyrodes pulverans	*C. nucifera*	D*	Brazil
Stenaleyrodes vinsoni	*C. nucifera, D. lutescens, P. dactylifera, Roystonea regia*	nr	Réunion, New Caledonia, Loyalty Islands

M, monocotyledons; D, dicotyledons; nr, none reported. The number of asterisks indicates the importance of the host category, e.g. M*, few monocotyledonous hosts; M***, many monocotyledonous hosts.

According to Byrne *et al.* (1990), whiteflies are reported from about 40 woody biennial or perennial crops, but are significant pests in about eight, one of which is coconut palm. But, while whiteflies are generally common on coconut and some other species of palms, typically occurring in small aggregations on the abaxial surfaces of fronds, dense infestations are observed on coconut palms only occasionally and their importance is usually eclipsed by pests deemed to be more damaging. For example, whiteflies were not even mentioned in lists of important pests of coconut palms provided by entomologists in several important coconut-growing regions, including Sri Lanka (Priyanthie Fernando), Brazil (Dalva Luiz de Queiroz Santana, Joana Maria Santos Ferreira), Quintana Roo, Mexico (Humberto Carrillo Ramírez), and Guerrero, Mexico (Laura Sampedro Rosas). They have never been reported as pests of date palm or African oil palm.

Of the exceptional species that are occasional pests of coconut palm, four are species of *Aleurodicus* (Aleurodicinae). The imagos of these species are white and, being aleurodicines, they are large for aleyrodids. They lay eggs in spirals, depositing white wax patches among them. As the immature stages develop, they produce a thick mass of flocculent white wax threads, which almost completely obscures them.

Aleurodicus cocois is an aleurodicine whitefly that attacks palms and other plants in tropical America. It was reported as the principal pest of coconut palms in Barbados in the first half of the 19th century (Curtis, 1846; see Box 3.3) and in Guadeloupe in 1920 (Dash, 1922). It is currently known to be distributed in Jamaica, the Lesser Antilles, Mexico, Central America and northern South America (Mound and Halsey, 1978). An additional palm host is *W. filifera* (Lepesme, 1947). It is one of several similar whitefly species that may be encountered on sea-grape (*Coccoloba uvifera*, Polygonaceae) bordering Caribbean beaches, and on guavas in the countryside. Two coccinellids, *Cryptognatha nodiceps* and *Exoplectra* sp., are recorded as predators of *A. cocois* (Mound and Halsey, 1978), and these and, presumably, additional natural enemies probably keep populations of this insect under control most of the time.

Aleurodicus pulvinatus was recently reported as a pest of coconut palms in St Kitts and Nevis in the Leeward Islands, West Indies. Currently, it is causing problems in Antigua (Gillian Watson, personal communication). It also attacks sea-grape, guavas and other tropical plants, and is

Box 3.3. A whitefly on coconut palms in the time of Wordsworth.

During the first half of the 19th century, the Industrial Revolution underwent its greatest expansion and Romanticism flourished in art and literature. For biologists, one of the more prominent events was Charles Darwin's voyage around the world on HMS *Beagle*. Had we lived during that period, we would have been writing about insects and palms with a quill or perhaps one of the new stick pens. Some of our illustrations might have been the newly introduced daguerreotypes. And it was during this period that modern applied entomology had its beginnings, as agriculture began to modernize and undergo a vast worldwide expansion. On the island of Barbados, coconut plantations were attacked by a previously unknown species of whitefly. *Aleurodicus cocois*, described by John Curtis (1846), was one of the earlier whitefly species described in scientific literature and one of the first insects reported as a pest of palms. Curtis, who sometimes used the pseudonym Ruricola, was the author of the eight-volume work *British Entomology*, and one of the first British professional entomologists. His discussion, published with his description of *A. cocois*, provides a glimpse into early Victorian applied entomology.

Aleurodicus cocois was first noticed when it became abundant on fronds of coconut palms on Barbados after a hurricane in 1831. A planter, Sir Robert Schomburgh, surmised that the whitefly was brought to Barbados not by the hurricane itself (the island is the easternmost of the West Indies), but on coconut palm seedlings imported from some other island for replanting after the hurricane. According to Sir Robert, the whitefly infestation was at levels sufficient to kill lower fronds, thus causing a decline in coconut production. It was Sir Robert who tentatively identified the insect as 'allied to *Aleyrodes*' and sent specimens to John Curtis in England.

Curtis described this 'white mealy fly' as a species of the genus *Aleyrodes*, while expressing an inclination to treat it as member of a separate genus. He noted its large size and details of structure that later authors would consider distinguishing characteristics of the subfamily Aleurodicinae.

The planters were desperate enough to contemplate eradicating the whitefly by uprooting all coconut palms on the island and replanting after a year. Curtis suggested a less drastic measure: he thought that applications of sulphur would be effective, and stressed the importance of applying it simultaneously on all palms, or when the insects were inactive. He recommended examining palm species additional to coconut as possible reservoirs of infestation, and commented that *Scymnus* beetles (Coccinellidae) destroyed the European *Aleyrodes*. *Aleurodicus cocois* was out of control, he suggested, because it was introduced into Barbados without its 'usual attendant antidote' (natural enemies). More than a century and a half later, a present-day applied entomologist's analysis of and recommendations for this problem would differ only in minor details.

probably often confused in the field with *A. cocois*. The two species can be distinguished reliably only by examination of microscope slides of the fourth instars (Martin and Watson, 1998).

Asian species of *Aleurodicus* are probably not congeneric with the neotropical species of *Aleurodicus* (Martin, 1996), but, in its relationships with palms, *Aleurodicus destructor* could be perceived as an Asian and Pacific counterpart of *A. cocois* (Fig. 3.22). Discovered in 1911 as a pest infesting coconut palms along the east coast of Negros Island, Philippines, the whitefly was subsequently found in additional islands of this archipelago, in some cases at outbreak levels (Mackie, 1917). Although hymenopterous parasitoids were associated with the whiteflies, they did not appear to curtail the whitefly populations sufficiently, and removal of infested fronds was recommended for control (Mackie, 1912). The species was subsequently recorded in additional localities in the Philippines and in Malaysia, Indonesia, Australia, New Guinea and the Solomon Islands (Mound and Halsey, 1978). Several dicotyledonous host plants have been reported as hosts, including *Annona squamosa* (Annonaceae), *Ficus* sp. (Moraceae) and *Banksia* sp. (Proteaceae) (Mound and Halsey, 1978).

Aleurodicus destructor continues to be a pest of coconut palm in the Philippines, but is not considered to be as serious a pest as, for example, the coconut scale insect,

Fig. 3.22. *Aleurodicus destructor* (Aleyrodidae), adults on coconut palm foliage. Photo by A.A. Loyola.

Aspidiotus destructor, partly because it does not attack the fruits. Natural enemies of *Aleurodicus destructor* include the predators *Scymnus* sp. (Coccinellidae), *Bacca* sp. (Syrphidae), *Chrysopa* sp. (Neuroptera), Formicidae and Araneae (Arachnida), and the parasitoids *Coccophagus* sp. (Chalcidoidea: Aphelinidae), and *Tetrastichus* sp. (Chalcidoidea: Eulophidae) (Mound and Halsey, 1978; Loyola, 1994).

Aleurodicus dispersus has been spread more widely around the world than any other aleyrodid that infests palms. Known as the spiralling whitefly, because of the pattern in which it lays its eggs (although this is a behavioural trait of many other whitefly species), its masses of fluffy, white, wax secretions are conspicuous on palm fronds (Russell, 1965). Like most palmivorous aleyrodids, it is polyphagous, having been reported on and considered an occasional pest of bananas and many tropical dicotyledonous crop plants, e.g. avocado, cacao, citrus, guava, mango, papaya, etc. (Table 3.4).

In a test in Florida comparing the total number of eggs laid and the survival of *A. dispersus* on seven different host plants, Cherry (1980) found that coconut palm (the only palm in the test) was second to *Bucida buceras* (Combretaceae) as a host. The broad, stiff fronds of palms and of seagrape are apparently exceptionally favourable for harbouring colonies of this whitefly. Thus, these plants are apt to be infested if *A. dispersus* is in the area (Weems, 1971; Cherry, 1980). However, host-plant preferences of the insect seem to differ with locality and conditions. In fact, in most areas it is considered more important on plants other than palms. For example, in Kerala, India, where 72 host plants of this insect were recorded, *A. dispersus* populations were dense on guava and 21 other dicotyledons, but low on coconut palm (Prathapan, 1996).

Described in 1965, *A. dispersus* was reported from 38 genera of 27 plant families (Russell, 1965). The specimens she examined had been collected from 1905 through the 1960s from diverse localities of tropical America, from Brazil through Central America, Florida and numerous Caribbean Islands. Russell also had specimens from the Canary Islands. Thirteen years after Russell's report, no changes were reported in the insect's known distribution (Mound and Halsey, 1978).

In 1978, *A. dispersus* was discovered on Oahu, in the Hawaiian Islands, representing a dramatic extension in its distribution, and within 3 years it was established on the islands of Kauai, Maui, Molokai, Lanai and Hawaii (Kumashiro *et al.*, 1983). Spreading westward across the Pacific, it was found in the Philippines by 1983 and the Malay Peninsula around 1990. It has since reached Thailand, southern India, Sri Lanka and the Maldive Islands (Martin, 1996). In 1992 it was found in Nigeria, West Africa, and was said to be present in additional African countries (Akinlosotu, 1993). It was recently reported in Madeira, 420 km north of the Canaries (Martin, 1996). Thus, in little more than a decade the species achieved a circumtropical distribution.

A situation involving *A. dispersus* in the Canary Islands appeared to mirror on a smaller scale the history of its worldwide dispersal, with a latent period of three decades followed by a population explosion and rapid expansion of its distribution. But this concept of the insect's history in these islands seems to have to been illusory, as discussed below.

First reported in the Canaries from a single collection on *Schinus terebinthifolius* on the island of Gran Canaria (Russell, 1965), *A. dispersus* remained an uncommon insect in the Canaries for many years, living on palms and many other kinds of plants. In 1990, there was a population explosion of a whitefly thought to be *A. dispersus* on the south side of Tenerife (Manzano *et al.*, 1995). By 1997, dense whitefly populations were present on palms and other plants in virtually all coastal areas of Tenerife and in some areas of Gran Canaria, with more limited infestations reported from the islands of Fuerteventura and La Gomera (Carnero *et al.*, 1999).

What happened? A sudden change in the insect or its environment, or the introduction of a second, better-adapted strain of the species? Martin *et al.* (1997) found an explanation when they discovered a new species of whitefly on Tenerife, which was very similar in appearance to *A. dispersus* and affected many of the same host plants. This species, *Lecanoideus floccissimus* (Colour Plate 10c), is native to tropical America, having also been found in Ecuador on African oil palms. The two species are difficult to distinguish in the field, and valid identifications must be verified by examining slide-mounted specimens under a compound microscope. In the Canaries, *L. floccissimus* has been collected from 29 genera in 16 plant families, including 15 species of palms.

Coccinellid predators, e.g. *Scymnus* sp., have been observed to attack both *A. dispersus* and *L. floccissimus* in the Canary Islands. A species of *Encarsia* parasitizes *A. dispersus* there (Martin *et al.*, 1997) and may be its principal population-regulation agent. No evidence has been found for a parasitoid of *L. floccissimus* in the Canaries. Apparently, the rampant spread of this whitefly has been possible partly because it has no natural enemies in these islands. Emergence holes were seen in the fourth instar of this species in Ecuador, indicating that this country could be a source of natural enemies for biological control of *L. floccissimus*. A recent undated circular, distributed by the Consejería de Agricultura, Pesca y Alimentación of the Canary Islands government, lists buprofezin, imidacloprid and summer oils as chemical controls for this pest.

Several decades ago, a combination of circumstances drew attention to *A. dispersus* as a possible vector of a serious palm disease. First, the presence of the insect in Key West, Florida, coincided, at least approximately, with the appearance there of lethal yellowing disease (q.v.). The earliest record of *A. dispersus* in Florida listed by Russell (1965) was 1957 in Key West. During the 1960s, populations there built up on coconut palm and many other species of plants. Lethal yellowing broke out in Key West in 1955 and was rampant during the early 1960s. It was suspected to be caused by a virus. Phytoplasmas, later implicated as the causal organism, were not known to cause plant diseases until the later years of that decade. Later, the spread of the whitefly to the upper Keys coincided with the appearance of lethal yellowing on Key Largo in 1970.

Meanwhile, in experiments conducted

in Jamaica, some immature palms exposed in cages to a whitefly, *Aleurodicus jamaicensis*, became affected with what appeared to be lethal yellowing (Romney, 1972). This was a tentative diagnosis, since the clearest symptoms of the disease are in the inflorescence and fruits (which immature palms lack), and laboratory tests for confirming diagnoses of this disease (Box 3.2) had not yet been developed.

Thus, these observations in Jamaica and Florida seemed to incriminate whiteflies as possible vectors of lethal yellowing (Russell, 1965; Weems, 1971). However, by 1972 it was determined that lethal yellowing was associated with phytoplasmas. Then as now, whiteflies were not known to transmit phytoplasmas. Additionally, although both lethal yellowing and *A. dispersus* invaded the Florida mainland during the early 1970s, based on observations since then their distributions do not coincide (F.W. Howard, unpublished). Similarly, no coincidence has been reported between whitefly species and lethal yellowing in Jamaica, Mexico or Central America. Finally, the transmission experiment in Jamaica referred to above was inconclusive, and further attempts to experimentally transmit lethal yellowing with whiteflies were unsuccessful (Romney, 1972). Thus, *A. dispersus* is not currently considered a putative vector of lethal yellowing.

Aleurodicus dispersus was considered a pest of palms and other ornamental plants in southern Florida in the late 1970s and early 1980s. During this period, Cherry (1980) observed no parasitoids of this species in Florida. In the late 1970s, an explorer of the Hawaii Department of Agriculture discovered natural enemies of *A. dispersus* in Central America, including *Nephaspis oculatus* (as *Nephaspis amnicola*) (Coccinellidae) and *Encarsia* sp. near *E. haitiensis* (Aphelinidae). These were released in the Hawaiian Islands, resulting in a 79% reduction of *A. dispersus* in lowland Honolulu and a 99% reduction in highland Honolulu (Kumashiro *et al.*, 1983). These natural enemies were then released in Florida. It was subsequently determined that the coccinellid had been in Florida all along and had apparently had no noticeable impact on *A. dispersus* populations in this state. The aphelinid, on the other hand, apparently failed to become established in Florida. By the early 1980s, populations of *A. dispersus* subsided in Florida. A parasitoid, *Euderomphale vittata*, which was apparently fortuitously introduced during that period, is believed to have caused this decline (Bennett and Noyes, 1989). In Florida, *A. dispersus* is currently distributed only in sporadic populations in the southern coastal regions of the peninsula and the Keys.

Aleurotrachelus atratus (Aleyrodinae) was described in 1922 from specimens collected from coconut palm in Bahia, Brazil (Lepesme, 1947; Mound and Halsey, 1978; Colour Plate 10d). Bondar (1940) considered it the most common aleyrodid on coconut palms in that region, noting that populations were often sufficient to cause leaf necrosis. Otherwise, it was not noticed much until recently, when it was found to have extended its distribution. It was collected for the first time in Florida in November 1989 on *Syagrus schizophylla* and subsequently found to be widely distributed in southern Florida on various palms, including coconut palm, African oil palm and *A. merrillii.* The Natural History Museum (London) collection contains specimens from the Canary Islands, St Helena, Antigua, Barbados, Nevis, Puerto Rico, Bermuda, Bahamas, Brazil, Colombia, Guyana and Venezuela (Gillian Watson, personal communication). A whitefly that appeared to be *A. atratus* was seen on coconut palms in Dominica and Costa Rica (F.W. Howard, unpublished).

Adult females on coconut palm in Florida have been observed resting near aggregations of 14–32 eggs. Based on our observations, *A. atratus* has three immature instars, the third corresponding to the fourth or ‘pupal’ stage of most aleyrodids (Fig. 3.23). Based on measurements of specimens of *A. atratus* mounted on slides, the lengths (mm) of different instars are as follows: first, 0.40–0.45 ($n = 7$); second, 0.60–0.72 ($n = 8$); and third, 1.00–1.10 ($n = 7$).

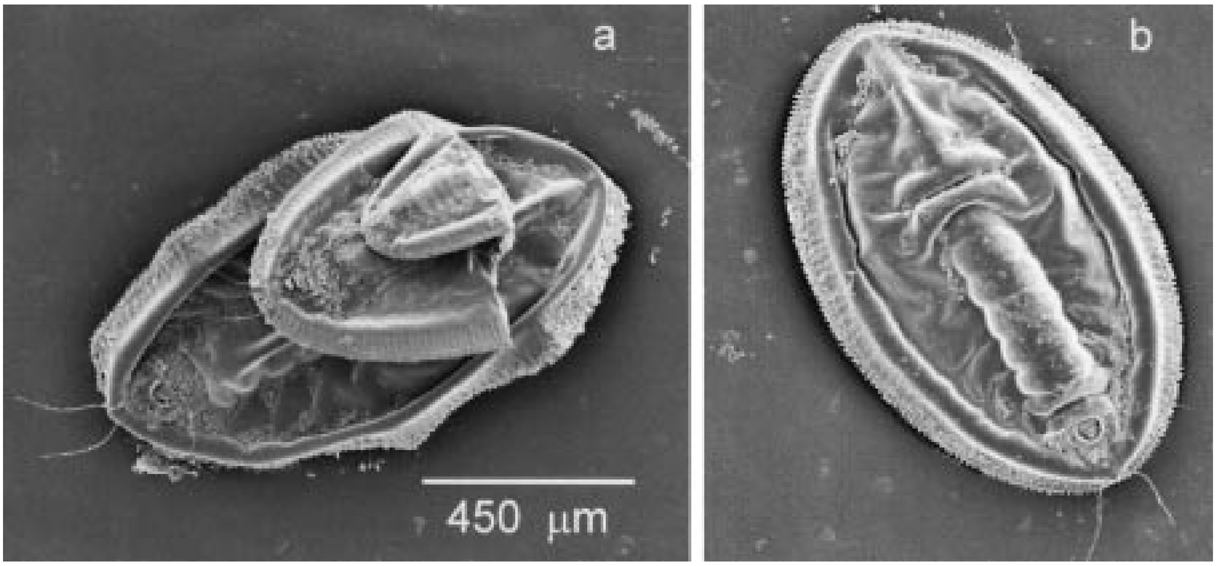


Fig. 3.23. *Aleurotrachelus atratus* (Aleyrodidae), SEM views of third-instar larvae. The second-instar exuviae may remain attached to the third instar (a), or fall off as in (b). The larval stage of *A. atratus* has three instars, instead of four as in most Aleyrodidae.

The survival of *A. atratus* in southern Florida was challenged by an unusually powerful tropical storm, Hurricane Andrew, on 24 August 1992. Observations of insects on palms were conducted north of the path of this category 4 storm in Fort Lauderdale, where, based on damage to trees and structures, we estimated that there were sustained winds of 90–150 km per hour for several hours. Although we had few prestorm population data on *A. atratus*, when we examined fronds of coconut palm 17 days after the storm we found that many whiteflies had survived. On the sixth frond of a young 'Panama Tall' coconut palm selected for examination, 58 of 84 leaflets were infested with *A. atratus.* Fifty randomly selected eggs examined with a hand-lens appeared to be turgid and viable. Five each of second and third instars selected for observation produced wax filaments within 24 h of our having removed them, indicating that they were alive. Adult *A. atratus* were present, some near egg clusters. Presumably they had emerged since the storm, rather than survived it in the adult stage. These observations indicate that whiteflies are well adapted to surviving tropical storms. This is probably true of sessile insects in general, especially those that infest palm fronds, since these are relatively wind-resistant.

Currently, *A. atratus* occurs in light populations on palms in southern Florida. Parasitoid exit holes were observed in final instars, but the parasitoid species have not yet been identified.

Coccoidea

The superfamily Coccoidea includes the mealybugs and the scale insects, grouped into 17–22 families, according to different authorities. Almost 8000 species have been described. Excellent reviews on the bionomics and ecology of the Coccoidea were published by Beardsley and Gonzalez (1975), Miller and Kosztarab (1979), Rosen (1990) and Gullan and Kosztarab (1997). These insects are distinctive for their sluggish or sessile habits, reduced morphology and the waxy secretions they produce. The sessile habit of the more advanced forms is more highly evolved than that of the Aleyrodidae, and the production of waxy secretions reaches a high degree of specialization. These secretions, which are mixtures of true waxes plus lipids, resins and other substances, are produced by integumentary wax glands, which range from thousands per individual in the more primitive Margarodidae (giant coccids) to less than 100 per individual in some species of the more advanced Diaspididae (armoured scale insects) (Brown, 1975; Foldi, 1991; Gullan and Kosztarab, 1997).

Viewed dorsally, the adult females of coccoids are typically elongate, elliptical or circular, and they are flat to hemispherical or globulous in profile, with little if any distinct demarcation between head, thorax and abdomen. The mature females of mealybugs (Pseudococcidae) and other less advanced taxa have functional legs. In Coccidae, which are more advanced than Pseudococcidae, the legs of mature females of some species are functional, but in others are reduced or absent. In the most advanced family, Diaspididae, mature females are always legless. Females of all Coccoidea are apterous. Metamorphosis of the females is gradual, usually taking place through two or more instars before attaining the mature stage. Females may live several months or more (Gullan and Kosztarab, 1997).

Male development proceeds through five or six instars. The last two are reminiscent of the prepupal and pupal stages of endopterygote insects and are sometimes referred to by those terms (see introduction to Sternorrhyncha).

Adult males are usually winged, but, with few exceptions, only the first pair of wings is developed and functional; the metathoracic wings are absent or reduced to halteres. The order Diptera and some species of Ephemeroptera are the only other insects that share the two-wing condition. Males are ephemeral and lack functional mouth-parts. Coccoidea are distinguished from other Sternorrhyncha in that all but some Margarodidae possess tarsi of one, rather than two, distinct tarsomeres. This feature is evident in the crawlers and males (Williams, 1991).

Many coccoids reproduce sexually, but an unusually diverse array of kinds of parthenogenesis is found in the superfamily. Most species are oviparous, but viviparity (giving birth to larvae) is more common than in most insect taxa.

The first instars, or crawlers, of Coccoidea are generally small, flat creatures with fragile legs and simple eye-spots, which probably provide only rudimentary vision. The crawler's function is to wander over the plant and select a feeding site. In the more advanced Coccoidea, e.g. Diaspididae, this and the male are the only mobile stages.

Most crawlers settle on the natal plant, i.e. the plant on which they were hatched, but a percentage of them may be lifted and carried by air currents. Some crawlers may be dispersed by phoresy or transported on host plants carried in marine drift (Williams, 1984). Tremendous numbers of airborne crawlers undoubtedly perish because they fail to land on suitable host plants. Such passive dispersal seems astonishingly inefficient, but it is obviously effective. Only one female crawler need land on a plant. When mature, it can attract a winged male, mate and initiate a population.

How far can scale-insect crawlers be dispersed by air currents? This question is often raised, especially in connection with control of scale insects in areas near sources of reinfestation. It is similar to the question of how far a feather can be dispersed by air currents: the distance is undoubtedly highly variable. Certain wind speeds, in combination with other factors, are probably optimal for dispersal of crawlers. Gentle winds with up-draughts would seem to be most effective for dispersal; very strong winds may blow crawlers off plants without depositing them on new hosts.

Families of the Coccoidea, from the relatively primitive, in which all stages are mobile, to the most advanced, in which all but the crawlers and males are sessile, are progressively more elaborately protected by their wax secretions. Mealybugs have at least limited mobility throughout life and produce a mealy or flocculent wax, which coats the body. Most species of Coccidae excrete a waxy coating over their bodies, which suggests a step towards the development of a true scale. Diaspididae produce and sculpt a protective scale, beneath which they reside.

All species of Coccoidea feed exclusively on plant juices by inserting long, sucking stylets into the host plant. When not inserted, as when crawlers are searching for a feeding site, the stylets remain coiled in a crumena, i.e. a special invagination. The crawlers and females of all stages feed. Males feed only in the first two instars; adult males have vestigial mouthparts. Species of Pseudococcidae, Margarodidae, Ortheziidae, Eriococcidae, Dactylopiidae, Kermesidae, Kerriidae, Coccidae, Cerococcidae, Lecanodiaspididae and Stictococcidae produce honeydew and probably in most cases are trophobiotic with ants (Formicidae) (Williams, 1984; Buckley, 1987). However, honeydew is not produced in Asterolecaniidae, Halimococcidae or the largest family, Diaspididae. Diaspidids are believed to return waste products to the plant via the mouth-parts or use them in fabricating the scale (Banks, 1990).

The structure of minute features, especially the wax-producing glands and the dermal structures that serve as conduits for the glandular products, is important in distinguishing families of Coccoidea. To observe these, the specimens must be cleared, stained, mounted flat on glass slides and examined under a compound microscope. Preparing and mounting the specimens is a rather lengthy process and requires considerable skill (McKenzie, 1956; MacGregor, 1972; Perricone, 1988; Wilkey, 1990). The taxonomically important features distinguishing families are discussed in detail in Kosztarab (1982), Carver *et al.* (1991) and Williams (1991) and an annotated key to coccoid families was published by Howell and Williams (1976). In fieldwork, however, most Coccoidea can be recognized, at least to family level, by the gross morphology of the insect and the waxy secretions, such as a scale or ovisac.

Ten families of Coccoidea (i.e. about half of the families of the superfamily) are significant on palms (Fig. 3.24). Much of the

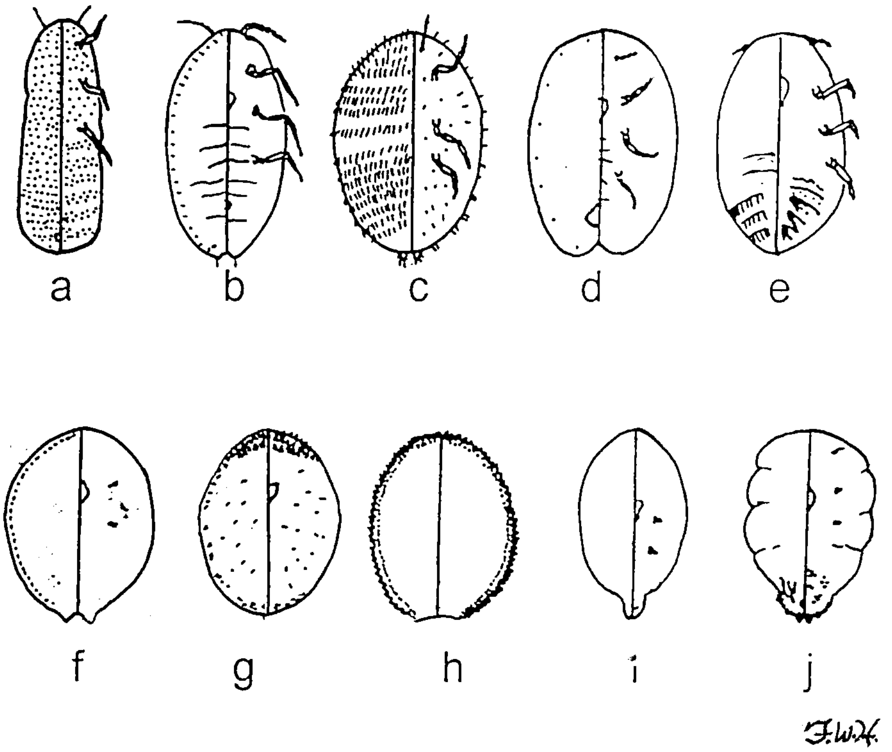


Fig. 3.24. Families of Coccoidea associated with palms. (a) Margarodidae. (b) Pseudococcidae. (c) Eriococcidae. (d) Coccidae. (e) Conchaspididae. (f) Asterolecaniidae. (g) Phoenicococcidae. (h) Beesoniidae. (i) Halimococcidae. (j) Diaspididae. Mature females are sketched as they are seen on microscope slides, with left half as dorsal view and right half as ventral view. After Kosztarab (1982).

information on host plants and geographical distribution of coccoids in this chapter was obtained from the excellent Internet web site, Scalenet (Ben-Dov *et al.*, 2000).

Margarodidae

The Margarodidae are considered to be the most primitive family and constitute the basal group of Coccoidea. Known as the giant coccids, the mature females are large for Coccoidea – up to 40 mm in length in an Australian species (Carver *et al.*, 1991) and, in many species, are mobile. Mature females may have thousands of wax pores (Foldi, 1991) and produce copious waxy filaments to cover their bodies and eggs. They have a high oviposition rate of several thousand eggs per female. Larvae of some occupy subterranean habitats associated with roots, forming cysts in the soil, known as 'ground pearls', in which they may remain for extended periods to survive unfavourable conditions, e.g. droughts. The family's best-known species is *Icerya purchasi*, the cottony cushion scale, a cosmopolitan, highly polyphagous species, which attacks many cultivated plants, but not palms.

About 375 species have been described (Ben-Dov *et al.*, 2000). Less than a dozen species of Margarodidae have been reported on palms. *Pseudaspidioproctus vayssieriellus*, known from African oil palm and *R. regia*, is said to be restricted to palms (Lepesme, 1947).

Icerya seychellarum was regarded as the most important pest of coconut palm in the Seychelles during the early part of the 1900s (Lepesme, 1947). *Margarodesia desmieri*, described as a new genus and species of margarodid in Côte d'Ivoire (Foldi, 1981), feeds in cysts 15–30 cm beneath the ground, associated with secondary and tertiary roots of African oil palm.

Pseudococcidae

The bodies of most species of Pseudococcidae (mealybugs) are covered with a white, powdery to granular waxy substance. This is secreted from numerous fine pores of diverse structure dispersed over the insect's body. Triangular triocular pores, with three elongated loculi, are typical of the Pseudococcidae (Foldi, 1991). The colour of the insect's body, often pink or yellowish, may show beneath the waxy layer. The margins often have waxy filaments. Mature females are usually elliptical from a dorsal view and convex from a side view and are usually about 3–5 mm in length. They bear simple eyes, a pair of well-developed antennae and functional legs. Segmentation of the abdominal region is distinct, but the divisions between head, thorax and abdomen are not readily apparent. Pseudococcidae typically fabricate an ovisac from their waxy secretions, in which they deposit hundreds of eggs. This may remain attached to the plant after the insect has died. Minute morphological structures have taxonomic value in distinguishing Pseudococcidae from other coccoid families. These, the province of the taxonomic specialist, include dorsal ostioles, ventral circuli, trilocular pores, cerarii, inner and outer layers of pores associated with the annular ring, and tubular ducts that are not invaginated.

Pseudococcidae are the second largest family of Coccoidea after Diaspididae. Putoidae, the giant mealybugs, are related to Pseudococcidae; some authors include them in this family. The two families combined comprise almost 2000 described species in 262 genera (Ben-Dov, 1994; Ben-Dov *et al.*, 2000).

Most species infest leaves and other above-ground plant parts, preferring folds, crevices and other protected sites. Some species infest roots. Mealybugs are usually observed in aggregations of several to many individuals, remaining for long periods in the same feeding sites. Their infrequent movements are slow and sluggish. They do not visibly respond to disturbances, even when the plant part they are feeding on is excised, partly because withdrawing their long, thin stylets from plant tissue is a slow process. They produce copious honeydew and are typically associated with ants.

Mealybugs often produce a white,

flocculent material in the vicinity of their colonies. Thus, a gardener repotting palms in a glasshouse in France in 1876 was concerned that the roots were infected with a fungus. He consulted an entomologist, who found a new species of mealybug, which he described as *Rhizoecus falcifer* (Künckel d'Herculais, 1878). The gardener's misidentification is still a common one.

Pseudococcidae are not usually highly host-specific. Most species are primarily associated with dicotyledons, but nearly a third of the mealybug species for which host records are available include *Gramineae* among their hosts and many species are strictly graminivorous. There are relatively fewer associations between mealybugs and gymnosperms, and fewer still between mealybugs and ferns (*Filicopsida*) (Ben-Dov, 1994).

Fifty-two (i.e. about 3%) of the known species of Pseudococcidae have been recorded on palms (Table 3.5). Most of these species are polyphagous and are primarily associated with dicotyledons. Palmivorous species are distributed widely in the Pseudococcidae, but half of them are in the genera *Dysmicoccus*, *Planococcus*, *Pseudococcus* and *Rhizoecus*. *Dysmicoccus* has the most palmivorous species (eight), including three species known only from palms.

The most commonly reported mealybug pests of palms are highly polyphagous species, which have been spread around the world, and in many cases they are known primarily as pests of crops other than palms. Examples include *Dysmicoccus brevipes*, *Nipaecoccus nipae* and *Pseudococcus longispinus*. Their wide adaptability, particularly to many kinds of host plants, is probably a principal factor in their wide dissemination, establishment and long-term survival in diverse localities.

Except for occasional records on other hosts, the following mealybugs are almost restricted to palms: *Dysmicoccus hambletoni*, *Dysmicoccus cocotis*, *Dysmicoccus finitimus*, *Neosimmondsia hirsuta*, *Palmicultor palmarum*, *Phenacoccus sakai*, *Planococcoides anaboranae*, *Pseudococcus portiludovici*, *Tylococcus malaccensis*, *Crinitococcus palmae* and *Cyperia angolica*.

Based on observations in Florida, mealybug infestations are fairly common on mature palms of certain species, but are often hidden in leaf axils and may go unnoticed. When populations become abundant, they sometimes spread on to exposed surfaces of the crown shaft, petioles and fronds. Although some mealybugs (e.g. *P. palmarum*) may cause important problems in mature palms in

Table 3.5. Pseudococcidae on palms (compiled from records in Ben-Dov, 1994, unless otherwise noted).

Species of Pseudococcidae	Palm hosts	Other hosts	Distribution
Chryseococcus arecae	*Rhopalostylis sapida*	M* D**	Australia, New Zealand
Coccidohystrix insolita	*Cocos nucifera*	D**	Eastern hemisphere
Crinitococcus palmae	*Caryota* sp.	nr	Philippines
Cyperia angolica	*Elaeis guineensis*	nr	Angola
Dysmicoccus boninsis	*C. nucifera*	M** D*	Pantropical
Dysmicoccus brevipes	*Areca catechu, Carpentaria acuminata, C. nucifera, E. guineensis, Phoenix dactylifera, Rhapis, Roystonea, Sabal bermudiana*	M* D**	Cosmopolitan
Dysmicoccus cocotis	*C. nucifera*	M*	Oceania, India
Dysmicoccus finitimus	*C. nucifera*	nr	Southern Asia, Malaysia
Dysmicoccus hambletoni	*E. guineensis*	nr	Ecuador

Table 3.5. *continued*

Species of Pseudococcidae	Palm hosts	Other hosts	Distribution
Dysmicoccus neobrevipes	*C. nucifera*	M* D**	Tropical America, Oceania, South-East Asia
Dysmicoccus nesophilus	*Balaka seemanni*	G* M** D***	Oceania
Dysmicoccus papuanicus	*C. nucifera*	M*	New Guinea
Ferrisia consobrina	*Metroxylon sagu*	M* D***	Pantropical
Ferrisia virgata	*C. nucifera, P. dactylifera*	M**	Cosmopolitan
Geococcus coffeae	*Chamaedorea*	M* D*	Cosmopolitan
Laingiococcus painei	*C. nucifera*	D**	Oceania
Laminicoccus flandersi	*Gronophyllum, Howea*	nr	Australia, New Zealand
Laminicoccus vitensis	*C. nucifera, Roystonea regia*	M*	Oceania
Leptococcus metroxyli	*C. nucifera, Metroxylon*	M*	New Guinea
Maconellicoccus hirsutus	*P. dactylifera, Phoenix sylvestris*	M* D**	Cosmopolitan
Maculicoccus malaitensis	*C. nucifera*	D*	Oceania
Neosimmondsia esakii	*Metroxylon amicarum, Ptychosperma ledermanniana*	M	Ponape (Caroline Islands)
Neosimmondsia hirsuta	*C. nucifera*	nr	Solomon Islands
Nipaecoccus annonae	*C. nucifera*	D*	Guadeloupe, St Vincent (Lesser Antilles)
Nipaecoccus nipae	*Areca* sp., *Arenga saccharifera, Calyptrogyne, Chamaedorea, Chamaerops excelsus, C. nucifera, E. guineensis, Gronophyllum, Howea belmoreana, Howea forsteriana, Livistona chinensis, Nypa fruticans, Pritchardia, Ptychosperma, Rhapis humilis, Sabal, Syagrus romanzoffiana*	M* D**	Cosmopolitan
Palmicultor palmarum	*A. catechu, C. nucifera, Dypsis lutescens, Latania glaucaphylla, R. regia, Veitchia* sp.	nr	Oceania, Asia, tropical America, Florida, Bermuda (Ben-Dov, 1994; Avas Hamon, unpublished)
Paraputo leveri	*C. nucifera*	D	Oceania
Phenacoccus gregosus	*Chamaedorea*	D*	Mexico, Central America
Phenacoccus sakai	*N. fruticans*	nr	Malaysia
Planococcoides anaboranae	*C. nucifera*	nr	Madagascar
Planococcus citri	*C. nucifera, Gronophyllum* sp., *P. dactylifera*	M* D***	Cosmopolitan
Planococcus ficus	*P. dactylifera*	D*	Cosmopolitan
Planococcus kraunhiae	*Trachycarpus fortunei*	M* D**	Asia, California
Planococcus lilacinus	*C. nucifera, P. dactylifera*	M* D***	Cosmopolitan

Table 3.5. *continued*

Species of Pseudococcidae	Palm hosts	Other hosts	Distribution
Planococcus minor	*A. catechu, B. seemannii*	M* D***	Cosmopolitan
Planococcus nigritulus	*P. dactylifera*	D*	Tanzania (West Africa)
Plotococcus neotropicus	*C. nucifera*	M* D**	Tropical America
Pseudococcus cryptus	*C. nucifera, E. guineensis*	M* D**	Cosmopolitan
Pseudococcus longispinus	*A. catechu, Chamaedorea elatior, D. lutescens, C. nucifera, Dictyosperma album, Howea* sp., *Metroxylon sagu, Roystonea* sp., *Phoenix canariensis*	G* M** D***	Cosmopolitan
Pseudococcus microadonidum	*C. nucifera*	M*	Oceania, Seychelles
Pseudococcus portiludovici	*C. nucifera, Latania verschaffeltii*	nr	Indian Ocean: Mauritius, Chagos Archipelago
Pseudococcus zamiae	*Howea* sp.	G*	Australia
Rastrococcus iceryoides	*A. catechu*	G* M* D***	Eastern hemisphere
Rastrococcus neoguineensi	*C. nucifera*	M* D**	Indonesia, New Guinea
Rastrococcus spinosus	*C. nucifera*	M* D**	South-East Asia
Rhizoecus americanus	*Areca* sp., *Chamaedorea elegans, D. lutescens, Coccothrinax argentata, Chamaedorea, Howea* sp., *Phoenix loureiri, S. romanzoffiana*	F* M** D***	Tropical America, Italy
Rhizoecus californicus	*Rhopalostylis sapida*	M* D**	New Zealand, California
Rhizoecus cocois	*C. nucifera*	nr	India
Rhizoecus falcifer	*Chamaerops humilis, Howea belmoreana, Howea forsteriana, P. canariensis, Phoenix roebelenii, Ptychosperma* sp. *Ptychosperma elegans, Sabal blackburniana*	F* M** D***	Cosmopolitan
Rhizoecus floridanus	*D. lutescens, P. canariensis, S. romanzoffiana*	M* D**	South-eastern USA
Rhizoecus hibisci	*P. canariensis, Sabal* sp.	M* D*	Japan, apparently Puerto Rico
Tylococcus malaccensis	*N. fruticans*	nr	Malaysia
Xenococcus annandalei	*C. nucifera*	M* D*	Australia, New Guinea, South-East Asia

F, ferns (Filicopsida); G, gymnosperms; M, monocotyledons; D, dicotyledons; nr, none reported. The number of asterisks indicates the importance of the host category, e.g. G*, few gymnosperm hosts, G***, many gymnosperm hosts.

plantations or landscape plantings, they are a more common problem on palms in the young seedling stage, especially when these are closely spaced, as they are in nurseries, seed-beds and glasshouses (F.W. Howard, unpublished).

Reyne (1948) in Indonesia observed that mealybugs and sooty mould were abundant on foliage of coconut palms in two villages but absent from coconut palms in the countryside between the villages. He attributed this to ants associated with houses in the villages.

Dysmicoccus cocotis is common on fronds and inflorescences of coconut palm on many islands of the South Pacific. Populations occasionally become dense enough to cause concern to coconut growers. Adult females are oval, yellow beneath their white wax coating and about 3 mm long. Simmonds (1921), cited by Williams and Watson (1988), reported it as a pest of coconut palm on several islands of Fiji, commenting that it was rapidly controlled by the coccinellids *Megalocaria fijiensis* and *Cryptolaemus montrouzieri*. In addition to coconut palm, it has been reported on *R. regia* on Viti Levu (Fiji), on *Phoenix* sp. on Niue (French Polynesia) and on *Pandanus odoratissimus* on Rarotonga (Cook Islands). A record of *D. cocotis* on *Calophyllum inophyllum* (Guttiferae) might be based on a vagrant specimen, as the species appears to infest only palm hosts and occasionally Pandanaceae (Williams and Watson, 1988).

A disjunct of *D. cocotis* was formerly thought to occur in southern Asia. Apparently this was based on a misidentification of *D. finitimus*, a different species of very similar appearance described recently by Williams (1994). The distribution of *D. finitimus* is Sri Lanka, the Laccadive Islands, Andaman Islands, southern India and parts of Malaysia. It is known only from coconut palms, and occasionally occurs in dense populations on this host.

Nipaecoccus nipae was originally described from *Nypa fruticans* in Demerara, Guyana (Maskell, 1893). This palm is native to Oceania and South-East Asia, where it grows on muddy coastal sites. Slide-mounted adult females of this insect are subcircular and about 2 mm long. In life, the body is a deep red, with a white or yellow, mealy, wax covering. The significance of the difference in the colour of the wax in different populations is not understood (Colour Plate 10f) (McKenzie, 1956).

Nipaecoccus nipae is a common pest of palms of various species in glasshouses in temperate regions of North America and Europe, occurring most commonly on species of *Howea* (McKenzie, 1956). It is often found on aerial parts and roots of containerized palms outdoors in Florida. It was reported as common on fronds of coconut palms in plantations and on leaves of several tropical fruit-tree species in Guadeloupe, but was not considered a pest (Balachowsky, 1957).

Palmicultor palmarum is a widely distributed mealybug, reported in the eastern hemisphere from many localities and in the western hemisphere from the Hawaiian Islands, Mexico, Jamaica, the Bahamas, Florida and Bermuda (Fig. 3.25). According to Cohic (1959), cited by Ben-Dov (1994), it did little damage to mature coconut palms but killed seedlings. It was recently introduced into Florida (Avas Hamon, personal communication), where it has been observed in dense aggregations in leaf axils and at the base of the spear leaf of *R. regia*, *Veitchia* spp. and *D. lutescens*. In several of these cases, the spear leaf became necrotic and the palm died; whether the mealybugs were lethal or secondary is not yet known (F.W. Howard, unpublished). Additional hosts are *A. catechu* and *Latania glaucaphylla*. There is one record from an unidentified legume (Ben-Dov, 1994).

Pseudococcus longispinus (Colour Plate 10e) is distinguished by the presence of a pair of extremely long caudal wax filaments, laterad of which is a second pair about half as long. Although these break easily, they are usually intact in at least some of the individuals in an aggregation (Johnson and Lyon, 1991). The marginal wax filaments are a quarter to half the width of the body. Slide-mounted adult females are 2.1–3.6 mm long (McKenzie, 1956).

Fig. 3.25. (*and opposite*) Infestation of mealybugs, *Palmicultor palmarum* (Pseudococcidae), on *Veitchia arecina*. (a) On spear leaf. Light-coloured insects are *P. palmarum* and darker insects are mostly parasitized *Coccus hesperidum* (Coccidae). (b) Damage to recently opened leaf associated with *P. palmarum*.

A common species in glasshouses, *P. longispinus* attacks many ornamental plants, including palms. A palm relative, the genus *Dracaena*, is said to be a preferred host in California (McKenzie, 1956).

Rhizoecus falcifer is a common pest of palms and other plants grown in glasshouses. It was originally described from *P. elegans* grown as a containerized palm in a glasshouse in France. The palm had been introduced years previously from Australia, the probable origin of this mealybug (Künckel d'Herculais, 1878).

Rhizoecus americanus occurs on the roots of at least 30 hosts, including dicotyledons and monocotyledons. At least nine species of palms are hosts. It has been reported from many localities in b

tropical America. Intensive collecting in Florida revealed that it was common on palms and other plants in that state. *Rhizoecus floridanus* is a similar species (Ben-Dov, 1994).

Eriococcidae

The Eriococcidae are distinguished from other families of the Coccoidea by the presence and distribution of tubular ducts, the structure of the anal ring, and other minute morphological features. A more obvious characteristic is that the mature female resides in a felted ovisac. They are commonly called 'felt scales'.

Eriococcids are not generally known as pests of palm plantations in the tropics, but, from 1989 to the present, *Sangicoccus* sp. near *truncatespinus* (determined by G.W. Watson) has been a pest on foliage of coconut palms in a plantation of 4500 ha in Palawan, Philippines (Ester Pacumbaba, personal communication).

Coccidae

The Coccidae are subcircular, elliptical to pyriform and flat to convex. They are probably the most frequently encountered sessile scale insects after armoured scales (Diaspididae) and are referred to as 'soft' scale insects to distinguish them from the latter. Coccids are generally larger at maturity than armoured scale insects. Adult females of most smaller species are not less than about 3 mm long, and females of some larger species are up to 12.5 mm long. The derm is membranous in immature forms and in young females, becoming heavily sclerotized in females of some species. Segmentation is indicated on the ventral but not the dorsal surface. In mature females, antennae and functional legs may be present or absent. The immature stages and mature females secrete a waxy substance from numerous pores distributed on the body, forming a smooth wax covering, although this is absent in some species. A conspicuous characteristic that distinguishes soft scale insects from other Coccoidea is the anal cleft. This is subtended by an operculum, formed of the anal opening covered by a pair of anal plates (Figs 3.24 and 3.26). Many species produce a conspicuous ovisac of waxy material. The Coccidae are the third largest family of Coccoidea after Diaspididae and Pseudococcidae, with 153 genera and more than 1000 species (Hamon and Williams, 1984; Ben-Dov *et al.*, 2000).

Female coccids undergo hemimetabolous metamorphosis, with two to three larval instars in the female and four in the male. Whether or not the mature females are mobile, the first-instar crawlers are generally the most active stage of coccids. They are usually elongate–elliptical, with simple eyes and with antennae and legs well developed in proportion to their body. The anal plates of crawlers bear long apical setae, which are lost with the moult to the second instar. Successive instars bear increasing numbers and varieties of ducts, pores and setae. Sexual dimorphism is recognizable in the second instar, for the male is more elongate than the female. The mature female emerges with the third or fourth moult. As in other Coccoidea, the male undergoes stages similar to prepupal and pupal stages, in which wing buds and other precursors of the adult stage develop. The alate males are similar to those of other coccoid families. Some species can reproduce parthenogenetically, but, if reproduction is sexual, males are attracted to females by pheromones (Hamon and Williams, 1984).

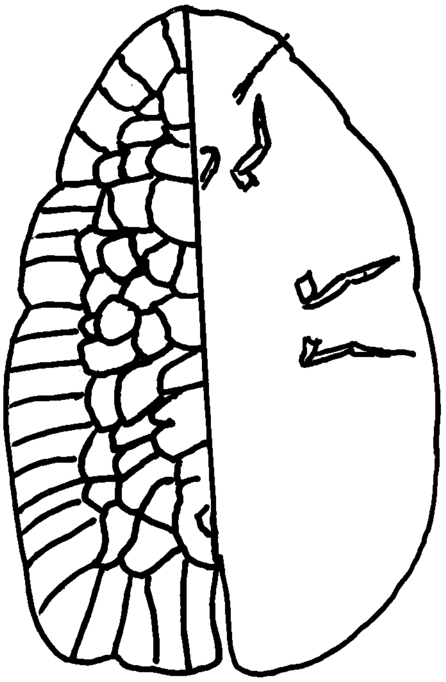


Fig. 3.26. *Eucalymnatus tessellatus* (Coccidae). Left, dorsal view; right, ventral view. After Lepesme (1947).

Forty species of Coccidae are known from palms (Table 3.6). Species that have been collected only on palms include *Ceroplastes hololeucus*, *Coccus acrossus, Paralecanium coccophyllae*, *Neosaissetia triangularum*, *Platylecanium elongatum* and *Pseudokermes palmae.*

In plantations, Coccidae are usually minor pests. For example, in coconut plantations in the Philippines, light populations of *Milviscutulus mangiferae* (known as the mango shield scale), *N. triangularum* and *Paralecanium quadratum* are often present, but at very low population levels. In the same plantations, *P. coccophyllae* is a rare coccid.

Table 3.6. Species of Coccidae reported on palm hosts (records compiled from Lepesme, 1947; Hamon and Williams, 1984; Ben-Dov, 1994; Chua, 1997; Penny Gullan, personal communication).

Species of Coccidae	Palm hosts	Other hosts	Geographical distribution
Avricus arborescens	*Cocos nucifera*	D*	Tropical Africa
Ceroplastes actiniformis	*Areca catechu* *C. nucifera*	M* D**	Asia
Ceroplastes ceriferus	*C. nucifera*	F* G* M* D***	Cosmopolitan
Ceroplastes cirripediformis	*Livistona chinensis*	M* D**	Cosmopolitan
Ceroplastes constricta	*Elaeis guineensis*	F G M D	Angola
Ceroplastes floridensis	*Acoelorraphe wrightii, C. nucifera, Chamaedorea elegans, Hyophorbe lagenicaulis, Nypa fruticans, Phoenix canariensis, Washingtonia filifera, Syagrus romanzoffiana*	F* G* M* D***	Cosmopolitan
Ceroplastes hololeucus	*E. guineensis*	nr	Angola
Ceroplastes rubens	*C. nucifera*	F* G* M* D***	Asia, Australia Oceania, Florida, Puerto Rico
Ceroplastes rusci	*Chamaerops humilis*	F G M D	Pantropical
Ceroplastes xishuangensis	*E. guineensis*	G (*Cycas*)	China
Coccus acrossus	*E. guineensis*	nr	Angola
Coccus acutissimus	*A. catechu, Dypsis lutescens, C. nucifera*	G* D*	Asia, Pacific, tropical Africa, Florida and Texas (USA)
Coccus capparidis	*Roystonea regia*	F* M* D***	Pantropical
Coccus discrepans	*C. nucifera*	D*	Asia
Coccus hesperidum	*Aiphanes caryotifolia, Archontophoenix alexandrae, A. oleracea, Arenga pinnata, Adonidia merrillii, Caryota mitis, Caryota urens, C. elegans, Chamaedorea erumpens, Chamaedorea microspadix, C. humilis, D. lutescens, C. nucifera, Howea forsteriana, Hyophorbe verschaffeltii, Phoenix dactylifera, Phoenix roebelenii, Ravenea* sp., *R. regia, Sabal palmetto, S. romanzoffiana, Washingtonia robusta*	F* G* M** D***	Cosmopolitan

Table 3.6. *continued*

Species of Coccidae	Palm hosts	Other hosts	Geographical distribution
Coccus longulus	*Archontophoenix cunninghamiana, A. catechu, C. microspadix, Livistona chinensis, Ptychosperma sanderianum*	G* M* D***	Cosmopolitan
Coccus viridis	*A. catechu, C. nucifera, C. elegans, S. palmetto, Sabal* sp.	M* D**	Pantropical
Eucalymnatus tessellatus	*Acrocomia* sp., *Archontophoenix alexandrae, A. catechu, Arenga engleri, C. mitis, Caryota rumphiana, C. urens, Caryota* sp., *C. elegans, Chamaedorea ernesti-augusti, C. erumpens, Chamaedorea tenella, C. nucifera, Dictyosperma album, Dypsis decaryi, D. lutescens, Heterospathe* sp., *Howea belmoreana, H. forsteriana, H. verschaffeltii, Hyphaene crinita, L. chinensis, N. fruticans, P. canariensis, P. roebelenii, Rhapis excelsa, Rhapis humilis, Roystonea* sp., *Sabal blackburniana, S. romanzoffiana, Trachycarpus fortunei, Washingtonia* sp.	F* G* M*** D***	Pantropical
Inglisia vitrea	*C. nucifera*	D**	Tropical America
Kilifia acuminata	*C. elegans, Roystonea* sp.	F* M* D***	Pantropical
Milviscutulus mangiferae	*C. nucifera*	F G M D	Pantropical
Milviscutulus pilosus	*C. nucifera*	D*	New Guinea, Solomon Islands (Penny Gullan, personal communication)
Neosaissetia triangularum	*C. nucifera*	nr	Philippines
Paralecanium cocophyllae	*Calamus* sp., *C. nucifera, Sabal adansoni*	nr	Malaysia, Philippines
Paralecanium milleri	*C. nucifera, E. guineensis*	D*	Malaysia
Parasaissetia nigra	*A. catechu, C. nucifera, E. guineensis, Erythea armata*	M** D***	Cosmopolitan
Platylecanium asymmetricum	*Pinanga* sp.	D*	Malay Peninsula
Platylecanium cocotis	*C. nucifera*	M*	Pacific
Platylecanium elongatum	Unidentified palm	nr	Indonesia
Protopulvinaria pyriformis	*C. erumpens*	M* D***	Pantropical
Pseudokermes palmae	Unidentified palm	nr	São Paulo State (Brazil)
Pulvinaria psidii	*L. chinensis, Washingtonia* sp.	F* G* D**	Pantropical

Table 3.6. *continued*

Species of Coccidae	Palm hosts	Other hosts	Geographical distribution
Pulvinaria urbicola	*Sabal* sp.	F* M* D***	Asia, Australia, Oceania, tropical America, Israel
Saissetia coffeae	*Butia capitata, C. nucifera,* *Cyphosperma* sp., *Hyphaene crinita,* *S. romanzoffiana*	F* G** M** D***	Pantropical
Saissetia miranda	*C. nucifera*	M* D***	Pantropical
Saissetia neglecta	*Latania loddigesii*	F* M* D***	Australasia, tropical America
Saissetia oleae	*Metroxylon* sp. *Phoenix* sp.	G* M* D***	Pantropical
Saissetia zanzibarensis	*C. nucifera*	D**	East Africa
Vinsonia stellifera	*C. nucifera* *N. fruticans*	F* M* D**	Pantropical

F, ferns (Filicopsida); G, gymnosperms; M, monocotyledons; D, dicotyledons; nr, none reported. The number of asterisks indicates the importance of the host category, e.g. G*, few gymnosperm hosts; G***, many gymnosperm hosts.

Coccidae that are of greatest pest potential are usually species that are cosmopolitan and polyphagous. *Coccus hesperidum* is a typical example. Such species are common in glasshouses, where they are more likely to be pests of palms than in plantations and landscape situations.

Eucalymnatus tessellatus is exceptional in having been reported as a serious coccid pest of palms outdoors. The female is a flat, brown, soft scale insect about 2 mm × 3 mm in size, with a distinctive mosaic pattern (Colour Plate 11a, Figs 3.26 and 3.27). Males are unknown.

The females give birth to larvae or lay eggs, which hatch promptly. Among Coccoidea, *E. tessellatus* has a low reproductive rate, producing less than two dozen larvae per female. First-instar larvae are purple-brown; second instars are green (Vesey-FitzGerald, 1940).

Although *E. tessellatus* is a very common scale insect in tropical countries on palms and many dicotyledonous trees, populations of this scale insect are usually sparse. For example, although in Florida one of its more common palm hosts is coconut palm, there are usually no more than a few of these scale insects per frond. Exceptionally dense infestations of up to about 200 scale insects on some leaflets have been observed, however (Colour Plate 11a; Fig. 3.27). In one such case, the palms had been sprayed repeatedly with insecticides to control *Cerataphis* sp. This may have disrupted natural control of *E. tessellatus*. Extensive sooty mould was on the palm foliage, which may have been supported by the honeydew of both the aphids and the scale insects.

Vesey-FitzGerald (1940) observed that *E. tessellatus* was scarce on coconut palms growing on poor soils in the uplands. Highly infested palms were more common on alluvial soils and coral sands. On alluvial soils, the incidence of *E. tessellatus* appeared to vary with soil quality and with the vigour of the palms.

Observations of *E. tessellatus* in the Seychelles indicated an indirect way in which this coccid may be deleterious to palms: it attracted predacious ants, which

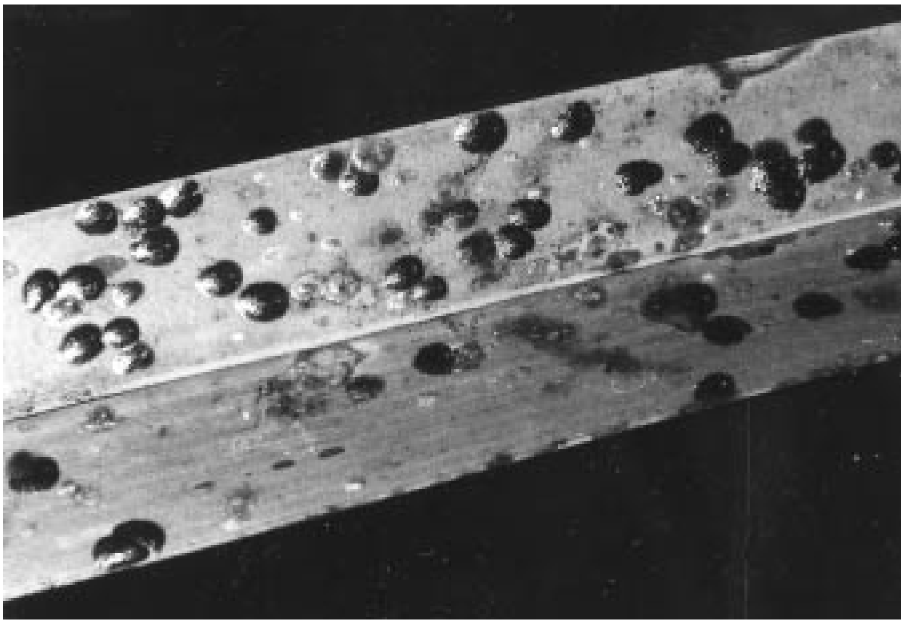


Fig. 3.27. *Eucalymnatus tessellatus* (Coccidae) infestation on leaflet of coconut palm. Photo by James V. DeFilippis.

attacked the natural enemies of armoured scale-insect pests (see *Ischnaspis longirostris*). It was thus decided that biological control of the armoured scale insects with parasitoids would be ineffective without introducing an effective biological control agent of *E. tessellatus*. *Chilocorus wahlbergi* (Coccinellidae), introduced from East Africa for this purpose, apparently caused the decline of *E. tessellatus* and thus facilitated control of the armoured scale insects. A fungus, *Vertecillium lecanii*, also attacked *E. tessellatus* in the Seychelles (Vesey-FitzGerald, 1940, 1953).

Wax scale insects are sometimes found on palms. These are coccids of the genus *Ceroplastes*, easily recognized by thick, waxy coverings with characteristic mounds or projections (Fig. 3.28).

Ceroplastes floridensis is a polyphagous, cosmopolitan wax scale insect that is fairly common on palms. Although it was described from Florida, it is native to Asia (Lepesme, 1947).

The greyish to pinkish-white waxy covering of the mature female is 1.0–3.5 mm wide and 3.0–4.0 mm long (Hamon and Williams, 1984). There are three generations per year in Florida. The species has been reported as far north as New York in the USA but does not overwinter in such localities (Johnson and Lyon, 1991). This scale insect sometimes occurs in dense enough populations on palms in nurseries or glasshouses to be of concern.

Vinsonia stellifera is a polyphagous coccid sometimes seen on palms (Fig. 3.29). Usually no more than a few individuals are

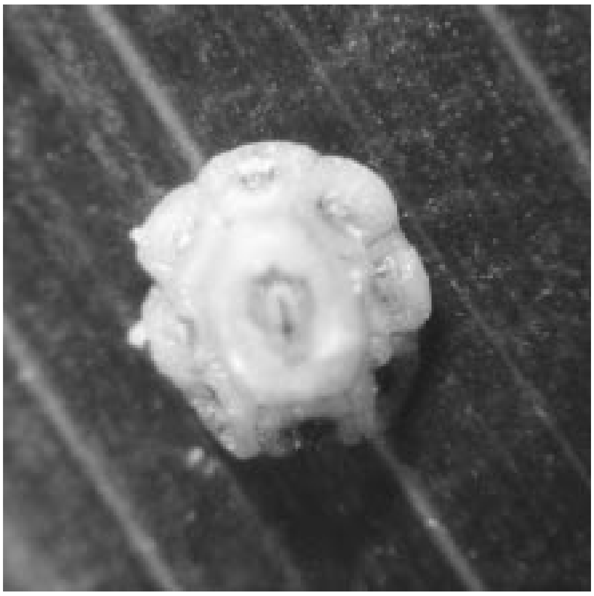


Fig. 3.28. Wax scale, *Ceroplastes* sp. (Coccidae) on coconut leaflet. Photo by Robin Giblin-Davis.

found on one palm, but it attracts attention because of its curious star shape.

Conchaspididae

The small family Conchaspididae occurs mostly in the tropics. The females have a highly sclerotized pointed abdomen, functional legs and prominent antennae (Fig. 3.24). The mature scale is conical and may look like a diaspidid scale, but without the first-instar exuviae. There are four genera and 30 species (Ben-Dov *et al.*, 2000). Five species are known from palms (Ben-Dov, 1981; Williams, 1991; Table 3.7). These interesting insects are not pests of palms.

Asterolecaniidae

The coccoid family Asterolecaniidae, with about 400 species (Ben-Dov *et al.*, 2000), is closely related and similar in appearance to Coccidae, with circular or oval, flat bodies and a separate, hardened, wax layer covering them, but are generally smaller, being about 2 mm or less in diameter (Fig. 3.24). Many species, including those on palms, lack anal plates or a well-developed anal cleft. The family is separated from other coccoid taxa by characteristics of the pores and ducts of the mature females. In particular, asterolecaniids and related groups have peculiar pores that occur in pairs, and thus each pair appears like the figure 8. These are referred to as 8-shaped, or geminate, pores (Ferris, 1937–1955; Russell, 1941). In Asterolecaniidae, they occur in marginal rows (Foldi and Lambdin, 1995).

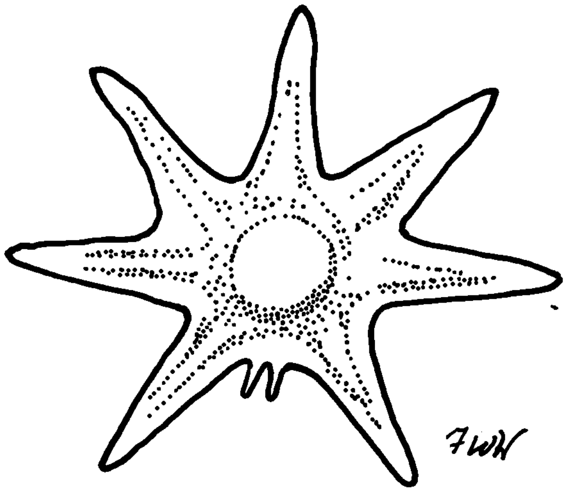


Fig. 3.29. *Vinsonia stellifera* (Coccidae), a pantropical soft scale insect sometimes seen on coconut palm foliage. After Lepesme (1947).

Asterolecaniids are called pit scales, because some species appear to reside in pits in the tissue of their host plant. Actually, they induce abnormal growth of tissue around them. The resulting structure is an ‘open’ gall. Asterolecaniids that attack diverse host-plant species may induce such galls in some species and not in others (Russell, 1941), indicating that different plants respond differently to the same scale-insect species. No galls produced by asterolecaniids are known in palms (Matile-Ferrero, 1996). In fact, few galls are known in this plant family (see p. 22, and cysts, p. 177).

Asterolecaniids are typically highly host-specific. Species of certain genera tend to occur on particular plant taxa: e.g. *Asterodiaspis* on oaks (*Quercus*), *Bambusaspis* on bamboos and *Palmaspis* on palms (Matile-Ferrero, 1996).

Russell (1941) revised the genus *Asterolecanium*, recognizing 156 species, 22 of which were associated with palms, 15 of these being new to science.

Table 3.7. Species of Conchaspididae reported on palms (from Ben-Dov, 1981).

Species of Conchaspididae	Palm hosts	Other hosts	Geographical distribution
Conchaspis diplothemii	*Allagoptera*	nr	Brazil
Conchaspis lepagei	*Astrocaryum ayri*	*Eugenia*	Brazil
Conchaspis pauliani	*Dypsis* sp.	nr	Madagascar
Conchaspis tsaratananae	*Dypsis decaryi*	nr	Madagascar
Conchaspis vayssierei	*Areca* sp.,*Cocos nucifera*, *Roystonea regia*	nr	Madagascar

nr, no record.

Bodenheimer (1951) created the genus *Palmaspis* for the palmivorous species. Matile-Ferrero (1996) redefined this genus and included 29 species specific to palms (Table 3.8). *Grammococcus* is a second palmivorous genus of asterolecaniids, with two species that attack palms (Miller and Lambdin, 1978).

Few palmivorous asterolecaniids are recognized as important pests of cultivated palms. The family as a whole has attracted little attention and thus is poorly known biologically. Most of the palmivorous species included in Russell's (1941) revision were described from specimens found, probably fortuitously, by various collectors over the years on wild palms in their native habitats. Wild palms have seldom been surveyed expressly for asterolecaniids, but, when such work was undertaken recently in the Amazon basin in Peru, nine species were reported for the first time from Peru, five of which were new to science (Matile-Ferrero, 1996). More than

Table 3.8. Species of Asterolecaniidae reported on palms (based on records in Matile-Ferrero, 1996, unless otherwise noted).

Species of Asterolecaniidae	Palm hosts	Habitat	Known geographical distribution
Asterolecanium epidendri	*Chamaedorea* sp., unidentified spp.	nr	Guatemala, Haiti
Grammococcus adetocorymbus	Unidentified palm	Foliage	Trinidad
Grammococcus corymbus	*Astrocaryum chonta, Elaeis guineensis, Scheelea brachyclada*	Abaxial leaf surface	Colombia, Peru, Trinidad
Palmaspis boliviae	*Euterpe precatoria, Jessenia bataua*	Adaxial and abaxial frond surfaces	Bolivia, Colombia, Peru
Palmaspis bondari	*Attalea funifera, Maximiliana elegans*, unidentified cocosoid species	Adaxial and abaxial frond surfaces	Brazil, Trinidad, Venezuela
Palmaspis degenerata	*Cocos nucifera, Maximiliana* sp.	Fronds	Brazil, Venezuela
Palmaspis dictyospermae	*Dictyosperma album*	nr	Round Island (Mauritius)
Palmaspis difficilis	*C. nucifera, Euterpe* sp.	Stems	Panama
Palmaspis distincta	*Attalea cohune*	Abaxial frond surface	Guatemala
Palmaspis elvae	*Bactris gasipaes*	nr	Peru
Palmaspis gilva	*A. cohune, Attalea gomphococca*	Abaxial frond surface	Panama
Palmaspis hilli	*Livistona humilis*	Abaxial frond surface	Australia
Palmaspis inlabefacta	*Chamaedorea* sp.	Spathe, fronds, stem	Mexico
Palmaspis inusitata	*Caryota* sp.	Adaxial frond surface	Venezuela
Palmaspis jesseniae	*Jessenia bataua*	nr	Peru
Palmaspis longifilum	Unidentified palm	nr	Brazil (Stumpf, 2000)
Palmaspis loretoensis	*Oenocarpus mapora*	nr	Peru
Palmaspis marfil	*Phytelephas macrocarpa*	nr	Peru
Palmaspis oraniae	*Orania philippinensis*	Abaxial frond surface	Philippines
Palmaspis pallida	*A. cohune*	Adaxial and abaxial frond surface	Panama

Table 3.8. *continued*

Species of Asterolecaniidae	Palm hosts	Habitat	Known geographical distribution
Palmaspis palmae	*Aiphanes* sp., *A. cohune. C. nucifera, E. guineensis, Elaeis oleifera, Guilielma* sp.	Adaxial and abaxial frond surface	Colombia, Costa Rica, Honduras, Jamaica, Panama, Peru
Palmaspis palmicola	*Archontophoenix* sp.	nr	Réunion (Mascarene Islands)
Palmaspis phoenicis	*Phoenix dactylifera*	Leaflets, rachis, fruits	North Africa and the Middle East
Palmaspis pinangae	*Pinanga* spp.	nr	Philippines
Palmaspis sabalis	*Sabal palmetto*	Adaxial and abaxial frond surface	Cuba
Palmaspis similis	*A. cohune, C. nucifera*	Leaflets, rachis, fruits	Honduras, Jamaica
Palmaspis singularis	Unidentified species	Stem	Philippines
Palmaspis spectabilis	Unidentified species	Adaxial leaf surface	Mauritius
Palmaspis truncata	*A. cohune, M. elegans*	Abaxial frond surface	Guatemala, Honduras, Mexico
Palmaspis ucayali	*C. nucifera*	nr	Peru
Palmaspis unica	*Calamus* sp.	Adaxial frond surface	Philippines
Palmaspis urichi	*B. gasipaes, Bactris major, Bactris minor*	Fronds, fruits, stems	Brazil, Granada, Mexico, Nicaragua, Panama, Peru, Trinidad

nr, not reported.

twice as many species have been described from tropical America as from the tropics of the eastern hemisphere.

Palmaspis similis was reported on fronds and fruits of coconut palm, on *Attalea cohune* in Honduras and from an unidentified palm in Jamaica, but it is not generally known as a significant pest of any of these palms (Russell, 1941). However, a recent shipment of coconut seednut imported into Florida from Jamaica was quarantined when some of them were found to be infested with *P. similis*.

Palmaspis dictyospermae is noteworthy for its involvement in an unusual conservation dilemma. It was described from *Dictyosperma album* in Mauritius (former Mascarene Islands), where this palm species is endemic. This palm is harvested for palm hearts and distinct varieties are recognized. *Palmaspis dictyospermae* was found on one of three varieties of *D. album* that occur in Mauritius, namely var. *conjugatum*. At the time that the insect was discovered on Round Island, Mauritius, there were only two palms of this species remaining on the island, both of var. *conjugatum*. This was thought to be perhaps the only place in Mauritius where this variety was isolated and thus not interbred with other varieties of *D. album*. The scale insects were abundant on the two palms and thus were a threat to their survival. Ironically, the scale insect itself was obviously a threatened species (Williams, 1986).

Palmaspis phoenicis is one of the few asterolecaniids consistently found on economic palms. Known as the green scale insect, it is considered a serious pest of date palms in Sudan and has also been reported from Iraq, Iran, Saudi Arabia, Israel, Egypt and Qatar. Its feeding causes chlorosis and eventual desiccation of the fronds and shrivelling and dropping of the fruits (Ali Abbas and El Nasr, 1992).

Asterolecanium epidendri is one of the few palmivorous asterolecaniids known in glasshouses in temperate regions. In addition to palms, it is a pest of Orchidaceae, *Anthurium* (Araceae), *Zamia* (Zamiaceae) and other ornamental plants commonly grown in such facilities. It has been collected from *Chamaedorea* sp. in Guatemala and diverse palms in Haiti. Believed to be of neotropical origin, it has been spread to some tropical and Mediterranean countries of the eastern hemisphere (Ferris, 1937–1955; Russell, 1941; Lepesme, 1947).

Diaspididae

The family Diaspididae, the armoured scale insects, is the largest family of Coccoidea, with about 400 genera and more than 2650 described species (Ben-Dov, 1990a, b; Ben-Dov *et al.*, 2000). The adult females are legless, with rudimentary antennae. The fourth to last abdominal segments are fused and sclerotized to form a flat pygidium. There are different kinds of wax pores on the dorsal and ventral surfaces of the pygidium, and a fringe of spines, plates (usually branched structures) and lobes on the margins. The insect constructs the scale by releasing wax from the pores and sculpting it with the marginal structures of the pygidium. In some literature, the insects themselves are referred to as scales, and the scale as the scale covering, test or armour. We find it simpler and clearer to refer to the animal as the scale insect and its protective structure as the scale. Not merely a waxy layer on the insect's body, as in most other Coccoidea, the scale of the armoured scale insect is indeed like a suit of armour, in that it is a protective structure separate from the body. Other coccoids, e.g. some asterolecaniids, have similarly separate scales. The defining characteristic of diaspidid scales is that they incorporate exuviae (the shed cuticles of the first and second instars) in a characteristic manner. As in other Coccoidea, the waxy filaments issue from special glands, reaching the integument surface through ducts. The wax filaments of most coccoids are cylindrical but in Diaspididae, Conchaspididae and Halimococcidae are flattened, double, hollow filaments, which are thought to provide exceptional strength and insulation. They are extremely hydrophobic (Foldi, 1991). An anal liquid cements them together and then hardens. Waste products may be incorporated in the scale. With each of the first two moults, the shed cuticle is incorporated into the scale. The waxy substance from which the scale is made is about half wax and about half proteinaceous substances (Foldi, 1990). It is white in most species, and brown, reddish, black or other colours or translucent to transparent in others. Many species incorporate material such as fragments of the host plant in their scales, thus modifying their appearance on different hosts (Foldi, 1990). Armoured scale insects fashion the substance into a shelter beneath which they reside. The plant surface provides protection of the ventral surface, but some species also have a ventral scale. Some species have groups of pores on the ventral surface (perivulvar pores).

The shape of the scales of females is usually either circular or pyriform to elongate, reflecting the forms of the insects that make and inhabit them (Stoetzel, 1976; Foldi, 1990). For example, females with circular or broadly turbinate shapes, which are typical of Aspidiotinae, produce circular to oval scales. With each of their two moults, they incorporate exuviae, so that, at maturity, the scale consists of three more or less concentric components. The central one consists of the exuviae of the first-instar larva. These typically have a thin coat of wax produced by that instar when it was settling on the host plant. These exuviae are in the centre of the wax-coated exuviae of the second instar. The third concentric component is an expanded circular flange, consisting entirely of the waxy substance produced by the mature female.

Females of the more elongate species, as exemplified by Diaspidinae, produce pyriform or otherwise elongate scales. Again, three components are visible, but with the first-instar exuviae at the cephalic end, succeeded by the wax-coated second-instar exuviae and the expanded waxy portion made by the mature female.

Pupillarial forms are exceptional, in that the adult female is enclosed in the second set of exuviae, which serves as the scale. Thus, only one set of exuviae is seen externally. Little or no waxy scale is made and there is usually a reduction in glandular structures. There are about 200 of such species. Those found on palms include *Fiorinia fioriniae* and *Fiorinia arengae*.

Scales of mature armoured scale-insect females range from 1 to 3.5 mm, with most falling within the range of 1.5–2.0 mm. The more elongate species tend to reach greater lengths than the round species (Foldi, 1990).

Since the scales of both males and females are cemented to the plant surface, they may persist for a long time after the insect that produced them has died, shrivelled and even partially decomposed. Armoured scale insects usually do not infest the very youngest fronds of palms. Commonly, the third or fourth oldest frond may have a sparse population, and subsequently the density of scales may increase with the age of the frond. A large portion of the scales on the lower (i.e. older) fronds of a palm may be the scales of dead insects that completed their development months previously. For this reason, it may often be ineffective to prune older, scale-encrusted fronds to control a scale insect.

Because the scales are the most obvious and easiest structures to examine, they are useful for routine field identifications by personnel who are familiar with the pests of particular crops in particular regions. For example, in many regions, experienced personnel routinely identify the common armoured scale insects on coconut palms by the appearance of the scales: *Aspidiotus destructor* (flat, circular, transparent scale), *Aonidiella orientalis* (flat, circular, thin, brown scale), *Chrysomphalus aonidum* (blackish, broadly conical scale with brown central exuviae) and *Pseudaulacaspis cockerelli* (white pyriform scale).

However, because the scales of many species are similar in appearance and those of the same species may look different on different hosts or even on different plant parts, the scales *per se* have limited diagnostic value. Entomologists relying on the scale for identification could overlook introduced or undescribed species. For example, prior to its description as a new species, *F. phoenicis*, a scale insect found on date palm in southern Iran, was probably often identified in the field as *Parlatoria blanchardi*, because the scales of the two species are similar. Where these species are sympatric, field identifications should be confirmed by laboratory examinations, as described below.

Taxonomically valid identifications and species descriptions of armoured scale insects have long been based almost entirely on the morphology of the mature females. They are the most commonly encountered of the adults. Although the females cannot be said to be rich in taxonomically useful structures, most species can readily be distinguished in this stage by the distribution and kinds of wax pores, the appearance and arrangement of lobes, plates and spines on the margins of the pygidium, and the arrangement and types of setae. Although additional external and internal structures of the females, morphology of males and immature stages, ultrastructure of wax pores, pigments, sperm and chromosomes have been shown to have taxonomic value (Miller and Kosztarab, 1979), characters of the mature female are adequate for identifying most species and the adult females continue to be the basis of diaspidid systematics (Takagi, 1990).

Some species are difficult to identify even from well-prepared slides of mature females. For example, *Aonidiella aurantii*, familiar as the California red scale insect of citrus, is sometimes reported from palms. Although some of these records are believed to be valid, most are probably misidentifications of *Aonidiella eremocitri*, which is probably common on coconut palms throughout the Pacific region (McKenzie, 1946; Williams and Butcher, 1987; Table 3.9).

Table 3.9. Species of Diaspididae reported on palm hosts (records compiled from Borchsenius, 1966, and Dekle, 1976, unless otherwise noted).

Species of Diaspididae	Palm hosts	Other hosts	Distribution
Diaspidinae			
Lepidosaphidini			
Andaspis hawaiiensis	*Ptychosperma*	D**	Cosmopolitan
Dentaspis substriata	Unidentified palms	nr	Uganda, Tanzania
Dinaspis aculeata	*Geonoma*	M*	Panama
Insulaspis duponti	*Cocos*	nr	Seychelles, Mariana Islands
Insulaspis gloveri	Unidentified Palmae	G* M* D**	Cosmopolitan
Insulaspis megregori	*Cocos*	D*	Oceania
Insulaspis vermiculus	*Cocos*	nr	Mauritius
Ischnaspis longirostris	*Acoelorraphe, Archontophoenix, Areca, Arenga, Attalea, Balaka, Borassus, Butia, Calamus, Chamaedorea, Chamaerops, Cocos, Coccothrinax, Copernicia, Dictyosperma, Dypsis, Elaeis, Howea, Hydriastele, Hyophorbe, Latania, Livistona, Pritchardia, Pseudophoenix, Ptychosperma, Raphia, Rhapidophyllum, Rhopalostylis, Roscheria, Roystonea, Sabal, Stevensonia, Syagrus, Trachycarpus, Veitchia,* Verschaffeltia, Washingtonia*	M* D***	Cosmopolitan
Lepidosaphes micronesiensis	*Clinostigma*	nr	Caroline Islands
Lepidosaphes unicolor	*Cocos*	nr	Philippines
Parainsulaspis bladhiae	*Cocos*	M* D**	Philippines, Taiwan
Parainsulaspis esakii	*Cocos*	M*	Oceania
Chionaspidini			
Aulacaspis phoenicis	*Phoenix*	nr	Sri Lanka
Aulacaspis tubercularis	*Cocos*	D*	Cosmopolitan
Chionaspis javanensis	*Cocos*	nr	Indonesia
Dentachionaspis pseudonivea	*Hyphaene*	nr	Somalia
Phenacaspis dendrobii	*Rhapis*	M*	China, Philippines
Phenacaspis eugeniae	*Howea, Livistona*	D*	Asia, Australia, Oceania
Phenacaspis inday	*Areca, Cocos, Corypha*	D*	Africa, Oceania
Phenacaspis kentiae	*Howea*	nr	Japan
Phenacaspis samoana	*Cocos*	nr	Samoa, Tonga
Phenacaspis sandwicensis	*Cocos*	M* D*	Hawaiian Islands, California
Pinnaspis aspidistrae	*Areca, Butia, Cocos, Howea, Rhapis, Syagrus*	F* G* M** D**	Cosmopolitan
Pinnaspis buxi	*Areca, Chamaerops, Cocos, Dictyosperma, Phoenix, Raphia, Rhapis, Thrinax, Trachycarpus*	F* M** D**	Cosmopolitan

Table 3.9. *continued*

Species of Diaspididae	Palm hosts	Other hosts	Distribution
Pinnaspis strachani	*Attalea, Chamaedorea, Chamaerops, Cocos, Dypsis, Elaeis, Howea, Livistona, Rhapis, Roystonea, Sabal, Syagrus, Trachycarpus, Verschaffeltia, Washingtonia*	G* M** D***	Cosmopolitan
Rolaspis chaetachma	*Phoenix*	D*	Southern Africa
Fioriniini			
Fiorinia arengae	*Arenga*	nr	Taiwan
Fiorinia fioriniae	*Areca, Chamaedorea, Chamaerops, Cocos, Dictyosperma, Dypsis, Howea, Hyophorbe, Latania, Licuala, Livistona, Phoenix, Phytelephas, Roystonea, Thrinax, Trachycarpus, Washingtonia*	G* M** D***	Cosmopolitan
Diaspidini			
Cryptaspidus nucum	*Cocos*	nr	Madagascar
Diaspis boisduvalii	*Acoelorraphe, Acrocomia, Archontophoenix, Areca, Bactris, Butia, Caryota, Chamaedorea, Chamaerops, Cocos, Corypha, Dictyosperma, Dypsis, Elaeis, Euterpe, Howea, Hyophorbe, Latania, Livistona, Nannorrhops, Phoenix, Ptychosperma, Rhapidophyllum, Rhapis, Roystonea, Sabal, Syagrus, Thrinax, Trachycarpus, Washingtonia*	M** D**	Cosmopolitan
Diaspis bromeliae	*Chamaerops, Phoenix, Syagrus*	M** D*	Cosmopolitan
Diaspis coccois	*Chamaerops, Cocos, Howea, Latania, Livistona, Phoenix, Roystonea*	M*	California, Jamaica
Gymnaspis grandis	*Lodoicea*	nr	Seychelles
Pseudaulacaspis cockerelli	*Acrocomia, Archontophoenix, Areca, Butia, Chamaerops, Cocos, Dypsis, Howea, Livistona, Phoenix, Rhaphidophyllum, Serenoa, Syagrus, Thrinax, Trachycarpus, Washingtonia*	M** D***	Cosmopolitan
Pseudaulacaspis pentagona	*Cocos, Phoenix, Pseudophoenix*	G* M* D***	Cosmopolitan
Pseudoparlatoria parlatorioides	*Butia, Chamaerops, Cocos, Dypsis, Howea, Phoenix, Ptychosperma, Roystonea, Sabal, Serenoa, Thrinax, Washingtonia*	M** D***	Cosmopolitan
Pseudoparlatoria turgida	Unidentified palm	D*	Panama

Table 3.9. *continued*

Species of Diaspididae	Palm hosts	Other hosts	Distribution
Parlatoriinae			
Parlatoriini			
Parlagena bennetti	*Cocos*	nr	San Andrés Islands (West Indies) (Mosquera, 1977)
Parlatoria blanchardi	*Hyphaene, Latania, Phoenix, Pritchardia, Washingtonia*	nr	North Africa, Middle East to India
Parlatoria crotonis	*Cocos*	M* D**	Cosmopolitan
Parlatoria fulleri		D*	France, Australia
Parlatoria mytilaspiformis	*Howea*	G* M* D**	Asia, Oceania
Parlatoria pergandii	*Archontophoenix, Cocos, Dypsis, Hydriastele, Latania, Phoenix, Ptychosperma, Syagrus, Trachycarpus*	G* M* D**	Cosmopolitan
Parlatoria pittospori	*Phoenix*	G* M** D***	Cosmopolitan
Parlatoria proteus	*Areca, Arenga, Butia, Caryota, Coccothrinax, Cocos, Dypsis, Howea, Hyophorbe, Latania, Livistona, Phoenix, Pritchardia, Pseudophoenix, Rhapidophyllum, Roystonea, Sabal, Syagrus, Thrinax, Veitchia,* Washingtonia*	G* M** D***	Cosmopolitan
Parlatoria serrula	*Cocos*	nr	Sri Lanka
Leucaspidini			
Lopholeucaspis cockerelli	*Bactris, Chamaedorea, Dypsis, Howea, Pritchardia*	G* M** D**	Cosmopolitan
Aspidiotinae			
Pseudaonidiini			
Duplaspidiotus tesseratus	*Roystonea, Sabal*	M* D**	Cosmopolitan
Furcaspis charmoyi	*Dictyosperma*	nr	Mauritius
Furcaspis oceanica	*Cocos, Nypa*	nr	Oceania
Neofurcaspis andamanensis	*Cocos*	nr	Andaman Islands
Pseudaonidia trilobitiformis	*Cocos, Dictyosperma, Hyphaene*	M** D***	Cosmopolitan
Stringaspidiotus curculiginis	*Corypha*	M** D*	South-East Asia
Tollaspidiotus mauritianus	*Dictyosperma*	nr	Mauritius
Aspidiotini			
Abgrallaspis cyanophylli	*Butia, Caryota, Cocos, Dypsis, Howea, Hyphaene, Livistona, Orbignya, Phoenix, Pritchardia, Ptychosperma Rhapidophyllum, Roystonea, Syagrus, Thrinax, Trachycarpus, Veitchia,* Washingtonia*	G* M** D***	Cosmopolitan
Abgrallaspis palmae	*Cocos, Elaeis, Phoenix*	G* M* D**	Cosmopolitan

Table 3.9. *continued*

Species of Diaspididae	Palm hosts	Other hosts	Distribution
Acutaspis albopicta	*Cocos*	M* D*	California, Mexico, Panama
Acutaspis perseae	*Sabal, Serenoa*	G* M** D***	Cosmopolitan
Acutaspis scutiformis	*Cocos*	M* D**	Mexico, Brazil, Argentina
Acutaspis tingi	*Cocos*	D*	Mexico, Colombia
Acutaspis unbonifera	*Attalea*	M**	Tropical America
Aonidia obtusa	*Verschaffeltia*	nr	Seychelles
Aonidiella comperei	*Cocos*	D*	Cosmopolitan
Aonidiella eremocitri	*Cocos*	M* D*	Australia, Oceania, California.
Aonidiella inormata	*Areca, Cocos, Metroxylon*	G* M* D**	Australia, Oceania
Aonidiella messengeri	*Phoenix*	D*	Taiwan, Ryukyu Islands
Aonidiella orientalis	*Archontophoenix, Chamaerops, Cocos, Copernicia, Dypsis, Orianopsis* (syn. *Orania*), *Phoenix, Roystonea, Sabal, Veitchia**	G* M* D**	Cosmopolitan
Aonidiella rex	*Elaeis*	D*	Congo
Aspidiotus coryphae	*Corypha*	nr	Philippines
Aspidiotus destructor	*Acoelorraphe, Archontophoenix, Areca, Arenga, Butia, Chamaedorea, Chamaerops, Coccothrinax, Cocos, Copernicia, Dictyosperma, Dypsis, Elaeis, Hyophorbe, Latania, Phoenix, Phytelephas, Raphia, Rhopaloblaste, Roystonea, Sabal, Syagrus, Verschaffeltia, Washingtonia*	G* M* D**	Cosmopolitan
Aspidiotus elaeidis	*Cocos, Elaeis*	nr	Pan-African
Aspidiotus fularum	*Cocos*	D*	Tropical Africa
Aspidiotus nerii (syn. *Aspidiotus hederae*)	*Areca, Chamaerops, Cocos, Corypha, Dypsis, Elaeis, Howea, Livistona, Phoenix, Pritchardia, Ptychosperma, Rhopalostylis, Sabal, Trachycarpus, Washingtonia*	G* M** D***	Cosmopolitan
Aspidiotus pangoensis	*Cocos*	nr	Fiji, Tonga, Samoa
Aspidiotus spinosus	*Arenga, Caryota, Cocos, Dictyosperma, Livistona, Phoenix, Rhapis, Roystonea, Sabal, Trachycarpus*	G* M* D**	Cosmopolitan
Aspidiotus varians	*Cocos*	nr	Tanzania, Madagascar
Chrysomphalus ansei	*Cocos*	D*	Seychelles
Chrysomphalus aonidum	*Acoelorraphe, Acrocomia, Archontophoenix, Areca, Balaka, Butia, Caryota, Chamaedorea, Chamaerops, Cocos, Copernicia, Dictyosperma, Dypsis, Erythea, Howea, Hyophorbe, Hyphaene, Latania, Livistona, Phoenix,*	G* M** D***	Cosmopolitan

Table 3.9. *continued*

Species of Diaspididae	Palm hosts	Other hosts	Distribution
	Pritchardia, Ptychosperma, Rhapis, Roystonea, Sabal, Veitchia, *Washingtonia*		
Chrysomphalus bifasciculatus	*Phoenix*	G* M** D***	Japan, Taiwan, Hawaiian Islands, California
Chrysomphalus dictyospermi	*Acoelorraphe, Acrocomia, Areca, Arenga, Attalea, Balaka, Butia, Calamus, Chamaerops, Cocos, Corypha, Dictyosperma, Dypsis, Drymophloeus, Heterospathe, Howea, Hyophorbe, Hyphaene, Latania, Livistona, Orbignya, Phoenix, Phytelephas, Ptychosperma, Rhapidophyllum, Roystonea, Sabal, Syagrus, Trachycarpus, Veitchia,* Verschaffeltia, Washingtonia*	G* M* D**	Cosmopolitan
Chrysomphalus diversicolor	*Dypsis, Phoenix*	G* M** D***	Eastern hemisphere
Chrysomphalus pinnulifer	*Cocos, Neodypsis, Ptychosperma*	G* M* D**	Cosmopolitan
Chrysomphalus propsimus	*Calamus*	nr	Sumatra (Indonesia), Venezuela (D'Ascoli, 1971)
Gonaspidiotus howardi (syn. *Hemiberlesia howardi*)	*Sabal*	D**	USA, Mexico
Gonaspidiotus minimus	*Chamaerops*	D*	Mediterranean region
Hemiberlesia lataniae	*Archontophoenix, Areca, Arenga, Attalea, Coccothrinax, Cocos, Corypha, Dictyosperma, Dypsis, Elaeis, Howea, Hyophorbe, Jubaea, Latania, Livistona, Orbignya, Phoenix, Pritchardia, Ptychosperma, Rhapidophyllum, Roystonea, Sabal, Syagrus, Thrinax, Veitchia,* Washingtonia*	G* M** D***	Cosmopolitan
Hemiberlesia palmae	*Cocos, Dypsis, Elaeis, Howea, Phoenix, Maximiliana* sp. (D'Ascoli, 1971)	G* M* D**	Cosmopolitan
Hemiberlesia popularum	*Phoenix*	D*	South-western USA
Hemiberlesia rapax	*Butia, Cocos*		Cosmopolitan
Lindingaspis floridana	*Howea, Phoenix*		Florida (USA), Asia
Lindingaspis mackenziei	*Cocos*	D*	Sri Lanka
Lindingaspis musae	*Elaeis*	M* D*	Tropical Africa
Lindingaspis rossi	*Cocos*	G* M** D***	Cosmopolitan
Lindingaspis tomarum	*Cocos*	D*	Guinea, Sierra Leone
Marginaspis thevetiae	*Cocos*	D*	West Africa

Table 3.9. *continued*

Species of Diaspididae	Palm hosts	Other hosts	Distribution
Melanaspis corticosa	*Ptychosperma*	M* D***	Southern Africa
Mycetaspis personata	*Areca, Cocos, Latania, Phoenix, Sabal*	M* D**	Cosmopolitan
Paraselenaspidus madagascariensis	*Raphia*	D**	Tropical Africa, Madagascar
Quadraspidiotus ostraeformis	*Phoenix*	G* D**	Cosmopolitan (extratropical)
Selenaspidopsis browni (Nakahara, 1984)	*Chamaedorea* sp.	nr	Mexico
Selenaspidopsis mexicana (Nakahara, 1984)	*Chamaedorea* sp.	nr	Mexico
Selenaspidus articulatus	*Chamaerops, Cocos, Dictyosperma, Dypsis, Elaeis, Howea, Hyphaene, Phoenix, Washingtonia*	G* M* D**	Cosmopolitan
Selenaspidus kamerunicus	Unidentified palm	D*	West Africa
Selenaspidus rufescens	*Cocos*	D*	Jamaica
Spinaspidiotus fissidens	*Hyphaene*	D**	Pan-African
Of unknown taxonomic position			
Aspidiotus chamaeropsis	*Chamaerops*	nr	France
Aspidiotus minutus	*Cocos*	nr	Jamaica
Aspidiotus palmarum	Unknown palm	nr	Europe (locality not specified)
nomen nudem:			
Aspidiotus simmondsi	*Cocos*	nr	Fiji
Diaspis vandalicus	*Cocos*	nr	Cuba
Leucaspis fulchironiae	*Phoenix*	nr	France

*Some records on *Veitchia* may refer to *Adonidia merrillii.*

F, ferns (Filicopsida); G, gymnosperms; M, monocotyledons; D, dicotyledons; nr, none reported. The number of asterisks indicates the importance of the host category, e.g. G*, few gymnosperm hosts; G***, many gymnosperm hosts.

Males are smaller than the females of their species, as are their scales. After the first-instar male settles and moults, the second instar forms a scale, incorporating the exuviae of the first instar. The scale of the second instar of some species is like that of the female, while in other species the male and female scales are different. The subsequent third and fourth instars develop within the scale without adding to it. The exuviae, except for those of the first instar, are very thin and pushed back inside the scale but not incorporated into the scale, as in the female. Therefore, the scale of most males is a parallel-sided, usually white, delicate wax structure, with the exuviae of the first instar at one end. In many species, the scale has one to three ridges or carinae (Foldi, 1990). Elongate, tricarinate scales are produced by males of many species.

The development of armoured scale insects is similar to that of Coccoidea in general. There are two larval instars in the female and four in the male (Fig. 3.30). Since all female stages past the crawler stage are sessile and the mobile male adult does not feed, the first-instar crawler is the only stage that is both mobile and capable of feeding. The crawlers hatch from eggs oviposited beneath the scale of the mother or, in viviparous forms, are deposited as larvae. Crawlers of most species are barely visible with a 10 hand-lens, being about 300 m long. They are oval in form, dorsoventrally flat, with functional legs that are too short to extend beyond the margins of insect's body and thus are not visible from a dorsal view. Their heads bear eye-spots and antennae. Most species have two long caudal setae (Howell and Tippins, 1990).

Crawlers usually wander for about an hour, but may continue this activity for up to a few days. The duration of this activity may be influenced by characteristics of the plant surface and other factors (Heriot, 1934; Hulley, 1962). Leaf veins and other obstacles that the crawlers encounter may trigger settling behaviour (Hulley, 1962; Koteja, 1990). Once a crawler selects a feeding site, it folds its legs and flattens itself against the plant surface to begin the lengthy procedure of inserting its stylets. First-instar larvae usually settle on the natal host plant. No longer 'crawlers', first-instar larvae feed for about a week before moulting to the next instar.

One function of the caudal setae of the crawlers is apparently that of increasing buoyancy in the air and thus enhancing dispersal (Hulley, 1962). In studies of several armoured scale-insect species, crawlers have been captured on glass plates with adhesive substances at varying distance from infested plants. Air dispersal may be more important for armoured scale insects of transitory hosts, such as grasses, than for tree-infesting species (Greathead, 1990).

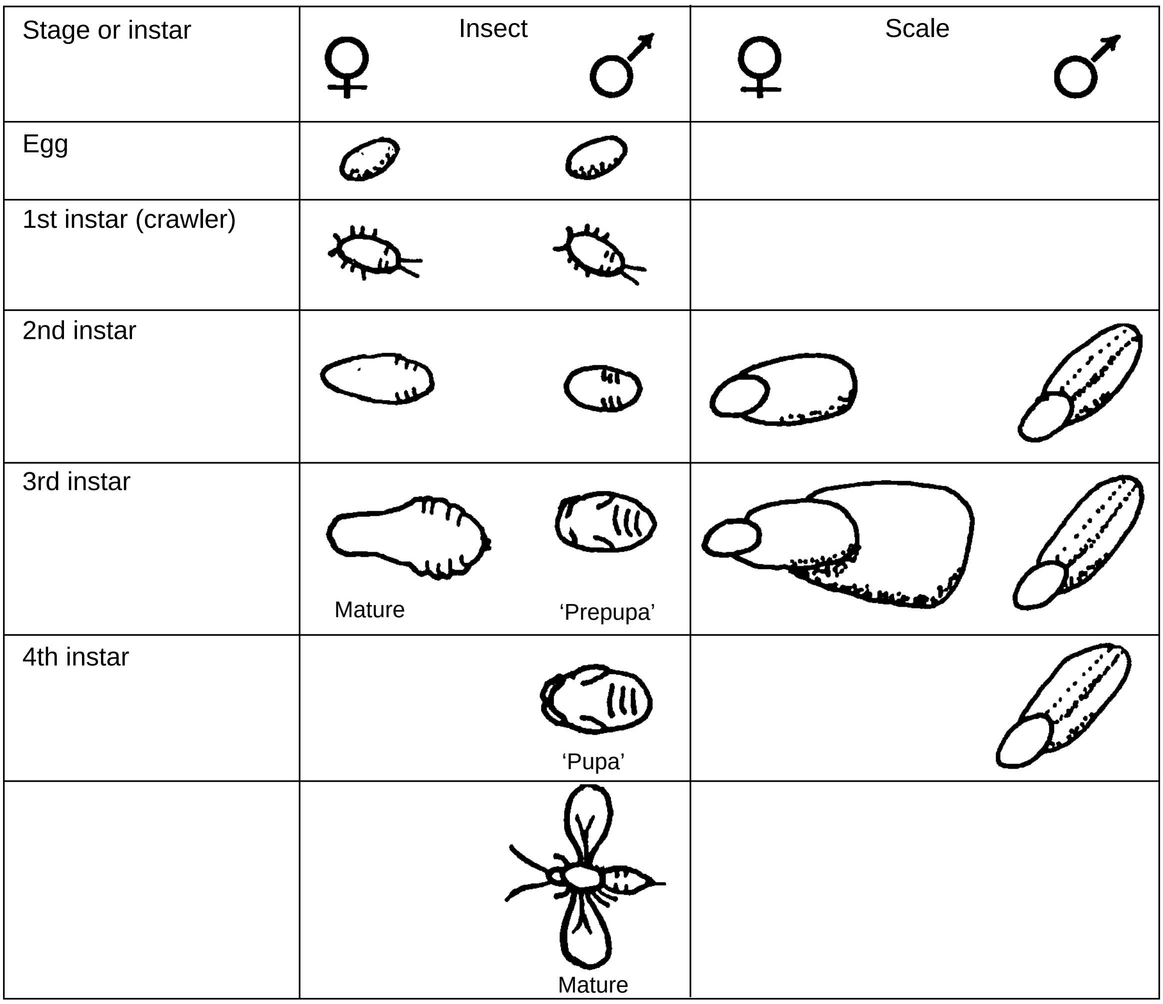


Fig. 3.30. Life stages and corresponding scale development in armoured scale insects. Females undergo two instars and then moult to the mature stage. During development, the scale is formed in three stages. Mature males emerge with the fourth moult; the external appearance of scales of males does not change after the second instar.

However, Reyne's (1948) studies on *Aspidiotus destructor* on coconut palms indicated that air dispersal was very important.

The second instar, occupying the same site as the first, differs greatly from it morphologically, having the same general form as the adult. Legs are lacking or reduced, and antennae are reduced. Armoured scale insects do not change the feeding site from that selected by the crawler. Thus, the cephalic end of the insect remains in place and growth is mostly posteriorly or both posteriorly and laterally in the more circular forms. The growth of the insect is reflected in the shape of the scale, as described previously.

Sexual dimorphism may be indicated in the first instar by differences in chaetotaxy, and becomes more apparent in the second instar. Female armoured scale insects of most species are about 1.0–1.5 mm in length. They are neotenic (i.e. sexually mature larvae), an unusual condition among insects. They are almost devoid of appendages and have only rudimentary eyes and antennae. Their stylets, which are much longer than the body, are extremely thin and flexible. For example, stylets of the females of *Aulacaspis tegalensis*, a species intensively studied by Williams (1970), are 0.3, 0.75 and 2.4 mm long in the first, second and adult stages, respectively. The mature female of this species is about 1.8 mm long. Armoured scale insects unwind their stylets from the crumena and insert them slowly with little control over the direction of their penetration. The salivary pump is disproportionately large, presumably an adaptation to force saliva down the long, fine salivary duct (Heriot, 1934; Takagi, 1990).

Armoured scale insects may feed in various tissues but are thought to be mostly phloem- or mesophyll-feeders. The path of the stylets may make some turns, but is generally parallel to the surface in a leaf and perpendicular to the surface if in stem tissue. When feeding on the monocotyledon sugar cane, the stylets of *A. tegalensis* penetrate an outer 0.1 mm layer of thick-walled cells of the stem (the rind) and then pass through parenchyma, avoiding vascular bundles. They terminate and feed in parenchyma cells (Williams, 1970). Feeding by armoured scale insects on palm tissue has not been scrutinized.

Armoured scale insects do not produce honeydew. They lack the filter chamber of other coccoids (Beardsley and Gonzalez, 1975) and, as mentioned, they probably return waste products to the plant or incorporate them in the scale (Banks, 1990; Foldi, 1990). However, there may be a weak association between some armoured scale insects and some ants: Vesey-FitzGerald (1940), studying scale insects on palms, observed that ants appeared to feed on the waxy bloom on scales of living diaspidids.

Because armoured scale insects beyond the crawler stage are immobile beneath a fixed scale, feeding takes place at almost the same site throughout life. With each moult, new stylets are formed and inserted in the plant tissue and never withdrawn. The scale is fabricated posteriorly by the pygidium from wax emitted by posterior wax glands. Anterior growth of the insect is restricted by the scale; thus the point where the stylets of an instar penetrate is slightly posterior to the insertion point of the preceding instar. One might say that the insect's body slides slowly backward as it grows, so that the stylets must reach over the gap created by this displacement. The extraordinary length and flexibility of their stylets may be compensatory for this mode of growth.

After the final moult, the mature female begins to enlarge the scale, but mates before it is completed, extending the pygidium slightly beyond the scale and emitting a pheromone that attracts the winged male. The males mate with females by extending the aedeagus under the scale and inserting it into the vulva of the female. The female then completes the scale (Williams, 1970).

Under tropical conditions, a female generally develops from the egg stage to the adult in a few weeks and lives as an adult for 1–3 months, during which time it may produce several hundred eggs or larvae. These accumulate beneath the scale, posterior to the female. As eggs are laid, the female gradually shrinks. The larvae may remain for a time beneath the scale, but eventually leave its protection to settle on the natal host plant or are spread to other plants, as already indicated.

The male armoured scale insect undergoes two larval instars, followed by two quiescent stages, sometimes referred to as the prepupal and pupal stages, and then emerges as an adult (Howell and Tippins, 1990). Adult males do not feed. They live only the few hours necessary for mating. Copulation in, for example, *P. blanchardi*, an armoured scale pest of date palm, takes place for only 2–3 min (Smirnoff, 1957). In diaspidids, there are exceptions to the rule that males of coccoids are winged. In *P. blanchardi*, some males have well-developed forewings, some are apterous and others are brachypterous. The males of *Comstockiella sabalis* (placed tentatively by many authors in Diaspididae) are apterous, as are some diaspidid relatives, such as Phoenicococcidae. Unlike Coccidae, Diaspididae are rarely parthenogenetic (Giliomee, 1990).

Limited in mobility during much of their lives, but provided with highly effective protective adaptations, armoured scale insects are best fitted for life on long-lived hosts. Although some armoured scale insects, notably the subfamily Odonaspidinae, infest grasses, most species infest dicotyledonous woody perennial plants. They may prefer certain plant parts, but are often eurymerous on above-ground plant parts. One species, *Aulacaspis yasumatsui*, which infests above-ground parts of Cycadaceae, was also found to infest roots of this host several centimetres below the soil (Howard *et al.*, 1999). Thus, it may be suspected that additional species are adapted to roots of their hosts. The family Diaspididae may be fundamentally adapted to live on stem tissue. Utilization of leaves and fruits may be a secondary evolutionary development, as suggested by observations on *A. tegalensis* infesting sugar cane (Williams, 1970). This species infests leaves only when its stem-infesting populations become extremely dense. Williams commented that scales are formed more readily on the firm surfaces of stems and adhere to them better and that the longevity of a leaf may be insufficient for full completion of the life cycles of some armoured scale-insect species. On the other hand, many armoured scale insects that infest conifers occur on foliage and not on stems. Conifer needles offer a relatively firm substrate and are continuously present. Armoured scale insects that infest the leaves of deciduous trees and shrubs must be adapted to survive periods when there is no foliage. Most of these species survive the winter (or dry season) as morphological variants, which move to the stems prior to leaf-fall.

Some armoured scale insects, e.g. *Pinnaspis aspidistrae*, which prefers ferns and monocotyledons, usually occupy leaves and are rarely on stems. Palms would seem to be exceptionally suitable hosts for leaf-infesting armoured scale insects. Their stiff fronds provide a good substrate for scales. Fronds are available year-round and each may last a year or more.

Several taxonomic systems have been followed for the Diaspididae, and current taxonomic research will probably result in new concepts (Ben-Dov, 1990a, b; Miller, 1990). For convenience, we use a modified version of Borchsenius's (1966) system, which may be outlined as follows:

- Family Diaspididae
  - Subfamily Diaspidinae
    - Tribes:
    - Ancepaspidini
    - Antokaspidini
    - Chionaspidini
    - Diaspidini
    - Fioriniini
    - Lepidosaphidini
  - Subfamily Parlatoriinae
    - Tribes:
    - Leucaspidini
    - Parlatoriini
  - Subfamily Aspidiotinae
    - Tribes:
    - Aspidiotini
    - Pseudaonidiini
    - Targioniini
  - Subfamily Odonaspidinae

About 6% of the 1890 species listed in Borchsenius's (1966) *A Catalogue of the Armoured Scale Insects (Diaspidoidea) of the World* were recorded on one or more species of palms. The palmivorous species are well distributed in different subfamilies and tribes. A notable exception is the totally graminivorous Odonaspidinae.

Most armoured scale-insect pests of palms are not restricted to them, but instead are polyphagous 'weedy' species that have been spread to many countries. Of the 43 principal armoured scale pests of the world listed by Beardsley and Gonzalez (1975), about 90% are polyphagous species that primarily infest dicotyledonous woody ornamental and fruit-trees, and about 35% of them have also been reported on palms (Borchsenius, 1966). Of the 56 major armoured scale-insect pests of ornamental plants listed by Miller and Davidson (1990), nearly all were polyphagous. None were restricted to palms, but palms were listed as hosts of 21% of them. Examples of these palmivorous species include (each followed by number of host-plant families): *Abgrallaspis cyanophylli* – 44, *A. orientalis* – 25, *Aspidiotus destructor* – 45, *Aspidiotus nerii* – 88, *Chrysomphalus aonidum* – 74, *C. dictyospermi* – 71, *Hemiberlesia lataniae* (Fig. 3.31) – 78, *Ischnaspis longirostris* – 31, *Parlatoria proteus* – 22, *P. aspidistrae* – 27, *Pinnaspis buxi* – 21, *Pinnaspis strachani* – 27, *Pseudaulacaspis cockerelli* (Colour Plate 11d, Fig. 3.32) – 21 and *Selenaspidus articulatus* – 31. A few of these (e.g. *A.*

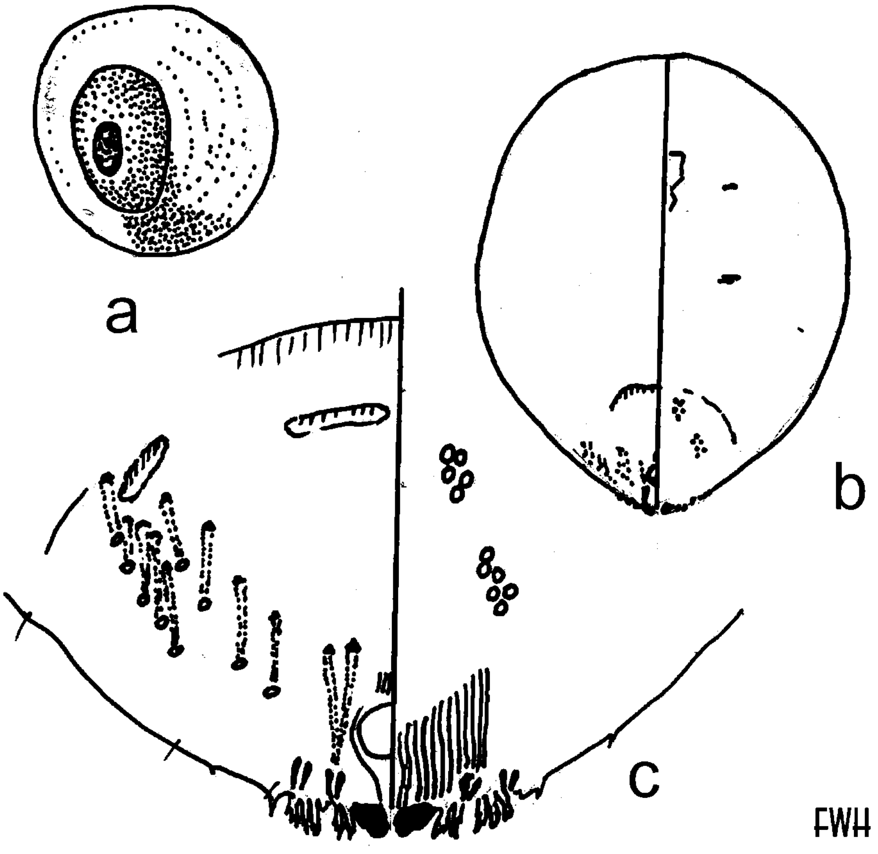
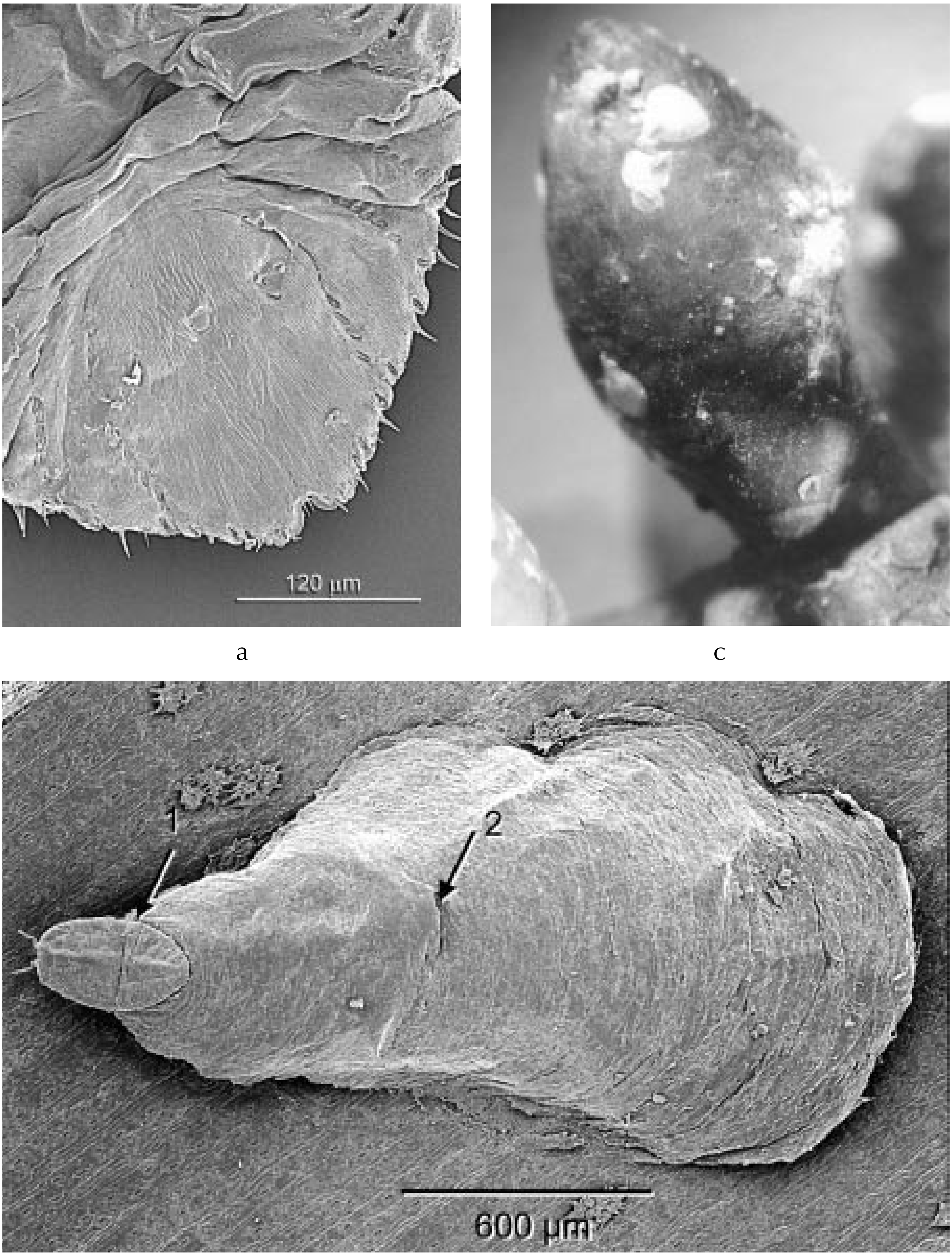


Fig. 3.31. *Hemiberlesia lataniae* (Diaspididae). (a) Scale of female. (b) Mature female, drawn from a cleared and stained specimen on a microscope slide. Left half is dorsal surface, right half is ventral surface. Each surface can be viewed separately by focusing the microscope. (c) Detail of pygidium. Characteristics of this subfamily, Aspidiotinae, are the more or less circular outline of the body, slender dorsal ducts and fringed 'plates' on the pygidial margin. Diaspidinae (see *Pseudaulacaspis cockerelli* and *Ischnaspis longirostris*) are circular or elongate, and have short, thick dorsal ducts, and spines on the margins rather than plates.



a

c

b

Fig. 3.32. *Pseudaulacaspis cockerelli* (Diaspididae: Diaspidinae), a widely distributed pest of palms and other plants. (a) Dorsal surface of pygidium (SEM view). Note spines on pygidial margin, a characteristic of the subfamily Diaspidinae. (b) Scale of female, showing three-part structure: (1) first-instar exuviae, (2) juncture of scales of second and third instars. The shape of the scale conforms to that of the insect itself; thus those of Aspidiotinae are usually circular and those of Diaspididae circular to elongate. (c) On fruit of *Dictyosperma album*, Florida.

destructor and *I. longirostris*) have been reported as important pests of palms in plantations. Most are primarily nursery and glasshouse pests, which thrive on diverse dicotyledons grown in the high plant densities and favourable growing conditions of nurseries and glasshouses, opportunistically infesting palms grown in the same facilities. That a disproportionate number of hosts are tropical fruit- and ornamental trees is probably a result of collecting bias: they are inspected more frequently than wild trees and shrubs.

Diaspis boisduvalii, *Diaspis bromeliae* and *Diaspis coccois* are among the exceptional armoured scale insects that have been observed mostly on monocotyledons. They are common on palms, especially in glasshouses.

Species known only from palms (except for rare records) include *Abgrallaspis palmae*, *Chrysomphalus propsimus*, *Fiorinia fioriniae*, *Gonaspidiotus minimus, P. blanchardi*, *Selenaspidopsis browni* and *Selenaspidopsis mexicana*. *Comstockiella sabalis* is restricted to palms, but is no longer placed in the Diaspididae.

Armoured scale insects are relatively unknown on palms in the wild, most attention having been focused on pests of economic palms. Species that await discovery are likely to occur in sparse populations.

The relatively few species that exploit palms find a highly favourable habitat: armoured scale insects are the most consistently encountered hemipterous pests of cultivated palms from the seedling stage to maturity. They are major pests of palms grown as plantation crops and landscape plants, and rival spider mites as pests of palms grown in nurseries and glasshouses.

Armoured scale insects are eminently adapted for long-range dispersal on host plants that are moved from one place to another. Unlike flying insects, they do not leave their host plant when it is disturbed, but remain on it, even during long ocean voyages. They are difficult for agricultural inspectors at ports of entry to detect, because of their small size and concealed habits. Their establishment in a new locality is facilitated because the major component of their habitat is the host plant upon which they have arrived. A study conducted in Louisiana serves to illustrate their propensity for invasion of new areas. About half of the armoured scale insects known to occur in that state are introduced species (Howard and Oliver, 1985). The situation is no doubt similar wherever a large array of exotic woody plants have been introduced.

Parlour palms became popular during Victorian times and, since then, small palms suitable for this purpose have been grown in nurseries and glasshouses for markets in distant localities. Many of the common scale-insect pests of palms and other ornamental plants were first reported in the USA in the late 19th century. Several decades ago, methods of transplanting large mature palms were developed. This led to the establishment of field nurseries where large palms could be grown for shipment elsewhere, creating ‘instant landscapes’. Vegetative propagation is not known for most palm species, but selections of the date palm have been propagated for centuries by separating buds (‘offshoots’) from stems. The modern California date industry was started from offshoots of various cultivars selected in North Africa and the Middle East. *Phoenicococcus marlatti* (in the diaspidoid family Phoenicococcidae) and *P. blanchardi* were introduced into the southwestern USA in this way. (The latter was eventually eradicated from that state. The former persists in California and recently became established in Florida (Avas Hamon, personal communication).

Some species of scale insects infest palm fruits. Thus, the voluminous traffic in fresh coconuts, fruits of peach palms, dates, etc. between producing countries poses some risk of spreading scale insects. Over longer distances, the risk is reduced because fruits of the economically most important palms (dates, coconuts, oil palm fruits, etc.) are generally dried, milled or otherwise processed in the producing countries. Seeds for planting are usually scraped to remove the fruit or fibrous mesocarp. Although coconuts used for seed propagation are generally not dehusked, they are usually dried before shipping, partly in order to reduce weight. In any case, by the time that the first leaf sprouts, the husk has generally been dry for at least a month. No stage of an armoured scale-insect species would be expected to survive this long without living plant tissue. Fumigation, as is required by regulatory agencies of some countries, further reduces any remaining risk of importing scale insects on coconut seednut. Sprouted coconuts present a different situation. They may provide a mode of long-distance spread of leaf-infesting armoured scale insects.

Ecological and economic factors should be considered in devising control strategies. Growers often rely on insecticides in nurseries where palms are grown as ornamental plants. This is partly because of consumer preferences for unblemished plants. Additionally, regulatory agencies may require that nurseries be treated when they are infested with pests, even though the insects may not have reached destructive levels. In commercial palm plantations, profit margins are lower, aesthetic damage is not a factor, and the environment, that of a tree grove, is suitable for biological control of scale insects. Landscape plantings of palms provide aesthetic value, but, because the plants are usually seen from a distance, blemishes may not constitute aesthetic damage. Profit margins, in fact, are almost undefinable. In Florida, the extensive palm plantings have similarities to tropical plantations. Thus, biological control is appropriate against armoured scale-insect pests of palms in these situations.

Parlatoria blanchardi (Colour Plate 12a, Fig. 3.33), a serious pest of date palm, is reported only on palm hosts. It is a good example of an insect pest adapted to palms in the BW climate (see Box 1.1). It is the major pest of date palms in some countries, e.g. Sudan (S. Ahmed Siddig, personal communication). It is known as the 'parlatoria date scale insect' and also as the 'white date scale insect', distinguishing it from the 'green' and 'red' date scale insects (q.v.). It is generally believed to be native to the Arabian Gulf countries (as is date palm). Commerce in date offshoots over the centuries spread it from there eastward into India and Central Asia and westward across the Middle East into North Africa and Turkey. It was spread overseas on offshoots to Australia and North and South America (Smirnoff, 1957). It has palm hosts additional to *Phoenix* spp. For example, in Niger it was observed on *Hyphaene thebaica* on sites devoid of *Phoenix* spp. (Stansly, 1984). In the south-western USA, it has been reported on *Washingtonia* spp. in certain cases where these were next to highly infested date palms (Boyden, 1941).

Boyden (1941) observed heavy infestations of this scale on *P. canariensis* in California. Although the Canary Islands date palm is one of the most ubiquitous ornamental palms in the world, *P. blanchardi* has not become widely distributed on it, no doubt partly because this sympodial palm is propagated from seeds, not offshoots.

The mature *P. blanchardi* female is about 0.8 mm long and reddish pink to reddish purple-coloured. Creamy-yellow individuals (Hussain, 1974) are probably callow (recently moulted) individuals. As is characteristic of Parlatorini, there are three pairs of well-developed pygidial lobes, which diminish only slightly from the median to the third pair (Fig. 3.33). The scale, 1.2–1.6 mm long, is pyriform and typically white (Hussain, 1974). Some populations have darker scales, and white and dark scales may be present on the same palms. This is believed to be due to individual variation and environmental differences (Cockerell, 1907).

In the original description of *P. blanchardi*, males were described as apterous (Targioni-Tozzetti, 1892), but further studies of this species revealed that winged, wingless and intermediate forms exist. Of 186 males examined by Stickney (1934b), 56% had fully developed wings and 25% were wingless; the remainder had micropterous wings. The apterous forms are well adapted to penetrating crusts of accumulated scales (Smirnoff, 1957). In Egypt, alate males predominate in the spring, and

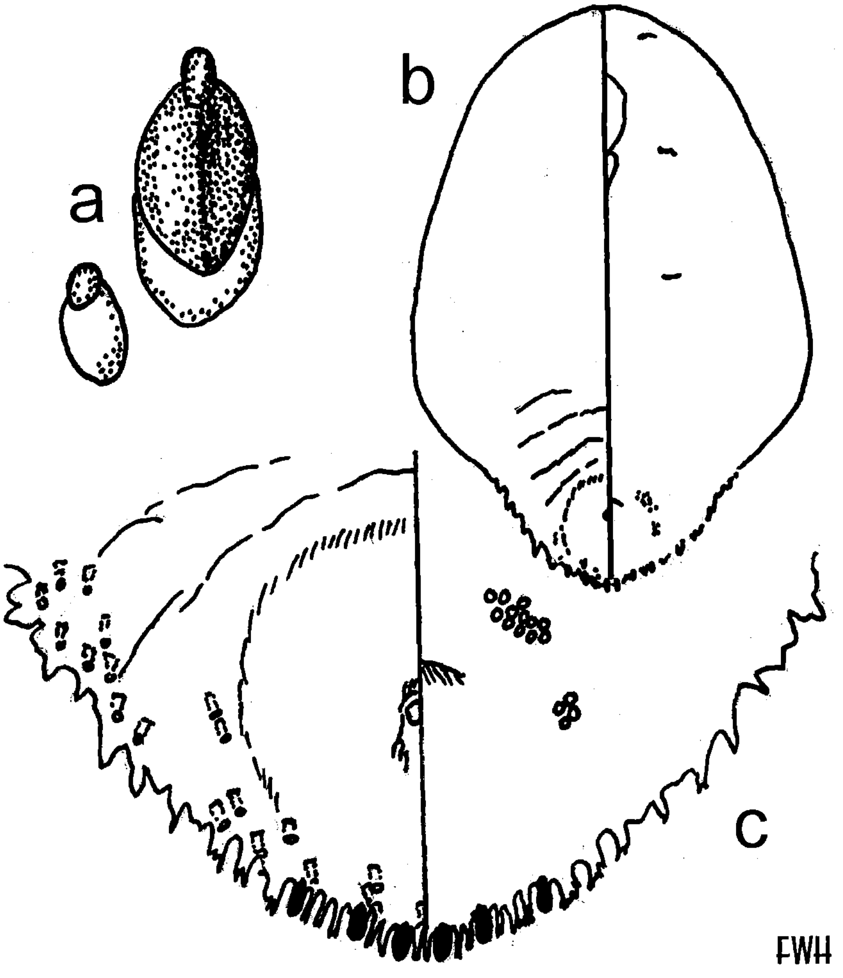


Fig. 3.33. *Parlatoria blanchardi* (Diaspididae: Parlatorinae), a pest of date palms. (a) Scales of male (left) and female (right). (b) Mature female. (c) Detail of pygidium. Left side is dorsal view, right side is ventral view. After Ferris (1937–1955).

apterous males predominate in the summer generation. The alate males fly at early dawn (El-Kareim, 1998). The scale of the male is elongate and much smaller than that of the female.

Parlatoria blanchardi commonly infests the leaf bases, where the insects are hidden by fibres. As populations increase, they infest first the older and then the younger foliage and finally fruits. High population density in autumn may result in infestation of fruit just prior to the date harvest (Benassy, 1990). In Basra, Iraq, numbers per pinna of older fronds were over 15,000 scales on the adaxial surfaces and over 7500 on abaxial surfaces (Hussain, 1974). It may be remarked that these counts were made on scales, and may not necessarily represent the numbers of live scale insects. Smirnoff (1957) estimated that a palm of 10–15 years of age may harbour up to 180 million of these scale insects. Curiously, *P. blanchardi* has surprisingly low fecundity for an armoured scale-insect pest. Females are reported to oviposit a mean of 9.6 and a maximum of 29 eggs (Smirnoff, 1957; Hussain, 1974; Benassy, 1990).

Armoured scale insects that infest leaves are typically on the abaxial surfaces, but *P. blanchardi* prefers the adaxial frond surfaces of date palms (Colour Plate 12a). For example, in Iraq twice as many scales were on the adaxial than on the abaxial surface (Hussain, 1974). This was consistent with observations in Saudi Arabia (Dabbour, 1981) and in the Thar Desert in western Rajasthan, India (Swaminathan and Verma, 1991).

The canoe-like structure of the induplicate pinna of *Phoenix* (Fig. 1.6) seems well suited to environmental conditions of the deserts. Because the laminae are turned upward, during much of the day they meet the uninterrupted intense sunlight obliquely so that they shade the adaxial surface of the pinna. Furthermore, the upturned laminae protect the adaxial surface from drying winds. Thus, the induplicate pinna also provides a haven for insects, undoubtedly attracting higher numbers of crawlers to settle, increasing survival rate, etc.

Parlatoria blanchardi typically has from three to four population peaks and the same number of overlapping generations per year. In Mauritania, during the cool season in January and February, when the mean daily temperatures are about 20°C and the minimum less than 14°C, the life cycle is completed in 90 days and populations diminish (Laudého *et al.*, 1970). Date palms continue to produce new fronds as long as the temperature is above about 10°C. During March and April, when mean temperatures are mild (21–32°C), the life cycle is completed in about 60 days. In the hotter, drier months of June through September, during which the temperature may rise above 40°C daily, the population declines, due to the death of a large portion of the scale insects. The life cycle of the survivors, however, takes only about 45 days. With cooler weather from October through December, a larger portion of the scale insects survives and populations increase in density again (Tourneur *et al.*, 1975). In plantings around oases (Colour Plate 2a), populations tend to be higher in the interiors than at the more exposed perimeters (Smirnoff, 1957).

Feeding by *P. blanchardi* on fronds causes necrosis of tissues. Heavily infested fronds turn yellow and die prematurely. Basakah (1987) reported on some of the chemical changes in date palm leaf tissue due to feeding by this insect. Offshoots heavily infested with this species become stunted. Fruits attacked by the insect shrivel and remain small and unmarketable. Losses of 70–80% of the date crop in 1 year and 50–60% in 3 years were reported in Morocco. In Morocco and Algeria infestations have commonly killed palms of 5–10 years of age (Smirnoff, 1957), but in Iraq heavy infestations were not lethal (Hussain, 1974).

One of the exemplary cases of eradication of a well-established insect pest was that directed against *P. blanchardi*, which was introduced into the USA on date palm offshoots from Algeria in 1890. The offshoots, which were imported for the then fledgling date industry in the south-western USA, were shipped via Washington, DC, where the US Department of Agriculture inspectors intercepted the scale insect. (They identified it as *Parlatoria ziziphi*, which otherwise has not been reported from palms. *Parlatoria blanchardi* was not yet known to science (Targioni-Tozzetti, 1892).) After repeated applications of a strong kerosene and soap emulsion, the scale insect appeared to have been eradicated and the offshoots were reshipped to the south-western USA.

In 1892, two palms at the University of Arizona experimental farm were found to be infested with *P. blanchardi* and, within the next 3 years, date palms in several localities in Arizona and California were found to be infested. In 1915, date palms near Laredo, Texas, planted from offshoots from Indio, California, in 1906, were found to be heavily infested.

Early eradication efforts, relying mostly on repeated kerosene and soap emulsion treatments and on cyanide fumigation, met with little success, but eventually a well-organized programme was inaugurated. It involved quarantine regulations to prevent movement of infested palms and mechanical control of the scale insect, combined with diligent inspections.

The fact that the pest was mostly confined to a single host species grown in discrete localities isolated by vast desert areas was undoubtedly a factor in making eradication a feasible goal. One must also credit the programme personnel for their perseverance and ingenuity, evident in their array of novel climbing equipment, illustrated and described by Boyden (1941).

These devices reveal great determination for meeting the different challenges that they encountered, but one fears that their designers may have been less than zealous with regard to job safety. They included a truck-mounted, collapsible tower, from which the date palm inspectors examined foliage while the truck was driven down rows of palms; it could be considered a predecessor of the hydraulic-lift truck developed decades later for tree work. Extremely tall and unstable-looking stepladders and similarly precarious extension ladders were employed for different situations.

The inspection procedures, described by Boyden (1941), should be studied in detail by those with more than a passing interest in pest regulatory work. Infested and uninfested groves were inspected repeatedly and with equal care. Thoroughness was favoured over speed. Industrial psychology was not neglected. For example, it was recognized that inspectors differed in efficiency and their efficiency was most likely to lapse during long intervals without finding scales. Additionally, different individuals examining the same palms were apt to look at them from different angles; thus one might see scales that the other inspector had missed. For these reasons, inspectors returning to a grove that they had previously inspected were assigned different rows, and grove assignments were occasionally switched between different inspectors.

But much of the success of the programme was also due to the 'mechanical control' method employed: it consisted in dousing palms with petrol and setting them ablaze! This idea came partly from 'a Mexican practice' of removing old persistent fronds from certain palms (probably *Washingtonia* and *Brahea* spp.) by burning, which did not appear to injure the palm permanently. An additional clue came from observations after the great earthquake and fire in San Francisco in 1906: in some quarters of that city, charred date palms stood above the ash and rubble, 'the only survivors of the catastrophe', and eventually produced new fronds and recovered (Forbes, 1907). Palms torched in the scale-insect eradication programme sprouted back within 2 years. Harsh and labour-intensive though it was, the programme resulted in eradication of the insect. The last remnants of the pest were eliminated in the Coachella Valley, California, in 1934. This was the first time – and one of only a few times – that a well-established insect was eradicated from a large region (Boyden, 1941; Gill, 1990a).

On small farms and in gardens in arid regions, where the isolated nature of the plantings might preclude rapid reinfestation, pruning of older fronds infested with *P. blanchardi* may be effective in controlling the pest (Siddig, 1975). However, frequent pruning may have long-term deleterious effects on palms.

Dabbour (1981) reported preliminary studies of the susceptibility *to P. blanchardi* of ten different cultivars of date palms. Swaminathan and Verma (1991) reported that 'Khadrawy' and 'Medjool' had > 500 scales per pinna, while six other cultivars, including 'Zahidi' and 'Migraf', had < 100 scales per pinna. Comparisons of numbers of *P. blanchardi* on six varieties of date palm in Iraq did not reveal well-defined differences (Hussain, 1974). In Tunisia, the cultivar 'Kentichi' was more resistant to the diaspidid than 'Deglet Noor', 'Aligue' or 'Khouaet Alig' (Khoualdia *et al.*, 1993).

Insecticides effective for control of *P. blanchardi* are similar to those used against armoured scale insects in general, e.g., dimethoate, which has systemic activity against all feeding stages, and malathion and other organophosphate contact insecticides, which are effective against crawlers (Avidov and Harpaz, 1969; Siddig, 1975). Chemical control may be warranted for emergency treatment of localized outbreaks, but may disturb natural or biological control for other pests, besides being expensive and difficult to implement in many situations where date palms are grown.

Although many natural enemies of *P. blanchardi* have been identified in localities of the Middle East and North Africa

(Smirnoff, 1957), the effect of any of these species by itself may be slight. *Aphytis phoenicis* (Aphelinidae) is one of a few species of parasitic Hymenoptera that is considered an important natural enemy of *P. blanchardi*. *Chrysopa* sp. (Neuroptera), found infrequently on date palms in Israel, may consume some of the scale insects. *Hemisarcoptes coccophagus* (Hemisarcoptidae) is a predacious mite that attacks *P. blanchardi* (Gerson and Smiley, 1990).

Twenty-five species of Coccinellidae are associated with *P. blanchardi* in Israel (Kehat, 1967) and 25 species in the area occupied by Tunisia, Algeria and Morocco (Smirnoff, 1957).

Species of *Pharoscymnus* and *Scymnus* are particularly widespread (Smirnoff, 1957), but any one species is often insufficient to control the scale insect. Natural enemies restrict the populations of some of these beetles while population fluctuations of others are poorly synchronized with those of the host. Several species of Cybocephalinae (Nitidulidae) attack this scale insect. In the Sahara region, 75% of the predacious insects are species of *Cybocephalus*. Three species, namely *Cybocephalus palmarum*, *Cybocephalus dactylicus* and *Cybocephalus flaviceps*, predominate, occurring in different proportions of the predator complex in different oases. *Cybocephalus nigriceps nigriceps* is also widespread in the Sahara region (Blumberg, 1973), and is the most prevalent of this group attacking *P. blanchardi* in Israel. However, as with cybocephaline beetles in general, their consumption rate of scale insects is low and their life history is asynchronous with that of their host (Benassy, 1990).

Two different biological control strategies for *P. blanchardi*, each of which may be applicable to different localities, were discussed by Benassy (1990): (i) enhancement of local natural enemies; and (ii) introduction of *Chilocorus bipustulatus* (Coccinellidae), a predator that has proved effective in controlling *P. blanchardi* in several localities.

In the first strategy, insecticide use is restricted and natural enemies are transferred, for example, on excised palm fronds, from local palm groves where they are relatively abundant to palm groves where they are scarce.

The second strategy can be illustrated by the example of biological control with *C. bipustulatus*, a widespread coccinellid that feeds on many scale insects and is sympatric with *P. blanchardi* in the Middle East and North Africa. Beetles of this species obtained in Iran successfully controlled *P. blanchardi* when introduced into Mauritania (Iperti *et al.*, 1970). Five other introduced coccinellids were not successful (Gaillot, 1967; Laudého *et al.*, 1970).

In 1973, *C. bipustulatus* was introduced near Agadés, in oases of the Sahara Desert in Niger (Colour Plate 2a). Both there and in Mauritania, the survival of the beetle during the hot, dry summer was poor and it only partially controlled *P. blanchardi* (Kaufmann, 1977). The next year, Stansly (1984) introduced the beetle from Agadés to the higher and cooler Aïr (Adine) mountains 125 km to the north-east, releasing them early in the morning or at the end of the day during rainy or relatively cool weather. Typically, 50 to 100 adult beetles were placed on three to five palms in the middle of a grove. Releases were made repeatedly. The presence of palms of different sizes and of some relatively dense plantings for harbouring beetles during the hottest period appeared to enhance their survival. After 2 years, the beetle was found at 25 release sites and had spread up to 15 km from some of them.

The beetle dramatically reduced *P. blanchardi* populations at release sites compared with date palm plantings where beetles were not released. Coccinellids, cybocephalines, *Hemisarcoptes* sp. (Acarina: Hemisarcoptidae) and a ‘liquefying’ disease were additional factors. Stansly (1984) suggested that biological control of *P. blanchardi* in Niger could be improved by planting small dense stands of date palms within the larger groves to provide refuge for the beetles during hotter periods, spraying the plants with food substances for the beetles and their larvae and introducing hymenopterous parasitoids.

Pharoscymnus horni (Coccinellidae) was the most abundant of several predators of *P. blanchardi* in the Thar Desert, India, consuming about 27 scale insects per beetle in 24 h (Swaminathan and Verma, 1991).

Chilocorus nigritus, known best as an important predator of *Aspidiotus destructor* on coconut palm in India and Sri Lanka, was observed as a natural enemy of *P. blanchardi* in Gujarat State, India. Larvae consume a total of about 437 of these scale insects each and imagos over 1000 each. The long life cycle, high consumption of prey, fecundity and adaptability to the Indian peninsula make this species of potential value for controlling *P. blanchardi* in that region (Muralidharan, 1994).

We are not aware of any published data on *P. blanchardi* in South America or Australia, where it was introduced decades ago (Tourneur and Vilardebo, 1975; Tourneur *et al.*, 1975).

Aspidiotus destructor, the coconut scale insect (Colour Plates 11b and 12f, Figs 3.34 and 3.35), is one of the most widespread pests of coconut palm. A highly polyphagous species, it has been recorded on 75 genera in 45 families of plants worldwide (Borchsenius, 1966), and is common on many species of the family Palmae (Table 3.9). In Florida, this species was recorded on 25 species of palms and 135 species of plants other than palms (Dekle, 1976). It is considered a pest on some of these plant species and is rare on others.

In Florida, although *Dypsis lutescens* and *Phoenix* spp., which are abundant palms, are reported as hosts, *A. destructor* is rarely observed on them outdoors (F.W. Howard, unpublished). No experimental work on preferences of *A. destructor* for different species of palms or different varieties of coconut palm have been published.

Of monocotyledonous hosts other than palms, banana is frequently reported in many countries. Other monocotyledonous hosts include *Pandanus* spp. (Pandanaceae) and *Carludovica palmata* (Cyclanthaceae) (D'Ascoli, 1971), both arborescent species. Most species recorded as hosts are dicotyledonous woody plants. *Aspidiotus destructor* has been listed as a pest of mango, guava and papaya (Taylor, 1935; Beardsley and Gonzalez, 1975; Chua and Wood, 1990).

The female is turbinate, is 0.95 mm long and has a delicate appearance, even for an armoured scale insect. The colour varies; there are orange, yellow and greenish-yellow forms. Taylor (1935) suggested that the insect's colour depended on the host plant, although this has not been investigated. The 'plates', highly branched structures on the pygidial margin, are well developed and form a characteristic lacy fringe (Fig. 3.36). The male, is about 0.7–0.8 mm and yellow, sometimes with a pink tint. The aedeagus is about one-third the length of the body. There are two simple eyes and two ocelli. The filiform antennae have ten antennomeres. The two wings are delicate, with reduced venation (Lepesme, 1947).

The scale of the female is round, about 1.2 mm in diameter, thin, whitish and semi-transparent, so that the insect's body and the eggs are visible through it (Colour Plate 11b, Fig. 3.34). The scale of the male is smaller and oval (Dekle, 1976).

The relative lengths of median and lateral lobes and other morphological features of the pygidium are highly variable in *A. destructor*, and some authors have described the more extreme variations as separate species or subspecies. Reyne (1948) described a subspecies, *A. destructor rigidus*, on Sangi (Indonesia), based on morphological and biological characteristics that distinguished it from the typical *A. destructor*. This may have been the 'Asian form', involved in a virulent outbreak of *A. destructor* on the island of Príncipe about 25 years later (Simmonds, 1960). Balachowsky (1957) recognized different strains, including the 'American', 'African' and 'Asian' forms. However, these forms may be found in any population of *A. destructor*, and the existence of distinct races or subspecies of this scale insect is unlikely (Reyne, 1948). At least seven forms described as separate species are currently considered synonyms of *A. destructor* (Borchsenius, 1966).

Except where otherwise cited, the following summarizes Taylor's (1935) detailed study of *A. destructor*. Females lay a mean

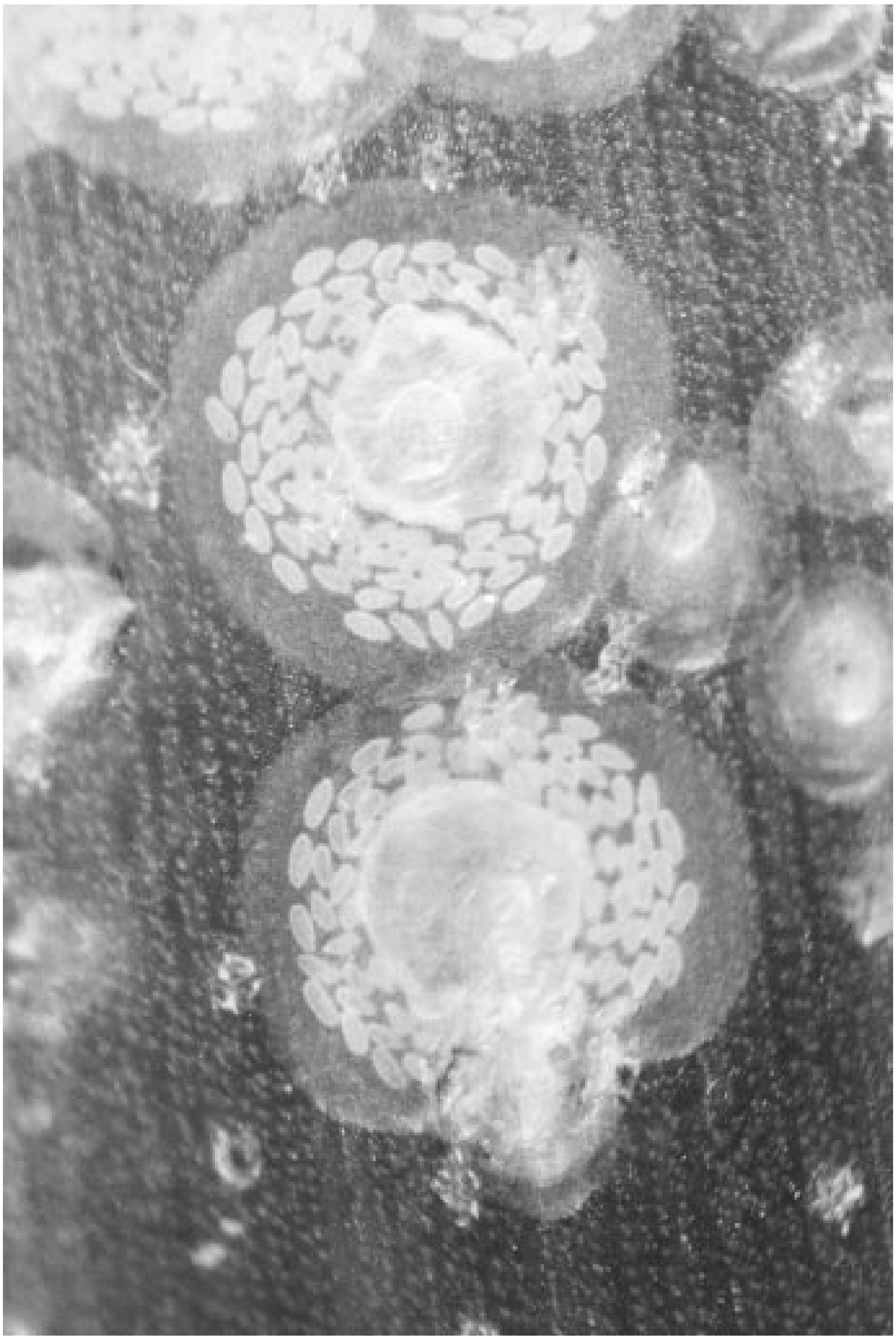


Fig. 3.34. Coconut scale, *Aspidiotus destructor* (Diaspididae), seen under a stereoscopic microscope. The female and eggs are visible through the transparent scale. Photo by Robin Giblin-Davis.

of about 90 eggs, pivoting on their stylets so that the eggs are laid in a circle. As eggs are laid, previously laid eggs are pushed out near the scale perimeter. Newly laid eggs near the insect's body are white, while older ones on the outside are yellow. They hatch in the order in which they are laid. Since the durations of the incubation period and the oviposition period of the female are both about 9 days, eggs begin to hatch about when the last eggs are laid.

Upon hatching, the yellow crawlers wander the plant surface for 2 to usually not more than 12 h. The crawlers do not survive more than 48 h without a host. At the end of their mobile period, the crawlers

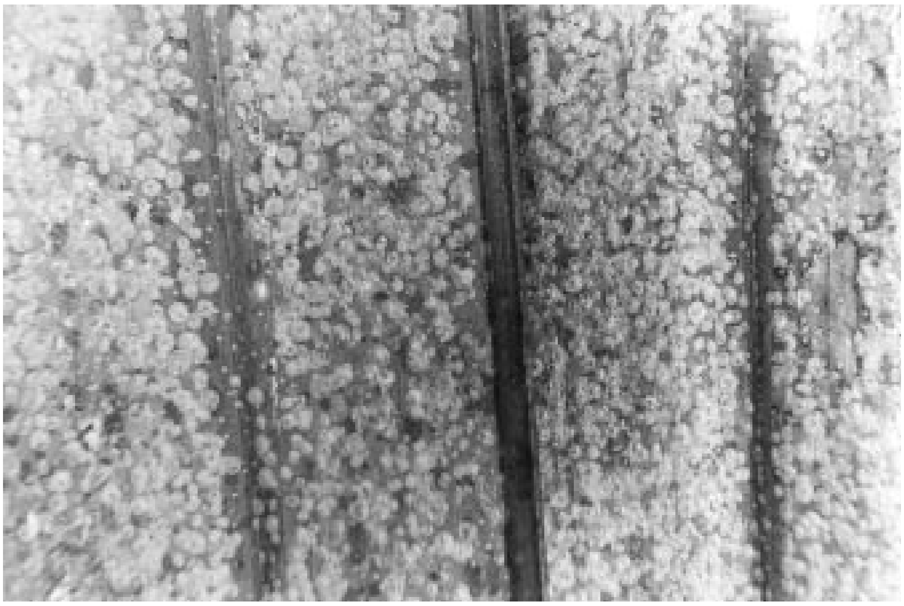


Fig. 3.35. Frond of *Livistona sp.* infested with *Aspidiotus destructor,* Florida.

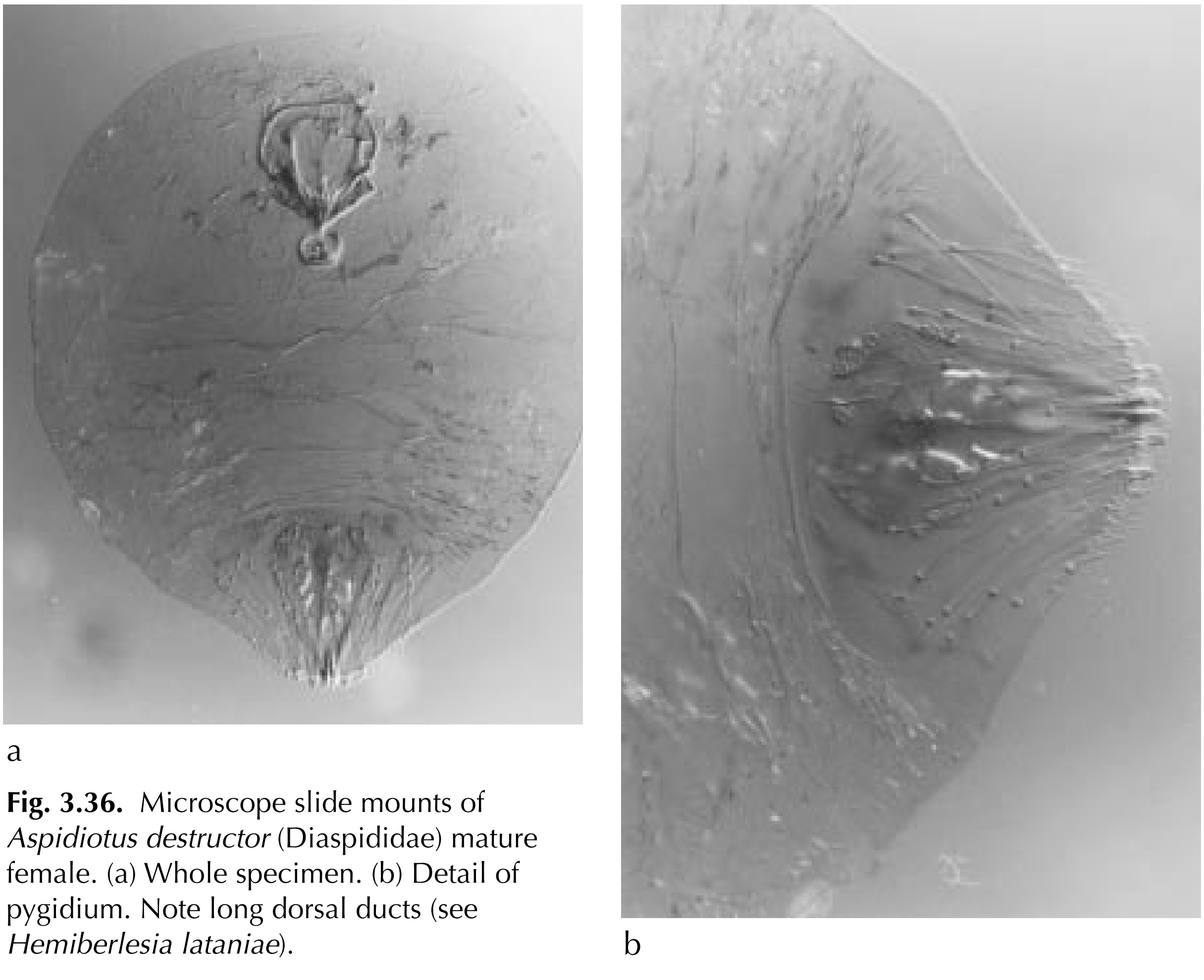


Fig. 3.36. Microscope slide mounts of *Aspidiotus destructor* (Diaspididae) mature female. (a) Whole specimen. (b) Detail of pygidium. Note long dorsal ducts (see *Hemiberlesia lataniae*).

settle and insert their stylets into the plant tissue. For the next 12 h, the settled crawler rotates slowly with its stylet as the pivotal point, while secreting waxy threads, which mat together to form the scale.

As in other coccoids, most crawlers settle within centimetres of where they hatch on the natal host, but can be spread, usually by air currents, to other hosts. Reyne (1948) in Indonesia trapped many crawlers on plates beneath coconut palms infested with *A. destructor* and suggested that there was a constant rain of larvae of this species from infested palms. He also trapped crawlers on adhesive-coated glass plates on a raft at distances of 50–500 m offshore and up to 1000 m from the nearest infested palm. Based on the trapping rate, he calculated that 35,000–60,000 crawlers could land on a mature coconut palm during 24 h.

Taylor questioned whether spread by air currents was important in Fiji, because infestations did not generally spread from palm to palm in the direction of prevailing winds and, on sites where the scale insect was abundant, the air was calm. However, such observations may not be entirely germane to the question of whether the crawlers disperse by air currents. For example, in coastal situations, the direction of the prevailing winds is different during the night and day. Also, gentle updraughts may do more to spread crawlers than stronger winds.

It is common for some batches of eggs to develop to either females or males. Sometimes, there is a succession of generations of mostly females followed by a generation of mostly males. Taylor observed that a preponderance of males was often antecedent to the concluding stages of an outbreak.

The stadia of immature stages are about 10 days each. As in other Diaspididae, *A. destructor* is sexually dimorphic in the second and subsequent instars. The scale insects mature in about a month.

Aspidiotus destructor commonly shares palm hosts with other armoured scale-insect species. For example, *C. aonidum* (Colour Plate 11c) and *A. orientalis* often occur with *A. destructor* on coconut palms in the Philippines and Florida. Usually, *A. destructor* is dominant in the Philippines, but outbreaks of *C. aonidum* have occurred (Gabriel, 1976). On San Andres Island in the Caribbean, *Parlagena bennetti* and *A. orientalis* occurred with *A. destructor* on coconut palms and different ones of these species were dominant in different blocks of palms (Mosquera, 1977). As in the case of *I. longirostris* and associated scale insects in the Seychelles (q.v.), where multiple species of armoured scale insects share a palm host, control of one of the species would be expected to result in an increase in others, because of reduced competition. In such cases, armoured scale-insect species should be targeted simultaneously, e.g. with omnivorous coccinellids.

The feeding of the first-instar larvae results in the formation of a tiny yellow area in the surrounding leaf tissue. This expands with the further feeding and development of the insect, and is most conspicuous on the adaxial leaf surface (Reyne, 1948). Dense populations of this insect cause large areas of the leaf to turn yellow (Colour Plate 12f). Field personnel highly familiar with this scale insect can recognize its damage from a distance, distinguishing it from that of other scale insects and from symptoms of nutritional deficiencies (Goberdhan, 1962; Beardsley and Gonzalez, 1975).

Reyne (1948) reported an unusually virulent outbreak of *A. destructor* on the island of Sangi, an island halfway between Celebes (Indonesia) and Mindanao (Philippines). The outbreak started in 1925 and spread over the island during the next 3 years. About 400,000 coconut palms were attacked, 30,000 of which died. In the Philippines, it is the most common armoured scale insect on coconut palm and is considered particularly damaging, because it attacks the fruits as well as the foliage, but it is much more damaging to palms in nurseries than to mature palms in plantations.

Evidence that severe infestations can curtail copra production was obtained on Príncipe, an island near the equator and off the coast of West Africa. Annual copra production had been about 1,350,000 kg from 1946 to 1954, but fell to nearly one-third of this in 1955, 3 years after *A. destructor* invaded the island (Simmonds, 1960).

The long-range spread of *A. destructor* may have been via human transport of many different kinds of plants. Movement of suckers (vegetative propagules) of bananas, which are preferred hosts, may have contributed substantially to the spread of this scale insect. In fact, in Fiji, where *A. destructor* was believed to have been introduced about 1905, it was considered a pest of bananas until 1916, after which it also became a major pest of coconut palm. The spread of this insect throughout the islands of the Fiji group was believed to have been partly on banana suckers (Taylor, 1935). Live females with eggs were once found on a banana fruit in a supermarket in Louisiana, far outside the insect's range. The banana had been imported from Honduras, suggesting that commerce in tropical fruits could also spread this insect (Howard, 1971).

The insect, believed to be native to the tropics of the eastern hemisphere, was described in 1869 from specimens on fronds of coconut palm on Réunion in the Indian Ocean, where it was highly destructive to these palms (Signoret, 1869). By 1902, it had reached several Caribbean islands (Goberdhan, 1962) and, throughout the 20th century, it was reported in one new locality after another in the tropical regions of the eastern and western hemispheres. Although pantropical by the mid-century, it continued to be reported in new localities, including Vanuatu in the Pacific in 1962 (Chazeau, 1981), the Hawaiian Islands in 1968 (Beardsley, 1970) and San Andres in the Caribbean in 1974 (Mosquera, 1977). It may have invaded Jamaica early in the 20th century, but was not recognized as a pest until the 1950s (Goberdhan, 1962).

According to some accounts, stressed palms are more susceptible to *A. destructor* than palms growing vigorously. Lever (1979) reported that palms in neglected coconut plantations were more susceptible, particularly those in which either the palms or wild plants were overly dense. He stated that well-spaced palms exposed to prevailing winds were less apt to be severely infested. Goberdhan (1962) indicated that palms under any kind of adverse conditions were more prone to attack by this pest. But Goberdhan emphasized that palms under drought conditions were more susceptible, while Lepesme (1947) and Lever (1979) reported that infestations were more severe in areas where rainfall was high. In such accounts, it is often not entirely clear whether the stressed palms were attacked by greater numbers of the scale insects or were less tolerant of the damage inflicted. In any case, these observations suggest that this pest can be controlled to some degree by good horticultural practices, but evidence thus far on the relationship between host condition and *A. destructor* is anecdotal and should be confirmed experimentally.

Many different chemicals have been applied to palms for control of *A. destructor*. Only recent examples will be given.

Dimethoate was effective in controlling *A. destructor* on coconut palm in a large area of southern Oman from 1984 to 1986. However, it was difficult because of the height of the palms (> 8 m tall), and was very expensive. Chemical control efforts are no longer necessary there, because the scale insect is under biological control (Kinawy, 1991).

Fish-oil–rosin soap, considered to be a relatively safe treatment, was found to be highly effective in controlling *A. destructor* in coconut palm nurseries in India (Jalaluddin and Mohanasundaram, 1989).

Over 40 predators and parasitoids are known to attack *A. destructor* (Beardsley, 1970). Parasitoids have not been as effective as predators. For example, *Aspidiotiphagus citrinus*, *Aphytis chrysomphali* (Aphelinidae) in Malaysia and *Comperiella unifasciata* (Encyrtidae) in Indonesia have often been reported parasitizing *A. destructor* during outbreaks, but apparently with little impact (Lever, 1964, 1979).

Aspidiotus destructor is under natural control in some areas, e.g. by the coccinellid *Chilocorus nigritus* in India and Sri Lanka (F.J. Simmonds, 1960, cited by Chua and Wood, 1990), *Chilocorus politus* in Indonesia and *Pseudoscymnus anomalus* in Micronesia. *Cryptogonus* sp., *Micraspis* sp. and *Scymnus* sp. are common predators of this insect in the Philippines. In many other areas, *A. destructor* is present in low populations, presumably checked by various natural enemies.

A biological control project against *A. destructor* in Fiji is often cited as a spectacular example of successful biological control, utilizing predators rather than parasitoids to control a scale insect. Taylor's (1935) detailed report of this work, of which a brief summary follows, would interest anyone engaged in biological control of scale-insect pests of palms.

Aspidiotus destructor became a serious pest of coconut palms in Fiji from about 1916 through the late 1920s. Parasitoids were imported in 1920 and 1927, but had little impact on the pest. In 1928, five species of Coccinellidae were introduced from Trinidad. Among these, *C. nodiceps* was effective, bringing the scale insect under control by 1929. It has not become a serious pest of coconut palms on Fiji since that time (Huffaker and Gutierrez, 1990).

Taylor (1935) analysed the characteristics of *C. nodiceps* that contributed to the success of this predator against *A. destructor* in Fiji: the beetle itself is free of important natural enemies in Fiji; larvae and imagos of *C. nodiceps* consume large numbers of *A. destructor*; the adults are long-lived; the beetle reproduces continuously throughout the year (as does its prey, *A. destructor*); it has a high reproductive rate; it disperses widely; and it survives when *A. destructor* populations almost disappear by feeding on other scale-insect species and also by finding isolated remnants of the *A. destructor* population.

Biological control of *A. destructor* with *C. nodiceps* was similarly successful in Príncipe. The scale insect was first observed on this island on a few palms in 1952 and within a few years had become widespread, causing a decline in copra, as explained. Coccinellids, hymenopterous parasitoids, predacious mites and fungi already present on Príncipe attacked the scale, but did not control its populations adequately. Parasitoids, for example, killed mature female scale insects, but surviving eggs may have allowed a resurgence in the scale-insect populations. In 1955, *C. nodiceps* was introduced from Trinidad, along with several additional coccinellids. Successful control was achieved within 2 years (Simmonds, 1960).

Aspidiotus destructor was reported on Efate Island (Vanuatu) in 1962 and became damaging to coconut palms. *Cryptognatha nodiceps* and two other coccinellids were introduced, but were ineffective in controlling the scale insect. However, *Rhyzobius pulchellus*, introduced from New Caledonia, brought it under control (Cochereau, cited by Chua and Wood, 1990). Nevertheless, by the late 1970s, the scale insect had spread widely in the archipelago. Of various coccinellids, *Rhyzobius satelles*, *P. anomalus* and *C. nigritis* were thought to be important in suppressing populations of the scale insect (Chazeau, 1981).

Efforts to control *A. destructor* with introduced predators have not always had spectacular results. From the early 1940s to the 1980s, there were many introductions of predators into various islands of the Caroline and Marshall Islands from foreign localities and from one island to another for control of *A. destructor*. Shreiner (1989) reviewed unpublished records of this work, noting that, in many cases, predators were released without evaluating their impact on the pest. In other cases, results were highly inconsistent. One coccinellid, *P. anomalus*, was said to control *A. destructor* successfully on some islands, but the pest was found to be abundant on the same islands in the 1980s. Moen, of the Truk Island group, was an example of an island where *A. destructor* was still damaging palms in the late 1980s, in spite of the presence of many predators imported to control it.

Several species of coccinellids (*Telsimia nitida*, *Scymnus luteus* and *C. nigritus*) and aphelinids (*A. chrysomphali* and *Prospaltella* sp.) were natural enemies of *A. destructor* in Sangi, but Reyne (1948) felt that the eventual crash of the scale-insect population was due to abnormal mortality of crawlers and a decline in fertility, rather than the effect of natural enemies. Chua (1997), however, suggested that natural enemies may have played some role.

In Malaysia and Mauritius, two predacious beetles, *Cybocephalus semiflavus* and *Cybocephalus* sp. (Nitidulidae), attacked *A. destructor* aggressively but failed to suppress populations satisfactorily (Lever 1964, 1979). Biological control of various armoured scale insects has been attempted with many species of *Cybocephalus*, generally with disappointing results. Their slow feeding rate and low degree of adaptability to different scale-insect hosts may be factors (Drea, 1990).

Aspidiotus destructor met with environmental resistance when introduced into the Hawaiian Islands, encountering formidable natural enemies that had been established years previously for the control of other scale-insect pests. *Rhyzobius lophanthae* was a principal predator of the pest on Oahu, along with *T. nitida* (Coccinellidae). A species of thrips and two hymenopterous parasitoids, namely *A. chrysomphali* and *Aphytis* sp. near *Aphytis lingnanensis* also attacked *A. destructor* in the Hawaiian Islands (Beardsley, 1970).

Although Trinidad was the source of *C. nodiceps* for at least two successful biological control projects targeting *A. destructor* (Fiji and Príncipe), and seven additional coccinellid species are predators of this scale insect on Trinidad, *A. destructor* is often of sufficient concern as a pest of coconut palm on that island for chemical control to be employed. Natural enemies of the beetles themselves may sometimes reduce their effectiveness as biological control agents (Goberdhan, 1962).

In summary, different species of coccinellids have been used effectively to control *A. destructor* in different localities (Table 3.10). Their success in any given locality cannot be predicted.

Ischnaspis longirostris, aptly called the black-thread scale insect, can easily be distinguished in the field from other common armoured scale insects. The distinctive scale of the mature female is shiny, black and extremely long and narrow. The scales reach a maximum of 3.5 mm long and are eight to ten times longer than wide (Colour Plate 12b, Fig. 3.37). The smaller scale of the male has rarely been observed (Newstead, 1901; Ferris, 1937–1955; Dekle, 1976). The scales are found on the fronds, petioles and fruits of palms. On fronds, they prefer abaxial surfaces (Vesey-FitzGerald, 1940). In light infestations on palms, the scales may be scattered on the abaxial frond surfaces and orientated parallel to the leaf veins. With crowding, some of the insects may encounter obstacles to development of their scales, such as other scales or leaf veins. In such cases, the scale bends abruptly, forming an L shape.

Table 3.10. Examples of attempts to control *Aspidiotus destructor* on coconut palms with coccinellid beetles.

Species of coccinellid	Imported from	Introduced into	Successful control?	Time period	Reference
Chilocorus nigritus	India	Oman	Yes	24 months	Kinawy, 1991
Chilocorus nigritus and *Chilocorus politus*	Sri Lanka Java	Mauritius	Yes	Several months; 1937	Moutia and Mamet, 1946
Cryptognatha nodiceps	Trinidad	Fiji	Yes	9 months; 1928	Taylor, 1935
Cryptognatha nodiceps	Trinidad	Príncipe Island	Yes	1 year; 1955	Simmonds, 1960
Cryptognatha nodiceps and other spp.	Trinidad	Efate Island {Vanuatu}	No	–	Cochereau, 1969, cited by Chua and Wood, 1990
Coccidophilus citricola	Chile	Easter Island	Yes	1990s	Renato Ripa, personal communication
Rhyzobius pulchellus	Vanuatu (other than Efate Island)	Efate Island	Yes	5 months; 1960s	Chua and Wood, 1990

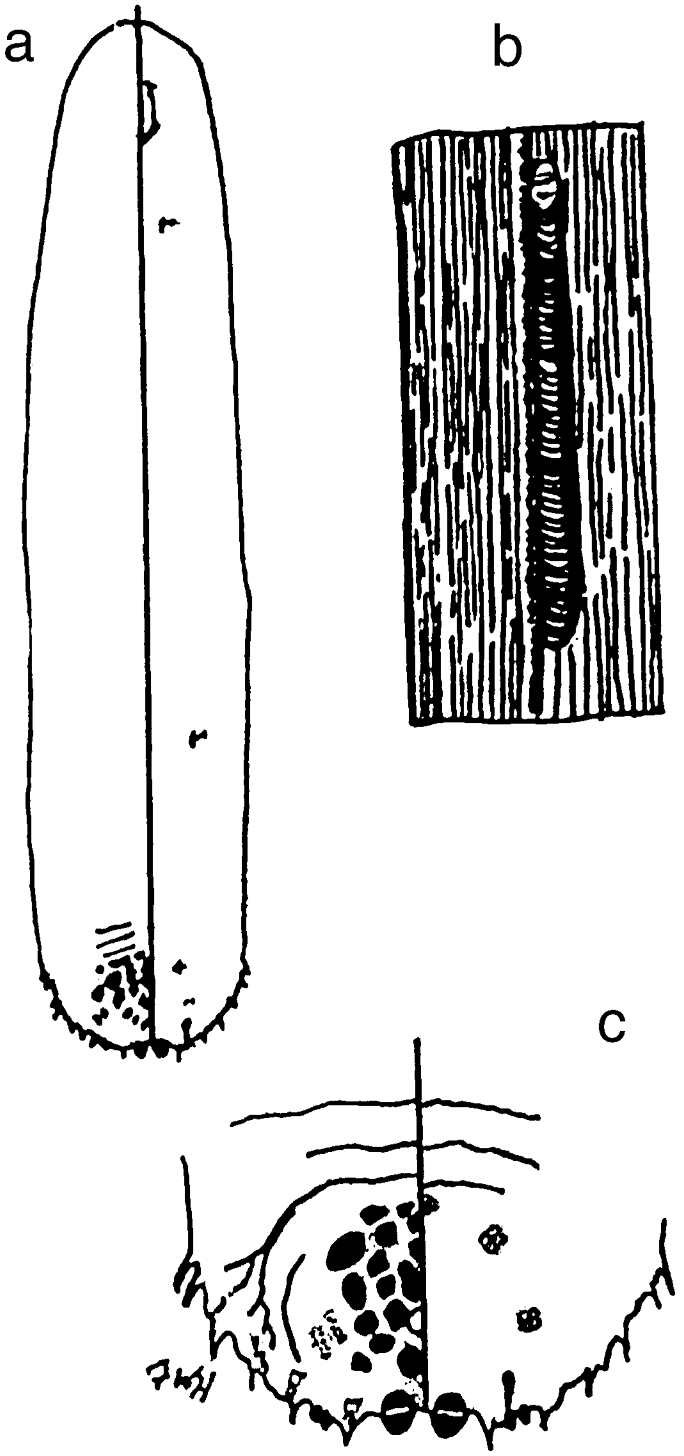


Fig. 3.37. *Ischnaspis longirostris,* (a) mature female (on microscope slide), (b) scale of female, and (c) detail of pygidium. Note spines on pygidial margin and short dorsal ducts, characteristic of subfamily Diaspidinae. Left side is dorsal view, right side is ventral view.

Although most of the hosts of this highly polyphagous insect are woody dicotyledons, it is one of the most frequently encountered armoured scale insects on decorative palms outdoors in warm areas and in glasshouses in cooler areas. Combining Borchsenius's (1966) and Dekle's (1976) host data, it attacks palms of 39 diverse genera and of multifarious geographical origins. Dekle (1976) stated that

Chamaedorea elegans, abundantly grown in nurseries and marketed for interiorscapes, was the most frequently reported host in Florida. African oil palm, coconut palm and *Raphia* spp. were preferred palm hosts in the Seychelles. Curiously, Vesey-FitzGerald (1940) observed that, in the Botanical Gardens in the Seychelles, palms exotic to those islands, but not endemic palms, were highly infested.

Like the scale it produces, the mature female has an unusual appearance for an armoured scale insect. No common species is as long and narrow. As seen on a microscope slide, the coarse reticulations of the dorsal surface of the pygidium are highly conspicuous. Additional unusual features are the wide spacing of the medial lobes, the pronounced sclerosis at the base of the second lobes and the arrangement of the perivulvar pores in five small groups (Fig. 3.37; Ferris, 1937–1955). The elongate body occupies a third of the anterior end of the scale; the space posterior to the insect serves as a chamber in which eggs are deposited and hatched.

Four to five developing eggs, visible within gravid females under magnification, are orientated with the long axis at right angles to the median of the insect. The anteriormost are indistinct and in the posteriormost the structure of the embryo is visible. The orange-coloured eggs hatch soon after being oviposited. Each female produces about 20–30 eggs, a relatively low reproductive rate for a scale insect. The yellow first-instar crawler, hatching soon after the egg is laid, is inactive at first and then leaves the mother scale and wanders on the plant for about 24 h. Crawlers moult to the elongate second instar in about 3 days (Vesey-FitzGerald, 1940).

Ischnaspis longirostris thrives under nursery conditions and is a common pest of palms and many monocotyledons and dicotyledons in glasshouses. In warmer areas, it commonly infests palms outdoors. Although it is usually no more than a minor pest outdoors, infestations can sometimes be serious.

During an outbreak in the Seychelles, Vesey-FitzGerald (1940) observed up to 135.9 scales cm^{-2} on leaflets of coconut palm, commenting that the scales persisted long after the death of the insect, so that an unknown portion of the masses of scales on older fronds may be those of dead scale insects. Crawlers may settle among and beneath scales of dead insects, so that the scales eventually form a thick crust (Vesey-FitzGerald, 1940). Two other armoured scale insects, *P. buxi* and *Chrysomphalus ficus* and a coccid, *E. tessellatus*, were present on coconut palms. Of these. *I. longirostris* was more evenly spread in plantations, while *C. ficus* and *P. buxi* were more localized. *Pinnaspis buxi* was considered the most damaging to individual palms.

These species were controlled by natural enemies in the Seychelles in the 1930s, and copra production increased substantially from 1940 onwards.

An unusual species with few close relatives, *I. longirostris* is almost certainly of eastern hemisphere origin. The additional species of *Ischnaspis* are three species known only from West Africa and one known only from India, none of them reported from palms (Borchsenius, 1966).

Vesey-FitzGerald (1940) reported that in the Seychelles infestations of *I. longirostris* were lighter on coconut palms growing in coral sands compared with those on alluvial or sedimentary soils, but no cultural control techniques have been developed to exploit this. The ‘Seychelles Tall’ and ‘Ceylon Tall’ tall varieties and a dwarf variety were equally susceptible to this scale insect.

Vesey-FitzGerald (1940) considered biological control to be the most economical method in the long run for controlling the complex of scale insects that infested coconut palms in the Seychelles in the 1930s, including *I. longirostris*, *P. buxi*, *C. ficus* and *E. tessellatus*. The latter two species were attacked by hymenopterous parasitoids, which did not keep the scale-insect populations adequately controlled. The trick would be to use natural enemies that would be more effective and that would have an impact on all of these scale-insect species, because, if only one or two of them were controlled, the population of the others could increase. Thus, a desirable characteristic of natural enemies was that they be polyphagous.

Coccinellid beetles, including *Chilocorus distigma*, *Exochomus ventralis* and *Exochomus flavipes* from East Africa and *C. nigritus* from India, were introduced and became established. *Exochomus* spp. were imported for control of *E. tessellatus*, while the *Chilocorus* spp. were for control of the armoured scale insects. However, *C. nigritus*, which became the most abundant species and apparently the principal natural enemy of the armoured scale insects, also consumed large numbers of *E. tessellatus*. Within months of the introduction of these beetles into the Seychelles, the populations of the scale-insect species were reduced below the level at which they caused economic damage (Vesey-FitzGerald, 1940).

Other diaspidoid scale insects

Several scale-insect taxa that occur on palms have been variously considered to be aberrant Diaspididae or to represent families closely related to the latter (Miller, 1990). These include taxa that we treat as the families Phoenicococcidae (genera *Phoenicococcus* and *Xanthophthalma*), Halimococcidae, Beesoniidae and *Comstockiella*. At present, the taxonomic placement of these groups is highly tentative.

Phoenicococcidae

Phoenicococcidae were formerly considered to be highly aberrant Diaspididae adapted to palms, but are currently recognized as a separate family, very closely related to the Diaspididae (Ben-Dov, 1990b). As in Diaspididae, there is a crawler stage (Fig. 3.40a), followed by a second instar, after which the insect moults to the mature female stage. The females are membranous, orbicular or elliptical, with reduced antennae, and are devoid of legs. The simple structure of the pygidium, devoid of the lobes, plates, spines and other marginal structures characteristic of the Diaspididae, and the presence of 8-shaped tubular ducts on the dorsum and sometimes the venter are characteristics that separate them from Diaspididae. They do not secrete and fashion scales, but cover themselves with a mass of waxy filaments. The apterous males mature in their fifth developmental stage. Nothing is known regarding their mating behaviour. The females are viviparous. The family has one genus, *Phoenicococcus* (Ben-Dov, 1990b). Some authorities (e.g. Kosztarab, 1982) also place *Xanthophthalma* in this family. Each genus has one species.

Phoenicococcus marlatti, the red date scale insect (Colour Plate 12c, Figs 3.38–3.40) is native to North Africa and the Middle East, where it frequently infests date palm. Based on a study of ancient

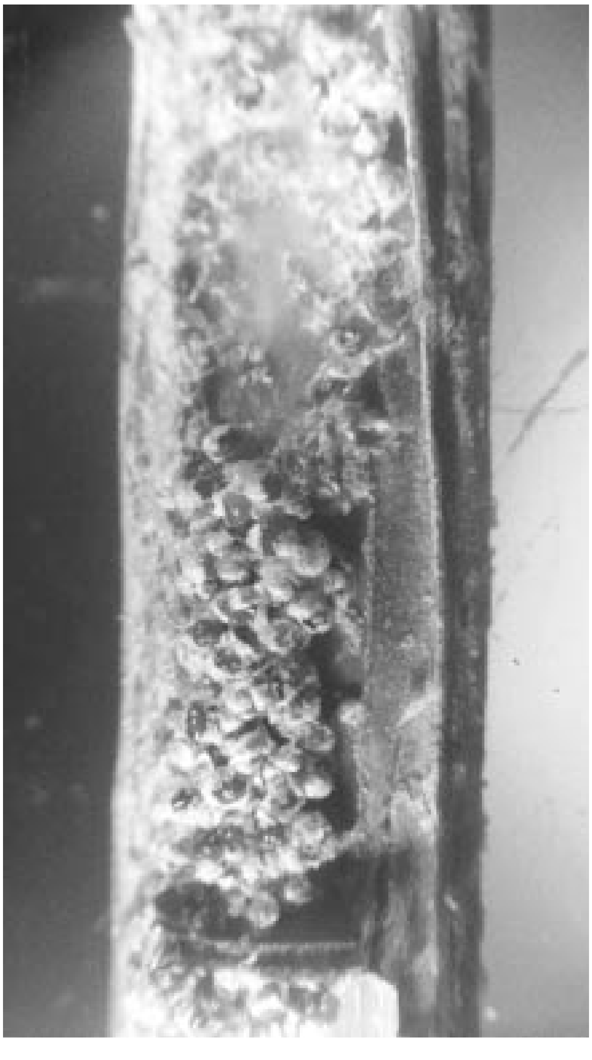


Fig. 3.38. *Phoenicococcus marlatti*. Infested young leaflet of *Phoenix canariensis*, Florida.

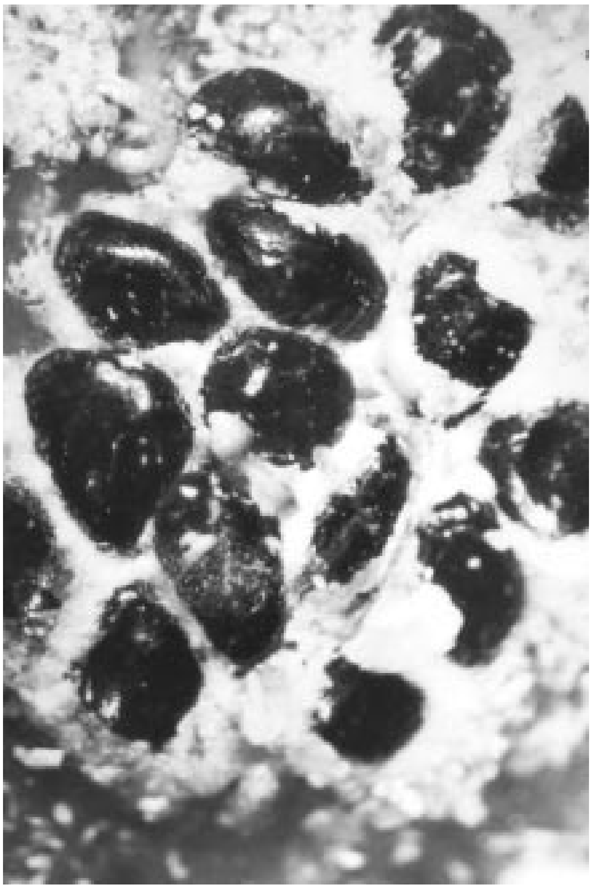


Fig. 3.39. *Phoenicococcus marlatti* (Phoenicococcidae), adult females on date palm stem, Elche, Alicante, Spain. Photo by Susi Gómez i Vives.

writings, Popenoe (1922) suggested that this scale insect may have a written history of 1300 years. It has been spread east to India (Muralidharan, 1993) and to the northern coasts of the Mediterranean, including Sicily (Sinacori, 1995) and Spain (Gómez i Vives *et al.*, 1996; Gómez i Vives and Ferry, 1999a). In the western hemisphere, it was introduced on date offshoots into Argentina and the south-western USA (Ferris, 1937–1955; Lepesme, 1947). It is occasionally found on *Phoenix* spp. in Florida, having been introduced there probably after 1990 (Avas Hamon, personal communication). In addition to date palm, it has also been reported on additional species of *Phoenix* and on *Calamus*, *Daemonorops* and *Pandanus* (Stickney *et al.*, 1950; Ben-Dov *et al.*, 2000). There is a curious record from *Eucalyptus* (Ben-Dov *et al.*, 2000).

The female, orbicular and about 1 mm in diameter (Fig. 3.40a) and of a deep red colour, typically occupies the stem underneath fibres behind overlapping leaf bases. Occurring in aggregations, the insects appear as small pink to red spherical bodies among masses of cottony secretions. At first glance, these infestations may appear to be a fungus. *Phoenicococcus marlatti* may also infest the bases of inflorescences or occupy roots below the soil. They tend to live underground during the scorching summers on the desert, rarely occupying exposed plant surfaces, such as the fronds, but they have been observed there in spring or during cool periods (Lepesme, 1947). In rare cases, the species has infested inflorescences severely enough to cause premature fruit drop. In their native home, *P. marlatti* populations are believed to be suppressed by high summer temperatures.

Differences in susceptibility among some date cultivars have been noted (Popenoe, 1973). But, since it is generally not a pest in its native home or in California (Nixon and Carpenter, 1978), little or no effort has been invested in the selection and breeding of resistant cultivars or other control measures for this insect.

Xanthophthalma concinnum has been collected from the abaxial frond surfaces of *Acrocomia, Cocos* (possibly *Syagrus*) and *Bactris* in Mexico and Central America. The adult female is oval to circular, about 0.4 mm long and membranous, except for reticulated sclerotizations on the posterior abdominal segments. The insect covers itself with waxy secretions and exuviae. While collecting in Chiriquí Province, Panama, in 1938, Ferris (1937–1955) observed that it was very common on various palms, especially *Acrocomia* sp. and *Bactris* sp.

Halimococcidae

The Halimococcidae are specialized and closely related to Diaspididae and Phoenicococcidae and were formerly included in one or other of these families (e.g. Ferris, 1937–1955; Borchsenius, 1966). The 20 known species are associated only with Palmae and Pandanaceae (Table 3.11; Carver *et al.*, 1991). The palm-infesting species tend to infest young, unfolded fronds, but *Colobopyga attaleae* was collected on fruits of *Attalea cohune* (Ferris, 1937–1955). The mature females have the

Fig. 3.40. *Phoenicococcus marlatti*. Microscope slide mounts of (a) crawler, (b) adult female. Collected from *Phoenix sp.* in Florida.

Table 3.11. Halimococcidae on palms (from Ben-Dov *et al.*, 2000).

Species of Halimococcidae	Hosts	Distribution
Colobopyga attaleae	*Attalea cohune*	Mexico
Colobopyga australiensis	*Howea* sp.	Australia
Colobopyga browni	*Pritchardia kahanae, Pritchardia martiodes, Pritchardia rockiana*	Hawaiian Islands
Colobopyga coperniciae	*Colpothrinax wrightii, Copernicia hospita*	Cuba
Colobopyga hedyscepes	*Hedyscepe canterburyana*	New Zealand
Colobopyga kewensis	*Borassus* sp., *Howea forsteriana*	Hawaiian Islands, Lord Howe Island, Tanzania
Colobopyga magnani	*Chamaerops humilis*	Argentina
Colobopyga pritchardiae	*Pritchardia hardyi, P. rockiana*	Hawaiian Islands
Colobopyga sabalis	*Sabal* sp.	Mexico
Colobopyga washingtoniae	*Washingtonia robusta*	Mexico
Halimococcus borassi	*Borassus flabellifer*	Sri Lanka
Halimococcus lampas	*Hyphaene* sp.	Natal
Halimococcus thebaicae	*Hyphaene thebaica*	Egypt
Madhalimococcus hyphaeneae	*Hyphaene* sp.	Madagascar
Platycoccus tylocephalus	Unidentified palm	Hawaiian Islands
Thysanococcus calami	*Calamus* sp.	Indonesia
Thysanococcus chinensis	*Calamus* sp.	South-east China
Thysanococcus madecassus	*Raphia* sp.	Madagascar
Thysanococcus squamulatus	*Calamus tetradactylus*	South-east China

appearance of tiny seeds about 1 mm long, with sparse wax at the margins (Fig. 3.24). They have been reported to reside in the sclerotized exuviae of the second instar (Ferris, 1937–1955), but Köhler (1987) reported that halimococcids form a scale that does not incorporate exuviae. Miller (1990) predicted that knowledge of the relationships between Halimococcidae and the other recondite palm-infesting scale insects (Phoenicococcidae, etc.) would greatly increase our understanding of the phylogeny of diaspidoids.

Köhler (1987) studied *Colobopyga coperniciae*, a halimococcid native to Cuba, on *Colpothrinax wrightii* in a glasshouse in the Jena Botanical Gardens, Germany. The first-stage larvae of *C. coperniciae* are similar to diaspidid crawlers. Second-instar larvae are heavily sclerotized, with distinct truncate abdomens, and, unlike second-instar diaspidids, have functional legs. The female, which is mature after two moults, is about 0.3–0.7 mm long, legless and similar in shape to a diaspidid female but typically with a bulbous posterior abdominal extension, bearing a simple pygidium devoid of lobes, plates, spines and the other marginal structures characteristic of the Diaspididae. The female begins forming its scale as it moults and sheds the second-instar exuviae. In contrast to the Diaspididae, the scale of the mature female *C. coperniciae* does not incorporate the shed exuviae of previous instars. It is a curious bottle-shaped structure, with an operculum, through which the larvae presumably escape. How the larvae do this is not understood, since they appear to be too thick to pass through the operculum. The scales vary greatly in shape and size, depending on their microhabitat and the proximity of other scales. The males of *C. coperniciae* are apterous and smaller than first-instar larvae.

Halimococcids generally go unnoticed, particularly by economic entomologists. Most of the known species have been discovered by zealous coccidologists examining herbarium material or wild palms in the field.

That *C. coperniciae* can be a serious pest under certain conditions was indicated by Köhler's (1987) observations on the palm in the glasshouse in Germany. The palm was brought from the Havana Botanical Gardens in May 1982. Presumably no scale insects had been detected on the palms. Within 6 months, *C. coperniciae* infestations had become serious and were not controlled with repeated insecticide applications (the chemical was not specified). After almost 41 months, the massive scale-insect infestation had caused the palm to lose nearly all its fronds.

Like many other palmivorous insect taxa, Halimococcidae are represented by some species on Pandanaceae. *Thysanococcus pandani*, which is not known from palms, is found on *Pandanus tectorius*, *P. utilis* and *Pandanus penangensis* in Java and Singapore (Stickney, 1934a).

Williams (1984) suggested that extant Halimococcidae may be relics of a family that was larger when palms were more widely distributed in Tertiary times, as indicated by fossil evidence (Uhl and Dransfield, 1987).

Beesoniidae

The family Beesoniidae contains nine species. Four species in the genus *Limacoccus* are restricted to palm hosts in tropical America (Table 3.12). The remaining five species, in the genera *Beesonia* and *Mangalorea*, are gall-makers on Dipterocarpaceae and other dicotyledons in Asia and Australia (Ben-Dov *et al.*, 2000). Among the most highly specialized of all Coccoidea, they are closely related to Phoenicococcidae, Halimococcidae and Diaspididae but their place among the higher Coccoidea has long been enigmatic. Foldi (1995) conducted a taxonomic revision of *Limacoccus* with a cladistic analysis of its relationship with other coccoid groups. While noting that the *Limacoccus*, group was arguably a separate family, Foldi assigned it to the Beesoniidae.

The mature females of *Limacoccus* spp. are generally orbicular, legless coccoids, with brown, highly sclerotized bodies (Colour Plate 12d, Fig. 3.41). In three of the known species, the margins are fringed

Table 3.12. Beesoniidae on palms (from Foldi, 1995).

Species of Beesoniidae	Host plants	Geographical distribution
Limacoccus brasiliensis	*Syagrus romanzoffiana*	Brazil
Limacoccus kosztarabi	*Astrocaryum chonta, Attalea speciosa, Orbignya polysticha*	Venezuela, Peru
Limacoccus serratus	*Attalea* sp.	Bahia (Brazil)
Limacoccus venezuelana	*A. chonta, Attalea maracaibensis, O. polysticha*	Venezuela, Peru

with integumentary projections, the exception being *Limacoccus venezuelana*, which has a smooth body margin (Foldi, 1995). Reproduction is viviparous. Female crawlers settle on the margins of unopened fronds, where they feed, secreting an amorphous substance. The second instar remains in the exuviae of the first instar. The exuviae split open along an ecdysial line, and the second instar secretes an amorphous substance through this opening. With movements of the body, the insect begins to form a tubelike shelter. As it is formed, the second instar extends out of the first-instar exuviae, occupies the shelter and extends it further (Fig. 3.42; Foldi, 1995).

The second-instar female eventually leaves the shelter and moults to the mature female, secreting a waxy substance, which pushes the exuviae outward. The female occupies a site on the plant a little removed from the shelter.

Male crawlers settle in groups near a female. Nothing is known of their development or of the mature males (Foldi, 1995). *Limacoccus kosztarabi* and *L. venezuelana* were described from

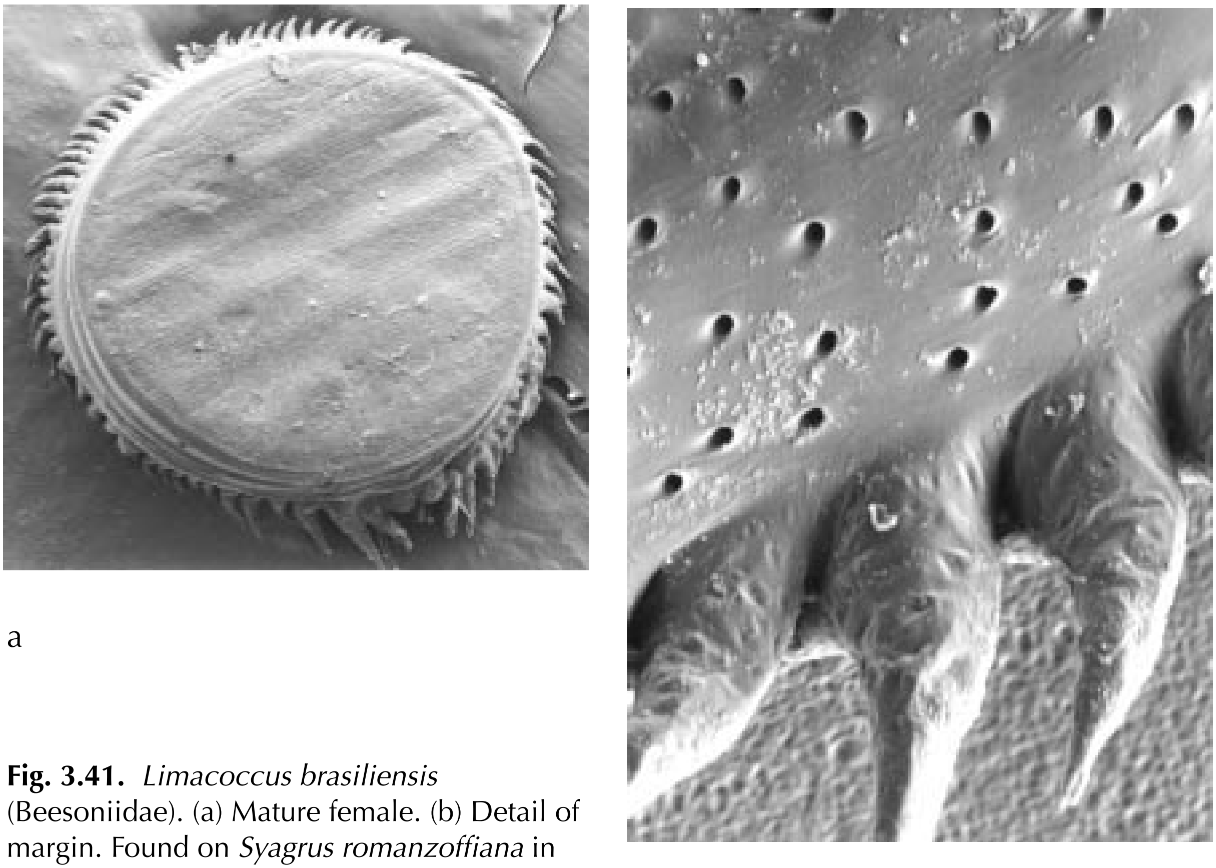


Fig. 3.41. *Limacoccus brasiliensis* (Beesoniidae). (a) Mature female. (b) Detail of margin. Found on *Syagrus romanzoffiana* in Italy. SEM views courtesy of Claudio Carrai.

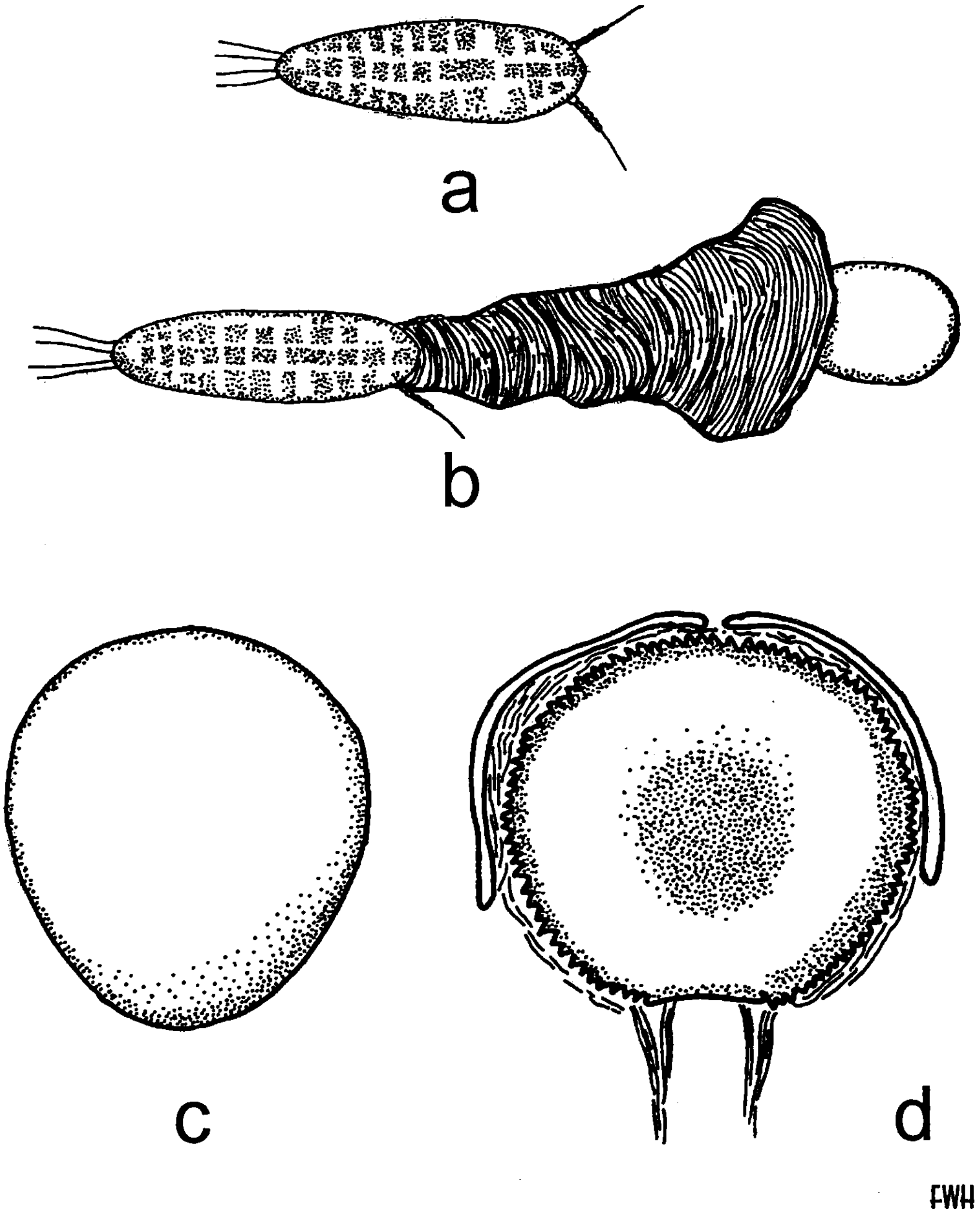


Fig. 3.42. Stages of Beesoniidae. (a) First instar. (b) Second instar constructing its tunnel. (c) Cyst form of second instar. (d) Adult female. After Foldi (1995).

Venezuela on *Attalea speciosa* and *Attalea maracaibensis*, respectively (Foldi, 1988a, b). Later they were both found frequently on *Orbignya polysticha* in the forests of the Upper Ucayali River valley, Peru (Couturier and Kahn, 1992). Couturier and Kahn's study was one of a relatively few attempts to characterize the coccoid fauna of wild palms. *Limacoccus brasiliensis*, native to Brazil, was found on palms, *Syagrus romazoffiana*, imported into Tuscany, Italy (Garonna and Carrai, 1993). Apparently it has not become established in Italy (Claudio Carrai, personal communication).

Comstockiella sabalis

The palmetto scale insect, *C. sabalis*, is very common on *S. palmetto*, an arborescent native palm distributed widely in the south-eastern USA (Fig. 3.43). The insect has been reported on the following palm hosts (Dekle, 1976): coconut palms, date palms, *A. wrightii, Butia capitata, C.*

Fig. 3.43. *Comstockiella sabalis*. This native scale insect is common on *Sabal palmetto* throughout its range.

humilis, Hyphaene crinita, Latania sp., *L. chinensis, P. canariensis, Rhapidophyllum hystrix, Roystonea oleracea, Sabal causiarum, Sabal minor, S. palmetto, Sabal etonia, Serenoa repens, S. romanzoffiana, Thrinax* sp. and *Washingtonia* sp. The species has also been reported on *Agave* sp. (Agavaceae). This host list contains almost twice as many palmate compared with pinnate palms, and conspicuous infestations of this scale insect are most often found on *S. palmetto* and other palms with palmate fronds (F.W. Howard, unpublished).

The adult female is turbinate, 0.6–1.0 mm long and light pink in colour. The margin of the pygidium is not like that of Diaspididae: it is irregularly crenate, notched at the apex and with no lobes, plates or paraphyses. The grouping of six perivulvar pores is an unusual feature. The dorsal ducts are extremely fine (Fig. 3.44).

The scale of the female is circular to irregular, 0.8–1.1 mm in diameter and white, with the exuviae near the centre. The male scale is similar but smaller.

The species has long been tentatively placed in the Diaspididae (e.g. Ferris, 1937–1955; Borchsenius, 1966; Miller, 1996), while authors have noted that the species is unique and not closely related to other diaspidids. Conspicuous differences are that the mature female of *Comstockiella* lacks the fringe of lobes and plates along the pygidial margin typical of the Diaspididae, and females do not consistently incorporate exuviae into the scale. The chromosome system (i.e. the way in which chromosomes divide during mitosis) is unusual (Brown, 1965; Miller and Kosztarab, 1979), but is shared with some species of Diaspididae and species in several other groups of Coccoidea. The males are apterous, like those of Phoenicococcidae, and share several other characteristics with them (Howell, 1979).

Comstockiella sabalis is distributed in Mexico, parts of the Caribbean and the south-eastern US coastal plains (Miller, 1996). It was first reported in Bermuda in 1921 and had spread throughout those islands by 1933. Here its host is *Sabal bermudana*, the most isolated and northernmost representative of *Sabal* (Bennett and Hughs, 1959). It is thus known throughout the northern portion of the range of the genus *Sabal*, but not from the southern portion, i.e. northern South America. The species is also known on palms in glasshouses in Europe (Miller, 1996).

Although this species is common, especially on *S. palmetto*, infestations are generally not conspicuous. Aggregations tend to be hidden between leaf segments of unopened fronds, in folds of unopened inflorescence spathes or on the base of petioles protected by the enveloping fibres. The occasional clusters of scales on exposed fronds or other surfaces are often empty or contain mostly parasitized or dead scale insects.

When introduced into Bermuda, *C. sabalis* became a severe pest of *S. bermudana*. Hymenopterous parasitoids

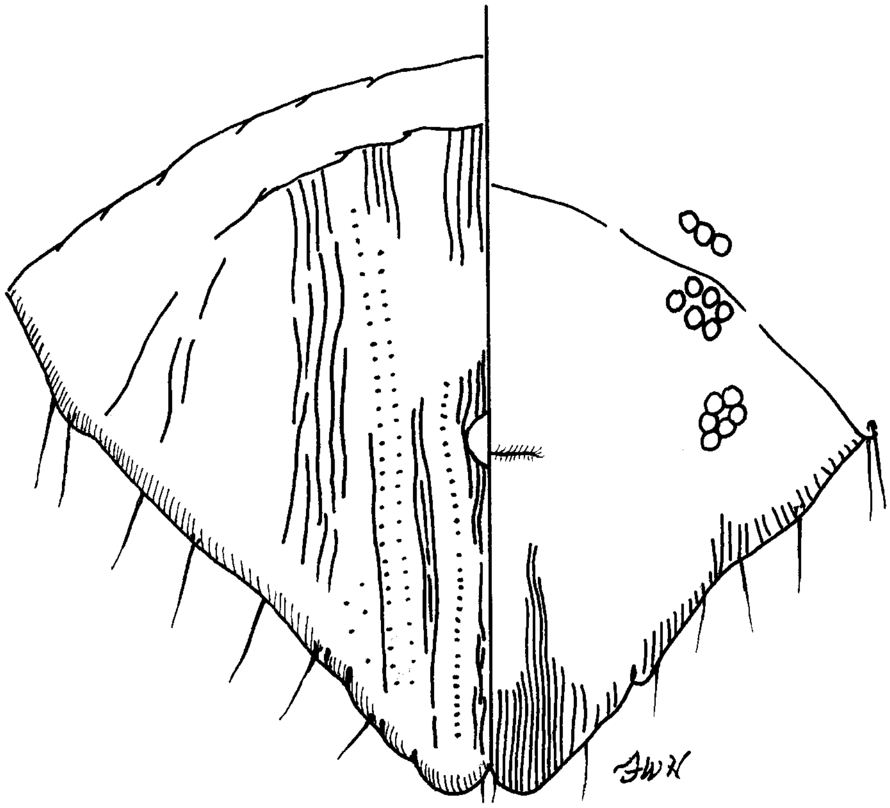


Fig. 3.44. *Comstockiella sabalis*, pygidium. Note lack of marginal lobes, plates and spines. Left side is dorsal view, right side is ventral view.

imported from Florida, principally species identified as *Physcus* sp. and *Encarsia portoricensis*, brought it under control by 1937. Subsequently, *Physcus* sp. was reported as apparently the main control agent of this scale insect in Bermuda (Bennett and Hughs, 1959). A recently described species, *Coccobius donatellae* (Hymenoptera: Aphelinidae), is the most common parasitoid that attacks *C. sabalis* in Florida and is believed to be the same species reported in the literature as *Physcus* sp., which was introduced into Bermuda in the 1920s. The introduced parasitoid identified as *Encarsia portoricensis* was also probably a misidentification of *C. donatellae* (Evans and Pedata, 1997).

Thysanoptera

Forrest W. Howard

Insects of the order Thysanoptera – thrips – are very elongate insects, less than a millimetre long. The distinctive tubelike wings of the imagos bear a fringe of setae (Fig. 3.45). Some species of thrips are phytophagous, but others feed on pollen or fungal spores or are predators. The phytophagous species typically congregate on the abaxial surfaces of leaves in groups, which are composed of nymphs and imagos. Their method of feeding involves rasping the surface tissues and sucking the juices released by the plant. This causes stippling and silvering on the leaves. The silvered areas where they have fed are peppered with the shiny black dots of their excrement (Colour Plate 12e).

Thrips can often be found on palms outdoors by close examination. They are typically common, but not numerous. Thrips on older fronds are probably often fungal-spore-feeders. Several species are pollen-feeders on many plants, including palms. Occasionally, phytophagous thrips species attack certain palms. *Heliothrips haemorrhoidalis* (Fig. 3.45) is probably the most common thrips that damages palm foliage. but there are additional species that do this

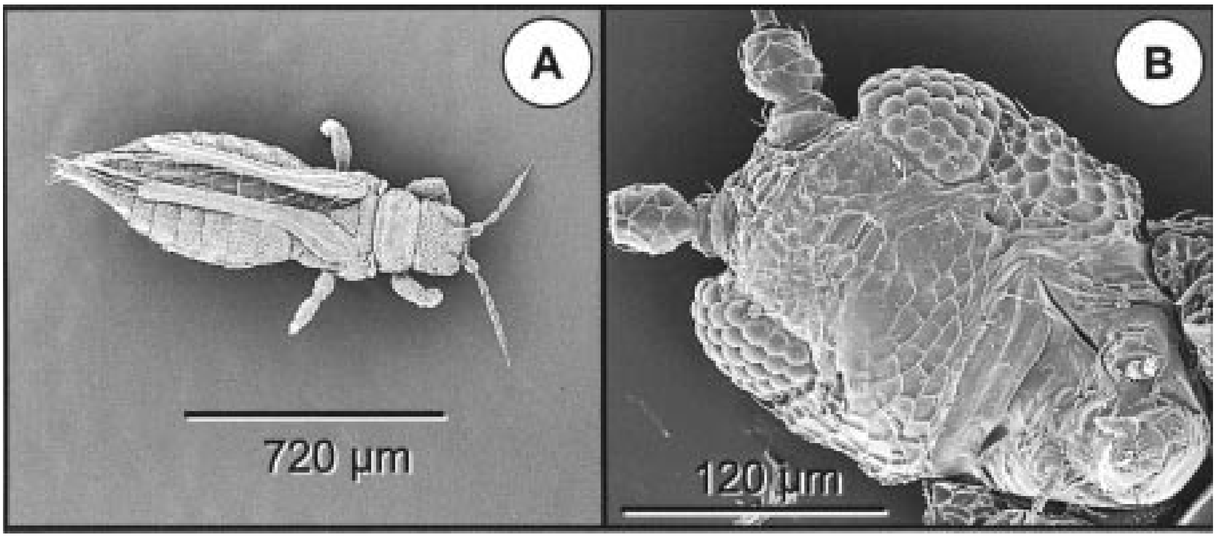


Fig. 3.45. Greenhouse thrips, *Heliothrips haemorrhoidalis* (Thysanoptera), collected from *Roystonea regia*, SEM view. (A) Adult. (B) Head, showing asymmetrical development of mandibles.

(Sakimura, 1986). Thrips are more likely to damage palms in interiorscapes or in nurseries than in landscape situations.

Acari

Dave Moore and Forrest W. Howard

Entomology is the science of the arthropod class Insecta. However, entomologists often extend their interest to another arthropod class, Arachnida, which contains the spiders, scorpions, mites, ticks and related taxa. Arachnida and insects share many similarities in their biology, ecology and impact on human activities, occupy the same basic habitats and interact together in various ways. Methods used in studying insects are generally applicable to studying arachnids.

Spiders (Araneae) of many species inhabit palms, where they prey on insects (Howard and Edwards, 1984). Many palms support a rich mite (Acari) fauna, which includes phytophagous and predacious species, in addition to species that feed on fungi, lichens, etc. However, since this book focuses on insects of palms, the subject of phytophagous mites of palms is treated only briefly.

Like other Arachnida, Acari have two body regions, a *gnathosoma*, with mouthparts and palps, and an *idiosoma*, i.e. body (Walter and Proctor, 1999). They pass through a maximum of six stages: egg, prelarva (reduced or lost in most species), six-legged larva, protonymph, deutonymph and adult. Most mites have three pairs of legs in the first developmental stage after hatching and four pairs in all other stages (except in Eriophyoidea, which have two pairs in the adult stage). The mouth-parts of Arachnida, including mites, are chelicerae. In plant-feeding and most parasitic species, these are modified as paired fang-like structures, which they thrust into host tissue to rupture cells in order to initiate the flow of fluids (blood or sap). They then press their oral opening over the wound to suck the fluid. Most mites are less than 1 mm long. There are three orders of Acari, with about 30,000 described species. All mites that are directly associated with palms are in the order Acariformes.

Mites that are primarily important on palm fruits are discussed in Chapter 4. Examples of mites important on palm foliage are discussed below.

Phytoptidae

Retracrus johnstoni feeds on the surfaces of fronds of coconut palm, *S. romanzoffiana* and *Chamaedorea* sp. Aggregations may appear to the naked eye as a fine powder on the abaxial frond surfaces. Feeding of the mite results in chlorotic flecking. Prolonged, heavy infestation results in extensive yellowing. Described from Colombia, it was not reported in Brazil until 1994 (Keifer, 1965; Schliesske, 1990; Ferreira *et al.*, 1994).

Retracrus elaeis, another mite known in tropical America, feeds on the abaxial frond surfaces of African oil palm, causing damage similar to that of *R. johnstoni* (Keifer *et al.*, 1982; Schliesske, 1990; Zenner de Polanía and Posada Flórez, 1992).

Tenuipalpidae

The family Tenuipalpidae, the false spider mites, consists of red or green mites of flattened form, which attack plants.

Raoiella indica, the coconut red mite, lives on foliage and is considered a major pest of coconut palm and *A. catechu* in India (Senapati and Biswas, 1990; Sathiamma, 1996). Several species of phytoseiid mites are natural enemies of *R. indica* (Somchoudhury and Sarkar, 1987). Population build-up was positively correlated with leaf moisture, crude protein and nitrogen levels in different coconut varieties (Sakar and Somchoudhury, 1989). Infestations are sometimes controlled chemically (Sakar and Somchoudhury, 1988; Jalaluddin and Mohanasundaram, 1990a; Jayaraj *et al.*, 1991). Spraying the foliage with water may also be effective (Senapati and Biswas, 1990).

Tetranychidae

The family Tetranychidae, known as spider mites, because of their propensity to spread webbing on their host plants, are green, yellow, orange or red mites, which live primarily on vascular plants (Fig. 3.46). They are the most important family of Acari that feeds on palm foliage. Their feeding on plant surfaces destroys chlorophyll-bearing cells, causing stippling, bleaching, yellowing or bronzing, followed by necrosis. Adult females live for several weeks, laying eggs daily, and may lay several hundred eggs in a lifetime. Spider mites develop from egg to adult in a few days and undergo many generations per year. Some species are very host-specific.

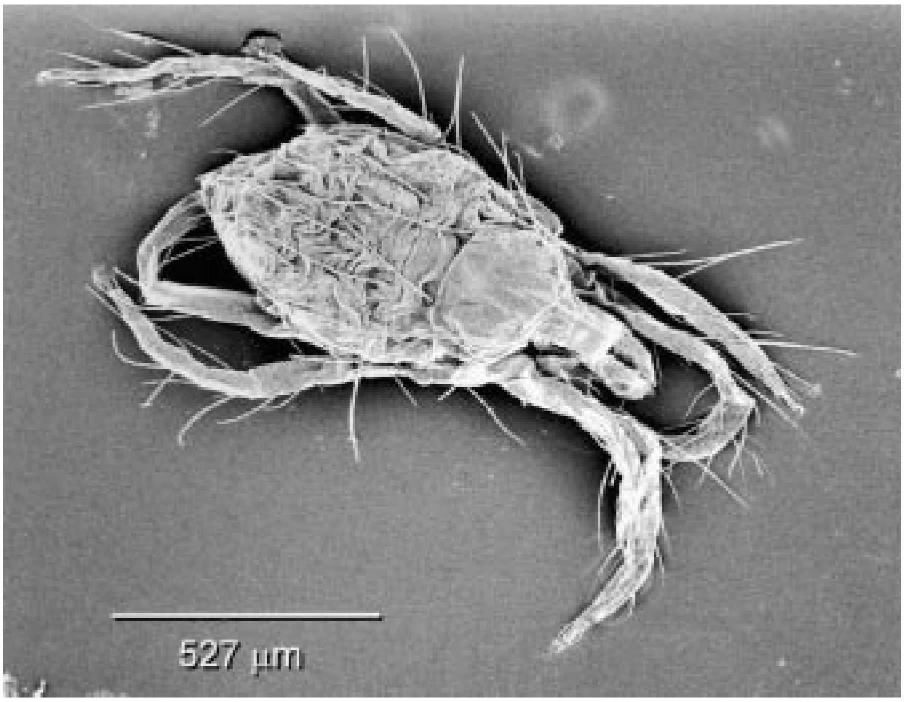


Fig. 3.46. A tetranychid mite from coconut palm foliage (SEM view).

Tetranychus urticae is a common spider mite on foliage of many species of palms in Florida. It is a green mite, with dark spots on either side of the abdomen, which are actually internal accumulations of metabolic wastes. A cosmopolitan pest, it attacks many species of woody plants in warm countries and is a glasshouse pest in colder regions.

Tetranychus mexicanus is a red spider mite, which attacks the foliage of coconut palm, African oil palm and diverse dicotyledonous trees in the American tropics. Its damage is less serious on palms than on its other hosts (Ferreira *et al.*, 1994).

Worldwide, at least 31 species of tetranychid mites have been reported from at least 31 species of palm (W. Calvin Welbourn, personal communication).

Eriophyoidea

Known as gall mites, rust mites or four-legged mites. Eriophyoid mites are discussed in Chapter 4 as pests of palm fruits. Numerous species of this superfamily have been found on palms by zealous acarologists equipped with microscopes, but otherwise they tend to go unnoticed and probably seldom, if ever, cause significant damage (Box 3.4).

Box 3.4. Dwellers in the secret garden: mites of the superfamily Eriophyoidea on palms.
James Amrine and Forrest W. Howard

> Où finit le télescope, le microscope commence. Lequel de deux a la vue la plus grande? (Where the telescope ends, the microscope begins. Which of the two shows the greater view?)
>
> (Victor Hugo (1802–1885), French poet, novelist, dramatist. *Les Misérables*)

Entomologists who observe insects of palms in the field may often be unaware that there is a world of much smaller arthropods inhabiting the foliage and fruits of the same palms. These denizens of a secret world may be revealed when the entomologist studies a sample of leaf or fruit tissue under the microscope. Mites of the superfamily Eriophyoidea (Colour Plate 13f, Figs 3.47 and 4.5), which are among the most minute arthropods, have been found on palms in various geographical regions. As can be seen in the following table, most species are known from the palms that are important as ornamental or crop palms. These have been discovered mostly by diligent acarologists; otherwise eriophyoid mites go unnoticed and probably seldom cause significant damage. Only meagre information is available concerning even the important economic species, *Aceria guerreronis* and *Retracrus elaeis.* Undoubtedly, many additional species of this mite family are associated with palms and await discovery.

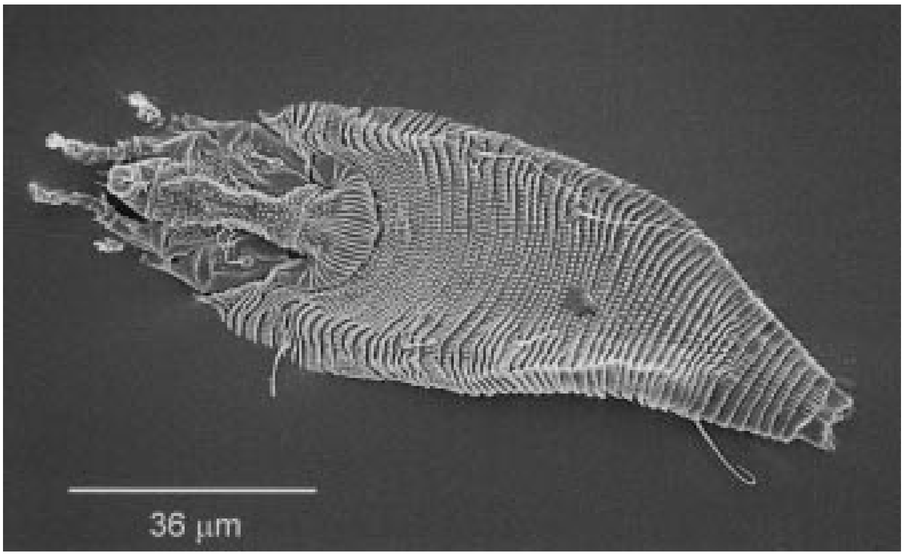


Fig. 3.47. *Acrinotus denmarki* (Acari: Eriophyidae) from *Roystonea regia* foliage (SEM view).

Box 3.4. *continued*

Species	Palm hosts	Plant part	Geographical distribution	References
Eriophyidae				
Aceria guerreronis	*Cocos nucifera*	Fruit	Tropical America, Africa, southern Asia	Moore and Howard, 1996
Acrinotus denmarki (Fig. 3.47)	*C. nucifera*, *Roystonea regia*	Fronds	Florida (USA)	Keifer, 1962b
Adenoptus chamaeropsi	*Chamaerops humilis*	Not stated	Southern Europe	Mitrofanov *et al.*, 1983
Amrineus cocofolius	*C. nucifera*	Fronds, fruits	São Paulo (Brazil)	Flechtmann, 1994
Amrineus coconuciferae	*C. nucifera*	Fronds	Florida (USA)	Keifer, 1962a
Colomerus novahebridensis	*C. nucifera*	Fruits	Oceania, Malaysia	Kang, 1981
Epitrimerus calami	*Calamus australis*	Fronds	Queensland (Australia)	Keifer, 1969
Epitrimerus elaeis	*Elaeis guineensis*	Fronds	Côte d'Ivoire	Boczek and Natcheff, 1989
Epitrimerus steveni	*C. humilis*	Not stated	Southern Europe	Mitrofanov *et al.*, 1983
Gilarovella canaliculata	*C. humilis*	Not stated	Southern Europe	Mitrofanov *et al.*, 1983
Nacerimina gutierrezi	*C. nucifera*	Fronds	Samoa	Keifer, 1979
Neocupacarus flabelliferis	*Borassus flabellifer*	Fronds	Bihar State (India)	Das and Chakrabarti, 1985
Notostrix attenuata	*C. nucifera*	Fronds	Philippines	Briones and Sill, 1963; Keifer, 1963
Notostrix exigua	*Euterpe edulis*	Fronds	Brazil	Flechtmann, 1998
Notostrix flabelliferae	*B. flabellifer*	Fronds	Tamil Nadu (India)	Mohanasundaram, 1982
Notostrix jamaicae	*C. nucifera*	Fronds	Jamaica, Costa Rica	Keifer, 1970; Schliesske, 1990
Phyllocoptes mariaui	*E. guineensis* × *Elaeis oleifera*	Fronds	Côte d'Ivoire	Boczek and Natcheff, 1989
Scolocenus spiniferus	*C. nucifera*	Fronds	Philippines	Keifer, 1962c; Briones and Sill, 1963
Tegonotus gutierrezi	*E. guineensis*	Fronds	Côte d'Ivoire	Boczek and Natcheff, 1989
Tumescoptes dicrus	*Phoenix reclinata*	Fronds	South Africa	Meyer, 1992
Tumescoptes phoenixi	*Phoenix canariensis*	Fronds	South Africa	Meyer, 1992
Tumescoptes trachycarpi	*Trachycarpus fortunei*, *Trachycarpus excelsa*, *C. humilis*	Fronds	China, California (USA)	Keifer, 1939b; Kuang, 1991
Phytoptidae				
Acathrix trymatus	*C. nucifera*	Fronds	Philippines, Florida (USA)	Briones and Sill, 1963; Welbourn, 1997
Mackiella borasis	*B. flabellifer*	Fronds	Tamil Nadu State (India)	Mohanasundaram, 1981
Mackiella phoenicis	*Phoenix dactylifera*	Fronds	California (USA)	Keifer, 1939a
Propilus gentyi	*Aiphanes* sp.	Fronds	Dept. of Santander (Colombia)	Keifer, 1975
Propilus spinosus	*Aiphanes* sp.	Fronds	Dept. of Santander (Colombia)	Keifer, 1975
Retracrus elaeis	*E. guineensis*	Fronds	Tropical America	Keifer *et al.*, 1982; Schliesske, 1990

Box 3.4. *continued*

Species	Palm hosts	Plant part	Geographical distribution	References
Retracrus johnstoni	*Chamaedorea elegans, C. nucifera, Syagrus romanzoffiana*	Fronds	Mexico, Costa Rica, Brazil	Keifer, 1965; Schliesske, 1990; Ferreira *et al.*, 1994
Rhynacus palmeus	*S. romanzoffiana*	Fronds	Brazil	Flechtmann, 1998
Diptilomiopidae				
Dialox stellatus	*C. nucifera*	Fronds	Philippines, Costa Rica	Keifer, 1962c; Briones and Sill, 1963; Schliesske, 1990
Diptacus borinquensis	*Roystonea* sp.	Fronds	Puerto Rico	Cromroy, 1958
Neodialox palmyrae	*B. flabellifer*	Fronds	Tamil Nadu State (India)	Mohanasundaram, 1983

4

Insects of Palm Flowers and Fruits

Dave Moore

> As vegetative structures, palms contend with the trees in the forest; fruiting, they summon bird and mammal; by flower they communicate through small insects and the wind.
>
> (E.J.H. Corner, British tropical botanist. *The Natural History of Palms*, Weidenfeld and Nicolson, London, 1966)

This chapter deals with the insects that are pollinators of palms, those that are herbivores of palm flowers and those that attack the fruits and seeds. Some insects play more than one of these roles, in which case they are discussed in the area where they are considered the more significant.

Insect Pollination in Palms

The Victorian naturalist the Reverend J.G. Wood sought the good in all things. Weevils eluded him. He wrote (Wood, 1874), ‘The hidden virtues of the weevils have yet to be discovered. That such virtues exist there can be no doubt, but at present they are so very deeply hidden that they are quite unknown’. His optimism would have been rewarded by the relatively recent knowledge that among their hidden virtues can be counted their importance in the pollination of palms.

Pollination of flowers may be biotic (carried out by animals) or abiotic. Abiotic pollination of most terrestrial angiosperms is by anemophily (wind pollination, or, more accurately, pollen transfer by air currents). The success of the angiosperms owes a great deal to entomophily (insect pollination) (Pellmyr *et al.*, 1991) and its development in some of the palms has led to great diversity of pollination mechanisms. Palms have a number of the characteristics associated with anemophily (Bertin, 1989), such as reduction of attractive flower parts, often limited production of nectar, little odour and the production of immense numbers of pollen grains. On the other hand, palms do not necessarily show close spacing of conspecifics, domination of the species composition of an ecosystem, coordinated flowering and short growing seasons, which are characteristics associated with anemophily (Whitehead, 1983). In fact, the pollen grains of many palm species have characteristics associated with entomophily, such as relatively large size and spiny or sculptured surfaces (Fig. 4.1). Entomophilous pollen may also be sticky. A formerly widely accepted view was that anemophily was of greater importance in palms than entomophily. The excellent review by Henderson (1986) leads to the conclusion that pollen transfer by insects, especially beetles, predominates in the palm family (Corner, 1966; Table 4.1).

In recent decades, there has been a significant shift in opinion concerning entomophily of palms. More accurately, there has been a shift from opinion to a state of limited knowledge (Schmid, 1970; Essig, 1971, 1973). Uhl and Moore (1977) studied floral structure and pollination in *Thrinax*, *Phoenix*, *Nypa*, *Ptychosperma*, *Bactris* and *Asterogyne*, and found that the last four were basically entomophilous. The first two were anemophilous, but even they had some structures that seemed to relate to entomophily. At the time of the study, the detailed floral biology was known for only about 5% of genera. The authors studied morphological, anatomical, chemical and other features and related them to mode of pollination and associated specific characteristics with beetle, bee, drosophilid and syrphid pollination. Many of the features cited could also relate to protection against herbivores.

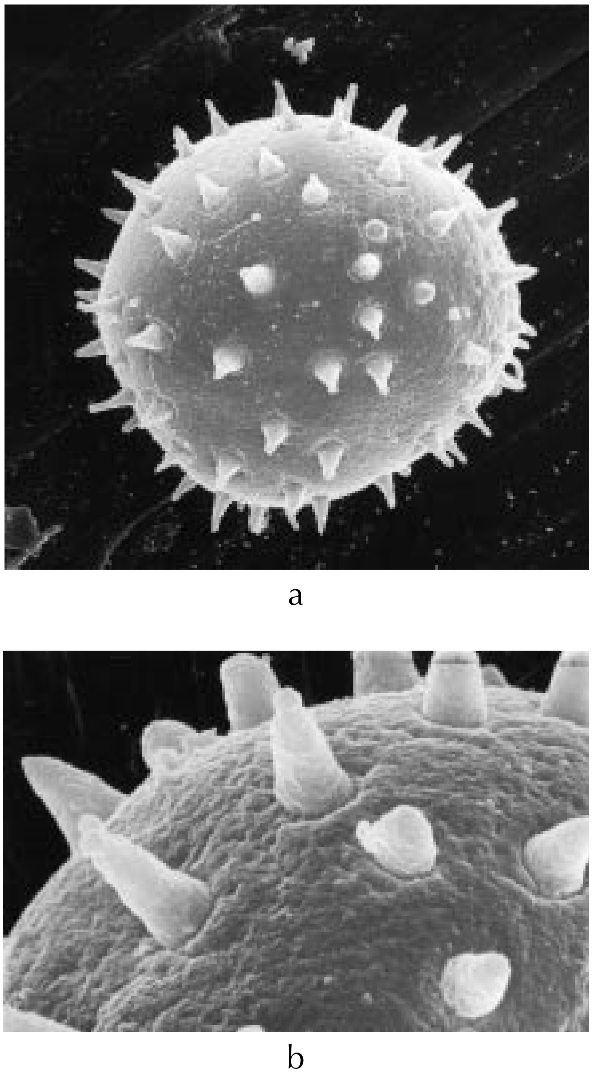


Fig. 4.1. (a) Pollen grain of *Caryota* sp. (b) Entomophilous pollen grains often have spines that are adapted to becoming lodged among insect setae. SEM view by Madeline Harley.

Pollinating insects and flowers have a mutualistic association mediated by the scent and the colour of the flower and the nutritional value of nectar and pollen (Harborne, 1988). Corner (1966) noted that little is known about the pollination of wild palms, but emphasized the discrete characters that palm species have that may make them attractive to animal pollinators. The story of insect pollinators of African oil palm suggests that cultivated palms also deserve more study.

The flowers of palms have odours of, for example, orange blossom, honey and sour milk. Odours may be important where visual stimuli are lacking, and many insects are very sensitive to low concentrations of volatile chemicals (Oleson and Balslev, 1990). The individual flowers of palms are typically small, but they occur bunched in inflorescences, which allow extensive foraging. The flowers may be of delicate hues, especially in contrast to many brightly coloured tropical blooms, but again, because of their occurrence in an inflorescence, often against green foliage or in the dimness of a dense forest, could be highly attractive. However, beetle pollinators, for example, often prefer dull, cream or greenish flowers and, having a poor colour sense, are often more reliant on other stimuli to attract them to inflorescences. Insects do not perceive the same spectrum of electromagnetic waves that humans recognize as colours. Thus, patterns in flowers may appear differently to them. Ultraviolet nectar guides, i.e. patterns that help guide insects to nectar sources within the flower, have been photographed, using special techniques. These techniques were used to examine flowers of several palm species, without finding ultraviolet patterns (F.W. Howard, unpublished).

Table 4.1. Arthropods associated with palm pollination (derived largely from Henderson, 1986, and references therein).

Palm subfamily and tribe	Palm genus	Insects associated with palm flowers and floral characteristics suggestive of entomophily
Coryphoideae		
Corypheae	*Chelyocarpus*	Odour probably attractive to beetles
	Cryosophila	*Derelominus* sp.; *Mystrops* sp. Strong lilac smell. Inflorescence temperature elevation
	Itaya	*Trigona* sp. bees dominate. Beetles and flies also important
	Thrinax	Beetles and thrips on *Thrinax excelsa*. Pink, scented flowers
	Trachycarpus	*Trachycarpus fortunei* possesses non-sepal nectaries
	Rhapidophyllum	Visited by *Notolomus* sp. (Derelomini). Flowers may be brightly coloured with dull bracts. Musky odour, especially from male flowers
	Chamaerops	Two pollen-eating *Derelomus* species recorded. *Chamaerops humilis* sometimes secretes nectar
	Rhapis	*Derelomus ueoni* breeds in *Rhapis excelsa*
	Livistona	Nectaries present
	Johannesteijsmannia	Different species have flowers, with odours ranging from sweet to sour. Nitidulid and staphylinid beetles, flies, thrips, ants and termites probably involved in unspecialized pollination
	Licuala	Nectar secretion
	Pritchardia	Flowers visited by bees, wasps and other insects. Nectar secretion in *Pritchardia martioides* and *Pritchardia rockiana*
	Serenoa	*Notolomus* sp. (Derelomini) and *Exoprosopa fascipennis* (Bombyliidae) (Colour Plate 13b) found on inflorescences
	Corypha	*Chrysomyia* spp. (Diptera: Calliphoridae). Yellow flowers, odour offensive or of sour milk. Sepal nectaries
	Sabal	*Sabal palmetto* visited by a range of insects, initially bees and flies, later by Coleoptera and Lepidoptera. *Apis mellifera*, although exotic, thought to be the major pollinator. Continuous nectar and odour production through the day. Sepal nectaries
Phoeniceae	*Phoenix*	*Apis mellifera* attracted to *Phoenix reclinata* and many bees to *Phoenix caespitosa*. Male flowers scented and nectaries possibly present
Borasseae		Sepal nectaries
Calamoideae		
Calameae	*Eugeissona*	Visited by a wide range of arthropods. Trigonid bees visit male flowers. Alcoholic smell resulting from fermentation of nectar
	Salacca	*Derelomus* species on male flowers of *Salacca zalacca* before visiting females, where they feed on nectar-like material. Females oviposit in female flowers, leaving the next day
	Daemonorops	Musty odour, crowded flowers, many beetles present
	Calamus	Musty or sour odour, crowded flowers, beetles, wasps and flies
	Calospatha	Musty odour, crowded flowers, many beetles present
	Ceratolobus	Penetrating odour. Staphylinid beetles, ants, thrips and Lepidoptera recorded on *Ceratolobus glaucescens*. Inflorescence enclosed except for small slits to let pollinators through
	Plectocomiopsis	Fragrant odours
	Plectocomia	Fragrant odours. Visited by insects, especially weevils

Table 4.1. *continued*

Palm subfamily and tribe	Palm genus	Insects associated with palm flowers and floral characteristics suggestive of entomophily
Nypoideae	*Nypa*	Visited by *Trigona* spp. and flies of the Drosophilidae. The bees were rarely found on female flowers, and the flies carried significant quantities of pollen. Dipteran larvae and occasional beetle larvae bred in the female flowers. Flower-buds brightly coloured, pollen orange and sticky and flowers with a distinct odour
Ceroxyloideae		
Cyclospatheae	*Pseudophoenix*	Many bees attracted by nectar
Ceroxylyeae	*Ceroxylon*	Many melyrid beetles found on male flowers of *Ceroxylon mooreanum*
	Ravenea	Curculionid and nitidulid beetles visit *Ravenea louvelii* and *Ravenea dransfieldii*. Inflorescence heating occurs and musty aroma. Other species, e.g. *Ravenea sambiranensis* and *Ravenea madagascariensis*, probably bee-pollinated
Hyophorbeae	*Hyophorbe*	Intense fragrance, bright orange flowers and sepal nectaries
	Synechanthus	Male flowers of *Synechanthus warscewiczianus* visited by many drosophilid flies, which later visited female flowers
	Chamaedorea	The bees of *Trigona tataira* and *Cholus* spp. weevils visited the flowers of *Chamaedorea wendlandiana*, but only the former were recorded as having carried pollen. Visitors to other palms include trigonid and halictid bees, chrysomelid beetles and drosophilid flies. Many palms of this genus have highly scented, brightly coloured flowers, with sticky pollen
Arecoideae		
Caryoteae	*Arenga*	*Apis mellifera* visit scented male flowers of *Arenga tremula*. Sepal nectaries
Iriarteae	*Iriartella*	Ants visit inflorescence
	Iriartea	*Iriartea ventricosa* and *Iriartea gigantea* visited by *Trigona* sp. bees. *Melipona* and *Apis* species also recorded. Beetles of secondary importance
	Socratea	*Socratea exorrhiza* considered beetle-pollinated and visited by large numbers of *Phyllotrox* sp. (Derelomini) and *Mystrops* spp. (Nitidulidae), including *M. basalis*, *M. dufaui* and *M. corpulentus*. Sepal nectaries in *S. exorrhiza*
	Catoblastus	*Phyllotrox* sp. and *Mystrops adustus* on *Catoblastus kalbreyeri*
	Wettinia	*Mystrops basalis, Mystrops teapensis, Phyllotrox* sp., flies and bees on male flowers of *Wettinia hirsuta*
Podococceae	*Podococcus*	Sepal nectaries
Areceae	*Manicaria*	Larvae probably breed in the flowers. Inflorescences with netlike bracts, which restrict entry of insects larger than pollinating nitulid beetles
	Leopoldinia	Scented male flowers
	Dypsis	Bee pollination in some *Dypsis* spp. Others have tiny, specialized flowers for small pollinators not yet studied
	Euterpe	Bees visited male and female flowers. Petals purple and nectar-like substance produced. Beetles of secondary importance
	Prestoea	*Prestoea decurrens* visited by *Trigona, Neucorynura* and *Lasioglossum* species bees and one species of halictid bee. Small flies may also visit
	Hyospathe	Few insect visitors, mainly ants, beetles and bees
	Archontophoenix	*Trigona amalthea* considered major pollinator of *Archontophoenix cunninghamiana*

Table 4.1. *continued*

Palm subfamily and tribe	Palm genus	Insects associated with palm flowers and floral characteristics suggestive of entomophily
	Rhopalostylis	Flies (mainly) attracted to exudates of male and female flowers
	Calyptrocalyx	Sweet scent, nectar produced
	Ptychosperma	*Ptychosperma macarthurii* is visited by *Trigona, Nomia* and *Homalictus* species bees and flies of the Syrphidae, Calliphoridae and Drosophilidae. *Nomia* sp. considered most important pollinator. Nectar secreted, pollen heavy and sticky
	Hydriastele	Bees of the genera *Nomia*, *Homalictus* and *Trigona* visited male flowers and collected pollen, but did not visit receptive female flowers. Drosophilid flies visited but considered unimportant. *Nodocnemus* spp. weevils (Derelomini) present. Musky odour of flowers and white sticky pollen
	Nenga	*Nenga gajah* has a marked odour and is visited by nitulids and trigonids
	Pinanga	Nitidulids and curculionids present on flowers of *Pinanga coronata*. Musty odour
	Areca	Pollen of *Areca catechu* collected by bees and other insects, which did not visit female flowers. Sweet-scented flower
	Iguanura	Male flowers attracted ants, flies, bees, wasps and weevils. Fewer insects visited the female flowers
	Marojejya	Inflorescence structures similar to those of palms known to be beetle-pollinated
Cocoeae	*Butia*	*Butia leiospatha* pollinated by bees, wasps, flies and curculionid and nitulid beetles
	Cocos	*Cocos nucifera* inflorescences are visited by many insects, but only a few are common to both male and female flowers. *Derelomorphus eburneus*, apparently restricted to coconut flowers, may be an important pollinator. Nectaries present and flowers sweetly scented. *Apis mellifera* considered important in many areas.
	Attalea	Beetle-pollinated
	Syagrus	Beetle or bee pollination predominates
	Orbignya	*Mystrop*s sp. found in numbers on *Orbignya martiana* flowers. Scented with nectaries
	Maximiliana	*Maximiliana martiana* visited by *Melipona* sp. bees
	Barcella	*Barcella odora* flowers are sweetly scented and visited by bees, flies and wasps
	Elaeis	Insect pollination important, especially *Elaedobius* spp. (Curculionidae). Female flowers strongly, but intermittently, scented
	Acrocomia	Curculionids, nitulids and scarabs implicated in pollination
	Aiphanes	Bees, flies and beetles implicated, depending on location
	Bactris	Bee and beetle pollination important. Flowers with musky odour. Scarabs important
	Astrocaryum	*Astrocaryum alatum* reported as beetle-pollinated. The scarab *Cyclocephala stictica* and *Mimeoma acuta* visited the flowers
Geonomeae	*Welfia*	*Welfia georgii* visited by six *Trigona* species
	Asterogyne	*Asterogyne martiana* is visited by many different insects. Weevils feed and breed in the flowers but syrphids may be the major pollinators. Flowers cream- or white-coloured, nectariferous with a sweet smell. *Asterogyne spicata* has bright orange male flowers with a strong scent, which are visited by bees

Table 4.1. *continued*

Palm subfamily and tribe	Palm genus	Insects associated with palm flowers and floral characteristics suggestive of entomophily
	Geonoma	Drosophilid flies may be important. Scented flowers, nectaries present
Phytelephantoideae	*Phytelephas*	*Phytelephas microcarpa* visited by bees, flies, staphylinids, nitulids and curculionids. One identified nitulid was *Mystrops teapensis*. The curculionids were thought to be the major pollinators. Strongly scented flowers. Scarabs also thought to be important pollinators
	Palandra	Scarabs, *Cyclocephala aequatoria* and *Mystrops costaricensis* reported on male flowers of *Palandra aequatorialis*
	Ammandra	Similar to *Phytelephas* and *Palandra* species. Curculionids, staphylinids, nitulids and hydrophilid beetles found on male flowers

The nutritive value of the tissues of the reproductive structures is also important. They are often rapidly growing, with many cells undergoing division, and may be high in easily metabolized nutrients and low in both the chemical and the physical defences associated with older tissues. The presence of nectar and pollen also adds to the nutritional value for herbivores. Nectar is high in sugars, but may also contain significant amounts of amino acids and lipids (Harborne, 1988). Pollen is often a nutritionally balanced foodstuff and is especially fed on by beetles. Starchy pollen is typical of self-fertilizing plants, while starchless pollen is more suitable for pollinators and often has higher levels of protein and lipids (Bertin, 1989).

The paucity of information on the pollination of palms reflects that of pollination of tropical plants in general (Fægri and van der Pijl, 1979). However, different groups of pollinating insects have important characteristics that may give clues about pollination in palms.

Henderson (1986) considered that most entomophily in palms could be grouped into beetle, bee or fly pollination. A fourth major pollinating order, Lepidoptera, is much less well represented on palm flowers.

Cantharophily (pollination by beetles), usually involving Nitidulidae and Curculionidae, is considered to be the most important category of entomophily in palms (Henderson, 1986). Genera of these large families appear to be specific to palm flowers, and the degree of specificity may be very marked (Syed, 1979, 1982). Other beetles, such as scarabs, may also be of importance but without exhibiting the same degree of specificity. Others, such as Staphylinidae, were thought to be regular visitors but not pollinators. However, staphylinid beetles are major pollinators of some plants, and many groups at present considered to be inconsequential or even harmful to plants may turn out to be valuable pollinators (Fægri and van der Pijl, 1979).

Cantharophily may be as characteristic of the tropics as bee pollination is of temperate regions (Fægri and van der Pijl, 1979). Palms evolved early in evolutionary times and are at least as old as any other group of flowering plants (Corner, 1966; Uhl and Dransfield, 1987). The earliest confirmed fossil records of palms are of *Sabal magothiensis* and *Palmoxylon cliffwoodensis* from the Upper Cretaceous period, about 84 million years ago (Uhl and Dransfield, 1987). *Nypa* pollen fossils from around the same period are known. Among the fossil beetles of the Jurassic period are some that resemble existing floricolous species (Crowson, 1981). Co-evolution between palms and pollinators could imply a long association with beetles. Beetle pollination is widespread among the more primitive angiosperms. It may have promoted the development of the angiosperm-type flower. What are now pollination attractants may have developed first as anti-herbivore defences (Vail, 1992). Some of the earliest beetles may have been pollinators (Crowson, 1981). However, fossil evidence also suggests that pollen-eating Lepidoptera and Diptera also appeared during the Cretaceous (Silberbauer-Gottsberger, 1990).

Fægri and van der Pijl (1979) noted that beetles were often deceived by false attractants, sometimes sexual, and could often be drawn to flowers by smells even if no nutritional reward was obtained. In many palms, the female flowers offer no nutritional reward and pollination is achieved by deception (Oleson and Balslev, 1990). Even when deceived into flowers, beetles probably obtain some benefit, such as shelter from enemies or from the elements, and heat from the rapidly metabolizing tissues in the flowers.

Several features associated with cantharophily relate to the relatively poor visual ability of most beetles. Beetle-pollinated flowers have few individual visual stimuli, so they are usually large or massed into large inflorescences. They are usually dull-coloured or white. If coloured, the colours tend towards the red end of the spectrum. They have easy access, being open and actinomorphic. They have strong odours and accessible food rewards, with many stamens, producing abundant pollen (Fægri and van der Pijl, 1979; Crowson, 1981).

Irvine and Armstrong (1990) suggested that beetle-mediated pollination is of two main types, depending on feeding. One type involves pollen- and nectar-feeders, which do little or no damage to flowers. The odours of this type tend to be sweet. The other involves primarily herbivores, which consume floral tissues as well as pollen or nectar. These flowers tend to have ripe fruit or musky odours.

Although much pollination may be carried out by generalist foragers, there are examples of highly specific mutualism, such as the pollinators of African oil palm.

Bees are the best-known pollinators and melittophily dominates biotic pollination in many areas. The typical floral characteristics associated with melittophily are brightly coloured zygomorphic flowers, with mild, fragrant odours. Bees are considered to be important in the pollination of coconut palm (Colour Plate 13a; Sholdt, 1966; Sholdt and Mitchell, 1967). Stingless bees such as *Trigona* spp. (Apidae: Meliponinae) have been observed on flowers of various palm species (Fig. 4.2). In general, other than the ubiquitous occurrence in inflorescences of many palm species, the value of bees as pollinators is presumed from such anecdotal information as the fact that tropical honey is largely dependent on palms (Corner, 1966).

Myophily (pollination by Diptera) shows a range of forms, from the highly specialized to the opportunist. Many are attracted by simple, pale blossoms and easily obtained nectar. These flowers often have little odour. Others are deceived by distinct, strong odours, indicating breeding or feeding sites. Myophily may be largely restricted to understorey species of palms, with flies of the Bombyliidae, Calliphoridae, Drosophilidae and Syrphidae being rather inefficient pollinators during the course of their feeding and breeding (Colour Plate 13b).

Pollination examples

African oil palm

The story of the studies into the pollination of the African oil palm is instructive. Native to West Africa, the palm was introduced into other regions. In some of these, such as South-East Asia, assisted pollination was necessary for adequate production and became a standard practice in plantations. The plant is monoecious; hence cross-pollination is obligatory. The debate over whether its flowers were anemophilous or entomophilous began early and appears to have been fuelled mostly by differing opinions rather than factual knowledge. Despite occasional reports suggesting that entomophily was of

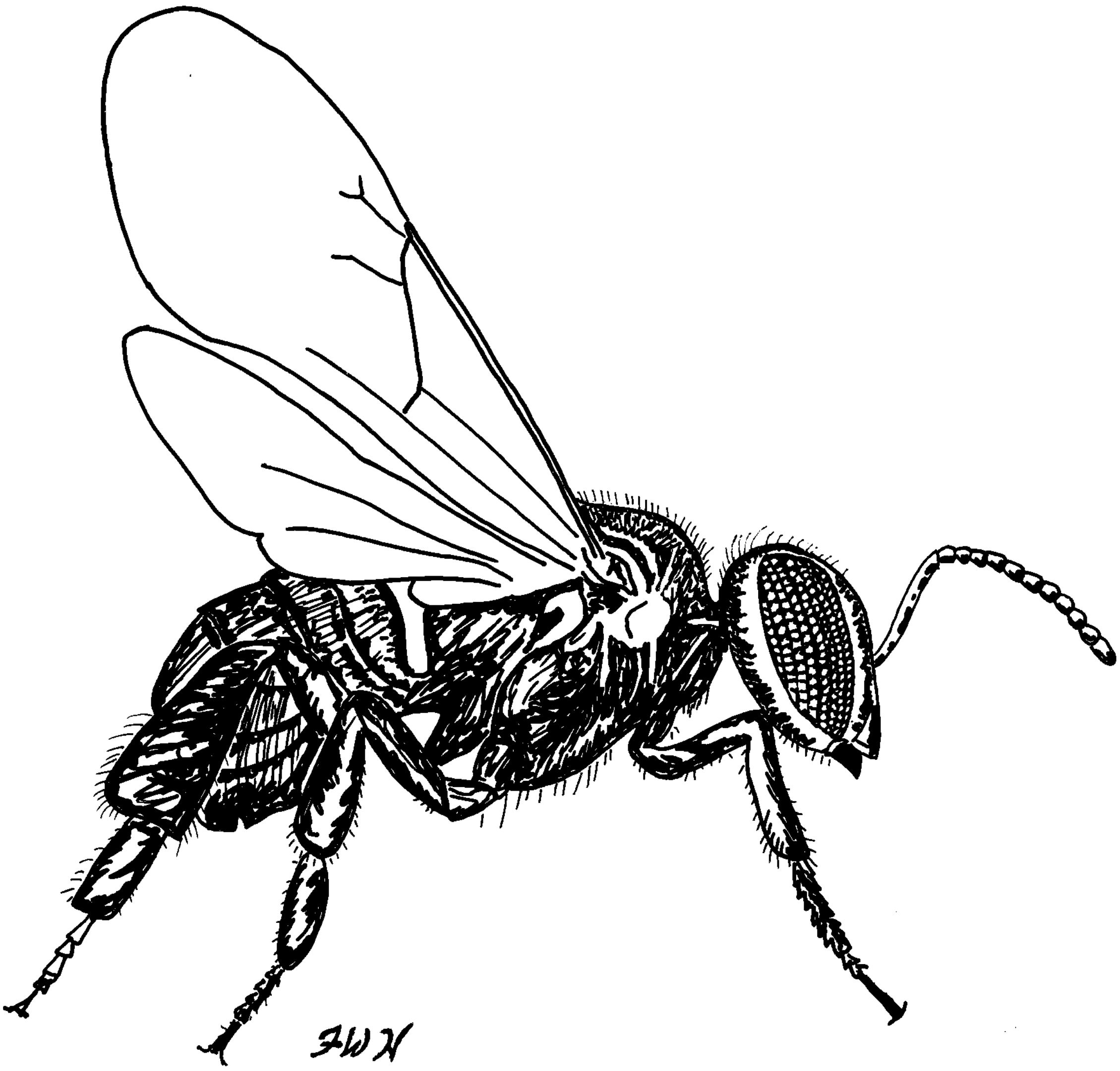


Fig. 4.2. A stingless bee (Apidae: Meliponinae). Meliponine bees are important in pollinating some palms. After M. Quick, in Naumann, I.D. (ed.) (1991) *The Insects of Australia.* Cornell University Press, Ithaca, New York.

importance, the opinion predominated that the pollen was transferred by air currents (Hardon and Corley, 1976; Purseglove 1985).

The issue was not resolved until R.A. Syed of the then Commonwealth Institute of Biological Control undertook a detailed study in Cameroon and Malaysia. In Cameroon, he found a large number of insects on male inflorescences, but fewer on female inflorescences. The species that he found frequently on one sex of inflorescence he rarely found on the other sex, which would have made it appear that insects were of little importance in pollination (Syed, 1979). However, Syed found that a large number of insects visited female inflorescences in intermittent swarms throughout the day. By netting all insects arriving in 4 s in every 15 min throughout the receptive period, he estimated that a single inflorescence was visited by 20,000 insects. Based on these more intensive observations, he discovered that all species that visited male inflorescences did indeed visit the female also. Insects were captured on the female inflorescence and examined microscopically for pollen. Species of *Elaeidobius* carried the largest number of pollen grains, of which the majority were viable (Fig. 4.3).

There was a much poorer complex associated with pollination in Malaysia. In Sabah, eastern Malaysia, a moth,

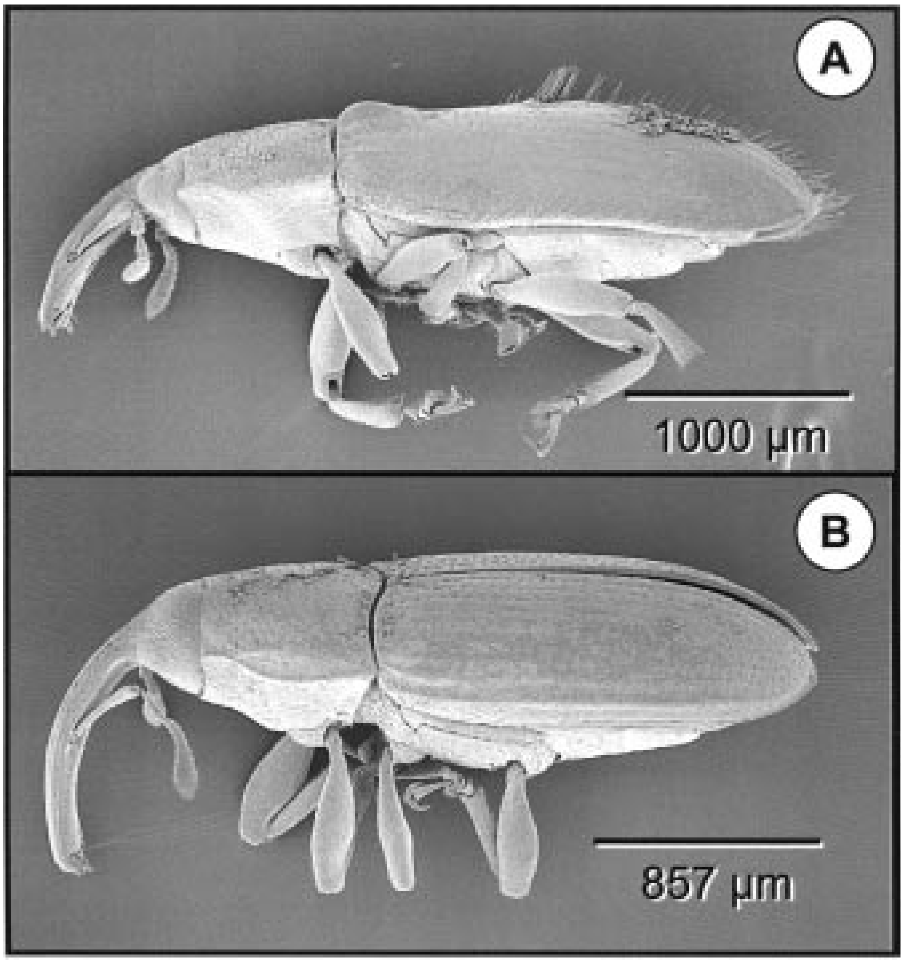


Fig. 4.3. *Elaeidobius kamerunicus,* (A) male and (B) female. This weevil is an important pollinator of African oil palm. Pollen grains are on elytra in A. SEM view by Robin Giblin-Davis.

Pyroderces sp. (Momphidae), was the only insect that apparently contributed to pollination. In western Malaysia, *Thrips hawaiiensis* began to arrive at the male inflorescence as the flowers opened. The majority were females and large numbers of eggs were laid, up to four in each flower. It was estimated that a single inflorescence could be visited by up to 200,000 thrips. The female inflorescences were also visited by many thrips, and a small assessment indicated that a proportion carried viable pollen grains.

Having determined that entomophily was important, further studies were carried out on the biology of the pollinators in Cameroon. Since *Elaeidobius* species are phytophagous, there was apprehension that they could damage African oil palms or other plants. However, it was evident that the weevils confined their feeding to palms. Species of the subfamily Derelominae (Curculionidae) live on the flowers of palms, especially *Elaeis, Cocos, Chamaerops* and *Sabal*, with the insects being specialized, at the generic level, to host (Lepesme, 1947). For example, the genus *Notolomus* is found on the flowers of *Sabal* species in the Americas and *Prosoestus* and *Elaeidobius* species on those of *Elaeis* in West Africa. A major pollinator of *Elaeis* in South America is *Mystrops costaricensis* (Nitidulidae) (Genty *et al.*, 1986). *Microsporum* sp. and, more especially, *Mystrops congolense* are responsible for most pollination of African oil palm in Madagascar, where the genus *Elaeidobius* is absent (Mariau and Genty, 1988). These are often attracted to female flowers, which produce an odour that mimics their normal mating and ovipositing environment.

Biological studies showed that *Elaeidobius* species did not even consume pollen. The imagos fed only on the inner parts of the male flowers, while larvae developed on the decomposing flowers (Syed, 1982). And, although *Elaeidobius* species visit the female flowers during anthesis, they obtain no benefit from them. Syed assumed that they were attracted by the odour of anise from the female flower.

The major *Elaeidobius* species, namely *E. kamerunicus*, *E. singularis*, *E. plagiatus* and *E. subvittatus*, have similar biologies. All but the last species visit exclusively flowers of the palm genus *Elaeis* (Mariau *et al.*, 1991). *Elaeidobius subvittatus* can maintain breeding populations on the South American oil palm, *Elaeis oleifera*. *Elaeidobius subvittatus* was superior in searching abilities to *E. kamerunicus*, but the latter maintained higher field populations and was responsible for higher levels of pollination in plantation situations. Male weevils carried significantly more pollen than the females, partly because of their larger body size but, more importantly, because males have more setae. The longitudinal groove in the pollen grain acts as a site of attachment to the tip of the setae (Dhileepan, 1992). *Elaeidobius kamerunicus* was selected for introduction into Malaysia to improve pollination, and thus fruit set, in African oil palm. The result has been dramatically increased oil palm fruit production (Ooi, 1982).

This weevil has since been introduced into many African oil-palm-growing regions in both the eastern and western hemispheres – however, not always with the same effect on fruit set. For example, in Sabah, inconsistencies in production during the year were possibly related to the reduction in weevil activity during the rainy season, and assisted pollination was used to make up for these losses (Donough *et al.*, 1995). Similar observations were made in southern India (Dhileepan, 1994). Assisted pollination was done in Peru in young African oil palms, because they did not produce enough male flowers to attract *E. kamerunicus* (Vera, 1996).

Based on studies in Rwanda, Jelínek (1992) suggested that palms may be obligatory hosts of imagos and larvae of at least two groups of Nitidulidae. These are *Mystrops* in tropical America and some Meligethinae in the eastern hemisphere. Three *Meligethinus* species were recorded most frequently: *M. humeralis*, *M. muehlei*, and *M. bisignatus*.

Epuraea subgenus *Apria* was associated with flowers of African oil palm. Four new *Epuraea* species were recorded, namely *E. lechanteuri, E. melanura, E. acuminata* and *E. kirejtshuki*. These comprised nearly 40% of the nitulids sampled (Jelínek, 1992).

Date palm

Since antiquity, date growers in the Middle East and North Africa have known that hand-pollinating the female flowers in spring resulted in increased yields of dates that year. The practice was described by Theophrastus in 301 BC and by other ancient Roman as well as medieval Arabic writers. The ancients were aware that the proximity of male palms resulted in more productive female palms, sometimes attributing this to the effect of the aroma of the male flowers on female fecundity. The idea that pollination of this dioecious plant is anemophilic goes back to the Renaissance, when sexuality in plants was beginning to be understood (Popenoe, 1973). In most commercial date regions, the palms are still pollinated artificially, either by hand or with mechanical dusters (Popenoe 1973; Nixon and Carpenter, 1978). However, circumstantial evidence indicates that entomophily is important in the genus *Phoenix* (Corner, 1966; Uhl and Moore 1977; Henderson, 1986). The fragrant male flowers attract some insects, but characteristics of the pollen itself closely match those typical of wind-disseminated pollen, such as size, smooth exine and non-sticky surface (DeMason and Chandra Sekhar, 1988).

Coconut palm

Despite the importance of coconut palm as a crop plant of major economic importance, a feature as fundamental as pollination is not well understood (Box 4.1). Child (1974) briefly described the debate over anemophily or entomophily.

The arthropod fauna associated with coconut palm varies widely, depending on geographical location (Lepesme, 1947). In the Hawaiian Islands, 51 species were found in coconut palm flowers, comprising 27 Diptera, 15 Hymenoptera, four Coleoptera, three Lepidoptera and one each of the Dermaptera and Hemiptera (Sholdt, 1966; Sholdt and Mitchell, 1967). Only 12 of these species were considered to be frequent and only seven were found regularly on both male and female flowers. These were the honey bee *Apis mellifera*, the wasps *Polistes exclamens*, *Polistes olivaceus* and *Polistes macaensis*, the ants *Paratrechina longicornis* and *Pheidole megacephala* and the black earwig *Chelisoches morio*. *Apis mellifera* was thought the most likely pollinator. Anemophily alone was deemed inadequate for coconut palm (Sholdt and Mitchell, 1967).

A derelomine weevil, *Derelomorphus eburneus*, is apparently specific to coconut palm flowers. It moves rapidly through male flowers and eats pollen and it was suggested that it breeds in the male flowers and could be a pollinator (Cock, 1985). The weevil occurs in Malaysia and the Philippines and its specificity adds weight to the view of a Melanesian origin of coconut palm. Other species of

Box 4.1. Keeping coconut varieties pure: applied pollination biology.
Eric H. Erickson and Forrest W. Howard

Pollination biology has practical implications for palm culture. For example, seednuts of coconut varieties are obtained by growing them in seed orchards, i.e. plantings of single varieties that are isolated to prevent cross-pollination with palms of other varieties. Because there is insufficient information on coconut pollination and the local factors that influence it, the distances that separate coconut-seed orchards from extraneous pollen sources have been chosen arbitrarily.

In recent years, coconut breeding has emphasized dwarf varieties and hybrids. Some dwarf varieties, such as the 'Malayan Red Dwarf', tend to be self-pollinating; however, cross-pollination sometimes takes place. For the production of hybrids, the male flowers are removed in the isolated blocks of palms and the female flowers pollinated artificially. In the production of both dwarf-variety and hybrid seednuts, isolation can help prevent genetic contamination.

The problem can be analysed by way of a hypothetical model, in which the honey bee, *Apis mellifera*, is the principal pollinator of coconut palm. (Indeed, this bee is extremely common on coconut flowers in many regions.) Honey bees do not normally forage more than a few hundred metres to about 3 km from the hive. In rare instances, honey bees may forage up to about 15 km for unusually rewarding nectar sources. Based on these considerations, a separation of 3 km might greatly reduce contamination of a coconut-seed orchard.

It has been shown, however, that, during close contact in the hive, honey bees may inadvertently transfer pollen to each other. Thus, bees foraging 3 km in one direction may rub pollen on to a nest mate, and the latter insect may then carry the pollen 3 km in the opposite direction. The significance of pollen transfer among nest mates in the hive undoubtedly varies with the viability of pollen of different plant species, but, to rule this factor out, an isolation distance of 6 km is indicated.

The involvement of pollinators additional to honey bees could further extend the isolation distance. For example, some species of solitary bees are known to forage much greater distances than honey bees.

Apicultural techniques may offer additional insurance against cross-pollination. One possible technique would be to 'load' the orchard with honey bees (about two colonies per hectare). This might result in more immediate pollination of the palms and prevent outcrossing when other pollinators arrive, and might reduce the nectar and pollen supply to the point that the orchard is less attractive to outside pollinators. Additionally, if flowers of other plants that are highly attractive to bees are more or less continually available in and near the orchard, foraging on palms outside the orchard might be reduced.

Coconut palms are believed to be facultatively anemophilous, but knowledge of the role of air currents in pollination of this palm is as meagre as that of insects.

Derelomorphus are thought to occur almost exclusively in palm flowers.

The pollen grains of coconut palm have a diameter of about 50 µm, which is larger than the 20–40 µm of most anemophilous pollens, and there is a prominent groove along the length of the grain, which is considered an adaptation more suited to entomophily than anemophily (Child, 1974). Although anemophily obviously occurs in coconut palm, the role of insects, especially bees, in pollination can no longer be seriously doubted.

Bactris *spp.*

Pollination of *Bactris* spp. is achieved almost exclusively by beetles, especially Curculionidae and Nitidulidae (Essig, 1971; Mora Urpí and Solis, 1980; Mora Urpí, 1982, 1983; Beach, 1984; Henderson, 1986; Listabarth, 1996). A curculionid, *Derelomus palmarum*, was reported by Mora Urpí and Solis (1980) to be the major pollinator of *Bactris gasipaes* in Colombia, with the scarab *Cyclocephala signata* of secondary importance. Stingless bees of the genus *Trigona* and drosophilid flies were of minor importance. In Amazonian Peru, *Phyllotrox* spp. (Curculionidae) and *Epuraea* (Nitidulidae) are the most important pollinators of the extensively cultivated *B. gasipaes*, visiting this palm from *Bactris bifida* and *Bactris monticola* in nearby primary forests (Listabarth, 1996).

Bactris spp. have unisexual flowers. On any single inflorescence, the period of female flowering is completed before any male flowers release pollen. Female flowers undergo anthesis in the late afternoon, withering by the next morning. On the afternoon of the second day, the small male flowers open, release their pollen and begin to fall within 2–3 h. Nitulids and curculionids acquire pollen while visiting male flowers while they are still open. As the male flowers wither, the beetles seek new flowers and may reach the female flowers of other inflorescences soon after they open and undergo anthesis. The female flowers are not a food source for these beetles and it appears that they are attracted to them by the musky odour which may be emitted by the male flowers, which are yet to open. While rummaging in the female flowers, they inadvertently plant pollen on the receptive stigma (Essig, 1971).

Pollination of *Bactris* spp. is crepuscular–nocturnal. When male flowers open the next day, the male beetles visit them to feed. The rapid withering of the male flowers forces the beetles to leave for another inflorescence, which is likely to be female. The system requires close synchrony and strong adaptive links between the beetles and the palm.

Aiphanes *spp.*

Borchsenius (1993) related types of pollination of three Ecuadorian *Aiphanes* species to flowering intensity and duration. *Aiphanes erinacea*, which is found between 600 and 2000 m in premontane and montane rainforest, was visited by 50 insect species from five orders. These were mostly Diptera (37 species from 16 families) and beetles (ten species from four families). *Aiphanes chiribogensis* is a solitary species from montane rainforests at altitudes between 1700 and 2100 m, visited by 22 species, mainly Diptera, on the staminate flowers and only three on the pistillate. Finally, *Aiphanes eggersii*, found in dry semi-deciduous forest in coastal plains, was visited by only two species, one bee and one wasp.

Borchsenius (1993) hypothesized that *A. eggersii*, which has the highest pollen/ovule ratio and a 1-week period of intensive staminate flowering, was the most suited to highly specialist, pollen-collecting bees. *Aiphanes erinacea* was considered to be an intermediate type, with fewer inflorescences and a slower inflorescence development, producing pollen over a longer period and attracting many Diptera, which were less demanding and were also less efficient pollinators. No bees were present, possibly because of the small anther size. *Aiphanes chiribogensis* represented the low-energy flowering system, with the inflorescence showing very slow development, with only a few flowers undergoing anthesis on a daily basis. There were fewer visiting insects, with a greater proportion of minute species of gnats and midges. The characteristics of this flowering system seemed to favour ant pollination (Hickman, 1974), but there was no evidence that ants were important in *A. chiribogensis*.

Borchsenius (1993) suggested that beetle pollination of palms in tropical America is restricted to the lowland areas, mainly below 1000 m, whereas fly pollinators operate up to 3000 m. In future studies of this type, identification of the insects to species level would be of great value in elucidating their relationships with the different palm species.

Orbignya phalerata

Orbignya phalerata is androdioecious, with individual palms being either androgynous and staminate or just staminate. *Homalinotus* spp. (Curculionidae) (Colour Plate 13e) and a species of Cerambycidae oviposit in the spathe. Pollen-robbing bees include *A. mellifera, Xylocopa frontalis*, *Melipona* spp., *Trigona* spp. and *Partimona* spp. Drosophilid flies are common but breed only on staminate flowers. Ant species present include *Camponotus, Crematogaster, Azteca* and *Pseudomyrmex*, but these groom themselves when in contact with pollen. The only species common on both types of inflorescence and considered to be the major pollinator was the nitidulid *Mystrops mexicana* (Anderson *et al*., 1988).

Dypsis *and* Ravenea *species*

A range of insect pollination systems occur among Madagascan palms (Dransfield and Beentje, 1995). Flowering itself varies; some species, for example, *Dypsis fibrosa* and *Dypsis pinnatifrons*, flower throughout the year, others, such as *Dypsis procera* and *Dypsis paludosa*, show seasonal flowering, while yet others flower at irregular intervals. Beetle and/or bee pollination predominates in the two genera, and flower structures and attributes such as smell and inflorescence heating reflect this. Bee pollination was suggested as quite widespread among the larger species of the two genera. *Ravenea sambiranensis* and *Ravenea madagascariensis* have sweetly scented flowers and loose, spreading inflorescences, suggesting bee pollination, but the former species, at least, is also visited by beetles. Other *Ravenea* species, such as *R. louvelii* and *R. dransfieldii*, are visited by curculionid and nitidulid beetles. The inflorescences of these palms have a musty smell. *Ravenea louvelii* has inflorescences almost hidden among the leaf bases and is probably beetle-pollinated.

Flowers of some *Dypsis* species, such as *D. pachyramea* and *D. remotiflora*, have tiny flowers around 1 mm in diameter. The specialized structures, which can exclude all but the tiniest of pollinators, suggests a highly evolved pollination system, which has not been studied (Dransfield and Beentje, 1995).

Some additional palms

Schmid (1970) pointed to features of *Asterogyne martiana* that suggest entomophily, including its habitat in dense, wet, forest undergrowth with still air and its white inflorescence. Aspects of the floral anatomy and pollen morphology of *Socratea exorrhiza* and *Iriartea deltoidea* can be related to their insect pollinators, which fall into the usual groups of beetles (*Phyllotrox* sp. and *Mystrops* sp.) and bees (*Trigona* spp.) (Henderson, 1985). *Notolomus* sp. near *N. basalis* (Curculionidae) was considered to be the likely pollinator of *Rhapidophyllum hystrix*, based on its frequency in the flowers, its small size, activeness and flight ability (Shuey and Wunderlin, 1977). In the rattan genus *Ceratolobus*, the inflorescence is enclosed, except for minute slits allowing pollinators through. *Manicaria* sp. inflorescences are enclosed with netlike bracts, which restrict entry by insects larger than their major pollinators, nitulid beetles (Dransfield, 1982). Inflorescence temperature elevation occurs in *Cryosophila albida.* The dynastine scarab genus *Cyclocephala*, with over 220 species, and the related genus *Erioscelis*, with four species, are common pollinators and have been implicated in the pollination of *Ammandra, Astrocaryum, Bactris, Palandra* and *Phytelephas* species. Scarab-pollinated plants generally exhibit strong odours, produced by elevating inflorescence temperatures by thermogenic respiration (Henderson, 1984).

Exceptional examples include *Salacca zalacca*, which Moncur and Watson (1987) suggested may be pollinated by small black ants (*Iridomyrmex glaber*), and *A. martiana*, which Schmid (1970) suggested may be pollinated largely by syrphid flies.

Summary and conclusions

It is now generally accepted that entomophily is more important in palm pollination than previously thought and that it falls broadly into the three types, illustrated by Henderson (1986). The first type, cantharophily, is of great importance, although whether it is predominant is open to some dispute. Members of the Nitidulidae and Curculionidae are of greatest significance. In the Nitidulidae, the genus *Mystrops*, in Central and South America, appears to be confined to palm flowers and comparable genera occupy the same niche in Africa. In the Curculionidae, the palm pollinators come from the Derelomini, whose genera, *Phyllotrox, Dereleminus, Derelomus, Meredolus, Notolomus, Nodocnemus, Derelomorphus*, *Prosoestus* and *Elaeidobius*, are confined to palm inflorescences (Henderson, 1986). In the second type, melittophily, the bees in the genera *Melipona*, *Apis* and *Trigona* are of most significance. Finally, myophily, by species of the Calliphoridae, Syrphidae and Drosophilidae, appears to represent the least specialized type, often confined to understorey palms. Wasps and ants (Hymenoptera) and thrips (Thysanoptera) are usually, at best, incidental pollinators of palms.

Silberbauer-Gottsberger (1990) proposed a hypothesis that the earliest palms were pollinated by generalists and cantharophily was derived through evolution. Wind pollination was also derived in palms very early and still occurs in both primitive and advanced palm species.

Great developments in knowledge of palm pollination have occurred in recent decades, but far more is yet to be discovered, even in the African oil palm, a species of major economic importance, which has been studied for decades. The pioneering work done on less well-known palms will undoubtedly be shown to be inadequate and often incorrect, but even the longest journey starts with the first step.

Coordinated multidisciplinary studies are especially needed to elucidate the pollination ecology of palms, one of the most exciting areas of research in palm biology.

Herbivores of Palm Flowers

Insects that are associated with the flowers of palms may be beneficial to the plant as pollinators, as discussed in the previous section. However, many of these same insects, as well as other insect species, damage flowers of palms by feeding on them. Several examples are discussed below.

Lepidoptera

Batrachedridae

The family Batrachedridae is closely related to Coleophoridae and Momphidae. Some authors have considered it a subfamily of one or the other of these families. The moths are small and brown or grey. The forewings are extremely narrow, with setae forming a fringed anal margin. The hind-wings are similar but narrower. The antennae are filiform.

Batrachedra amydraula, the lesser date moth, is a pest of date palm from the Arabian Peninsula west to Pakistan (Hussain, 1974; Ahmad, 1987). The adult is dull yellow-white speckled with grey, with a wing-span of about 10–13 mm. The larva is 12–15 mm when fully developed.

The imagos fly in April and oviposit on or near inflorescences. The larvae bore into the bases of immature date fruits and sometimes consume seeds, in varieties in which these are tender. In Iraq, there is a second and third generation by the end of the summer. Damaged fruits wither and are shed. Infestation levels vary by locality and over time. Losses of up to 75% of the crop have been recorded in some localities (Carpenter and Elmer, 1978).

No resistance in the many cultivars exposed to the lesser date moth has been reported (Hussain, 1974).

Parasitoids in the family Braconidae control the caterpillar naturally in many areas. Farmers in the Arabian Peninsula bought and used predatory ants, *Crematogaster* sp., to control *B. amydraula* until the introduction of DDT. The predator is still to be found.

Some chemical treatments of female inflorescences at the time of pollination are effective in controlling the larvae (Blumberg *et al.*, 1977; Al Sammarraie *et al.*, 1989; Sayed and Ali, 1995). Since entomophily is relatively less important in date palms than in palms in general, insecticide treatment of the flowers is unlikely to interfere with pollination.

The larva of *Batrachedra arenosella* (Lepidoptera: Batrachedridae) is a predator of scale insects, feeding on them from within a silken web that it spins (Nielsen and Common, 1991). It has been reported to attack coconut palm and African oil palm in the eastern hemisphere (Lever, 1979), but this is possibly another species. We refer to the palmivorous species as *B. arenosella*, but suggest that its identification is questionable. The small moth, sometimes referred to as the lesser coconut spike moth, has been reported widely in the tropics of the eastern hemisphere (Fig. 4.4) (Lever, 1979). The female oviposits on inflorescences that are well developed but not yet open and undergoing anthesis. The caterpillar, yellowish brown with a dark brown head, eats the male and female flowers, turning the latter black. There is no consensus as to whether the damage is of any consequence. Several hymenopterous parasitoids of eggs, caterpillars and pupae have been reported. *Celonus* sp. (Braconidae), released on Flores Island, Indonesia, parasitized the pupae of *B. arenosella* and became established, but spread slowly (Baringbing, 1986).

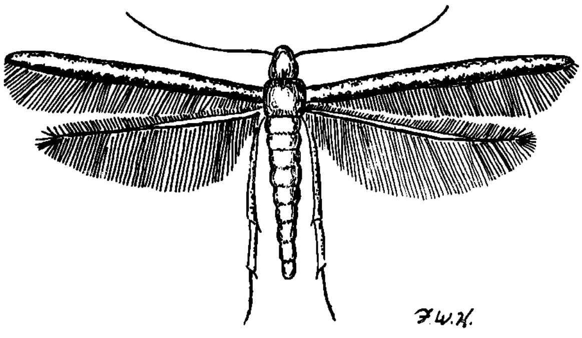


Fig. 4.4. *Batrachedra arenosella* (Lepidoptera: Batrachedridae). The caterpillars of this species are associated with infructescences, but are possibly largely predators of scale insects. After Lepesme (1947).

Ifeda perobtusa (syn. *Batrachedra perobtusa*), known in Brazil and northern South America, is a moth of 8–10 mm in wingspan. The small white to pinkish larvae, 6–7 mm in length at maturity, live among male flowers of palms and feed on pollen from coconut palm and the cocosoid palms *Syagrus* spp. and *Attalea* spp. They pupate among fibres of the palm (Bondar, 1940).

Batrachedra nuciferae was recently reported for the first time as a pest of coconuts in Venezuela (Arnal *et al.*, 1998).

Cossidae

The Cossidae are a family of moths whose larvae are borers, usually in stems but sometimes in roots. The imagos of some species are quite large, with wing-spans of several centimetres.

Acritocera negligens, the coconut spathe borer, has been reported from Fiji. The female lays large, flat, oval eggs in the spathe. Upon hatching, the larvae bore into the spathe and attack the male flowers at the distal end of the inflorescence. They rarely feed on the female flowers at the proximal end. The caterpillar takes about 26–30 days to reach full size, after which it leaves the spathe, drops to the ground and pupates in the soil. The complete development probably takes about 3 months. Its effects on yield appear to be small. In some cases, other insects, such as *Tirathaba rufivena*, may enter through the holes made by *A. negligens* in the spathes (Lever, 1979).

Pyralidae

The Pyralidae are one of the largest families of moths. The imagos are mostly small to medium-sized grey or brown moths, with prominent labial palps and long, filiform antennae. The larvae are typically cryptophagous, occurring as leaf-miners or rollers or stem or fruit borers.

The genus *Tirathaba* contains about 30 species, but many of these could be synonyms. Marked morphological variations and sexual dimorphism confuse the identity of some of these species (Waterhouse and Norris, 1987). Several species have been recorded as attacking the flowering spike of coconut palm in South-East Asia and the Pacific and at least some of these attack a range of other palms.

Tirathaba rufivena, the coconut spike moth or oil palm bunch moth, an important pest of palms in the Philippines and elsewhere in South-East Asia, has also been reported attacking inflorescences of African oil palm, *Areca catechu*, *Nypa fruticans*, *Plectocomia* spp., *Pritchardia pacifica* and *Roystonea regia* (Colour Plate 13c, d; Abad, 1983).

The female moth, with a wing-span of about 28–35 mm, has greyish forewings with green iridescence, red veins and black spots near the margins. The male is silver-grey with a dark band at the margin. The female lays white eggs, singly or in batches of two to 15, in the fibrous sheath surrounding the base of the flower spike. These turn yellow, then orange and then black when about to hatch. After a 5-day incubation period, the eggs hatch and the young larvae begin feeding on newly opened male flowers. They are white at first, but turn light or dark brown. The larval stage, with five or six instars, lasts about 12 days. The later instars attack the female buttons, causing premature shedding of these. The pupa, enclosed in a reddish-yellow cocoon, which incorporates frass and parts of flowers, is located in the inflorescence (Gallego and Abad, 1985).

Young palms are more heavily damaged because their crowns are more compact than those of older palms and often some of the inflorescences remain within the sheath, creating an ideal situation for the larvae. Debate over pest status centres around the amount of natural flower loss. The loss of male flowers is considered to be of little significance, because they are produced in vast excess. Female flowers are also produced in excess, with as much as 70% of them shed within 2 weeks of emergence of the inflorescence (Child, 1974). If caterpillar feeding results in still higher losses of flowers, coconut production may be reduced. This probably happens only in a portion of the cases. The larvae tend to attack the overcrowded female flowers, which are the ones most liable to be shed naturally. In addition, subsequent inflorescences may compensate for losses by retaining a higher portion of female flowers. Thus, losses in production are most apt to result when spike moths attack large numbers of female flowers on multiple inflorescences of the same palm.

The continuing controversy over whether *Tirathaba* attack causes yield losses goes back to earlier coconut entomologists, including T.H.C. Taylor, R.W. Paine and G.H. Corbett, who formed different opinions on the subject. A more recent view was that short-term yield reductions are probable and that coconut palms adequately compensate in the long term (Cock *et al.*, 1985). It was shown conclusively in the Philippines that a severe attack on young dwarf palms resulted in total loss of production, but Waterhouse and Norris (1987) considered that, in general, the moth had little or no effect on coconut production.

Populations of *T. rufivena* are normally regulated by an intricate complex of natural enemies. Some of these have been introduced from one area to another in biological control efforts against the spike moth – for example, the introduction of *Apanteles tirathabae* (Braconidae) from Java into Fiji in the 1930s and of *Argyrophylax basifulva*

(Tachinidae) from Fiji to the Philippines in the 1980s (Gallego and Abad, 1985). The braconid *Apanteles tirathabae* parasitizes young *Tirathaba* larvae, emerging from the host to spin a solitary white cocoon. This braconid may in turn be parasitized by any of four hyperparasitoids: *Aphanogmus manilae* (Ceraphronidae), *Irichohalticella tirithabae* (Chalcidae), *Perilampus* sp. (Perilampidae) and *Eurytoma* sp. (Eurytomidae). *Telenomus tirathabae* (Scelionidae) is an egg parasitoid. *Venturia palmaris* (Ichneumonidae) is a solitary parasitoid that attacks the young larvae, its progeny emerging from the host prepupa. *Argyrophylax basifulva* (Tachinidae) parasitizes *T. rufivena* by laying microtype eggs on coconut palm inflorescences. Microtype eggs are minute eggs produced by some parasitic insects. They are consumed by larvae feeding on plant tissue and hatch internally in the host. Other recorded parasitoids include *Erycia basifulva* (Tachinidae) and the pupal parasitoids *Anacryptus impulsator* (Chalcidae)*, Melanichneumon muciallae* (Ichneumonidae) and *Trichospilus pupivora* (Eulophidae). Insect pathogens, such as *Beauveria bassiana* and *Metarhizium anisopliae* (*Deuteromycotina*), have been tested against *T. rufivena*. These are not commonly found on pyralids in nature but are likely to cause some mortality in laboratory tests. Allied to low levels of natural infection are the difficulties of application in palms. These fungi may not be the most profitable line to investigate for control purposes.

Tirathaba mundella, *Tirathaba fructivora* and *Tirathaba leucotephras* are species similar to *T. rufivena*, which attack various palm species in South-East Asia (Lepesme, 1947).

The caterpillars of *Hyalospila* (syn. *Atheloca*) *ptychis*, known from Brazil and Cuba, develop on recently opened inflorescences of coconut palms and the cocosoid palms, *Attalea* spp. The adult moth has brown forewings, with purplish, black and white markings, and a wing-span of 18 mm. The hind-wing is transparent, with a brown border. The caterpillars, about 15–16 mm long when fully developed, are white with a brown head. They bore into the female flowers to feed on mesocarp tissue. Their damage causes flowers to abort or, if not, develop into deformed fruits. The larvae do not develop in pollinated hardened-off female flowers or developing fruits (Bondar, 1940; Ferreira *et al.*, 1994).

Cadra (syn. *Ephestia*) spp. are pests of palm fruits and are discussed in that section, but *Cadra cautella* may also attack male and female flowers of coconut palm (Bondar, 1940).

Arenipses sabella, the greater date moth, is generally distributed throughout the date-growing regions of North Africa, the Middle East and northern India (Carpenter and Elmer, 1978; Al-Azawi, 1986; Wiltshire, 1988; Talhouk, 1991).

The adult is a pale brown moth with a silvery abdomen, with a wing-span in the female of 40–42 mm. The larva is reddish brown with a darker head. The second abdominal segment has lateral yellow spots and the remaining segments four dark brown spots dorsally, each with a long seta. Fully developed, the larvae are 23 mm long (Hussain, 1974).

The imagos fly in spring, females ovipositing on or near unopened spathes. Upon hatching, the larvae may bore into spathes or petioles of young fronds. If spathes are open, they bore into the inflorescence, but remain for periods externally in a silken tube. A second generation begins in July–September. The second-generation larva overwinters in a white cocoon located in the crown of the palm. In spring, the larva pupates for about 2 weeks, after which the imagos emerge for the spring flight (Hussain, 1974).

Several species of Braconidae are parasitoids of *A. sabella*. In Iraq, pseudoscorpions are plentiful among the fibres at the bases of petioles and are thought to be important in the control of this caterpillar (Hussain, 1974).

Chemical control methods that are effective against *Batrachedra amydraula* are probably generally effective against *A. sabella*.

Spectrobates ceratoniae (syn. *Ectomyelois ceratoniae*), the carob moth, has become an important pest of dates in Israel during the recent decade (Daniel Blumberg and Moshe Kehat, personal communication) and also in California. During dry summers, the moths oviposit and larvae develop in fruits of the previous season that have lodged in leaf axils. Moths later emerge and attack developing fruits. Application of malathion dust is effective in controlling the pest in California (Warner *et al.*, 1990).

Coleoptera

Curculionidae

The larvae of *Diocalandra taitense*, the Tahiti coconut weevil, and *Diocalandra frumenti* (syn. *Diocalandra stigmaticollis*), the four-spotted coconut weevil, bore in roots, petioles, inflorescences and fruits of palms. *Diocalandra taitense* is reported on coconut palms, while *D. frumenti* attacks palms of the genera *Areca, Borassus, Elaeis* and *Nypa* and also *Sorghum* (Gramineae) (Lever, 1979).

Diocalandra taitense is native to the South Pacific and was introduced into Madagascar and the Hawaiian Islands. *Diocalandra frumenti* has a more extensive geographical range, from mainland Africa, Madagascar, southern India, through South-East Asia and the Pacific (Hill, 1987).

The imagos of both species are shiny black, about 6–8 mm in length, with four large reddish spots on the elytra (Hill, 1987). The life cycles are similar. Eggs are laid in crevices in stems of palms and hatch in 4–9 days. The larval stage lasts 8–10 weeks. The pupal stage takes 10–12 days. A cocoon is not formed. Damage to fruits can result in premature shedding, but the impact of these insects on production has not been assessed, and some entomologists consider them secondary invaders.

Himatidium neivae (Chrysomelidae) is a small beetle that causes superficial damage to developing coconuts in Brazil. The adults are about 6 mm long and the mature larvae slightly longer. They both feed on the surfaces of the fruits, especially in the protected sites where two coconuts touch. Although the damage is quite superficial, it can affect the market value of green coconuts sold for coconut water (Ferreira *et al.*, 1994).

Natural enemies include a braconid parasitoid, a predacious histerid beetle and a predacious rhagionid fly (Lever, 1979).

Hemiptera

Coccoidea

In general, Coccoidea are eurymerous and thus may infest any green part of a palm, including the fruits. *Parlatoria blanchardi* (q.v.) is a noteworthy example of an armoured scale insect (Diaspididae) that primarily infests the fronds but may become a serious pest of the fruit. Larger palm fruits that develop over many months, such as those of coconut, *Borassus, Lodoicea*, etc., would appear to be ideal for scale insect development, but also a good hunting-ground for predators and parasitoids of scale insects.

Many mealybug species have been reported on palm fruits, but they are rarely recorded as being of significance. *Dysmicoccus cocotis*, *Pseudococcus cryptus* and *Planococcus lilacinus* can be found in large numbers on coconut palm peduncles, causing drying of the inflorescence and button shedding (Fernando and Kanagaratnam, 1987). *Pseudococcus longispinus*, *P. cryptus* and *Rastrococcus iceryoides* have all been recorded from fruits of date palm.

Mealybugs have been the target of a number of successful biocontrol programmes, generally employing solitary parasitoids from the Encyrtidae, Aphelinidae and Platygasteridae (Moore, 1988). Coccinellid predators are also very important in regulating mealybug numbers. Sap-feeders, such as mealybugs, are often symptomatic of the more general ill-health of the plant or of relatively temporary disturbances. Drought, for example, may result in an increase in soluble nitrogen levels in a plant, increasing the reproductive success of an insect. The insect attack, in turn, weakens the plant and delays its return to health.

Hymenoptera

Formicidae

Interrelations are demonstrated by reports of largely indirect ant damage in Guyana, where coconut palms grew poorly. The ants (*Azteca* sp.) maintained colonies of *Nipaecoccus nipae*, protecting them against parasitoids and predators, and also interfered with pollinating insects. Ant control resulted in the practical elimination of the mealybug, with a subsequent improvement in plant health (Rai, 1977).

Herbivores of Palm Fruits

Dave Moore and Forrest W. Howard

The development of the fruit is a rapid process during the initial phase, at which point insect attack may be considerable. This is followed by a maturation phase, with increasing size and physical strength of the fruit, enabling it to better tolerate damage. The final mature stage is relatively rarely attacked by insects. During the final phase, plant defences are aimed at larger herbivores, as are features that attract herbivores that spread the seeds. Most examples of the insects of the developing fruit come from studies of plantation palms, but there is information on seed predators of wild palms.

Acari (see also Acari, Chapter 3)

Eriophyidae

Aceria guerreronis (syn. *Eriophyes guerreronis*), the coconut mite, attacks the developing fruits of coconut palm, causing distortion of the fruit. It is one of the most notorious pests of coconut (Colour Plate 13f, Figs 4.5 and 4.6; Moore and Howard, 1996).

During two decades of having been first described from specimens collected in the state of Guerrero, Mexico (Keifer, 1965), it was found to occur in many parts of tropical America and in West Africa (Doreste, 1968; Mariau and Julia, 1970; Zuluaga Cardona and Sánchez Potes, 1971; Arruda, 1974; Mariau, 1977; Griffith, 1984). The pattern in which it was reported in new countries did not suggest an even spread from some epicentre. In fact, it was found in Rio de Janeiro, Brazil, in 1965 (Ferreira *et al.*, 1994), the same year that it was described from specimens from Mexico, and on the east coast of Mexico a decade after having been reported in West Africa (Olvera-Fonseca, 1986). Whether the mite was spread from West Africa to the Americas or vica versa remains an intriguing question.

Because the mites reside beneath the perianth and, in any case, are invisible to the naked eye, their presence on a palm is usually not detected until their damage is visible. Even then, the damage may go unreported for a long time. As a result, the circumstances of their introduction and establishment in many countries have been especially enigmatic. It has seemed to some

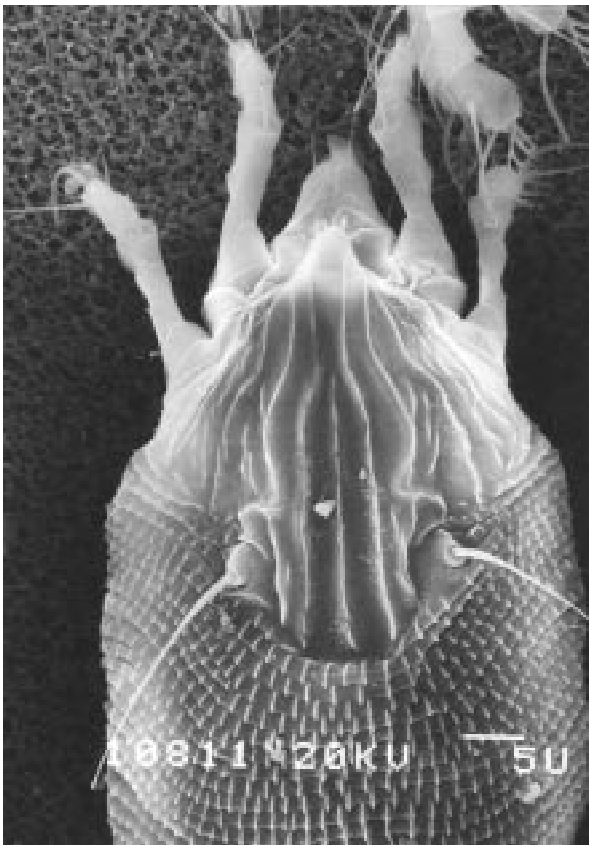


Fig. 4.5. *Aceria guerreronis* (Acari: Eriophyidae), cephalothorax. SEM view by Gregory Erdos.

Fig. 4.6. Coconuts damaged by the coconut mite, *Aceria guerreronis* (Acari: Eriophyidae), Dominican Republic.

observers that only since the 1960s has the mite been introduced from one country to another in the Americas and West Africa. According to another view, the mite had long infested coconut palms at low levels in many countries, but only recently have populations exploded. Indeed, some farmers and other local residents of some countries claim to have been aware of such damage for many decades prior to its scientific discovery.

Local residents tended to attribute the appearance of this pest to events. For example, in St Lucia, the use of the fungicide benomyl on bananas was proposed as a factor: since it is both a fungicide and an acaricide, it may have killed fungi or predacious mites that normally controlled *A. guerreronis.* Both in St Lucia in the early 1980s and in Guerrero in the early 1960s (Ortega *et al.*, 1965), outbreaks of *A. guerreronis* followed hurricanes, and it was suggested that they were responsible, either by blowing *A. guerreronis* from somewhere or by causing stress in the palms that increased their susceptibility to mite damage. However, vast portions of the range of *A. guerreronis* are never subjected to severe tropical storms (e.g. Brazil, West Africa).

In recent years, *A. guerreronis* has been spread further, having been found in Tanzania (David Romney, personal communication), Kerala State, India (Sathiamma *et al.*, 1998) and most recently (1999), in Sri Lanka (Priyanthie Fernando, personal communication). The mite is a particularly serious threat in southern India and Sri Lanka, since husk fibre is one of the important coconut products of that region.

The largest stage of *A. guerreronis*, the adult female, is 205–255 μm in length and 36–52 μm in width, enabling them to penetrate and live in very small spaces. They colonize young fruits, first penetrating between the tepals and feeding on the inner surfaces of these. During the first month of growth of the fruit, the tepals are extremely tight, but, as the fruit grows, sufficient spaces develop to allow the mites access to the protected meristematic surfaces of the fruit (Howard and Abreu-Rodriquez, 1991). Reproductive activity takes place under the perianth, where spermatophores have been observed (Moore and Howard, 1996). Rapid multiplication, with development cycles of around 10 days, results in colonies of up to thousands of mites (Mariau, 1977). Their feeding damages the soft, white tissue beneath the perianth. As this damaged tissue expands from beneath the perianth and is exposed to the air, it turns brown and becomes suberized.

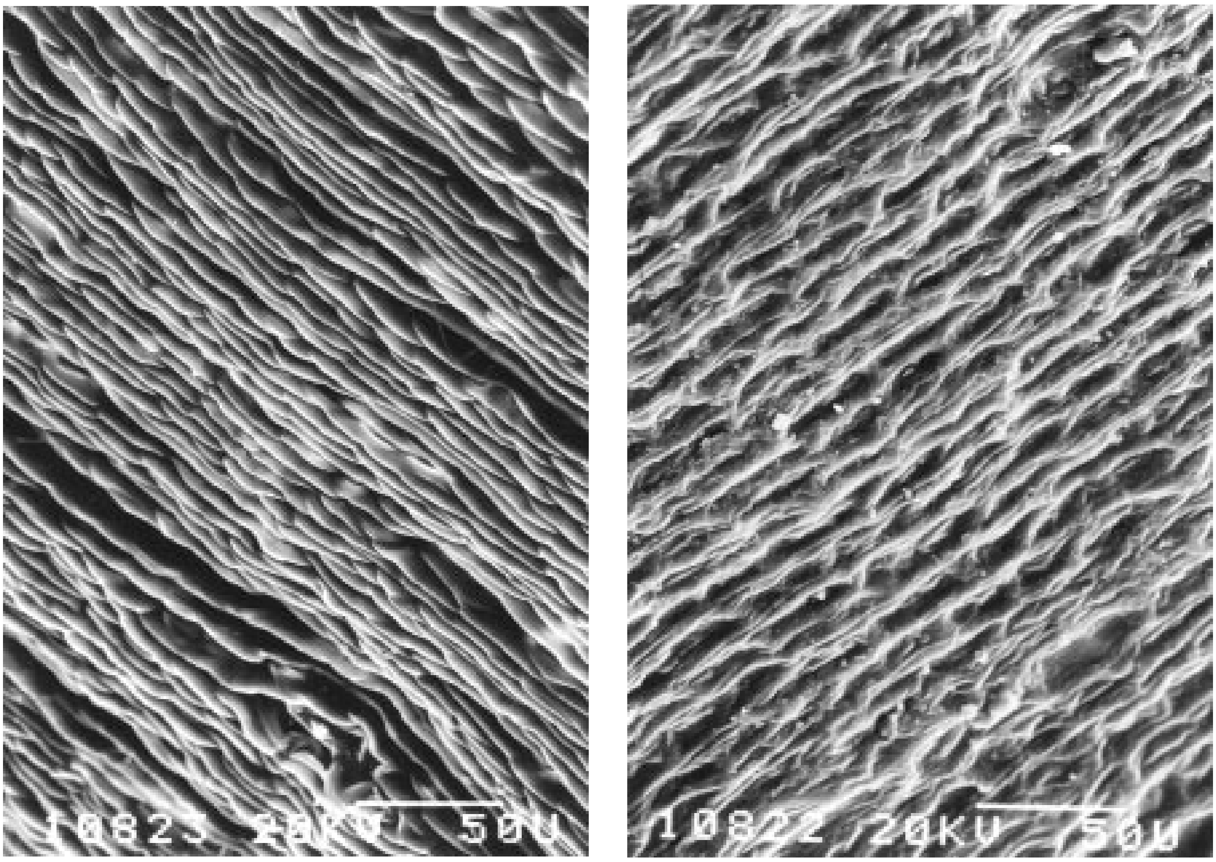
The damage by this mite is not a true gall, but seems to be a non-specific response of plant cells to superficial injury (Fig. 4.7). Simple mechanical damage and even the effects of cold temperatures in Florida can result in necrotic areas on coconuts, which, at least superficially, resemble damage by *A. guerreronis.* Also, unlike true galls, the modified plant tissues do not supply the gall-maker with food and shelter. Their shelter is the perianth and their food the juices of the fresh meristematic tissue. They have no contact with the suberized tissue that results from their feeding.

The damage to coconuts in tall palms is easily recognized from the ground. On young fruits, early damage is visible as a triangular white patch, which extends from beneath the perianth and which soon turns brown. As the fruit grows, this expands as a brown, corklike area with deep fissures and sometimes gummy exudates. The damaged area may cover half or more of the coconut's surface (Fig. 4.6). Coconuts that are highly infested may become greatly distorted as they grow. The damage was formerly thought to cause much premature shedding of coconuts, but this is not the case (Mariau, 1986).

In countries where *A. guerreronis* is present, the percentage of palms with this mite's damage usually varies greatly at different sites. In dense plantings, 90–100% of the palms often have this damage (Zuluaga Cardona and Sánchez Potes, 1971; Estrada Ortiz and Gonzalez Avila, 1975; Howard *et al.*, 1990; Laura Sampedro, personal communication).

Reduction in copra yield was estimated at about 30% annually in Guerrero, Mexico (Hernández Roque, 1977), and up to 50% in Côte d'Ivoire (Mariau, 1986). In a more recent survey in Jamaica, a 70% reduction of copra was measured in individual infested coconuts, but overall the loss varied between 1 and 9%, as most coconuts were only lightly damaged (McDonald, 1996). Losses may be compounded because the compacted fibres of the mesocarp make dehusking more difficult. In areas such as Puerto Rico, where coconut water is a principal product, mite-damaged coconuts are commonly avoided by customers.

In addition to damaging fruits, *A.*



a b

Fig. 4.7. Surfaces of coconut. (a) Surface never exposed to *Aceria guerreronis*, showing wax layer. (b) Surface fed on by *Aceria guerreronis*, with damaged wax layer. SEM views by Gregory Erdos.

guerreronis is reported as a pest of coconut seedlings in Brazil (Ferreira *et al.*, 1994). This has not been observed in other countries.

Other than coconut palm, the only additional reported host of *A. guerreronis* is *Lytocaryum weddellianum* (Flechtmann, 1989). The mite was collected from this species grown as an ornamental palm in an urban area (Carlos Flechtmann, personal communication). In the wild, *L. weddellianum* occurs in shady forests at 800–1800 m in south-eastern Brazil, which is not a coconut palm habitat. The palm is popular as an urn palm in Europe (Uhl and Dransfield, 1987). It has not been determined whether the mite is common on this host.

The mites are dispersed passively by air currents. The large target that a palm provides helps ensure that some mites arrive on hosts, especially if multiple palms are densely planted. Once on a palm, *A. guerreronis* presumably crawls until it arrives on young fruits. They are negatively geotactic and can move from older to younger inflorescences. Phoresy undoubtedly plays a role and herbivores, pollinating insects and their predators probably carry mites to new inflorescences (Hall and Espinosa, 1981; Moore and Alexander, 1987a). A morphological form of the female, thought to be a deutogine (an overwintering form), may be an adaptation for surviving unfavourable periods (Rosas Acevedo *et al.*, 1995).

Researchers studying *A. guerreronis* who have removed the perianth of large numbers of coconuts have occasionally found additional mite species. Many of these are thought to be detritus feeders or other casual visitors. A few are known or thought to be phytophagous, but these generally cause only light damage. Those that are members of predacious families are assumed to be natural enemies of *A. guerreronis*. Mites that occupy this cryptic habitat are not likely to behave normally under a bright microscope lamp; nevertheless, some mites have been observed to prey on *A. guerreronis* (Table 4.2).

These suspected natural enemies have generally been in small numbers, and there has been no indication that their impact on coconut mite populations is ever significant (Howard *et al.*, 1990). On the other hand, at least in southern Florida, coconut mite damage sometimes wanes in certain areas, due to causes that have not yet been determined. Predacious mites could possibly be a factor.

Two fungi specific to eriophyid mites, *Hirsutella thompsonii* (Hall *et al.*, 1980; Hall and Espinosa, 1981) and *Hirsutella nodulosa* (Cabrera and Dominguez, 1987), have been isolated from *A. guerreronis*. *Hirsutella thompsonii* caused up to 100% mortality to *A. guerreronis* when colonies were directly exposed to it at 100% relative humidity (Hall *et al.*, 1980). A commercial preparation of *H. thompsonii* applied in the field in Guerrero, Mexico, resulted in 25–75% mortality of *A. guerreronis* (Espinosa and Carrillo, 1986). Sampedro and Rosas (1989) tested the pathogenicity to *A. guerreronis* of seven strains of *H. thompsonii* in the laboratory. Although five of these strains were isolated from eriophyid mites other than *A. guerreronis*, all were pathogenic to the latter. However, the two strains isolated from *A. guerreronis* in Veracruz and Guerrero, respectively, caused the highest mortality of mites (64.9% and 88.4%, respectively). These suspensions were effective when sprayed on infested coconuts without lifting the perianth, which is how they would have to be applied in a practical situation. Microbial control was not effective in studies in St Lucia (Moore *et al.*, 1989).

Aceria guerreronis causes greater damage in some varieties of coconut palm than in others. In Benin, Mariau and Julia (1970) observed that damage was far less in a tall variety from Cambodia than in adjacent coconut palms of other varieties. Since this variety had a large round fruit, they suggested that the close fit of the perianth against the fruit surface might prevent entry of the mite. Julia (1979a) alluded to similarly round-fruited resistant varieties in Brazil, São Tomé and Côte d'Ivoire. Although, as additional varieties were observed, this factor appeared to be less consistent, some varieties with more elon-

Table 4.2. Mites associated with *Aceria guerreronis* beneath the perianth of coconuts.

Species	Family	Locality	Evidence of predation	Reference
Bdella indicata	Bdellidae	Côte d'Ivoire	Observed	Julia, 1979a
Bdella distincta	Bdellidae	Puerto Rico	Observed	Howard *et al.*, 1990
Tydeus sp.	Tydeidae	Florida	Unknown	Howard *et al.*, 1990
Paralorryia sp.	Tydeidae	Guerrero, Mexico	Unknown	Estébanes, 1978
Amblyseius largoensis	Phytoseiidae	Florida	Observed	Howard *et al.*, 1990
Neoseiulus baraki	Phytoseiidae	Puerto Rico	Unknown	Howard *et al.*, 1990
Neoseiulus mumai	Phytoseiidae	Florida	Observed	Howard *et al.*, 1990
Neoseiulus paspalivorus	Phytoseiidae	Florida, Cuba	Observed	Howard *et al.*, 1990; Rodríguez, 1990
Typhlodromips sabali	Phytoseiidae	Guerrero, Mexico	Unknown	Estébanes, 1978
Two unidentified species	Phytoseiidae	Côte d'Ivoire	Observed	Julia, 1979a
Lupotarsonemus sp.	Tarsonemidae	Côte d'Ivoire	Observed	Hall *et al.*, 1980
Rhynchotarsonemus sp.	Tarsonemidae	Florida	Unknown	Howard *et al.*, 1990
Steneotarsonemus furcata	Tarsonemidae	Puerto Rico, Colombia	Unknown	Zuluaga Cardona and Sánchez Potes, 1971; Howard *et al.*, 1990
Unidentified species	Tarsonemidae	Côte d'Ivoire	Observed	Julia, 1979a
Tyrophagus putrescentiae	Acaridae	Florida	Unknown	Howard *et al.*, 1990
Lasioseius phytoseiodes	Ascidae	Colombia	Unknown	Zuluaga Cardona and Sánchez Potes, 1971
Lasioseius sp.	Ascidae	Puerto Rico	Unknown	Howard *et al.*, 1990
Proctolaelaps bickleyi	Ascidae	Colombia	Unknown	Zuluaga Cardona and Sánchez Potes, 1971

gate and highly angular coconuts do indeed seem to be relatively susceptible. However, some varieties with more rounded coconuts are also susceptible. In extensive observations in Côte d'Ivoire, damage by *A. guerreronis* was greater in 'West Africa Tall', 'Malayan Yellow Dwarf', 'Malayan Green Dwarf' and 'Mozambique Tall' than in the 'Port Bouet 121' hybrid, 'Malayan Tall', 'Tahiti Tall' and 'Cameroon Red Dwarf', and there was no obvious resistance factor consistently associated with the varieties with less damage. Curiously, the relatively undamaged 'Port Bouet 121' hybrid is a cross between two varieties that sustained greater damage, namely 'Malayan Yellow Dwarf' and 'West Africa Tall' (Julia, 1979a; Mariau, 1986; de Taffin *et al.*, 1991). In Cuba, 'Criollo' (probably a synonym. of 'Jamaica Tall') was said to have more damage due to *A. guerreronis* than 'Indio Verde' (Suárez, 1991). In Costa Rica, 'Atlantic Tall' (syn. 'Jamaica Tall') was more often infested than was 'Malayan Yellow Dwarf' (Schliesske, 1990). In St Lucia, tall types with green and rounded coconuts tended to have less damage due to *A. guerreronis* (Moore *et al.*, 1989).

Moore (1987) explained how the arrangement of tepals on coconuts partly determines where *A. guerreronis* can penetrate and feed. For example, damage is apt to be concentrated where minute spaces exist because a tepal overlaps an adjacent tepal. Further work of this kind could reveal resistance mechanisms in particular palms or varieties.

Under some conditions, damage by *A. guerreronis* is greater during dry periods, possibly because the growth of the fruit is slower and thus young developing tissue is subjected to mite damage over a longer period of time (Mariau, 1986).

Chemicals have been tested for control of *A. guerreronis* (Mariau and Tchibozo, 1973; Hernández Roque, 1977; Griffith, 1984; Moore and Alexander, 1987b; Moore *et al.*, 1989). However, chemical treatments generally reduce damage only if applied repeatedly and would have to be continued indefinitely. Chemical control has not been viewed as a good long-term control method for *A. guerreronis*, because of the potential problems of residues in coconuts, hazards to workers and the environment and the potential development of resistant strains of the mite.

The coconut is most susceptible to invasion by *A. guerreronis* during the first few months of its development. Thus, research should be focused on host-plant differences and cultural techniques that might protect the coconut during this critical period (Moore and Alexander, 1987a).

Colomerus novahebridensis is an eriophyid mite that appears to occupy an ecological niche similar to that of *A. guerreronis*, attacking the meristematic tissues of the coconut beneath the perianth (Kang, 1981; Moore and Howard, 1996). Since *C. novahebridensis* is known only from South-East Asia and the Pacific, the species do not overlap geographically (Hall *et al.*, 1980). The damage by both species is almost identical, but *C. novahebridensis* is not significant as a pest. In most areas where it occurs, it is found on few palms and does only slight damage to the coconuts. West African cultivars growing in the Philippines and Malaysia sometimes show significant levels of damage.

Amrineus cocofolius was described from specimens from coconut palms in Brazil in 1994 (Flechtmann, 1994). By early 2000, it was reported as causing damage to coconut fruits that affected their fresh market value (Joana Maria Santos Ferreira, personal communication).

Tenuipalpidae

The family Tenuipalpidae, the false spider mites, consist of red or green mites of flattened form that attack plants.

Dolichotetranychus sp., reported from Sri Lanka, causes similar damage to that of *A. guerreronis* and *C. novahebridensis.* Different coconut cultivars exhibit different levels of response, with West African forms being the most susceptible (Fernando and Kanagaratnam, 1987). A species of *Dolichotetranychus* is also reported to attack fruits of *A. catechu* in Kerala, India (Davasahayam and Nair, 1982).

Brevipalpus phoenicis, the scarlet mite of tea and the red and black flat mite of citrus, sometimes attacks coconut fruits in India, causing a corky ringlike band around the fruits. Attack on young fruits can cause premature shedding (Jagadish *et al.*, 1983).

Tetranychidae

The family Tetranychidae, known as spider mites because of their propensity to spread webbing on their host plants, consists of green, yellow, orange or red mites, which live primarily on vascular plants.

Oligonychus afrasiaticus, the Old World date mite, attacks date fruits, causing them to turn from green to silvery in colour. The fruits begin to crack, shrivel and turn reddish in colour. The mite may also attack date palm foliage. The species occurs wherever date palms are grown in Africa and the Middle East. In Libya, this mite was said to be more damaging to palms in inland oases than on the coast. In Iran, the mite caused 40% loss of the date crop in some districts. There are as many as ten generations per year and mites are continuously present on date palms, but the population peaks during the hotter months. Neglected palms are said to be more susceptible than palms under good horticultural care (Hussain, 1974; Carpenter and Elmer, 1978).

Oligonychus pratensis is similar to *O. afrasiaticus*. It shares some of the same range with the latter species in North Africa and the Middle East, but is also known in California. There it is known as the date mite. This mite is also a pest of Bermuda grass, *Cynodon dactylon*, and other turf grasses, in which context it is known as the Banks grass mite. In date groves, the mite overwinters on grass hosts (Carpenter and Elmer, 1978).

Additional tetranychid mites of importance on palms include *Oligonychus tylus*, which has become an important pest of dates in Israel during the past decade (Daniel Blumberg and Moshe Kehat, personal communication), and *Oligonychus* *indicus*, which attacks fruits of *A. catechu* in Kerala, India (Davasahayam and Nair, 1982).

Tarsonemidae

The family Tarsonemidae contains small to minute mites of diverse feeding habits. The family includes fungivores, parasitic mites, predators of arthropod eggs and phytophagous mites.

Mites in the family Tarsonemidae are small to minute, with diverse feeding habits. The family includes fungivores, parasites, predators and phytophagous mites.

A species of *Tarsonemus* has been found in small colonies (maximum of 100 mites) occupying the meristematic zone beneath the perianth of young coconuts in Florida and Puerto Rico. The damage associated with this mite is similar to but much less extensive than that of *E. guerreronis*. In observations in Florida, about 1% of the young coconuts with damage that might be identified as that of *A. guerreronis* was actually due to *Tarsonemus* sp. (Howard *et al.*, 1990).

Hemiptera

Coreidae

The family Coreidae, with about 2000 species (Dolling, 1991), comprises often robust bugs. A good field character is that the veins in the membranous distal portion of the hemelytron are more numerous than in closely related bug families, including Lygaeidae and Pyrrhocoridae. Most species feed on fruits, typically causing necrotic areas, probably due to toxic substances in the saliva. A number of species of the subfamily Dasyninae in various parts of the world damage coconuts, resulting in premature fruit shedding and scarring of older fruits.

Amblypelta cocophaga, known in the Solomon Islands, attacks a wide range of plants, but coconut palm is the main palm host (Lever, 1979). The adult females are largely rusty-coloured dorsally, yellowish ventrally and about 15–16 mm in length. The principal oviposition site is on the underside of the fronds in the basal recesses of the leaflets. The first-instar larvae search for the inflorescences, only a small percentage arriving on the flowers. Development from egg to adult takes more than a month. Damage to young coconuts is typical of the family Coreidae.

In a study in coconut plantations, the predatory ants, *Oecophylla smaragdina* (Fig. 2.8) and *Anoplolepis longipes*, were important in regulating populations of the bugs when not themselves attacked by other ants, especially *Pheidole megacephala* and *Philidris myrmecodiae* (Way and Khoo, 1991).

Mixed cacao and coconut palm plantations provided a better ecosystem for *O. smaragdina* and for another ant, *Dolichoderus thoracicus*, which benefited from a greater abundance of honeydew-secreting Homoptera in this habitat. Of the two species, *O. smaragdina* dispersed more actively and was the more effective in controlling *A. cocophaga* (Way and Khoo, 1991).

A eulophid, *Anastatus axiagasti*, is a locally common egg parasitoid and several hymenopterous and tachinid parasitoids have been introduced into the Solomon Islands, but their effect is thought to be unimportant. Since a few punctures from a single insect can cause severe enough damage to cause premature fruit shedding, this insect causes significant loss at such low population densities that natural agents seldom suppress it sufficiently (Lever, 1979).

Pseudotheraptus wayi is found on a number of hosts, including palms, in coastal areas of eastern Africa and Zanzibar. A single puncture of a young coconut fruit can cause shedding even up to the third month of development. The adult insect is reddish brown on its dorsal aspect and paler, with pink spots, ventrally. The female is 13–15.5 mm long, the male slightly smaller. Development from egg to imago takes about a month and imagos live more than 2 months. The female may lay over 100 eggs and there may be up to nine generations in a year. The average density is about one bug per palm (Lever, 1979).

An ant, *Oecophylla longinoda*, controls the coreid but can itself be effectively replaced by antagonistic ants, which do not control the pest. These include *Pheidole* sp., *Anoplolepis longipes* and *Crematogaster* sp. Egg parasitoids include *Ooencyrtus albicrus*, *Ooencyrtus utetheisae* (Encyrtidae), *Anastatus* sp. (Eupelmidae) and *Coriophagus zanzibarae* (syn. *Halictophagus zanzibarae*) (Strepsiptera). These alone cannot reduce the very low populations of *P. wayi* below the economic threshold. Tachinid flies are major parasitoids of coreids, but none are known to be effective against *P. wayi*.

Lohr (1992) reported that in Tanzania a pugnacious ant, *Anoplolepis custodiens*, played a significant role in control of *P. wayi*, but protected the palm aphid, *Cerataphis brasiliensis* (as *Cerataphis variabilis*). In this case, *C. brasiliensis* did no economic damage in coconut palm. Rapp and Salum (1995) found that reduced weed control resulted in reduced damage by *P. wayi*, because under these conditions an ant, *P. megacephala*, which normally forages on the ground, was more likely to occupy palms and prey on the bug.

Pseudotheraptus devastans occupies a niche in West Africa comparable to that of *P. wayi* in East Africa and *A. cocophaga* in Melanesia. The imagos are 15 mm in length and of a red-brown colour, with the abdomen pale green ventrally. Both adult and young feed on coconut flowers and fruits of 9 months of development or less, causing premature shedding. Older fruits show scarring and gum exudates. The fruits that finally mature are usually reduced in size, scarred and distorted. Serious attacks are rare, but when they do occur can cause 50–80% yield loss. Development from egg to adult takes over a month.

The critical threshold for chemical treatment is when: (i) there are an estimated 30 individuals (all stages) per hectare; and (ii) less than 60% of the palms are colonized by the very effective predacious ant, *O. longinoda*. Control by this ant can be disrupted by more competitive ant species, such as *Camponotus* sp.

The three major species above have obvious similarities of ecology and control by ant species. Their geographical separation is interesting, as *A. cocophaga* presumably evolved over a long period of time with coconut palm, whereas the African species are probably recent associates.

Paradasynus rostratus, recognized as a pest of coconuts in southern India in 1961, has come to be known as the nut crinkler, in reference to the permanent furrows and crinkles with gummosis that form from lesions where they have fed just beneath the perianth. In laboratory observations, the eggs were laid on or near to the inflorescence and hatched in 8–10 days. The nymphs passed through five instars during 30 days, and adults lived for 50 days (Kurian *et al.*, 1976, 1979). The damage reduces the weight and volume of coconuts and the weight of copra and oil (Nair *et al.*, 1997). The losses vary by site, and have been extensive in some plantations (Visalakshi *et al.*, 1992).

Since natural control is sometimes insufficient for controlling coreid pests of coconut, control with insecticides has been investigated (e.g. Kurian *et al.*, 1976). But, in addition to the usual problems of worker safety, possible residues in coconuts and disruption of natural control of pests, insecticides applied to inflorescences are likely to interfere with pollination. Biorational products, such as neem products, may offer a solution. In laboratory tests, neem products were effective against the larvae of *Amblypelta lutescens lutescens*, a coreid bug not associated with palms (Huwer, 1997).

Additional species of coreids in the genera *Amblypelta, Pendulinus, Paradasymus, Galaesus, Theraptus* and *Asynus* have been reported from coconuts in the tropics of the eastern hemisphere, especially Asia and the Pacific. They are probably not significant pests and their taxonomy and bionomics have not been studied (Lepesme, 1947; Lever, 1979).

Leptoglossus lonchoides, which was reported damaging fruits of *Bactris gasipaes* in Central Amazonia, is one of the few coreid bugs reported on a palm other than coconut (Couturier *et al.*, 1991).

Pentatomidae

Pentatomidae associated with palms complete their cycle on the petioles or on the spathes of the inflorescence (see Pentatomidae, Chapter 3).

Axiagastus cambelli attacks male and female flowers and immature fruits of coconut palm and *A. catechu*. It is known in the Solomon Islands, Vanuatu and New Guinea, including the Bismarck Archipelago.

This stink bug is about 15 mm long and blackish, with yellow legs and markings. The female oviposits in clusters of about 15 eggs at the base of the petiole or inflorescence spathe. The larvae develop in about a month and a half, passing through white, followed by yellow stages, and are finally orange with black markings.

Unlike coreid pests, *A. cambelli* is of significance only when it occurs in high numbers. The damage can result in fruit fall, probably due to loss of sap rather than the injection of toxin. Two egg parasitoids are known (Lepesme, 1947; Lever, 1979).

Lepidoptera

Batrachedridae

Batrachedra amydraula, the lesser date moth, is a pest of date fruits from India to the Middle East. The female, a whitish moth finely speckled with brownish scales and a wing-span of about 10–13 mm, lays its tiny eggs on the fruit stalk and the emerging moths enter the young fruit from the calyx end (Talhouk, 1991). The fruit begins to decay and the caterpillars feed on the decaying tissue and complete their development. Second-generation moths lay on the developing fruits, but by this time the level of parasitism is so high that the damage is limited. During its diapause, many generalist predators attack it. Larvae frequently damage three or four fruits during their development. Its pest status is disputed: in some areas, it is rarely a pest and may be more often beneficial in thinning the fruits (Talhouk, 1991), while other reports cite almost complete fruit loss due to attack (Kranz *et al.*, 1977; Carpenter and Elmer, 1978).

Pyralidae

Plodia interpunctella, a cosmopolitan insect known as the Indian meal moth, is sometimes a pest of dates, either under plantation conditions or during the postharvest phase.

The adult moth is 1 cm long, with grey and brown wings. When attacking date palms, the female oviposits on the fruits. The eggs hatch in 4–20 days. The larvae develop to pupae in 3–4 weeks, reaching a length of 13 mm. In the field, the pupae are located on the date bunches or among fibres of the stem. In packing facilities, they may pupate in the boxes (Hussain, 1974).

The larvae prefer the drier, relatively mature dates in the bunches, entering fruits either through existing breaks or by directly boring into them and sometimes into the seeds, lining their galleries with webbing with incorporated frass. It is considered only a pest of the growing crop in the USA. In Africa and the Middle East, it is largely a pest of stored dates (Carpenter and Elmer, 1978).

Several species of the genus *Cadra* attack dates. Most are postharvest pests, but some species attack growing dates. One of the better-known species, the raisin moth, *Cadra figulilella*, is a pest of the growing fruit only in California. In North Africa and the Middle East, it attacks the stored fruit. The almond or fig moth, *Cadra cautella*, is largely a pest of harvested dates. Several additional species are pests of postharvest dates in the Middle East and North Africa (Carpenter and Elmer, 1978) and of copra.

Noctuidae: Catocalinae

Larvae of *Litoprosopus futilis*, the palmetto caterpillar, feed on the inflorescences of *Sabal palmetto* and sometimes on those of *Serenoa repens* in the south-eastern USA. While these palms are generally free of these insects, dense populations of the caterpillars are sometimes experienced, in which case the bloom of palmetto is thought to be seriously reduced. This has economic implications for producers of 'palmetto honey'. After completing their larval development, the larvae drop to the ground on silk threads and pupate in the soil (Dekle, 1968; Covell, 1984).

Coleoptera: Nitidulididae

Nitidulidae are usually small, dark beetles. Species of the subfamily Carpophilinae typically feed in the pulp of dried fruits. Several species of nitidulid beetles attack ripened dates. They are usually minor pests. In California, these include *Carpophilus dimidiatus*, *Carpophilus hemipterus, Urophorus humerali* and *Haptoncus luteolus*. *Carpophilus hemipterus* and other species attack dates in North Africa and the Middle East (Carpenter and Elmer, 1978).

Seed Predation

Dave Moore

By convention, herbivory of the seeds by insects is termed predation because the whole organism is usually killed. Most seed predation is by vertebrate herbivores. The coloration of many palm fruits appears to be well suited to bird predation, with distribution of the seed being the benefit to the plant. Most insect species feed on the seed while it is still in the immature fruit, before the danger of being consumed along with the seed by a larger herbivore (Janzen, 1976; Smythe, 1989). This early attack may also bring problems, as many plant defences, such as palatability-reducing compounds or toxins are concentrated in the young fruit and are reduced as the fruits mature (Stiles, 1989). A few studies on palms do reveal examples of very high levels of insect predation, but it is also likely that herbivory on fruits will lead to seed loss, without direct predation of the seed. It is also true that foliar herbivores can cause such damage as to reduce seed production more than may occur with seed predation.

The seed predators are one of the most interesting groups, as they attack the ultimate purpose of the existence of the plant. Resource allocation in relation to reproduction can be measured in many ways, such as the proportion devoted to seed production or the proportion devoted to all the reproductive structures that ultimately produce the seeds. In reality, all resources are allocated to reproduction, as the purpose of roots, trunk and leaves is to enable the plant to reproduce and the success of a plant is reflected in how well it does this. Damage done to any plant tissue will influence this, but the seed predators attack the culmination of effort by the plant. As such, their influence on the success of the population should have a more immediate impact than any other type of herbivore, with the exception of those that kill the plant.

The major insect seed predators that have been studied are beetles, which may eliminate almost the entire seed crop of a species in a certain year and locality. Most work on seed predators has been from the Americas, from Mexico southwards, and usually the insects involved are in the family Bruchidae and, more occasionally, Scolytinae (Curculionidae). Relatively few scolytines are spermatophagous. Usually they consume ectosymbiotic fungi in the galleries they excavate in the wood or phloem or inner bark of their hosts. Bruchids are more widely known from Leguminosae, many of which accumulate large amounts of the unusual amino acid L-canavanine. This is toxic to insects, apparently because it tends to replace arginine in protein synthesis, disrupting the process.

Most of the palm seed eaters are from the more primitive groups of the family Bruchidae, such as the Pachymerinae, a group that does not attack canavanine-producing plants.

Insect seed predators

The common genera of Bruchidae involved in predation of palm seeds are *Caryborus, Pachymerus* and *Caryobruchus*. For example, *Caryobruchus gleditsiae* has been recorded feeding on the fruits and seeds of *Sabal mexicana* and *Sabal uresana*. *Scheelea rostrata* and *Scheelea zonensis* suffer heavy predation by Bruchidae, with *Caryobruchus buscki* probably a major species (Janzen, 1971; Bradford and Smith, 1977). Usually adult Bruchidae do not rely heavily on the seed for nutrition, which is normally supplied from pollen and nectar, but they cause damage when boring through the seed for oviposition or emergence (Johnson and Kestler, 1987). The larvae are responsible for most feeding damage. *Scheelea zonensis* (syn. *Attalea butyracea*) produces one or two large infructescences each year, each carrying up to 1000 fruits, which ripen over a 5–7-month period. Most of the fruits have a single seed in a stony endocarp, surrounded by an oily mesocarp and tough exocarp. The exocarp and mesocarp are removed by vertebrate predators, so that the endocarp is vulnerable to oviposition by *Caryobruchus giganteus*. The first-instar larvae bore through the endocarp and, even if the larvae do not survive, the seed dies. Over 80% of the early-ripening fruit can be destroyed. Late-season fruits are less severely attacked, as there is only one generation of adult beetles each year and their numbers are greatest at the beginning of the season (Wright, 1990). The oviposition behaviour of the beetle may have influenced the flowering and fruit set of the palms. The high oviposition activity during the peak flowering time subsides before the late-flowering palms have produced ripe fruit.

Some fruits of *S. zonensis* contain two or three seeds. Multiseeded fruits may have a survival advantage. If attacked by a single bruchid, one or two seedlings may still emerge, despite destruction of a seed. Harms and Dalling (2000) observed almost 25% seedling emergence from fruits showing signs of attack by bruchids, but from which no bruchids emerged. This may be attributable to premature death of the beetle or a failure of bruchid larvae to penetrate the endocarp. Whether the presence of a bruchid inhibits attack by others is not known. If so, the bruchid that dies prematurely may be protecting the seed from others. No single seed produced both a seedling and a beetle, showing that successful development of the insect kills the seed.

Most bruchids that feed on seeds appear to be highly specific. Janzen (1980) studied 110 species attacking a range of plants (only one of which was a palm) and found that almost 90% had no more than two hosts. Of the hosts, 95% were attacked by three or fewer seed eaters. Leguminosae are the most frequent hosts, with the Palmae providing under 5% of known hosts. Unlike with the Leguminosae, the specificity with palm hosts does not relate to secondary compounds. This may be nutritionally based. Pollen of the host may be a necessity for the adult beetle (Johnson and Kestler, 1987). Of interest was the rarity of parasitoids. In the majority of seed-eater species studied, parasitism was absent, although *Eupelmus cyaniceps* has been recorded from *C. gleditsiae* feeding on the seeds of *Sabal minor*. This could reflect the temporal characteristics of host availability. With long periods without suitable hosts, specific parasitoids are unlikely to occur in large numbers. It may also reflect an absence of host cues, with the initial damage to the fruit being done by rodents. However, perhaps the imagos are attacked by as yet undiscovered parasitoids.

A scolytine, *Coccotrypes carpophagus*, feeds on the seeds of a number of palm species, including *Euterpe globosa*. The female beetle bores through the endocarp after the fleshy exocarp has rotted off or been eaten by a rat (Janzen, 1972). The damage by the female and her progeny usually kills the seed. By the end of the fruiting season, over 99% of the seeds may be killed by the scolytine. Janzen suggested that the herbivore pressure on *E. globosa* in Puerto Rico resulted in the strong fruiting synchrony characteristic of the palm and that it was a dominant factor controlling palm replacement. The synchrony of fruiting could be an adaptive feature of the palm. The absence of seeds over a period of time causes the scolytine population to drop, so that the new season's fruit has a short period when predation is low. In consequence, the palm populations were higher than characteristic of most tropical trees. This synchronization also makes control by specific natural enemies very difficult. Janzen (1972) also hypothesized that fruiting synchrony was a possible strategy because of the island habitat and that it would not occur on the mainland of Central America.

A scolytine, *Xyleborus ferrugineus*, was reported to infest fruits and seeds of *Euterpe edulis* and *Euterpe oleracea* in Brazil, leading to an 80% reduction in seed germination (Zorzenon and Bergmann, 1995).

One of the reports from outside the Americas is of the scolytines of the Seychelles, studied by Beaver (1987), who reported spermatophagous *Coccotrypes* species. All these species are arrhenotokous, showing inbreeding polygyny or sibling mating, usually with the single male of a brood mating with his sisters. An unfertilized female will produce an all-male brood and may mate with one of her offspring to produce a female-biased brood. Five species were recorded to attack palm seeds. *Coccotrypes carpophagus* was a doubtful species reported from palm seeds only. *Coccotrypes cardamomi* and *Coccotrypes dactyliperda* attacked *Nephrosperma vanhoutteanum* seeds on the forest floor after the pericarp had been removed by ants and other insects. Predation of up to 70% of the seeds was recorded. *Coccotrypes declivus* attacked *Verschaffeltia splendida*, and *Coccotrypes laticollis* was occasionally found in *N. vanhoutteana*. Because of the levels of predation, Beaver (1987) suggested that the spermatophagous species could be important in reducing the regeneration of the two palms.

Coccotrypes dactyliperda, the date beetle, is a frequent, cosmopolitan pest of date palm and of other palms. It is probably the best studied scolytine of palms, because of its economic importance. It is a pest of green, unripe dates, sometimes causing a 30–40% yield loss (Blumberg and Kehat, 1982), and also of mature palm seeds. The adult beetle bores a small (1 mm diameter) round hole in the fruit, which soon drops from the palm, even if only the fruit, and not the stone, has been penetrated. The female lays eggs within 24–48 h after penetrating the stone and resultant progeny remain in the stone until they become adult. Mated females produce larger numbers of progeny. About 85% of the progeny of the mated females are females. Unmated females, as with the scolytine mentioned above, produce only males (Blumberg and Kehat, 1982). The imagos may overwinter inside date stones. In Greece, *C. dactyliperda* males were recorded as 1.4 mm long and 0.4 mm wide, compared with female dimensions of 2.2 mm and 0.5 mm. The progeny of fertilized females showed a marked sexual bias, with 72% being female (Vassilaina-Alexopoulou *et al.*, 1986).

Coccotrypes dactyliperda can have a significant effect against seedlings. Seed-beds of *Howea forsteriana* in the Canary Islands have been recorded as severely damaged. Species in 18 genera of palms have been reported as hosts, including African oil palm, *Chamaerops excelsus, Chamaerops humilis*, *Phoenix canariensis* and *Livistona* spp. (Siverio and Montesdeoca, 1990).

Bernabo (1990) surveyed seeds of date palm, *P. canariensis, Trachycarpus excelsa* and *C. humilis* in Genoa, Italy. The scolytine *Dactylotrypes longicollis* (syn. *Dactylotrypes uyttenboogaarti*) was often found in seeds of *C. humilis*, rarely in *P. canariensis* and not at all in the remaining two species. The author noted that *C. dactyliperda*, present in Italy, was not found in the palms examined. Other workers found that *P. canariensis* was a relatively common host compared with *Phoenix pumila*, *T. excelsa*, *Butia* *eriospatha* and *C. humilis*. These slightly different results may have reflected different climatic conditions at the time of study.

The case of *Hypothenemus hampei* (Scolytinae), the coffee-berry borer, illustrates that relationships between seed borers and their natural enemies are only beginning to be elucidated. Despite being well studied for 60 years, a new parasitoid was discovered during studies in 1987/88. In the 1920s and 1930s, researchers studied the parasitoid *Prorops nasuta*, a bethylid, which typically provides maternal care for its offspring. At around the same time, a braconid, *Heterospilus coffeicola*, was described. This lays an egg inside an infested coffee berry and the resultant larva, an aggressive predator, goes on the rampage. Little is known about this rare parasitoid/predator, as it has proved impossible to rear in the laboratory. *Cephalonomia stephanoderis* was found in West Africa in 1961. Another bethylid parasitoid, it appears to be a better competitor than *P. nasuta*. Then a species representing a new genus was discovered in Togo, West Africa. This was *Phymastichus coffea*, a parasitoid that attacked adult *H. hampei* (Borbon-Martínez, 1989; LaSalle, 1990). It was reported to attack the adult female and lay either one or two eggs. A female adult would emerge from the egg laid in the abdomen and a male from the egg laid in the thorax! The story seemed unbelievable. Within months of this discovery in Togo, it was found in Kenya (Murphy and Moore, 1990), where it had obviously been present for many years, probably since well before the studies made in the 1920s. However, parasitoids attacking imagos are unusual and entomologists rarely look for them and, consequently, rarely find them. Later, another species of this genus, *Phymastichus xylebori*, was discovered from another scolytine, namely the macadamia nut borer, *Xyleborus perforans* (J. LaSalle, personal communication).

Although attention is drawn to the extremely high levels of predation, the consequences for the host population dynamics are difficult to predict. The presence of the host proves that sometimes predation at these high levels may not be fatal to the population. Similarly high levels occur with other host insect systems (Janzen, 1969). Seed predation could theoretically regulate palm populations if it reduced seed density below that to which it would be reduced by density-dependent mortality factors (Fenner, 1985). However, the perennial nature of the plant makes this unlikely. The palm may produce very high numbers of seeds or rely upon years unfavourable to the herbivore to achieve a good proportion of seedlings.

Interactions between vertebrate and insect seed eaters

Seed predation has been the subject of many ecological studies, some of which have been multidisciplinary, leading to knowledge of fascinating systems. Lott *et al.* (1995) studied *Normanbya normanbyi*, a single-stemmed large-seeded palm in northern Queensland, Australia. The fruit has a bright, pink, fleshy exocarp and was thought to be dispersed in clusters of various sizes, by cassowaries, *Casuarius casuarius* (Aves: Casuariformes). These large birds feed on fallen fruit in rainforests. The seeds are also attacked by *Coccotrypes* spp. and two species of earwigs. The eggs of the borer were apparently laid inside the seed and the larvae ate the endosperm, while the earwigs attacked the germinating seeds via the radical and ate both embryo and endosperm. Strictly speaking, the earwigs are attacking the seedling rather than the seed. The earwigs were responsible for 85% of seed loss due to insects, which, in turn, were responsible for 24% of seed mortality generally. Insect attack was density-dependent. Dispersal of low-density seed lots away from the parent palm resulted in lower rates of insect predation. Overland water flow turned out to be the most important method of dispersal of viable seeds. Although only 0.6% of seeds survived to seedling stage, the fruit production of *N. normanbyi*, at around 1000 seeds or more per year, was sufficient to maintain populations of the palm.

Both rodents and Bruchidae eat the seeds of *Scheelea* spp. The palms produce a vast number of seeds early in the season, of which around 70% are bored by Bruchidae, with this proportion decreasing over the season (Forget *et al.*, 1994). In contrast, the proportion attacked by rodents early in the season is low but rises to nearly 90% by the season's end. Early in the season, the rodents avoided bruchid-infested seed and could do so because of the surfeit of food. However, later in the season, rodents were less reluctant to consume bruchid-infested seeds. The earlier the bruchid egg was laid, the greater the chance of survival of the progeny to adult.

Caryobruchus chiriquensis, a seed predator of *Phytelephas aequatorialis*, appears to depend heavily for its success on rodent herbivores, which consume the mesocarp (Pedersen, 1995). In trials, intact seeds and those stripped of their mesocarp were exposed to *C. chiriquensis*. All seeds stripped of the mesocarp were infested whereas none of the intact seeds were. The Bruchidae were more efficient at infesting stripped seeds in pasture than in forest.

Generally, the insect seed eater is more influenced by the vertebrate herbivore than vice versa. Sometimes the insect may depend on preliminary attack of the vertebrate herbivore to allow its own entrance. Often the insect is vulnerable to the vertebrate consuming the infested seed.

Seed Dispersal

There is little evidence that insects play a positive role in the dispersal of palm seeds. Zona and Henderson (1989) described zoochory (i.e. animal-mediated seed dispersal) in over 70 genera and 100 species of palms. Insect mediation was claimed for only three palms, namely *Butia leiospatha*, *Syagrus loefgreni* and *Allagoptera arenaria*. Unidentified beetles were implicated in dispersal but they were probably seed consumers, burying the palm fruits up to 10 cm deep after ovipositing on them. Germination was not recorded but was unlikely to be significant. Thus, the main effect of insects on populations of viable seeds of palms is in reducing their numbers. This activity is more intense in the immediate vicinity of individual palms (where there is a greater concentration of seeds) than in seeds that have been dispersed away from the parent palm.

Seeds of palms are dispersed mostly by vertebrate animals, including birds and mammals, which eat the fruits and pass the seeds at some distant site (Forget, 1991; Dransfield and Beentje, 1995). Many palms have spiny trunks and other parts which are viewed as adaptations to discourage climbing mammals (Fig. 1.3; Janzen, 1969; Essig, 1971; Smythe, 1989; Tomlinson, 1990). These would be less effective against birds, which are generally the main dispersal agent of palms (Corner, 1966; Herrera, 1981; Snow, 1981). Abiotic factors play a role in dispersing seeds of some palms, e.g. water in the case of palms that grow in swamps and on shorelines (Kubitzki, 1991) and presumably gravity in palms that grow on steep slopes.

An example of the role of vertebrate animals compared with insects in dispersal of palm seeds is provided by the black palm, *Astrocaryum standleyanum*. The palm may produce three to six pendulous infructescences in a year, with 300–800 brightly coloured fruits on each, producing a strong aroma. Bruchid beetles, *Caryobruchus* sp., are capable of destroying almost all the seeds. But agoutis, *Dasprocta punctata* (Mammalia: Rodentia), prove beneficial to the palm in removing the edible pulp, including the beetle larvae and eggs, before burying the seed (Smythe, 1989).

Effects of Insect Herbivory on Plant Reproduction

Some associations between phytophagous insects and plants could be considered mutualistic, because the insect, in obtaining nutrition, enhances the fitness of the plant (Vail, 1992). For example, reduction in fruit set may result in larger and fitter fruits, and may stimulate the plant to produce greater numbers of fruits than would otherwise have occurred. The sacrifice of individuals of a species, because they are young, weak or old, may be of general benefit to the population as a whole. It has been suggested that early chemical attractants for pollinating insects evolved from herbivore deterrents (Pellmyr *et al.*, 1991). The evolution of insect pollination was of prime importance for the success of many angiosperm species.

Various adaptive features compensate for the damage by herbivores. Perhaps as a response to losses, the flowers are produced in enormous numbers and, especially for the male flowers, the vast majority can be sacrificed. Female flowers are also produced in excess and physiologically induced abortion is common. Pest attack may result in fewer fruits, but these are fitter and the end result can be more favourable to the plant. There is always a problem of how many resources can be allocated to the reproductive process: too many and the adult is weakened and this lowers or entirely removes its reproductive potential for the future, but inadequate allocation deprives the flowers and fruits of the chance of success.

An advantage of flowering at intervals may be to escape the attack of some insects. In different species of palms, flowering varies from monthly to once in a lifetime. Palms that flower annually sometimes miss a year, allowing them to build up reserves and also depriving herbivores of feeding and reproductive possibilities. Periodic flowering at long intervals reduces the time of opportunity for the herbivore to an occasional period, and increases the chance that, on some occasions, herbivore activity will be reduced, due to climatic or other reasons. Regular flowering at short intervals ensures flowering during some seasons when insect activity is reduced, and allows the establishment of a rough equilibrium with beneficial insects regulating the herbivore populations.

Synchronized flowering of populations or individuals at intervals is a way of escaping consumers, because the flowers are not continuously available. In some areas, date palms have two annual flowerings, with a major flowering followed later in the year by a few palms producing a few inflorescences. Although this probably resulted as an adaptation to climatic conditions, it may be beneficial in avoiding some insect pest attacks.

Individual flowers may be unprotected for very short periods of time. The spathe provides a physical barrier and, after opening and undergoing anthesis, the male flowers may die within a day.

Palms have adaptations that attempt to ensure the availability of flower-pollinating insects, while reducing the availability for herbivores. The problem is similar for anemophilous palms, which have to release and receive pollen without overexposure of the reproductive tissues to potential herbivores.

Protection begins with the tissues that will develop into the inflorescences, which may be surrounded by woody leaf bases, often with spines and thorns (Tomlinson, 1990). The flowers are often protected by the presence of tannins and physical structures to interfere with herbivores (Savage and Ashton, 1983), and female flowers especially are often very tough and not very nutritious. Not surprisingly, female flowers usually have more protection than their more ephemeral male counterparts. Another adaptive feature that may reduce loss to herbivores is the small size of palm flowers, causing the herbivore to expend excessive energy while foraging (Fenner, 1985). This may have to be balanced with the need for pollination, carried out by quite large insects.

Many of the features that reduce the effects of herbivores on the flowers are also relevant to the fruits. An overproduction of developing fruits is common. *Bactris gasipaes* and *Orbignya martiana* produce up to 600 seeds per year. In *Rhopalostylis sapida* of New Zealand, the maximum is about 1500 seeds per year (Enright, 1987). This may increase the chances of some being missed by consumers. Fruits that are damaged by insects may have fallen anyway, due to a number of causes.

The lack of dormancy of many tropical seeds limits the time available for seed eaters to attack and may be a response to the high level of activity of seed consumers in the tropics (Fenner, 1985).

Although it is more difficult for insects to find seeds dispersed a distance from the parent plant, the bruchid beetles, *Pachymerus* spp. and *Caryobruchus* spp., find seeds of *S. rostrata* that are dispersed via simulated rodent dispersal, with some of the seeds in clumps (Janzen, 1976). Bird dispersal probably results in scattered distribution, which may enable a high portion of the seeds to escape.

Development of a hard layer inhibits or prevents successful ingress. The hard endocarp of *Scheelea* defeats the attempts of many larvae to enter the seed (Wilson and Janzen, 1972). This has consequences in terms of resource allocation. Fewer, better-protected seeds should result. Development of sclerenchyma, raphides and silica deposits increases the physical defences of many fruits and, in the lepidocaryoid palms, there is development of overlapping triangular scales (Tomlinson, 1990).

Multiseeded fruits may have greater survivorship than single-seeded fruits (Bradford and Smith, 1977). Again, there is a trade-off, as each seed is smaller from a multi- than from a single-seeded fruit, which decreases the chances of the resultant seedling from successfully establishing.

The fruits of some lepidocaryoid palms have mucilage canals and some *Daemonorops* species produce large quantities of resin. These may provide some defence against small organisms.

5

Borers of Palms

Robin M. Giblin-Davis

> It can be said that for every tree there is a worm.
>
> Theophrastus, Greek philosopher, *c.* 371–287 BC

Several insect groups have evolved ways of searching for, finding and boring into palms, using them as hosts. A borer is defined here as an insect that makes a tunnel by chewing or burrowing into the stem, crown, unopened inflorescences, flowers, fruits, peduncles, petioles, fronds or roots of a palm. Nearly all insects that bore in plant tissue belong to the endopterygote orders Lepidoptera, Coleoptera, Diptera or Hymenoptera, although some exopterygotes, such as termite species, can bore in live palm tissue. The larva is usually the borer, although the imagos of some species of beetles (e.g. Scarabaeidae, Lucanidae, Scolytinae and Platypodinae) can also be borers. Most insect borers of palms attack wounded or stressed palms, but they can attack healthy palms on occasion or when insect populations reach epidemic (epizootic) proportions. Notable exceptions include the palm rhinoceros beetles, whose imagos can bore into healthy, live, palm crowns and the palm-pollinating weevils, whose larvae bore the male florets of the palm and then serve a critical role as pollinators (see Chapter 4; O'Brien and Woodruff, 1986). Imagos (e.g. carpenter bee, *Xylocopa californica arizonensis* (Xylocopidae) (O'Brien and O'Brien, 1966) and the larvae of some xylophagous insects, e.g. Brentidae, Buprestidae, Lucanidae, some Cerambycidae, Passalidae and Isoptera, are borers in dead palms and are not discussed unless they affect live palm tissue at some point in their life cycle.

Insect borers that use palms as hosts are found in the following taxa:

- Coleoptera
  - Curculionidae
  - Bostrychidae
  - Bruchidae
  - Lymexylidae
  - Scarabaeidae
  - Lucanidae
  - Cerambycidae
- Lepidoptera
  - Castniidae
  - Tineidae
  - Glyphipterigidae
- Isoptera

The Bruchidae are borers in seeds and are discussed in Chapter 4.

Coleoptera

Curculionidae

The most diverse family of organisms in the world is the Curculionidae, commonly known as the snout beetles or weevils (Fig. 5.1). They are recognized by an elongated rostrum ('snout'), with small mandibles at the distal end (Fig. 5.2). There are more than 60,000 described species of weevils, with many more still to be named. Their

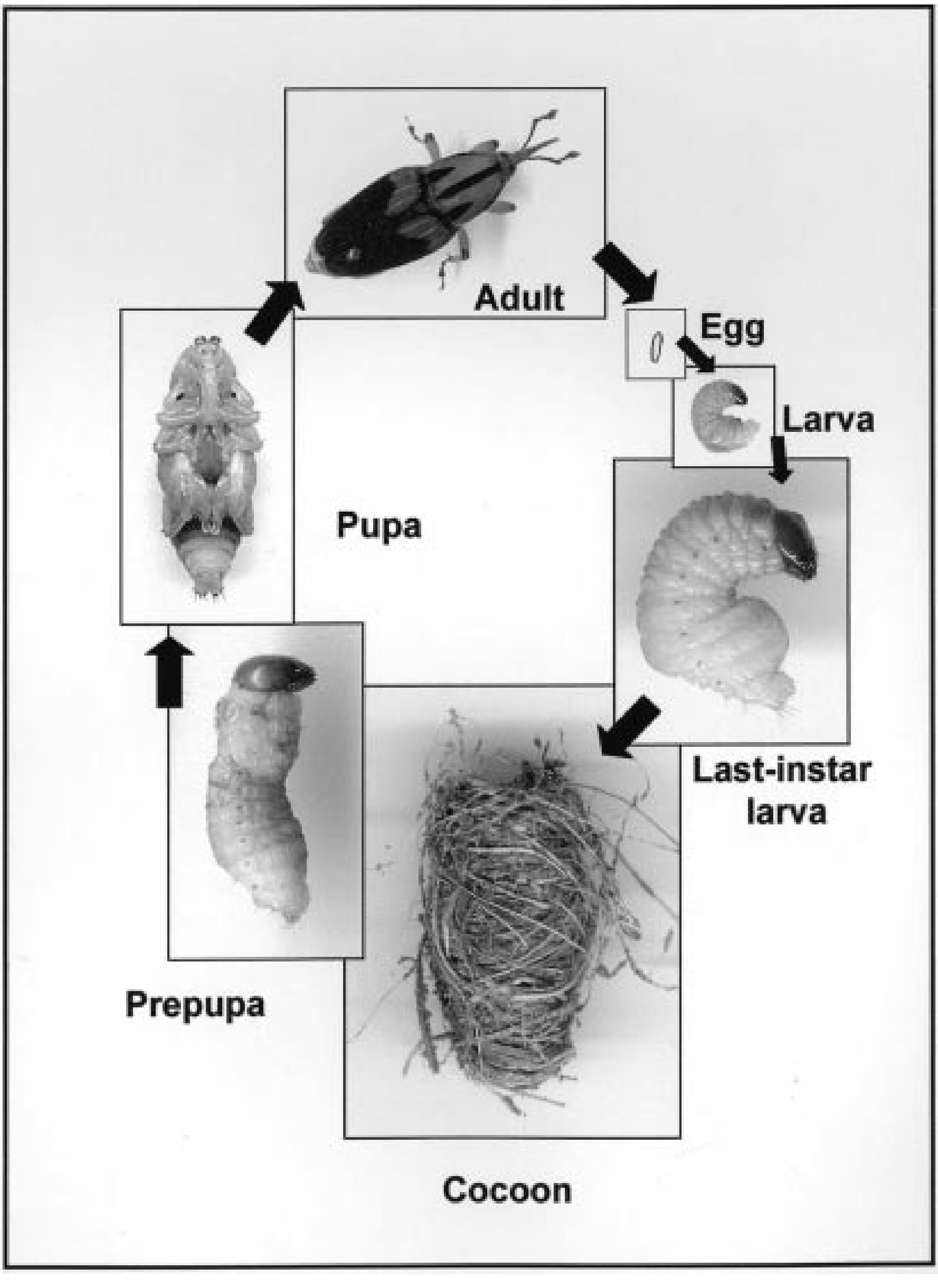


Fig. 5.1. Holometabolous life cycle illustrated by that of a typical weevil borer, *Metamasius hemipterus* (Coleoptera: Curculionidae: Sphenophorini). Photos, drawings and SEM views in this chapter by Robin Giblin-Davis unless otherwise noted.

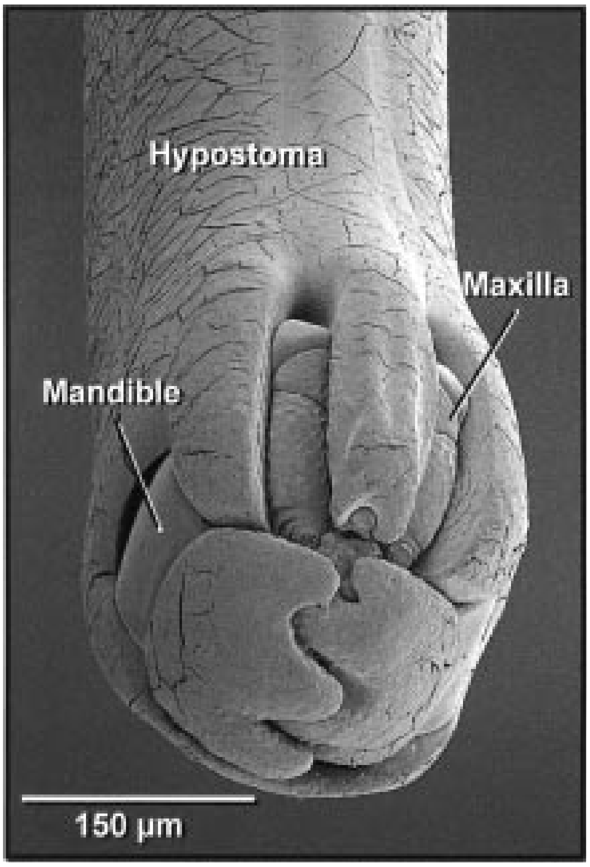


Fig. 5.2. The distal tip of the rostrum of *Metamasius inaequalis* showing small mandibles. SEM view.

success may be due to their specialization as borers of plants at the time of the radiation of the angiosperms in the mid- to late Cretaceous. Many weevils have narrow host ranges, often being family- or genus-specific. In most palm-associated weevils, the host range is polylectic or broad within the Palmae and sometimes including other monocotyledons, such as sugar cane (Gramineae), banana (Musaceae) and pineapple (Bromeliaceae). In contrast, the palm-pollinating weevils (borers of male flowers) tend to be oligolectic, with genus- or species-specific breeding host ranges (Charles O'Brien, unpublished observations).

Adult weevils are usually cryptic, taking refuge between petiole bases, unopened inflorescences, floral peduncles or damaged sites caused by larval feeding in the crown and/or stem of the palm, where they oviposit. Most palm-associated weevils use the small opposing mandibles at the tip of their extended rostrum (Fig. 5.2) to prepare an oviposition site in specific plant tissues. Egg production is usually in the range of 30–400 eggs per female, with eggs being laid individually. Larvae, which have a distinct head capsule, are apodous and move peristaltically. There are usually five to ten instars. While devouring all or parts of the inside of the host, larval stages gain protection from most predators, parasites and external abiotic factors. In contrast to the imagos, larvae possess large mandibles (Fig. 5.3) for chewing host tissue and may be involved in casual or strict associations with microorganisms (fungi and/or bacteria) (Nardon *et al.*, 1985). They often turn an orange-yellow colour prior to the prepupal stage. The larva typically uses fibre from the host to make a cocoon and pupates within the host, often in petioles or the stem periphery (Fig. 5.1). Many Derelomini (palm-flower weevils) leave the host and pupate in a cell in the soil (Charles O'Brien, personal communication). Both the prepupa and pupa move in a characteristic lateral spin within the cocoon. Because of drastic differences in the quality and quantity of food that the larva may find, palm and sugar cane weevils can exhibit large size polymorphism, which often leads to confusion about the identity of the weevil species. In addition to damage done directly by larval palm weevils, species in tropical America can be vectors of the lethal, nematode-caused, red-ring disease or the chronic little leaf of palms (see Box 5.2).

Known weevil borers of palms fall into seven subfamilies: Dryophthorinae (syn. Rhynchophorinae), Cholinae, Baridinae, Erirhininae, Petalochilinae, Scolytinae and Platypodinae. Of these groups, palm-associated members of the Dryophthorinae are the most damaging to palms worldwide. These long-snouted weevils are among the largest and most interesting-looking insects in the world. They attracted the attention of early entomologists. *Rhynchophorus* (from Greek *rhynch*, snout) was first used in 1795 by J.F.W. Herbst and *Rhina* (now *Rhinostomus*) was first used by Pierre Andre Latreille in 1802. Four tribes within the Dryophthorinae are significantly repre-

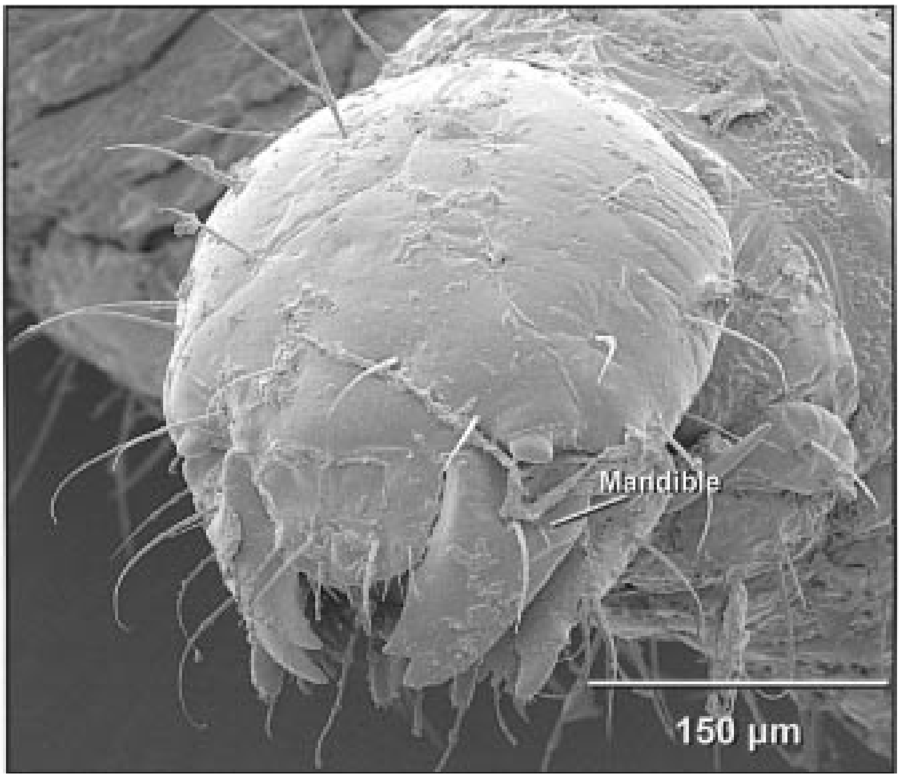


Fig. 5.3. Face-view of the larva of a typical weevil borer (*Diaprepes abbreviatus*).

sented on palms: the Rhynchophorini, including *Rhynchophorus* (Figs 5.4 and 5.5) and *Dynamis* (Fig. 5.6); the Sphenophorini, including *Metamasius* (Figs 5.1, 5.8–5.10), *Rhabdoscelus* (Fig. 5.11) and *Temnoschoita*; the Diocalandrini; and the Orthognathini, including *Rhinostomus* (Figs 5.12 and 5.13), and *Mesocordylus* (Wibmer and O'Brien, 1986; Zimmerman, 1992; May, 1993). Rhynchophorini tend to be large (15–50 mm), aggressive colonizers of the crown of wounded, stressed or healthy palms, often killing the host. Sphenophorini are medium-sized weevils (10–15 mm), often with wider host ranges within monocotyledons, usually attacking wounded or healthy petioles and rarely causing the death of the palm. Diocalandrini are small weevils (< 10 mm), which attack all parts of the palm, including roots, fronds, fruit stalks and, occasionally, the crown. Members of the Orthognathini vary in size (10–52 mm) and typically attack the stem of dying palms.

Dryophthorinae: Rhynchophorini

Species of *Rhynchophorus* and *Dynamis* are commonly called palm weevils, in reference to their usual hosts. Hosts of *Rhynchodynamis*, an obscure genus from Brazil, are not known. Palm weevils are large insects (imagos up to 50 mm long × 20 mm wide; larvae up to 64 mm long × 25 mm wide). The late-instar larvae are a food source for people in some tropical areas (see Box 5.1). The imagos are generally black and glossy in *Dynamis* (Fig. 5.6), but species of *Rhynchophorus* can range from reddish brown with variable black markings (Fig. 5.4) to all black with a matt to glossy finish (Fig. 5.5). Some *Rhynchophorus* species, e.g. *R. cruentatus, R. phoenicis, R. quadrangulus* and *R. ferrugineus*, are highly variable in body colour. There are good species keys available for *Rhynchophorus*, *Dynamis* and *Rhynchodynamis* in Wattanapongsiri (1966). However, some species of *Dynamis* in these keys have been synonymized.

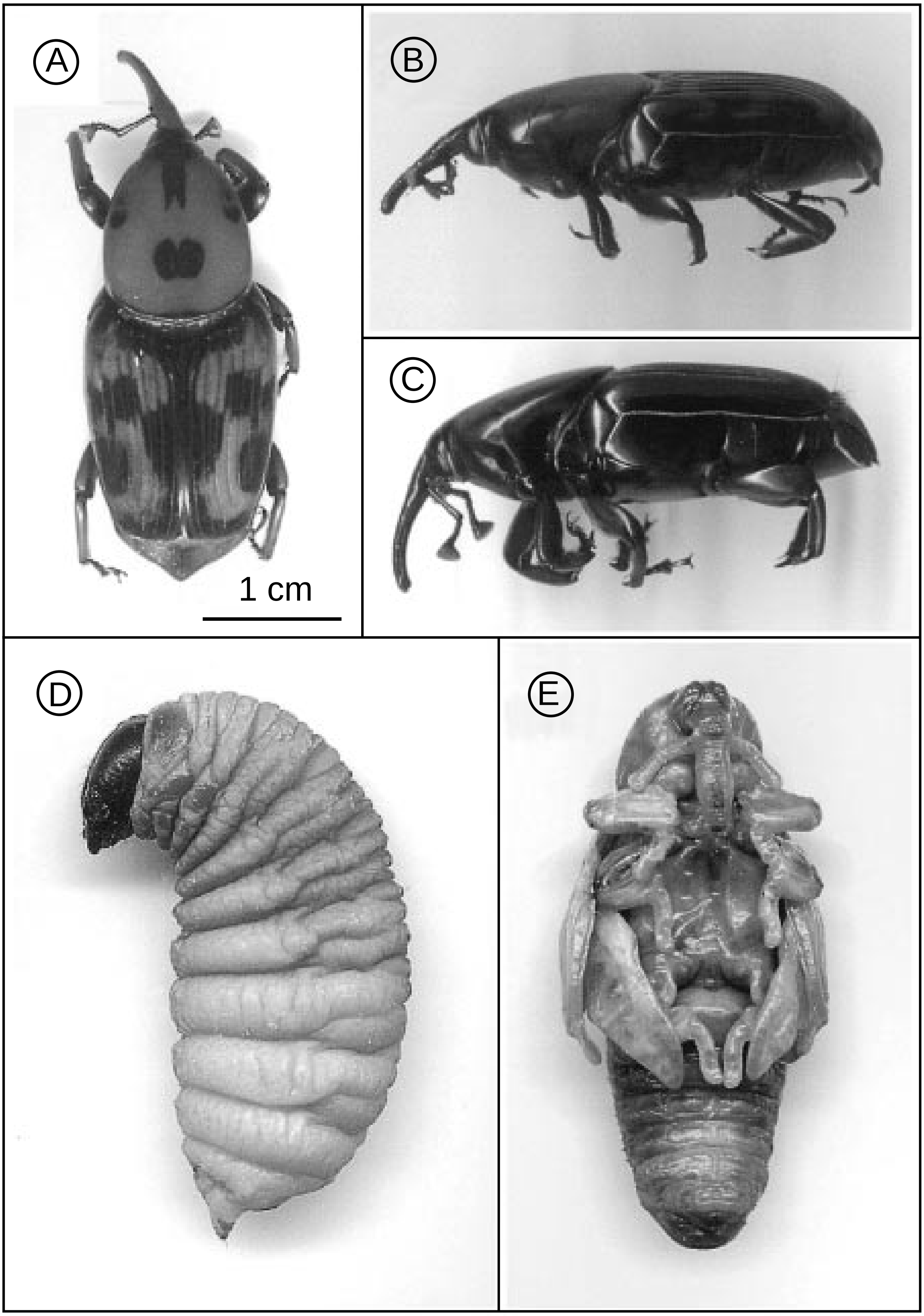


Fig. 5.4. *Rhynchophorus cruentatus* (Coleoptera: Curculionidae: Rhynchophorini). (A) Dorsal aspect of female. (B) Lateral view of male. (C) Lateral view of female. (D) Lateral view of last-instar larva. (E) Ventral view of pupa.

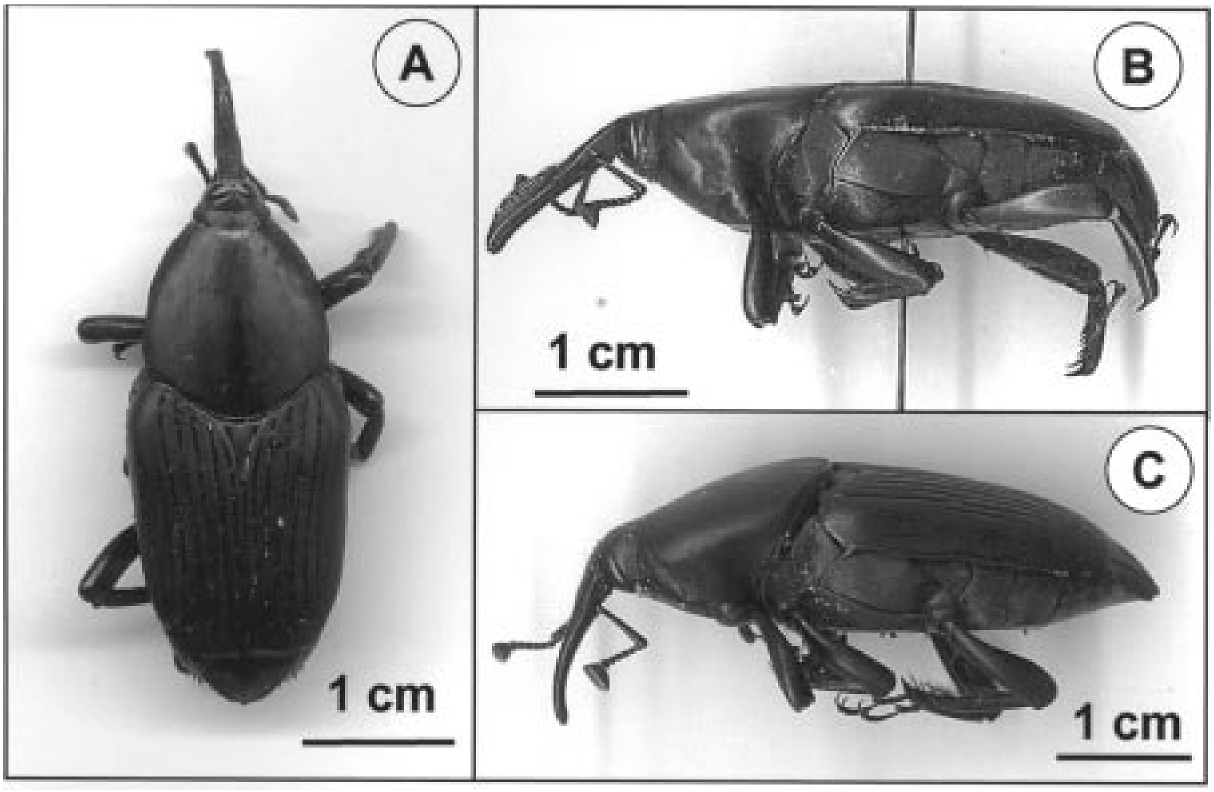


Fig. 5.5. *Rhynchophorus palmarum* (Coleoptera: Curculionidae: Rhynchophorini). (A) Dorsal aspect of male. (B) Lateral view of male. (C) Lateral view of female.

Wibmer and O'Brien (1986) recognized three species: *Dynamis borassi* (Fig. 5.6), *Dynamis nitidulus* and *Dynamis peropacus*.

The three species of *Dynamis* are restricted to Central and South America, whereas the ten named species of *Rhynchophorus* are distributed worldwide, mostly in tropical regions, as follows (Wattanapongsiri, 1966): *Rhynchophorus palmarum* in Mexico, Central and South America and the southernmost Antilles (Colour Plate 14a, Fig. 5.5); *R. cruentatus* in Florida and the coastal regions of the south-eastern USA from South Carolina to Texas (Colour Plate 14b, Fig. 5.4); *R. phoenicis* throughout central and southern Africa; *R. quadrangulus* in west-central Africa; *Rhynchophorus bilineatus* in New Guinea; *R. ferrugineus* (Colour Plate 14c), which is probably the same species as *Rhynchophorus vulneratus* (Hallett *et al.*, 1993), which is native to South-East Asia and has recently been introduced elsewhere (see below); *Rhynchophorus distinctus* in Borneo; *Rhynchophorus lobatus* known from Solok (Sumatra, Indonesia); and *Rhynchophorus ritcheri* in Peru.

Relatively little is known about *Dynamis*, possibly because it is easily confused with the commonly observed *R. palmarum*, the American palm weevil, in areas where their distributions overlap. *Dynamis borassi* is a pest of coconut palm in Ecuador, Colombia and Brazil, where it attacks and destroys unopened inflorescences. It has been reported to attack and develop in the inflorescences of *Astrocaryum carnosum* and *Astrocaryum chonta* from Peruvian Amazonia (Couturier *et al.*, 1998b) and is attracted to the maturing fruit of *Astrocaryum standleyanum* in Colombia (Giblin-Davis *et al.*, 1997). It can also attack the crown of coconut palm and may vector the red-ring nematode to this palm (Gerber *et al.*, 1990). *Dynamis nitidulus* and *R. palmarum* cause similar damage in plantations of *Bactris gasipaes*, grown in Peruvian Amazonia for heart of palm production. Both weevils oviposit in the cut

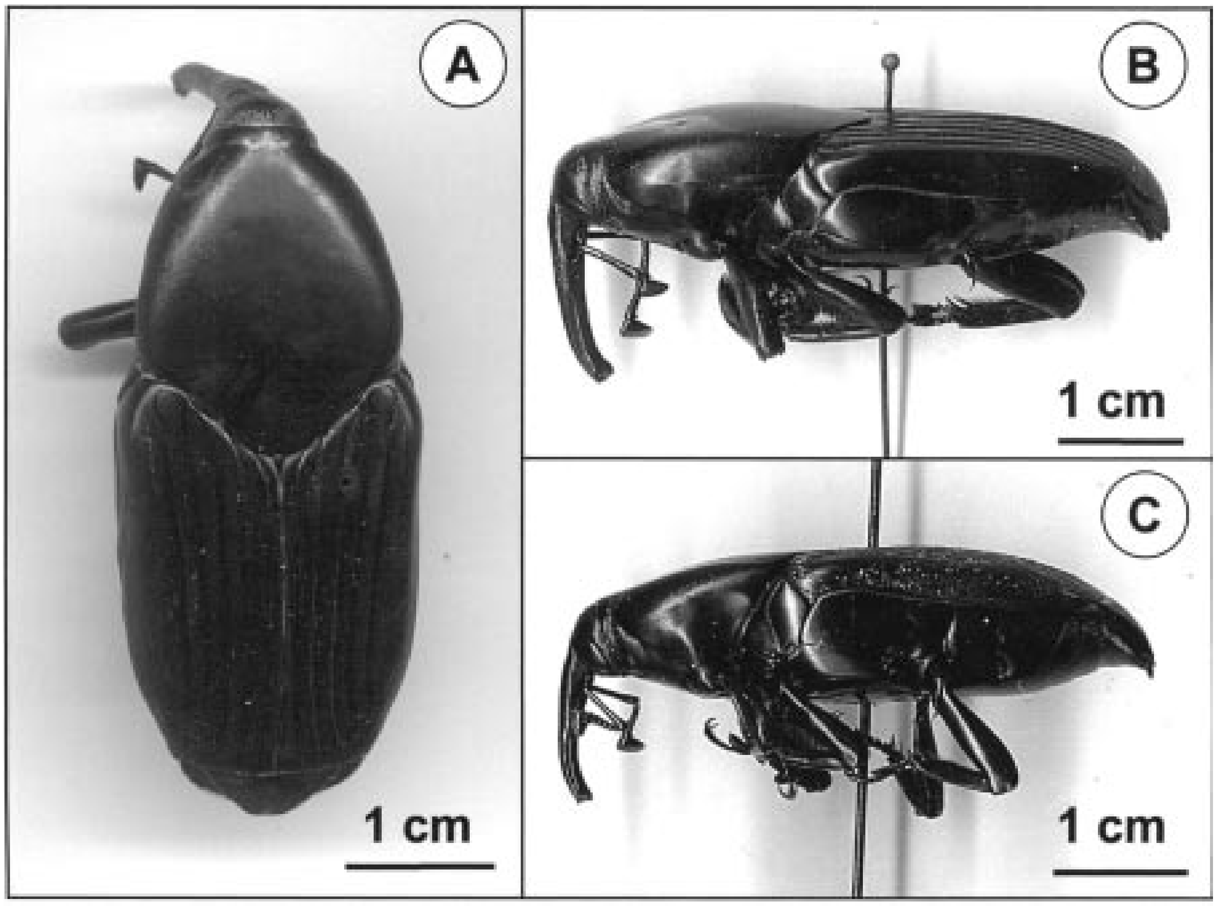


Fig. 5.6. *Dynamis borassi* (Coleoptera: Curculionidae: Rhynchophorini). (A) Dorsal aspect of male. (B) Lateral view of male. (C) Lateral view of female.

stems after harvest of the crowns for heart of palm, resulting in larval infestations that kill the bunching plant and curtail normal palm regeneration, which is critical for production (Vásquez *et al.*, 1998).

Most of the described species of *Rhynchophorus* are considered major pests of coconut palm in tropical regions of the world (Wattanapongsiri, 1966). *Rhynchophorus cruentatus* is rarely a problem in coconut palm in Florida, except in lightning-damaged palms. We have not observed *R. cruentatus* developing in lethal yellowing-killed palms in Florida. Similarly*,* *R. palmarum* has not been observed in lethal yellowing-killed coconut palms in locations such as Belize, where both the disease and the weevil occur. Apparently, something about this phytoplasma-caused wilt makes palms unsuitable for palm weevils.

Because of their relatively wide host range within the Palmae, species of *Rhynchophorus* can cause problems for other species of palms. For example, *R. cruentatus* is a pest of recently transplanted (i.e. stressed) *Sabal palmetto* and healthy *Phoenix canariensis* and has been reported from more than ten other species of palms (Giblin-Davis and Howard, 1989b).

Rhynchophorus ferrugineus, a weevil native to South-East Asia, is a pest of coconut palm in the Philippines (Gabriel, 1976). It has recently become the major pest in date palm groves all around the Arabian Gulf (Abdulaziz Al-Alajlan and S. Ahmed Siddig, personal communications). The species is also a recently introduced pest in the famous date groves of Elche, Spain (Gómez i Vives and Ferry, 1999a). The insect takes advantage of wounds made during vegetative production practices (removal of offshoots). It is the only palm weevil that has been introduced into

Box 5.1. Palms and entomophagy.
Robin M. Giblin-Davis

Entomophagy (the eating of insects) is known in various species of primates, including *Homo sapiens*. It is quite common in hunting/gathering cultures and is presumed to be an important source of nutrition for contemporary and early humans (Ponzetta and Paoletti, 1997). It is integrated into many cultures of Asia, where princes of antiquity served weevil larvae to distinguished guests. Early naturalists, including Pierre Andre Latreille and Alfred Russel Wallace, described entomophagy among American tribes (reviewed by Ghesquière, 1947).

In 1705, Maria Sybilla Merian (see *Brassolis sophorae*) reported that indigenous people of Suriname consumed *Rhynchophorus palmarum*, which they referred to as gru-gru (Ghesquière, 1947). A common criterion for deciding whether an animal is fit for human consumption is the food that it eats (Holt, 1988). Thus, it is not surprising that some of the insects that are intimately associated with palms as borers are eaten by humans. Palm-associated weevils, especially species of *Rhynchophorus*, are among the most important insects consumed worldwide (possibly because of their worldwide distribution and the fact that their larvae taste like coconut-cured bacon). In fact, *Rhynchophorus* distribution patterns might, in part, be connected with their importance in human diets and the movement and activities of early humans.

Optimal foraging theory predicts that the overall efficiency of obtaining a food source will determine the popularity of an insect species and stage in a human diet (Bukkens, 1997). Thus, *Rhynchophorus* larvae (Fig. 5.4D), which are large, tasty, nutritious and abundant, are often managed resources, which are harvested from felled or intentionally damaged palms (DeFoliart, 1997). Analyses of the nutritional value of *Rhynchophorus* species are reviewed by Bukkens (1997). In general, these weevils represent an important source of fat, protein and complementary amino acids relative to the staple foods consumed. For example, the overall amino acid score for *Rhynchophorus bilineatus* (syn. *Rhynchophorus ferrugineus papuanus*) in Papua New Guinea is low, but relatively high for lysine and leucine, which complement the low levels in the consumed staples of sago palm, sweet potato and taro (Bukkens, 1997).

In Ecuador, *R. palmarum* is one of the most commonly used food insects. In the 1950s in the Napo area, a missionary, Angel de Ucar, introduced the African oil palm as an ornamental plant. Indigenous Quechuas who were living near the mission traditionally cut healthy *Mauritia flexuosa* from swampy forests and *Bactris gasipaes* to attract palm weevils for oviposition, harvesting the resulting weevil grubs and pupae several weeks later for food. These people presupposed that the intended use of the African oil palm by the missionary was to 'rear fatter weevils for the bishop'. Thus, the African oil palm is known in this area as 'chontaduro del obispo', i.e. 'bishop's palm'. In Ecuador, larvae of *Castnia* spp. (Lepidoptera: Castniidae) (Fig. 5.19) and larvae and pupae of *R. palmarum* (Fig. 5.5), *Dynamis* spp. (Fig. 5.6) and *Rhinostomus barbirostris* (Fig. 5.12) are served boiled with salt, cooked with onions or eaten alive, as are imagos of several species of *Metamasius* (Figs 5.1 and 5.8). The latter are said to be similar in taste to peanuts (Onore, 1997).

In Papua New Guinea, the larva of *R. bilineatus* is the most widely eaten insect, where it is a by-product of sago starch production (Mercer, 1997). The sago weevil larvae are eaten alive or boiled or roasted or mixed into sago pancakes (Mercer ,1997). Typically, weevils are produced from the stump and cabbage remaining after the harvest and processing of the sago palm, *Metroxylon sagu* (Fig. 1.5e). In some areas, the spiny-trunk sago palm, *Metroxylon rumphii*, which is not eaten because of inferior-quality starch, is cut and prepared for weevil production (each palm producing 500–600 grubs) (Mercer, 1997). A complicated ceremonial life has evolved around the production and consumption of larvae of *R. bilineatus* in parts of Papua New Guinea (Ponzetta and Paoletti, 1997). Sago weevil production appears to be a sustainable system, because sago palms are hapaxanthic and only mature palms, just prior to flowering and death, are cut. It is fortunate that these palms regenerate well in swamps that are not considered suitable for agriculture (Mercer, 1997).

Palm weevils are a potential mini-livestock, suitable for protein production on small farms (Beets, 1997). In fact, DeFoliart (1997) argues that increased palm weevil production for food could be tied into more efficient recycling of dead and dying palms for disease and insect control. Also, coconut palm, bagasse (from sugar cane) and other agricultural-processing waste products could be recycled into production of weevils and/or *Oryctes* (palm rhinoceros beetle) larvae (Colour Plate 15e) for human consumption.

a large number of countries. This may be related to its association with *Phoenix dactylifera*. This is one of the few palms that is propagated by offshoots and, if these are shipped between countries, weevils could possibly be transported in them. *Rhynchophorus phoenicis* is known to attack African oil palm, date palm, *Phoenix reclinata* and *Borassus* spp., among others. *Rhynchophorus palmarum* is a pest of African oil palm (mostly in association with the red-ring nematode). Additional palm hosts include *B. gasipaes* and about 21 other species. Most of the weevils' hosts other than palms are monocotyledons, such as sugar cane, pineapple and banana (Wattanapongsiri, 1966).

In general, *Dynamis* and *Rhynchophorus* are multivoltine species, which lay between 30 and 832 eggs during a 42-day ovipositional period (Wattanapongsiri, 1966; Giblin-Davis and Howard, 1989b; Weissling and Giblin-Davis, 1994). Eggs hatch within 2–4 days and larvae bore into the palm petiole or stem. There are six to 20 instars, which end in a prepupal stage 25–105 days later. The last instar can be quite large, weighing between 3 and 14 g. The prepupal stage lasts 2–14 days. Pupation lasting 8–50 days occurs in the petioles and stem periphery. The life cycle can take from 45 to 180 days. Adult longevity is about 26–117 days (Wattanapongsiri, 1966; Giblin-Davis and Howard, 1989b).

Late-instar larvae can kill palms by destroying the apical meristem (i.e. palm heart, or bud) (Giblin-Davis and Howard, 1989a). Palms appear to have defences that must be overcome by palm weevils or their associated organisms, such as the red-ring nematode, *Bursaphelenchus cocophilus*. Stressed *S. palmetto* exposed to *R. cruentatus* adults became infested with their progeny, while healthy palms did not (Giblin-Davis and Howard, 1989b). In contrast, apparently healthy *P. canariensis* was a susceptible and suitable host for *R. cruentatus* (Giblin-Davis *et al.*, 1996b), suggesting that there are different physical and/or chemical defences conveying host suitability and susceptibility (Schuiling and Van Dinther, 1981; R.M. Giblin-Davis, unpublished data). The crown shaft of royal palm (*Roystonea* sp.) prevented *R. palmarum* infestation under natural conditions, but weevils developed and transmitted red-ring nematode if the crown shaft was damaged (Blair, 1969).

Association of *R. palmarum* (Gerber and Giblin-Davis, 1990; Giblin-Davis, 1993), *D. borassi* (Gerber *et al.*, 1990) and *Metamasius hemipterus* (Fig. 5.1; Mora *et al.*, 1994) in tropical America with the red-ring nematode may affect the population dynamics of the weevils. Deposition of nematodes into wounds of healthy palms can cause red-ring disease (RRD) (Box 5.2) within 2–4 months (Fig. 5.7; Giblin-Davis 1993). Palms dying from RRD, in turn, produce kairomones that attract palm weevils. Thus, red-ring nematode is a lethal agent that increases the potential number of hosts for palm weevils. Their cross-attraction to host kairomones and aggregation pheromones increases the probability of associating with and vectoring the dispersal stage of the nematode. *Rhynchophorus* spp. and *M. hemipterus* are also associated with or even rely on other microorganisms in dead or dying hosts (Griffith, 1987; Giblin-Davis *et al.*, 1989). For example, diets lacking debittered yeast are not suitable for rearing *R. cruentatus* (Weissling and Giblin-Davis, 1995).

The abundance of adult palm weevils undergoes seasonal changes (see Box 1.1). *Rhynchophorus palmarum* abundance increases from the end of the rainy season throughout most of the dry season in coconut palm plantations in Trinidad (Hagley, 1963) and in the dry season in oil palm plantations in Brazil (Schuiling and Van Dinther, 1981), Costa Rica (Morales and Chinchilla, 1990), Honduras (Chinchilla *et al.*, 1990) and Colombia (Cabrales *et al.*, 1994). In Florida, *R. cruentatus* (Weissling *et al.*, 1994a) and *M. hemipterus* (Peña *et al.*, 1995) are more abundant in spring, before the onset of the rainy season. *Rhynchophorus palmarum, R. ferrugineus* and *M. hemipterus* have crepuscular flight patterns (Rochat, 1987; Gunawardena and Bandarage, 1995; R.M.

Box 5.2. Red-ring disease (Fig. 5.7).
Robin M. Giblin-Davis

Red-ring disease (RRD) was first reported from coconut palm in Trinidad in 1905 and is currently distributed from the Yucatán Peninsula in Mexico south through Central America into the Lesser Antilles and South America. The disease is caused by the red-ring or coconut palm nematode, *Bursaphelenchus cocophilus* (syn. *Rhadinaphelenchus cocophilus*), a stylet-bearing, plant-parasitic roundworm (order Aphelenchida). RRD is one of the most important wilt diseases of coconut palm and African oil palms in tropical America, causing up to 10–15% annual losses (Giblin-Davis, 1993). It is vectored to healthy and stressed palms by palm and sugar cane weevils (*Rhynchophorus palmarum*, *Dynamis borassi* and *Metamasius hemipterus*), which carry as many as 10,000 juvenile nematodes internally (Gerber and Giblin-Davis, 1990; Gerber *et al.*, 1990; Mora *et al.*, 1994). The nematodes survive poorly without a palm or insect host, suggesting obligatory relationships with both hosts. Palm and sugar cane weevils are attracted to moisture in the frond bases and/or semiochemicals, produced by wounds on healthy palms and by stressed palms, and/or male-produced aggregation pheromones, which recruit both sexes of weevils to the host for mating and oviposition (Giblin-Davis *et al.*, 1996a). Nematodes are apparently transmitted to palms during oviposition or other activities by the weevils (Griffith, 1968). Only a few nematodes are necessary in wounds for successful RRD establishment (Griffith, 1968). In coconut palms, symptoms are first observed 28 days after inoculation, with peak populations of nematodes occurring about 42 days later (Goberdhan, 1964). Palm and sugar cane weevils colonize palms with RRD and their larvae become associated with the dispersal stage of the nematodes, carrying them through metamorphosis to the adult stage, which vectors them to the next palm.

Although most palm species appear to be susceptible to inoculation by red-ring nematode, disease severity and symptoms are variable (Griffith and Koshy, 1990; Giblin-Davis, 1993). Generally, very young palms (< 2 years old) are not susceptible. Most coconut palm varieties are highly susceptible and produce classical red-ring symptoms: a typical wilt, with premature coconut fall (except for mature coconuts) and premature yellowing and senescence of progressively younger fronds, which break at the petiole and hang. Cross-sections reveal anthocyanin-red pigments, which occur throughout the stem as a ring just inside the periphery, in the cortex of roots and in the petioles (Colour Plate 14d, e). Dispersal-stage (third-stage) nematodes can be harvested from this discoloured tissue in large numbers (up to 11,000 nematodes per gram of tissue). Nematodes occur intercellularly in ground parenchyma of the discoloured tissue. Nematode-caused damage near the xylem vessels appears to induce tyloses (growth of parenchyma cells into the xylem through pits), causing vascular occlusion. Vascular destruction in monocotyledons is irreversible, because there is no cambium tissue for repair. Thus, coconut palms with RRD usually die within several months of infection. In African oil palm, stem rings are thin and brown or cream-coloured and can be very irregular in shape, often extending less than the entire length of the stem with 0 to 5000 nematodes per gram of tissue. Infected African oil palms and older coconut palms sometimes exhibit a chronic disease, called ‘little leaf’, which can eventually lead to RRD (Chinchilla, 1988). Palms with little leaf reduce their new frond emission rate and abort inflorescences, causing a drop in fruit production. Propagating red-ring nematodes can be recovered from the unpresented fronds near the region of elongation, where they cause necrotic lesions that stunt the new fronds and give the crown the appearance of a feather duster (Chinchilla, 1988).

The major recommendation for RRD control has been the early removal and destruction of red-ring-diseased and/or *R. palmarum*-infested palms to break the cycle and reduce the chance for epizootics (Giblin-Davis, 1993). As soon as palms with RRD or *B. cocophilus*-induced little-leaf symptoms have been detected, they should be destroyed. In coconut palm, the disease can be confirmed by examining stem tissue extracted with a coring device for evidence of discoloured tissue and red-ring nematodes. In African oil palm, stem-coring for evidence of necrosis and red-ring nematodes is not reliable (Chinchilla, 1988). Palms should be sprayed with an insecticide (e.g. methomyl) and killed with 100–150 ml active ingredients (48.3%) of the herbicide monosodium acid methanearsonate (MSMA) or other herbicide, which is injected or placed into the trunk (Chinchilla, 1988; Griffith and Koshy, 1990). Occasionally, palms injected with MSMA will harbour weevil larvae. Therefore, once the palm is dry, it should be cut and sectioned to make sure that weevils are not present. Palms that are heavily infested with weevils should be cut, sectioned and treated with an insecticide, such as methomyl, trichlorfon, monocrotophos, carbofuran, cabaryl or lindane (Chinchilla, 1988), or burned.

Box 5.2. *continued*

Recent research in African oil palm plantations suggests that concerted aggressive phytosanitation and mass trapping with traps baited with sugar cane and synthetic aggregation pheromone (Rhyncholure; racemic 6-methyl-2-hepten-4-ol; ChemTica International) reduce the numbers of *R. palmarum* and change their distribution patterns (from highly aggregated to random), while reducing RRD incidence (Oehlschlager *et al.*, 1995a). At mass-trapping onset, most *R. palmarum* were captured in 'border' traps of the test site, suggesting removal of potential immigrants before entry into the study area (Oehlschlager *et al.*, 1995a). A combination of perimeter and 'internal' traps is most effective for mass trapping (Chinchilla *et al.*, 1993). More than 62,500 weevils (~94 weevils ha^{-1} month^{-1}) were captured during the study, with RRD incidence decreasing by more than half (Oehlschlager *et al.*, 1995a). We hypothesize that this strategy may be less effective in coconut palm, which is much more suitable and susceptible as a host to RRD and the American palm weevil. Also, the logistics of concerted area-wide control efforts for managing RRD in coconut palm may prove difficult, because it is generally grown on small farms.

Giblin-Davis, unpublished). The flight of *R. cruentatus* in the laboratory was not correlated with time of day or feeding status but increased with increasing temperature and decreasing relative humidity (r.h.) (Weissling *et al.*, 1994a).

Application of the systemic insecticide monocrotophos to coconut palm in South India in an early stage of infestation with *R. ferrugineus* was curative (Rajamanickam *et al.*, 1995), but this method may involve the usual disadvantages of chemical control. Infestations of *Rhynchophorus* and *Dynamis* in palms are difficult to accurately detect prior to serious damage to the apical meristem. Once this damage is obvious, the palm may die. Experiments using non-invasive methods of detecting larval chewing with an automobile technician's stethoscope and a portable electronic sound detector have not been successful in early detection of *R. cruentatus* in Canary Islands date palms in Florida (Hunsberger *et al.*, 2000). A variety of contact adulticides, e.g. lindane and chlorpyrifos, are effective against *Rhynchophorus* species (Giblin-Davis and Howard, 1989b). Thus, preventive treatment should involve prophylactic applications of contact insecticides at times when palms have been wounded to reduce establishment of weevils, in concert with early removal of palms at the first signs of larval weevil infestations. *Phoenix canariensis* infested with *R. cruentatus* in Florida should be cut down and removed when the fronds begin to droop and larval frass can be observed in gallery windows in the petioles. At this point, mean total weevil counts per palm are often over 100, with more than 65% as larvae and more than 25% of these being > 2.5 cm in length. About 20 larvae are needed to cause a lethal infestation. Palms with these symptoms are dying because of irreparable damage to their apical meristems, and attempts to save them are ineffectual. A delay in destroying the palms allows weevils to emerge and attack nearby palms.

Several natural enemies hold promise for biological control of *Rhynchophorus* spp., including nematodes in the families Steinernematidae and Heterorhabditidae, the bacterium *Micrococcus roseus* (Griffith, 1987), tachinid parasites, *Billaea* (syn. *Paratheresia*) *rhynchophorae* from Bolivia (Candia and Simmonds, 1965), *Billaea menezesi* from Brazil (Moura *et al.*, 1995), and a cytoplasmic polyhedrosis virus (CPV) from *R. ferrugineus* from India (Gopinadhan *et al.*, 1990). *Billaea rhynchophorae* has been reported from *D. borassi* from Peruvian Amazonia (Couturier *et al.*, 1998b).

Management of borers with semiochemicals is a recent development (Box 5.3). DeFoliart (1997) asked whether expanded food markets could provide an opportunity to combine palm-weevil larvae mini-livestock production with more efficient recycling of dead and diseased palms in an integrated pest management (IPM) programme for weevil and/or RRD control (see Box 5.1).

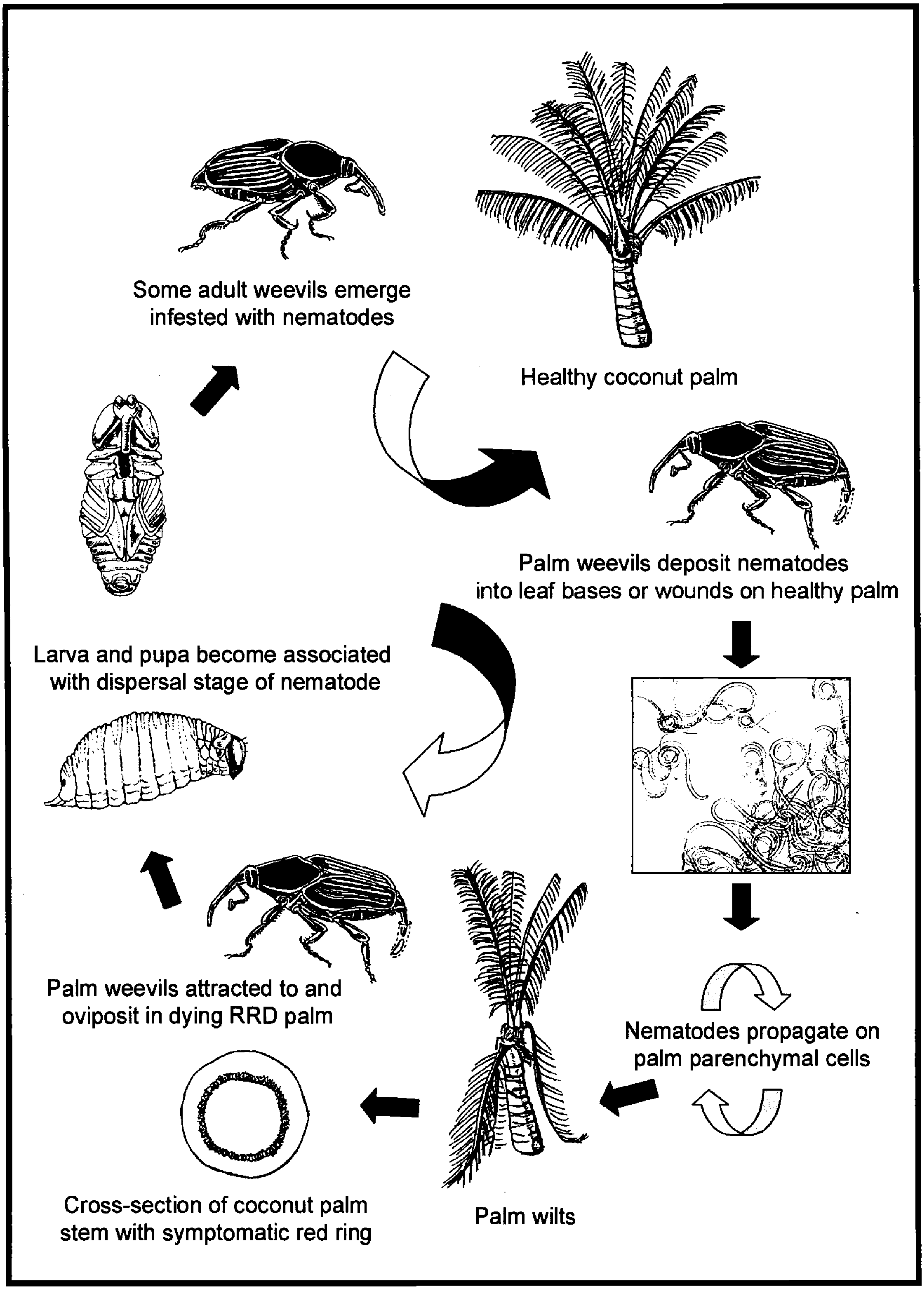


Fig. 5.7. Generalized representation of the association between the red-ring nematode, palm weevils and palms.

Box 5.3. Semiochemicals for management of borers.

Robin M. Giblin-Davis

A relatively recent alternative to conventional pesticides is the use of very small amounts of insect behaviour-modifying chemicals (IBMC) or semiochemicals. Semiochemicals are defined as chemicals that act as signals between organisms (Dusenbery, 1992). Pheromones are semiochemicals that act intraspecifically, whereas kairomones act interspecifically, benefiting the receiver (Dusenbery, 1992). These chemicals are crucial for life-sustaining functions of insects, including food and mate location, reproduction and defence. The semiochemicals that are easiest to exploit for management of insects are aggregation and sex pheromones. Insects use these chemicals to locate food and mates. Aggregation pheromones attract imagos of both sexes. They appear to be common in certain weevil groups, including the palm weevils (Giblin-Davis *et al.*, 1996a), and palm rhinoceros beetles (Hallett *et al.*, 1995). While monitoring is primarily used to achieve more efficient timing of insecticide application, mass trapping is used to actually lower pest populations. Sex pheromones are common to many moth species, including *Opogona sacchari*, and are used for monitoring. Because they are attractive to one sex only, they are rarely used for mass trapping. Population suppression via sex-pheromone application utilizes the strategy of confusion or mating disruption. In this strategy, many point sources of a female sex pheromone are placed in the environment. These compete with females for males. Both aggregation and sex pheromones are being investigated as attractants to lure pests to traps containing delayed-action biological control agents or pesticides, which the visiting pests would then spread throughout their population. Because most semiochemicals are species-specific, one can target an individual pest without indiscriminately harming beneficial predators in the agricultural or urban environment.

The semiochemicals that are actually used in operational programmes are synthetic preparations of the natural products produced by the host or pest. These chemicals have relatively low toxicity, are easily biodegraded and are used in extremely small quantities. For example, to lower the incidence of red-ring disease, which is caused by the nematode *Bursaphelenchus cocophilus* and vectored chiefly by the American palm weevil, *Rhynchophorus palmarum*, traps baited with aggregation pheromone of the weevil are placed at densities of one for every 5 ha in African oil palm plantations where red-ring disease is a problem. This mass trapping lowers red-ring disease by 85% over a year and consumes only 0.6 g ha^{-1} year^{-1} of pheromone (Oehlschlager *et al.*, 1993a).

Dryophthorinae: Sphenophorini

The Sphenophorini are the New and Old World billbugs. Species of the genus *Sphenophorus* attack and develop in grasses (Vaurie, 1978), whereas members of the genus *Metamasius* (Figs 5.1, 5.8 and 5.9) and *Metamasius inaequalis* (syn. *Paramasius distortus*) (western-hemisphere genera) and *Rhabdoscelus* and *Temnoschoita* (eastern-hemisphere genera) can attack *Palmae*, sugar cane and *Bromeliaceae*.

There are 15 species of *Metamasius* associated with palms in tropical America: *M. anceps, M. bruneri, M. canalipes, M. cinnamominus, M. dasyurus, M. ensirostris, M. flavopictus, M. hebatatus, M. hemipterus, M. inaequalis, M. maculiventris, M. mosieri, M. pygidialis, M. sierrakowsykyi* and *M. tectus* (Vaurie, 1966). The West Indian sugar cane borer, *M. hemipterus* (Colour Plate 15a, b, Figs 5.1, 5.8 and 5.9), which comprises three different subspecies, is distributed in Florida, the West Indies, Mexico and Central and South America (O'Brien and Wibmer, 1982; Wibmer and O'Brien, 1986). This species is probably the most damaging member of the genus to palms. It attacks more than ten species in Florida (Giblin-Davis *et al.*, 1994b, 1996b, c). Certain palm species seem to be more affected by *M. hemipterus* than others. *Phoenix canariensis* and *Ravenea rivularis*, which have soft or fleshy frond bases, or palms with crown shafts allowing weevils into the moist recesses between the exsheathing frond base and the next frond base, such as *Roystonea* and *Hyophorbe*, seem to be more prone to damage by *M. hemipterus* in Florida than palms with hard and split frond bases, such as *Sabal* species (R.M. Giblin-Davis, unpublished

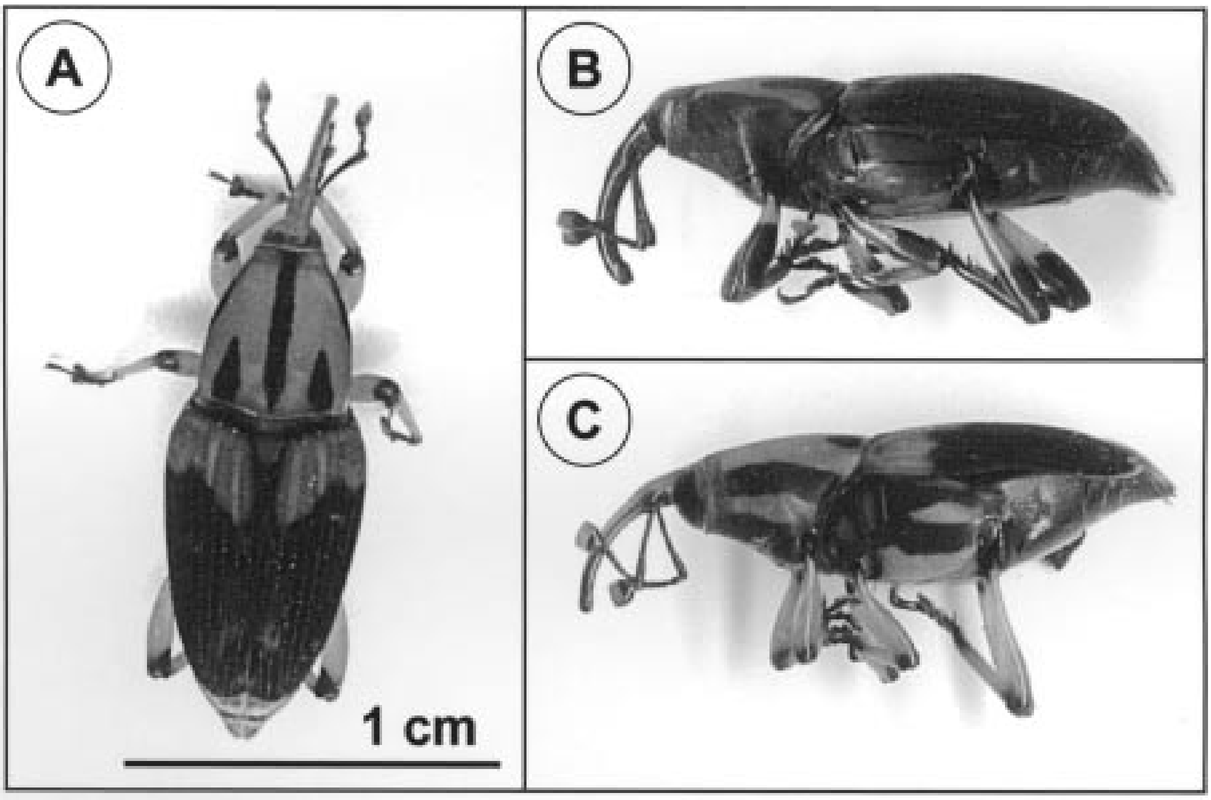


Fig. 5.8. *Metamasius hemipterus* (Coleoptera: Curculionidae: Sphenophorini). (A) Dorsal aspect of female. (B) Lateral view of male. (C) Lateral view of female.

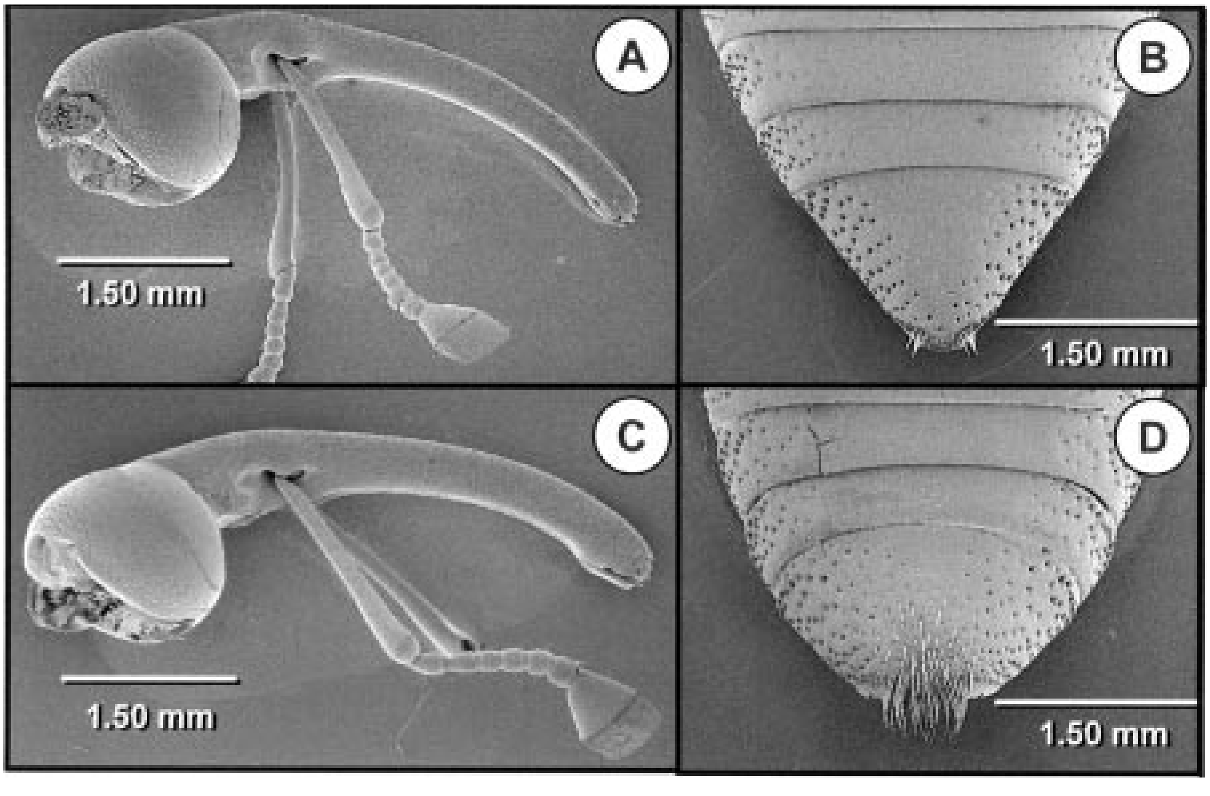


Fig. 5.9. *Metamasius hemipterus*, sexually dimorphic characters. (A) Lateral view of female head. (B) Ventral view of fifth abdominal segment of female. (C) Lateral view of male head. (D) Ventral view of fifth abdominal segment of male.

observations). *Metamasius inaequalis* appears to attack the pruned frond bases of African oil palm in Central and South America (Giblin-Davis *et al.*, 1996a; Pérez *et al.*, 1997). *Metamasius hebatatus* attacks frond bases of *Roystonea* and *Iriartea* (Vaurie, 1966).

The imagos of *M. hemipterus*, which can live for 60 days, are attracted to wounds due to rats, pruning, etc., where they oviposit an average of 500 eggs per lifetime (Castrillon and Herrera, 1980). Eggs hatch in about 4 days and larvae begin to feed. Larvae typically bore in the leaf bases, where they complete development in about 2 months, although they can also be found attacking the stem. Affected palms are often characterized by the production of an amber-coloured and gummy exudate and chewed plant tissue issuing from windows in the galleries at the bases of fronds, where they break prematurely (Colour Plate 15c, Fig. 5.10). The damage is rarely lethal. After about 7 weeks, larvae construct a fibrous pupal case, similar to that constructed by *R. cruentatus* (Woodruff and Baranowski, 1985). Pupae transform to imagos in about 10 days and may immediately break free of the cocoon or may remain within the cocoon until conditions are favourable for emergence (Woodruff and Baranowski, 1985).

The entomopathogenic nematode, *Steinernema carpocapsae* (the 'All' strain), was effective against the larvae but not the imagos of *M. hemipterus* in laboratory and field tests (Giblin-Davis *et al.*, 1996b). These bioassays also demonstrated that imagos of *M. hemipterus* were killed by labelled rates of a variety of commercial formulations of contact and systemic insecticides. In a field test with *Metamasius*-infested

Fig. 5.10. Damage by *Metamasius hemipterus*. (a) *Phoenix canariensis* × *Phoenix dactylifera* hybrid with drooping fronds due to damage to the petioles. (b) Galleries in cross-section of *M. hemipterus* in *P. canariensis* petioles, revealed when petioles were pruned, Florida. Photos by Forrest W. Howard.

P. canariensis, lindane and imidacloprid had the greatest effect on the percentage mortality of total weevils present per palm (> 60%), followed by *S. carpocapsae* (8×10^6 infective juveniles per palm, i.e. 51%) and acephate, which was statistically equal to the controls (14%). Control palms harboured over 200 *M. hemipterus* per palm in the petioles and stem periphery. Because of the potential for high weevil production per palm and the cryptic habitat of the boring stages, chemical insecticides and/or entomopathogenic nematodes must be applied frequently and over a long period of time for effective management (Giblin-Davis *et al.*, 1996b).

Natural enemies of *M. hemipterus* include ants of the genus *Tetramorium* and a complex of generalist predators, e.g. *Hololepta quadridentata* (Histeridae) and *Propagalerita bicolor* (Carabidae) (Peña *et al.*, 1995). The naturally occurring entomopathogenic fungus *Beauveria bassiana* is an important mortality factor for *M. hemipterus* in Florida and, under optimal conditions of high temperature and r.h., may occur as epizootics (Peña *et al.*, 1995). Reduction of cultural practices that wound the fronds or stems of susceptible palms should reduce damage caused by these weevils. Also, this weevil appears to be most damaging in consistently moist and shady situations.

The eastern-hemisphere palm-associated Sphenophorini have life histories similar to those of the western-hemisphere genera, attacking recently cut petioles and other wounds. *Temnoshoita quadrimaculata* (syn. *Temnoshoita quadripustulata*) is a weevil pest of bananas and of African oil palms in nurseries, those recently planted in the field and those in the early bearing stage (Lepesme, 1947; Asante and Kumar, 1986). In mature oil palm plantations, pruned palms had higher numbers of adults of this weevil than palms that were not pruned, and palms greater than 10 years of age were more susceptible than younger palms (Asante and Kumar, 1987). Inflorescences of older palms can be severely damaged, leading to significant tunnelling through both dead and living tissue near the point of entry. Damage includes premature withering of fronds and necrosis of the terminal shoot. Young palms can be killed by damage to the crown and apical meristem. Mated females lay 200–400 eggs singly into wounds after a 16-day preovipositional period. These hatch in about 3–4 days. The length of the larval phase ranges from 25 to 46 days. Pupation, which lasts from 5 to 12 days, occurs in the petioles. This weevil also attacks coconut palm and species of *Bactris, Livistona*, *Raphia* and *Roystonea.* Additionally, it attacks pseudostems of banana and sugar cane stalks (Lepesme, 1947; Asante and Kumar, 1986, 1987). In Ghana, imagos ranging in length from 8 to 15 mm, are dark brown, with two reddish spots on each elytron (i.e. so as to form a pattern of four dorsal spots). The genus *Temnoshoita*, reviewed by Marshall (1938), is morphologically close to members of the subgroup *Canalipes* of the western-hemisphere genus *Metamasius* and to members of the eastern-hemisphere genus *Rhabdoscelus*, except for the pygidium, which is very large in most species (Vaurie, 1966).

Predators, such as the ponerine ant *Paltothyreus* sp., unidentified tabanid fly larvae and a number of Reduviidae, were observed preying upon pupae and larvae of *T. quadrimaculata* (Asante and Kumar, 1986). Unidentified hymenopterous parasitoids were observed emerging from larvae of this weevil.

The New Guinea sugar cane weevil, *Rhabdoscelus obscurus*, is a damaging pest of sugar cane and of palms grown as ornamental plants (Fig. 5.11; Chang and Curtis, 1972; Napompeth *et al.*, 1972; Halfpapp and Storey, 1991). Symptoms are very similar to those described for other Sphenophorini, with characteristic production of a jelly-like substance from weevil-caused holes in frond bases and trunk. This weevil is about 10 mm long, tan- to dark brown-coloured with patterns of light and dark on the pronotum and elytra. Apparently, it is native to New Guinea. However, in the past 100 years, *R. obscurus* has been spread by humans in sugar cane south and east to Queensland (Australia), Polynesia and

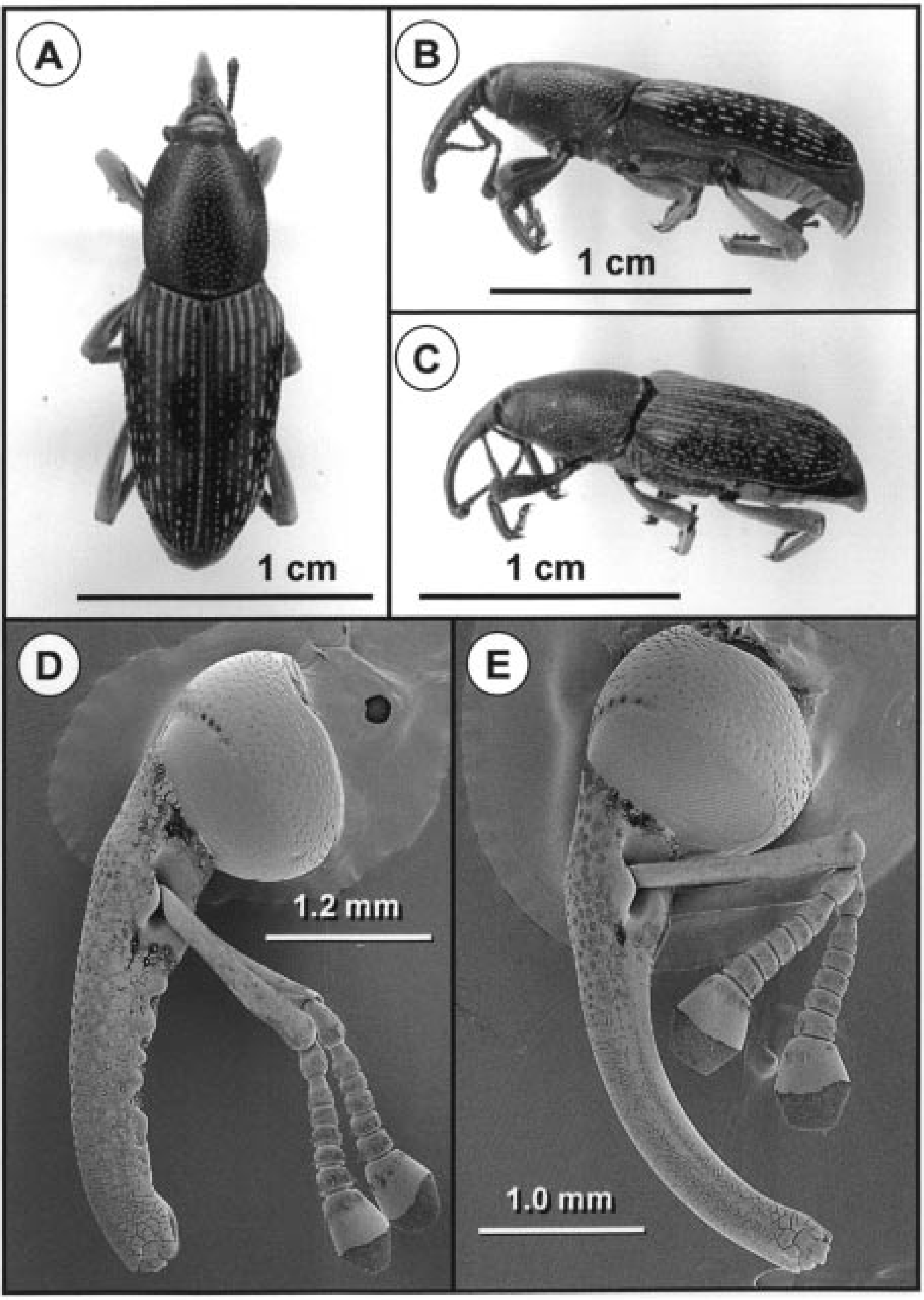


Fig. 5.11. *Rhabdoscelus obscurus* from Queensland, Australia (Coleoptera: Curculionidae: Sphenophorini). (A) Dorsal aspect of male. (B) Lateral view of male. (C) Lateral view of female. (D) SEM lateral view of male head. (E) SEM lateral view of female head.

Micronesia and north to the Hawaiian Islands (Chang and Curtis, 1972; Napompeth *et al.*, 1972; Halfpapp and Storey, 1991). *Rhabdoscelus obscurus* attacks healthy, damaged or stressed sugar cane stalks, pseudostems of bananas and *Strelitzia reginae* and crowns, sheaths or stems of palms, where the larvae bore and develop to imagos (Napompeth *et al.*, 1972; Halfpapp and Storey, 1991). This species is multivoltine and the life cycle takes about 13 weeks, with the egg, larval and pupal stages lasting about 6, 80 and 8–14 days, respectively (Lever, 1979). Recently, *R. obscurus* has been reported from 24 species of native and exotic palms, including coconut palm, *P. canariensis*, *Roystonea* spp. and *Hyophorbe lagenicaulis* (Halfpapp and Storey, 1991). Catastrophic primary infestations of *R. obscurus* in coconut palm were reported from Guam in the early 1960s (Bianchi and Owen, 1965). These apparent epizootics may have been caused by rapid population expansions in mature coconut palms damaged by earlier typhoons. In addition, *R. obscurus* is highly variable in morphology, colour and host preference and may not be one species (Bianchi and Owen, 1965). Its congener, *Rhabdoscelus asperipennis*, is injurious to coconut palms on certain islands in Micronesia (Ngesebus, Peleliu, Ngemelis and Aulong). This weevil is morphologically different from and larger than *R. obscurus* and causes damage similar to the Rhynchophorini (e.g. *Rhynchophorus*), with larval development in the rachides sometimes moving into the apical meristem and stem, causing the death of the palm. Infestations often occurred in 10-year-old coconut palms in regions of the plantation that were densely shaded with other vegetation (Bianchi and Owen, 1965). The Asiatic palm weevil *Rhabdoscelus lineaticollis* attacks seedlings of *Hyophorbe* in Taiwan (Ta *et al.*, 1998). There are no comprehensive keys to the species of *Rhabdoscelus*.

Cultural controls for *R. obscurus* in ornamental palms in Australia include: (i) not using sugar cane bagasse (which is attractive to weevils) in the potting medium or as a mulch; (ii) removing dead fronds to reduce harbourage sites; and (iii) painting pruned surfaces with acrylic paint to reduce the attractiveness of wounds (K.H. Halfpapp, personal communication). Chlorpyrifos has been effective for prophylactic treatment of seedling and older palms during active times of the year for *R. obscurus* in Australia: March–April, July–August and December–January (Brough *et al.*, 1994). A tachinid fly, *Lixophaga sphenophori*, has been used for classical biological control of *R. obscurus* in the Hawaiian Islands with some success (Beardsley, 1993) and in Queensland (Halfpapp and Storey, 1991). Other natural enemies include the histerids *Plaesius javanus* and *Platysoma abruptum*, the elaterid *Simodactylus* sp. and the rhagionid fly *Chrysopilus* sp. (Halfpapp and Storey, 1991).

It has long been known that fermented sap exuding from dead or wounded palms or moist fermenting tissue from palms, various fruits, sugar cane stalks and molasses (plus water) can be highly attractive to palm-associated members of the Dryophthorinae (Chittenden, 1902; Giblin-Davis *et al.*, 1996a). For example, peak attraction of *R. cruentatus* to chopped and fermenting *S. palmetto* crown and stem tissue occurs about 24–72 h after cutting, whereas cut surfaces of felled palms remain attractive for 35 days (Weissling *et al.*, 1992). Relatively dry palm tissue (e.g. stem of *Serenoa repens*) or molasses (without water) are less attractive to *R. cruentatus* and *M. hemipterus*, suggesting that volatile chemicals from fermentation of moist and stressed, damaged or dying host plant tissues with high sugar content provide olfactory cues to attract palm weevils (Giblin-Davis *et al.*, 1996a).

Laboratory and fieldwork with *R. obscurus* provided the first evidence that males of palm and sugar cane weevils (Dryophthorinae) produce male- and female-attracting aggregation pheromones for intraspecific communication (Chang and Curtis, 1972). Subsequently, male-produced aggregation pheromones have been demonstrated and identified for many palm weevils in the Dryophthorinae (e.g.

D. borassi, R. palmarum, *R. cruentatus*, *R. phoenicis*, *R. ferrugineus*, *R. vulneratus*, *M. hemipterus, M. inaequalis and R. obscurus*) (references for each cited in Giblin-Davis *et al.*, 1996a). Pheromones that have been identified so far are eight-, nine- or ten-carbon, methyl-branched, secondary alcohols. (4*S*, 5*S*)-4-Methyl-5-nonanol (ferrugineol) is the major aggregation pheromone for *R. ferrugineus, R. vulneratus, R. bilineatus, M. hemipterus* and *D. borassi* and a minor component for *R. palmarum*. (5*S*, 4*S*)-5-Methyl-4-octanol (cruentol), (3*S*, 4*S*)-3-methyl-4-octanol (phoenicol) and (4*S*, 2*E*)-6-methyl-2-hepten-4-ol (rhynchophorol) are the main aggregation pheromones for *R. cruentatus, R. phoenicis* and *R. palmarum*, respectively. Pheromone is apparently produced by two modified salivary glands in the prothorax of males of *R. palmarum* and passed to the mouth for regurgitation and distribution on the male's rostral setae or into the digestive tract and out to the environment in the faeces (Sánchez *et al.*, 1996, 1998). Plant kairomones strongly enhance pheromone attractiveness.

Generally, 3 mg day^{-1} of synthetic pheromone plus insecticide-treated plant tissue constitutes a highly attractive trap bait. Typically, the (*S*)-enantiomer or (*S, S*)-stereoisomers are produced by the weevils and elicit a behavioural response. Inexpensive racemic blends of synthetic pheromones can be used, because the non-natural stereoisomers present in synthetic pheromones do not interfere with weevil attraction. For experimental and commercial use, racemic pheromone with an indicator dye is hermetically sealed in a polymer membrane release device (ChemTica International, San José, Costa Rica) for slow and constant pheromone dissemination (~3 or 7 mg day^{-1} at 25°C for 2–3 months (Oehlschlager *et al.*, 1995a, b).

Lethal traps baited with aggregation pheromones alone or host kairomones alone are not very attractive to palm weevils, but in combination synergize attractiveness eight- to 20-fold (Giblin-Davis *et al.*, 1996a). These weevils appear to be opportunistic oligophages, responding to volatile substances from early fermentation of wounded or stressed hosts and recruiting conspecifics over longer distances with male-produced aggregation pheromones (Jaffe *et al.*, 1993; Weissling *et al.*, 1994b). Some host kairomones may also have long-range attraction potential (Gunawardena *et al.*, 1998).

Potential kairomones identified by electroantennograms from fermenting palm or sugar cane tissue include the 'palm esters', namely, ethyl acetate, ethyl propionate, ethyl butyrate and ethyl isobutyrate for *R. phoenicis, R. cruentatus, R. palmarum, R. bilineatus, R. ferrugineus* and *R. vulneratus* (Gries *et al.*, 1994a). Ethyl propionate (30 mg day^{-1}) was the only palm ester tested that synergized field attraction of *R. phoenicis* to (±)-phoenicol (Gries *et al.*, 1994a). Ethyl acetate, ethyl propionate, ethyl butyrate, ethyl isobutyrate, ethyl (*S*)-(–)-lactate and ethanol at various release rates synergized field attraction of *R. cruentatus* to (±)-cruentol (Giblin-Davis *et al.*, 1994a), and ethyl acetate of unknown release rate enhanced field attraction of *R. palmarum* to (±)-rhynchophorol (Jaffe *et al.*, 1993). Each of the fermenting sugar cane volatiles – ethyl acetate (30 mg day^{-1}), ethyl propionate (20 mg day^{-1}) and ethyl butyrate (20 mg day^{-1}) – equally enhanced field attraction of *M. hemipterus* to metalure (racemic 4-methyl-5-noranol and 2-methyl-4-heptanol in an 8:1 ratio) (Pérez *et al.*, 1997). None of the palm esters tested so far with pheromone have been as effective as palm or sugar cane tissue in enhancing pheromonal attractiveness to *Rhynchophorus* species (Jaffe *et al.*, 1993; Giblin-Davis *et al.*, 1994a, 1996a; Gries *et al.*, 1994a; Pérez *et al.*, 1997), suggesting that there may be additional unknown palm kairomones or that the ratios of tested components were not effective. Peak field attraction of chopped palm or sugar cane tissue within 2–5 days indicates proportional changes in volatile chemicals from fermentation over time, affecting optimal attraction of weevils to traps (Weissling *et al.*, 1992; Hallett *et al.*, 1993; Gries *et al.*, 1994a). Proportional changes in volatile chemicals from fermenting or fermented palm sap can be attributed to the abiotic conditions and microflora present (Samarajeewa *et al.*, 1981; Nagnan *et al.*, 1992).

Ethyl acetate released at 400–900 mg day^{-1} significantly enhanced attraction of *M. hemipterus* to metalure, sugar cane or both (Giblin-Davis *et al.*, 1994a, 1996c). Because ethyl acetate at 400–1600 mg day^{-1} is not repellent to *R. cruentatus* or *M. hemipterus* (Giblin-Davis *et al.*, 1994a, 1996c), it may be used to increase the 'active space' of a trap, improve short-range orientation towards weevils or arrest them near traps. In Australia, ethyl acetate similarly affects *R. obscurus* (R.M. Giblin-Davis, unpublished). Ethyl acetate release rates of 400–1600 mg day^{-1} may seem high but may be competitive with levels produced by large damaged palms (Giblin-Davis *et al.*, 1996a). When ethyl acetate is perceived by male *R. palmarum*, it stimulates pheromone production (Jaffe *et al.*, 1993; Sánchez *et al.*, 1996). If this is true for *M. hemipterus* or other Dryophthorinae, high rather than low relative release of ethyl acetate from traps could induce natural pheromone production by nearby weevils.

Sugar cane is one of the cheapest and best sources of kairomones to enhance attraction of palm weevils to pheromone-baited traps. Other tissues, such as pineapple, *S. palmetto* or molasses plus water, were equally synergistic in trapping trials with *R. cruentatus* and *M. hemipterus* (Giblin-Davis *et al.*, 1994a, b, 1996a). African oil palm stem cubes, molasses on a sponge or molasses-impregnated mesocarp was not as effective as sugar cane for *R. palmarum* (Oehlschlager *et al.*, 1993a). Increasing quantities of sugar cane or host tissue generally increases the attractiveness of the pheromone-baited trap (Oehlschlager *et al.*, 1993a, b; Giblin-Davis *et al.*, 1994b, 1996a), but optimal quantities should be based on a cost–benefit analysis.

Capture of neotropical palm weevils in lethal traps baited with aggregation pheromones of heterospecifics suggests synomonal pheromone (benefit to both) activity. For example, *D. borassi, M. hemipterus* and *M. inaequalis* are attracted to the aggregation pheromone of *R. palmarum. Metamasius inaequalis* also responds to the aggregation pheromone of *M. hemipterus* (Giblin-Davis *et al.*, 1996a). In October 1993, two lethal pitfall traps (Giblin-Davis *et al.*, 1994b) baited with devices releasing 3 mg day^{-1} each of ferrugineol, 2-methyl-4-octanol and 2-methyl-heptanol for 10 days at Rancho Grande, Rondonia, Brazil, captured seven different species of weevils, including six species of Sphenophorini: 25 specimens of *M. hemipterus hemipterus*, five specimens of *Metamasius cerasinus*, three specimens of *M. cinnamominus*, one *Metamasius tuberculipectus*, one *M. tectus*, 13 specimens of *Alloscolytoproctus peruanus* and one specimen of the Cossoninae, *Stenommatus* sp. (C. O'Brien and R.M. Giblin-Davis, unpublished). Cross-attraction of sympatric weevils may have evolved because it is adaptive in overcoming a palm's defence, allowing time-efficient use of a temporarily suitable resource. Minor volatile components may serve as intra- or interspecific semiochemicals mediating resource partitioning. Niche divergence and larval cannibalism in *R. palmarum, M. hemipterus, D. borassi* and *M. inaequalis* may reduce interspecific competition in a host occupied by multiple species of weevils. Some of these compounds may also serve as weevil host indicators for predatory insects. Further work with pheromone combinations in palm weevils could result in an optimally designed trap for monitoring or mass-trapping multiple palm weevil species where they co-occur.

Rhynchophorus spp. are harboured in the crowns of healthy and wounded palms (Weissling and Giblin-Davis, 1993) and moist fermenting garbage (Chittenden, 1902). The cryptic behaviour of *R. cruentatus* may be an adaptation for conserving water. This weevil has high cuticular permeability, resulting in desiccation in dry environments (Weissling and Giblin-Davis, 1993). In a bioassay with choices between low- and high-r.h. environments, *R. cruentatus* preferred high r.h., suggesting that this weevil had hygroreceptors that locate moist harbourage sites (Weissling and Giblin-Davis, 1993). High r.h. is probably necessary for semiochemical-baited traps and can be provided by using soapy water, pesticide-treated sugar cane or palm or wet sponges or towelling.

Different trap designs have been tested to optimize the capture of palm weevils. Large bucket traps with a good surface area placed on the ground or attached to palm trunks are available (Oehlschlager *et al.*, 1993b). Captured weevils are killed with pesticide (i.e. carbaryl, carbofuran, lannate)-treated sugar cane (Oehlschlager *et al.*, 1993a) or with soapy water in the bottom of traps (Weissling *et al.*, 1994b). *Rhynchophorus* species usually fly into the vicinity of a trap to land on fronds, the palm trunk or the ground and then walk into the trap (Oehlschlager *et al.*, 1993a). *Metamasius hemipterus* is smaller and more agile in flight and, unlike large species of *Rhynchophorus*, may not require a large landing surface. A lethal pitfall trap (Giblin-Davis *et al.*, 1994b) appears to be most effective for *M. inaequalis*, suggesting that these weevils may occupy pruned or fallen fronds or petioles at the base of the stem at or below the soil surface. Cut palms baited with pheromone and treated with insecticide can also be used as effective traps (Moura *et al.*, 1997).

In trap-height studies with *R. palmarum* (Oehlschlager *et al.*, 1993a, b) and *M. hemipterus* (Giblin-Davis *et al.*, 1996a), traps associated with possible landing areas were superior to suspended traps. For example, traps on the ground captured more *R. palmarum* than those that were pole-suspended 1.7 or 3.3 m above ground. In contrast, traps attached to palm trunks at 0, 1.7 and 3.3 m heights were equally effective (Oehlschlager *et al.*, 1993a, b). Unlike *R. palmarum, M. hemipterus* was captured equally in ground traps and pole-suspended traps (1 m) (Giblin-Davis *et al.*, 1996a).

Trap silhouette and colour have not yet been intensively studied, but colour is apparently not a critical parameter of an optimal trap design for *M. hemipterus* or *R. palmarum* (Giblin-Davis *et al.*, 1996a).

Dryophthorinae: Diocalandrini

Two palm-associated species of the Diocalandrini cause premature yellowing of palm fronds and emergence holes in new and old fronds and premature shedding of fruits. The palm-weevil borer, *Diocalandra frumenti*, is a small (6–8 mm long), shiny black weevil with four red to brownish-yellow to blackish-brown spots on the elytra. The closely related *Diocalandra taitensis* is also small (6–7 mm long) and is black with dark reddish markings on the thorax and elytra. *Diocalandra taitensis* is known to attack only coconut palms, is distributed in New Guinea, Solomon Islands, Melanesia and Polynesia and was introduced into the Hawaiian Islands and Madagascar. Severe losses of young fruits of coconut palm have been reported from Tahiti and the Line Islands (Kiribati). Stem damage at all heights has been reported from Madagascar (Lever, 1979). *Diocalandra frumenti* can cause the death of mature specimens of *P. canariensis* in Queensland and has been recorded from coconut palm, African oil palm, *Areca*, *Nypa*, *Borassus* and five other species of palms (Lever, 1979; K.H. Halfpapp, personal communication). It is reported from Zanzibar (Tanzania), India, Sri Lanka, Thailand, the Malay Peninsula, Indonesia, New Guinea, Solomon Islands, Guam, northern Queensland (Australia) (Lever, 1979), Taiwan (Ta *et al.*, 1998) and Ecuador (Wibmer and O'Brien, 1986). Eggs of both species may be deposited in inflorescences, the base of the petioles or peduncles or in cracks near adventitious roots at the base of the stem. Larvae eclose about 4–8 days later and bore into tissue, causing a gummy exudate near the gallery entrance. The larval stage, lasting 8–10 weeks, can damage any parts of the palm, including roots, fronds and fruit stalks, and may cause premature fruit drop. In frond infestations, larvae typically bore from the petiole distally. The pupal stage, which occurs without a cocoon, lasts 10–12 days. In some cases, severe damage to the crown can cause the death of the palm. There are no registered pesticides for this weevil in northern Queensland. Cultural practices are similar to those recommended for *R. obscurus* (K.H. Halfpapp, personal communication). Painting wounds with tar and covering adventitious roots at the stem base with soil have also been recommended (Lever, 1979). The same generalist predators of *R. obscurus* attack *Diocalandra* species (Lever, 1979).

Dryophthorinae: Orthognathini

Members of the weevil tribe Orthognathini are unique in that their mandibles are not clasping or pincer-like with smooth inner surfaces and the mouth-parts are generally hidden by a ventral plate and by the mandibles (Fig. 5.13). Palm-associated Orthognathini include two species of *Mesocordylus* of the tropics of the western hemisphere (Vaurie, 1970b) and seven species of *Rhinostomus* of the western- and eastern-hemisphere tropics (Vaurie, 1970a, 1977). *Mesocordylus striatus* and *Mesocordylus subulatus* have been recovered from palms or their flowers (Vaurie, 1970b). Members of the genus *Rhinostomus* are nocturnal. They attack old, damaged, fallen or dead palms. The imagos can be separated from related groups by their thicker outward-curving, laterally trilobed mandibles and by features of the legs, antennae and pronotum (Figs 5.12 and 5.13). The eyes of adult *Rhinostomus* nearly touch when viewed from above (Vaurie 1970a). Males of the coconut palm weevil, *Rhinostomus barbirostris* (Figs 5.12A, B and 5.13), differ greatly from females (Fig. 5.12C) and possess very long, outstretched beaks, with reddish-gold hairs emerging from all sides, giving the head the appearance of a bottle-brush. These weevils are black and vary in length from 14 to 58 mm long. In some species, the black elytra have white or yellowish spots or stripes. The long front legs and large size of many specimens make them interesting weevils to watch. The

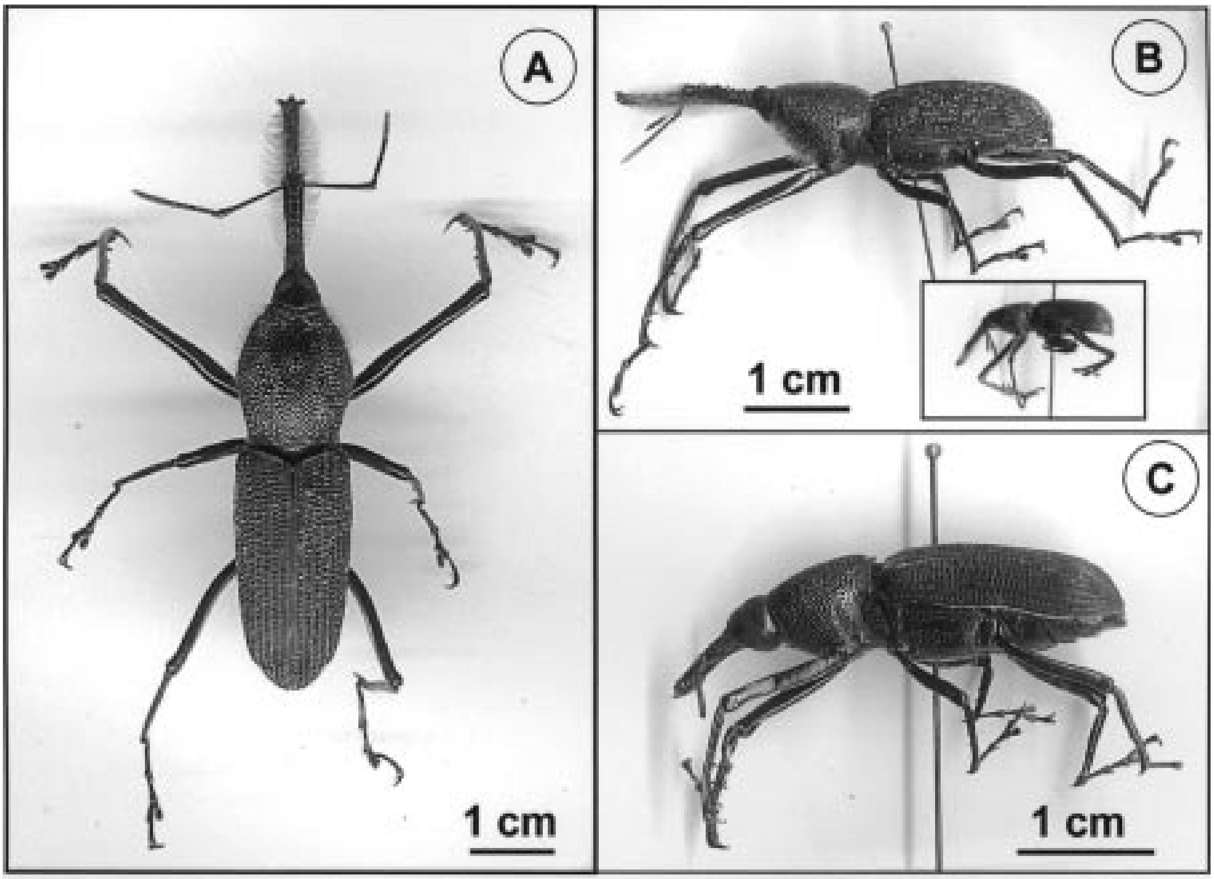


Fig. 5.12. *Rhinostomus barbirostris* (Coleoptera: Curculionidae: Orthognathini). (A) Dorsal aspect of a large male. (B) Lateral view of a large male; inset, a small male. (C) Lateral view of female.

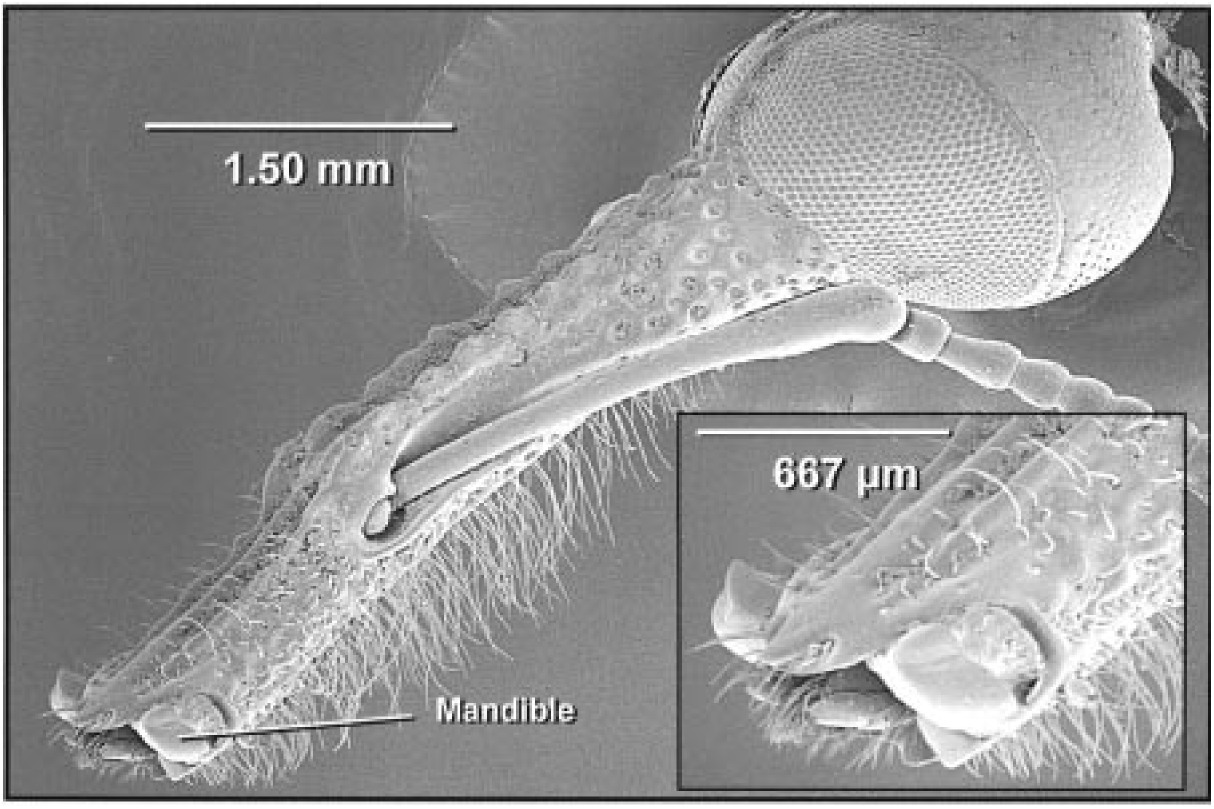


Fig. 5.13. *Rhinostomus barbirostris* (Coleoptera: Curculionidae: Orthognathini). SEM of a small male's head; inset, close-up of characteristic mandibles.

genus was revised (Vaurie, 1970a) and there are good keys available for *Rhinostomus* (Vaurie, 1970a, 1977).

The two most important species are *R. barbirostris*, occurring from southern Mexico south throughout Central America, Trinidad and South America (except Chile), and *Rhinostomus niger*, occurring throughout tropical Africa, Madagascar and the Comoro Islands (Vaurie, 1970a). *Rhinostomus quadrisignatus* occurs in South America from French Guiana and eastern Brazil to western Brazil, Ecuador and Peru. *Rhinostomus thompsoni* is distributed from Panama south through Colombia to Ecuador. Three species are distributed on islands: *Rhinostomus oblitus* in Cuba and Hispaniola, *Rhinostomus scrutator* in Hispaniola and possibly Montserrat, and *Rhinostomus meldolae* from Asia (Vaurie, 1970a).

Hosts for *R. barbirostris* include coconut palm, African oil palm, four species of *Syagrus* (including the popular ornamental palm, *S. romanzoffiana*) and three species of *Attalea* (Vaurie, 1970a). Hosts for *R. niger* include coconut palm, African oil palm and a rattan palm, *Raphia vinifera* (Vaurie, 1970a). *Rhinostomus oblitus* has been reported from coconut palm and *Roystonea regia* (Vaurie, 1970a).

Rhinostomus generally chooses old or otherwise stressed palms. Females come out of hiding from the crown at night and locate hardened areas of the trunk, where they bore a 4-mm-diameter hole, using a combined punchlike action of the unusual mandibles and rostrum (Fig. 5.12). The mandibles have three lateral teeth and are contoured, with a concavity on the outside and a convex inner surface, so that they never fully come together (Fig. 5.13). The tip of the beak with the mandibles closed is forced down into stem tissue and then opened and retracted to enlarge the hole. An alternative explanation is that the opening and closing of the mandibles could be orchestrated, like a swimmer's breast-stroke, under pressure from the beak, allowing the weevil to dig increasingly deeper into hard tissue (Vaurie, 1970a). The female deposits a white, round, 2-mm-diameter egg into the hole and then secretes a cream-coloured cover, resembling a scale insect. The female will also use damaged areas caused by a weevil, *Homalinotus coriaceus* (Cholinae), as oviposition sites. The apodous larvae are recurved, with a melanized pronotum and yellow spots and an abruptly truncated last segment. They grow to 20–50 mm long by 7–20 mm wide. In Ecuador, they serve as a food source for humans (see Box 5.1). Nutrition plays an important role in the size of larvae and resulting imagos (Fig. 5.12B). Larvae tunnel horizontally inward. Sometimes frass and juice are expelled from the stem at the beginning of larval boring, revealing symptomatic stains. As the larvae grow, they work their way upwards in the stem, until they create a tunnel to the stem periphery, where they pupate (Bondar, 1940). There are conflicting reports about whether a cocoon composed of palm tissue fibres is made (Vaurie, 1970a). Stems riddled with their galleries may be toppled by strong winds. The life cycle is estimated at less than 3 months (Vaurie, 1970a) to as long as 6 months (Bondar, 1940). The imagos are present throughout the year in Brazil, but are more common and damaging from October to March (Bondar, 1940).

There are several natural enemies for *Rhinostomus*, including histerid beetles, ants, parasitic insects and woodpeckers (Vaurie, 1970a). Management should be focused on phytosanitation. The removal and destruction of old, stressed and dying palms (including, in tropical America, red-ring-diseased palms) reduce breeding sites and the possibility that large populations will develop. During renovation of unproductive African oil palm and coconut palm plantations in Costa Rica, large populations of *R. barbirostris* can develop on herbicide-poisoned or bulldozed palms that are not subsequently treated with insecticides (Carlos M. Chinchilla, personal communication).

Cholinae: Cholini

The weevil subfamily Cholinae contains some of the largest and most fanciful weevils in the world (Vaurie, 1973). They are black to brownish weevils, with tuberculated or smooth surfaces, which are often patterned with white, grey, brownish or yellowish scales or setae (Fig. 5.14). The pronotum is usually wider than long and most species are about 20 mm long (range 8–50 mm) (Vaurie, 1973). As in the Dryophthorinae, larvae of the Cholinae bore into stems and branches of monocotyledons (palms, grasses, orchids and bromeliads). This contrasts with the majority of the morphologically allied subfamily Hylobiinae, which live in pulp or seed of the fleshy fruits of dicotyledons (Vaurie, 1973). Little is known about the life history of most Cholinae, except a few species of the genera *Homalinotus, Ameris* (syn. *Amerrhinus*) and *Odontoderes*, which are borers in palms, and the species of *Cholus*, which attack orchid bulbs. The palm-associated Cholinae are members of the tribe Cholini, which can be distinguished from the sister tribe Rhinastini by the first tarsomere, which is smaller than the second and narrowly constricted at the base (Vaurie, 1973). There are 21 species of *Homalinotus*, of which five (*H. coriaceus* (Fig. 5.14A, B)*, H. deplanatus, H. nodipennis, H. porosus* and *H. validus*) have been reported as pests of various genera of palms, most notably coconut palm (Bondar, 1940; Lepesme, 1947; Vaurie, 1973; Wibmer and O'Brien, 1986; Ferreira *et al.*, 1994). Four more *Homalinotus* species (*H. depressus, H. histrix, H. lherminieri* and *H. pectinis* (Fig. 5.14C)) are known to be associated with palms (Vaurie, 1973; R.M. Giblin-Davis, unpublished). The genus is distributed mostly in South America. Three species (*Homalinotus dorsalis, H. pectinis* and *H. validus*) also occur in Central America, and three species in Trinidad and the Lesser Antilles (*H. depressus, H. lherminieri* and *Homalinotus umbilicatus*) (Vaurie, 1973). Most species of *Homalinotus* are distributed in the

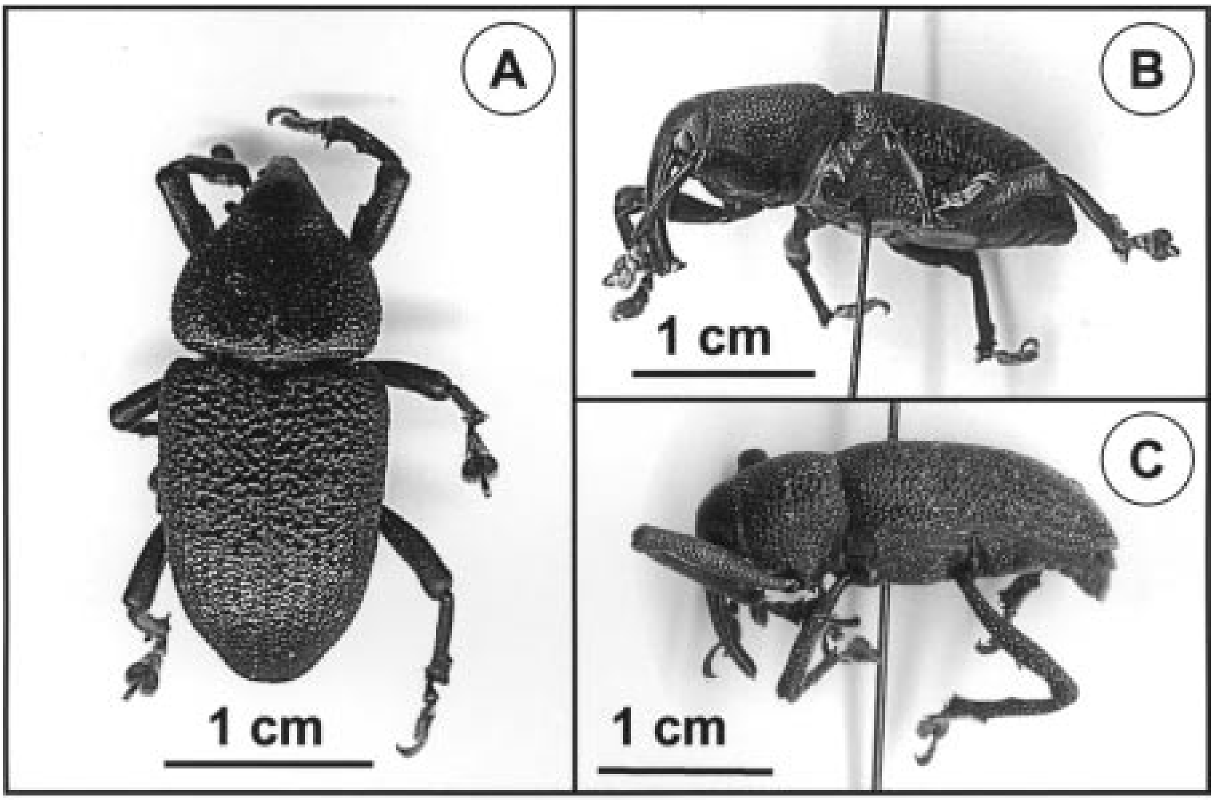


Fig. 5.14. *Homalinotus coriaceus* (Coleoptera: Curculionidae: Cholinae) from Brazil, (A) dorsal and (B) lateral views. (C) *Homalinotus pectinus* from Colombia, lateral view.

Amazon River basin west to the rivers of Peru, south-west to Bolivia and south to Paraguay and north-eastern Argentina. They have been reported in all of the countries of South America, except Chile and Uruguay (Vaurie, 1973). Vaurie (1973) presented an excellent taxonomic revision of the genus, with species keys.

Most of what is known of the ecology of *Homalinotus* is extrapolated from observations of *H. coriaceus* in Brazil (Colour Plate 13e, Fig. 5.14A, B; Bondar, 1940; Ferreira *et al.*, 1994). It has been considered the most serious pest of coconut palms in Brazil (Dalva Luiz de Queiroz Santana, personal communication). The behaviour and ecology of *H. pectinis* in Colombia are similar (R.M. Giblin-Davis, unpublished). These weevils are borers of floral peduncles of coconut palm. The native hosts for *H. coriaceus* are *Syagrus coronata, Attalea funifera, Attalea piassabossu, Attalea burretiana* and *Diplothemium caudescens*, in which the weevils bore the rachis of older fronds. Coconut palm, when present, appears to be a preferred host because of its relative succulence. *Homalinotus* species are very secretive and large numbers can easily go undetected. The most obvious damage in coconut palm is feeding damage on the peduncle, buds of female flowers and young fruit and abortion of fruits. *Homalinotus coriaceus* also causes damage to old fronds, new inflorescences and the trunk. In young coconut palms, prior to fruiting, eggs are laid in the frond sheath, where the larvae bore and develop, eventually descending to the stem, where they are protected by the frond sheaths. The larva creates a cocoon of fibre and pupates in a superficial gallery in the surface of the stem. In older fruiting palms, eggs are laid in the floral peduncles, where larvae bore and then descend to the trunk. Larval damage to the fruiting stalk undermines structural integrity and nutritional flow, causing abortion of fruit and peduncle. Older fronds break off prematurely. The imagos can live without food for about a month, and have longevity approaching 2 months (Bondar, 1940; Vaurie, 1973). Damage from *Homalinotus* is not fatal, but can create wounds that attract more damaging pests, such as *Rhynchophorus, Dynamis* and *Rhinostomus*. Sanitation (frequent inspection of palms and removal of infested infructescences and fronds) is important in managing *H. coriaceus*. Malathion applied to the bunches and leaf bases at 3-month intervals was highly effective in reducing populations of this weevil (Ferreira *et al.*, 1994).

Two other genera in the Cholinae are associated with palms; (i) *Ameris ynca* (syn. *Amerrhinus ynca*), which attacks the inflorescences and petioles of coconut palm, *Copernicia cerifera* (the economically important carnaúba wax palm), *Syagrus coronata, Syagrus picrophylla, D. candescens* and other species of palms and is distributed in Brazil, Peru, Argentina, Paraguay and Bolivia (Bondar, 1940; Vaurie, 1975); and (ii) *Odontoderes transversalis* (syn. *Odontoderes bondari*), which breeds in the petioles and fronds of coconut palm and is distributed in eastern Brazil (Vaurie, 1974). The biology and control of *A. ynca* are discussed by Ferreira *et al.* (1994). The species is considered one of the more serious pests of coconut palm in Bahia State, Brazil (Joana Maria Santos Ferreira and Dalva Luiz de Queiroz Santana, personal communications). The larvae make galleries of 6–8 mm in diameter and 30–40 cm long. The galleries become packed with frass, some of which becomes mixed with sap, exudes from the gallery openings and falls on to petioles and into leaf axils. The petiole becomes weakened and breaks easily. Pruning of infested fronds may reduce infestations in plantations (Ferreira *et al.*, 1994). See Vaurie (1974, 1975) for taxonomic descriptions and keys to these species and Wibmer and O'Brien (1986) for nomenclatural clarification.

Baridinae: Madarini

The Baridinae are usually small black weevils (3–5 mm long), with long, curved rostra whose larvae bore into the immature male and/or female florets of palms (Bondar, 1940). Species of tropical America in the tribe Madarini attacking palms include *Parisoschoenus obesulus*, *Parisoschoenus expositus* and other species of that genus, *Microstrates ypsilon*, *Microstrates bondari* and *Tonesia melas* (Bondar, 1940; Ferreira *et al.*, 1994). In Coto, Costa Rica, large numbers of *P. expositus* are commonly recovered from freshly cut surfaces of African oil palm fronds, where they can undergo their life cycle (C.M. Chinchilla and R.M. Giblin-Davis, unpublished). *Parisoschoenus obesulus* prefers young tender tissue, and larvae often eat the mesocarp of female florets of coconut palm (Bondar, 1940).

Baridinae: Centrinini

Centrinini are similar in size, colour and appearance to Madarini, but palm-associated species are often covered with setae, as is *Palmocentrinus lucidulus*, or with punctation, as is *Palmocentrinus punctatus* (Bondar, 1940). *Palmocentinus lucidulus* larvae bore the floral rachides, causing abortion of female florets (Bondar, 1940). Other palm-associated species in this tribe include *Dialomia discreta* (Bondar, 1940) and *Limnobaris calandriformis*, which can be recovered in large numbers from the freshly cut surfaces of African oil palm fronds in Colombia and has been suggested as a possible vector of red-ring nematode (Calvache *et al.*, 1995).

Erirhininae: Derelomini

Palm-associated Derelomini are usually minute to small, yellowish-brown insects. Most are 1.0–2.5 mm in length. The largest is 8 mm long. They are oligolectic borers of the male flowers and visitors of female flowers of palms, in what may be a highly co-evolved mutualistic system of pollination for food (O'Brien and Woodruff, 1986). Some species bore in palm spathes. There are potentially hundreds of species of these palm-associated borers to be studied and described (Charles O'Brien, unpublished).

Anchylorhynchus trapezicollis occurs in Brazil (Bondar, 1940; Vaurie, 1954; Wibmer and O'Brien, 1986). *Elaeidobius* is a genus of the eastern hemisphere. *Elaeidobius subvittatus* (14-day life cycle) and *Elaeidobius kamerunicus* (Fig. 4.3) (21-day life cycle) are native to Africa and major pollinators of African oil palm. They have been introduced into South-East Asia and the Americas to enhance pollination of this palm (see Chapter 4). There are two other species that are involved in pollination of African oil palm in Africa: *Elaeidobius singularis* (life cycle of 8 days) and *Elaeidobius plagiatus* (life cycle of 14 days) (Mariau and Genty, 1988).

Petalochilinae

Petalochilus lineolatus (syn. *Petalochilus attaleae*) is similar in size and colour to the Baridinae. It is associated with the flowers of *A. funifera* (Bondar, 1940; Vaurie, 1954). *Petalochilus gamellus* adults were collected from pupal cells in the flower spathes of a spiny palm in Suriname (Charles O'Brien, unpublished).

Scolytinae and Platypodinae

Ambrosia beetles (Scolytinae and Platypodinae) are small (< 5 mm long) derived weevils, usually without a rostrum (Fig. 5.15). The larvae are similar in appearance to the larvae of other weevils, in that they are grublike, apodous and broadly C-shaped, and are white to cream-coloured, with a well-developed head capsule. Adult ambrosia beetles look superficially like powder-post beetles but can be distinguished from them because they possess elbowed antennae, with a club, and four visible tarsomeres. Most Scolytinae are either: (i) true bark beetles, which feed on phloem tissue beneath the bark; or (ii) ambrosia beetles, which do not feed on wood but form galleries in it, in which they cultivate specific fungi, which serve as their food source (Solomon, 1995). Of the Scolytinae, the ambrosia beetles are probably the best adapted to palm stems, because of their lack of reliance upon specific plant tissues. Monocotyledons, such as palms, have small vascular bundles enclosing phloem and xylem elements,

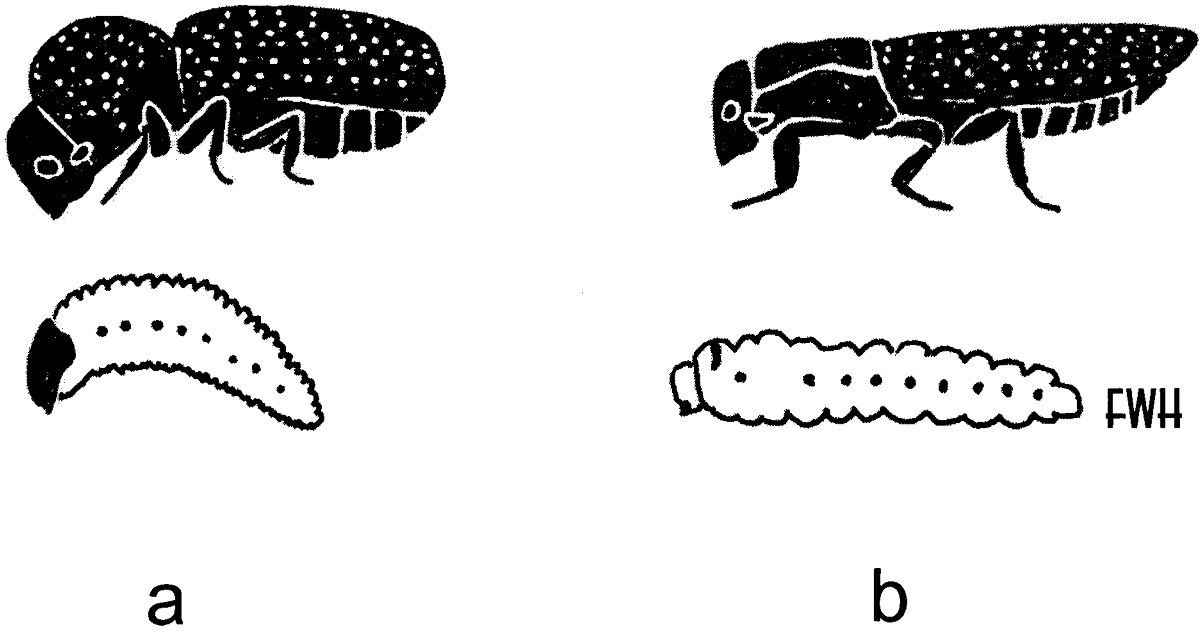


Fig. 5.15. General characteristics of ambrosia beetles (Coleoptera: Curculionidae) that bore in palm stems. (a) In Scolytinae adults, the head is concealed from above by the pronotum, and the larvae are C-shaped. (b) In Platypodinae, the head is visible from above, and the larvae are rectilinear. Drawings by Forrest W. Howard.

which are distributed throughout stem tissue (Fig. 1.12). In contrast, in dicotyledons, the phloem tissue occurs as a layer under the bark. Platypodinae are tropical and subtropical ambrosia beetles. Some ambrosia beetles use the stem tissue of palms for their galleries, while true bark beetles, which feed on phloem, are not adapted to palms, because of the lack of aggregated phloem tissue.

These yellowish to reddish-brown beetles are tiny (usually 1.5–3.0 mm long). The imagos bore into the stem and overwinter (in temperate climates) in brood chambers. In the spring, some adult females mate with apterous males and emerge at night to find new suitable hosts. An unmated female can produce two to three haploid males, which she mates with to produce female progeny. Other females do not leave the host and continue to reproduce until the host is no longer acceptable, often extending parental galleries. Single foundress females create new entrance galleries in a new host and are often joined by other females. Entrance and exit holes in the palm stem and petioles are usually about 1 mm in diameter, with abundant powder-like frass exuding from the hole (Colour Plate 14f). Galleries are created relative to moisture levels and tissue hardness, regardless of tissue depth. In palms, galleries tend to run arbitrarily through most of the lower stem tissue (Fig. 5.16). Females deposit eggs near the ends of galleries in groups of two to six, which hatch in 6–10 days. Adult females usually have a specialized structure, the mycetangium, for storing and carrying fungi to introduce into new galleries. These yeast-like fungi (*Ascomycetes*: *Endomycetales*) are cultivated by imagos within their tunnels and serve as food (ambrosia) for larvae and imagos. The larvae do not make cocoons but pupate freely in the galleries. The life cycle takes about 2–4 weeks (Lever, 1979; Solomon, 1995).

Entomologists occasionally receive enquiries from growers, who observe ambrosia-beetle damage in one or several palms and are concerned that the beetles might be primary pests. But, although they have been alleged to be primary pests in some circumstances (Paine, 1934; Mahindapala and Subasinghe, 1976), a tenet of entomology is that ambrosia beetles are almost always secondarily associated with dying trees, and this applies to palms. This damage can be prevented by good horticultural practices. Once

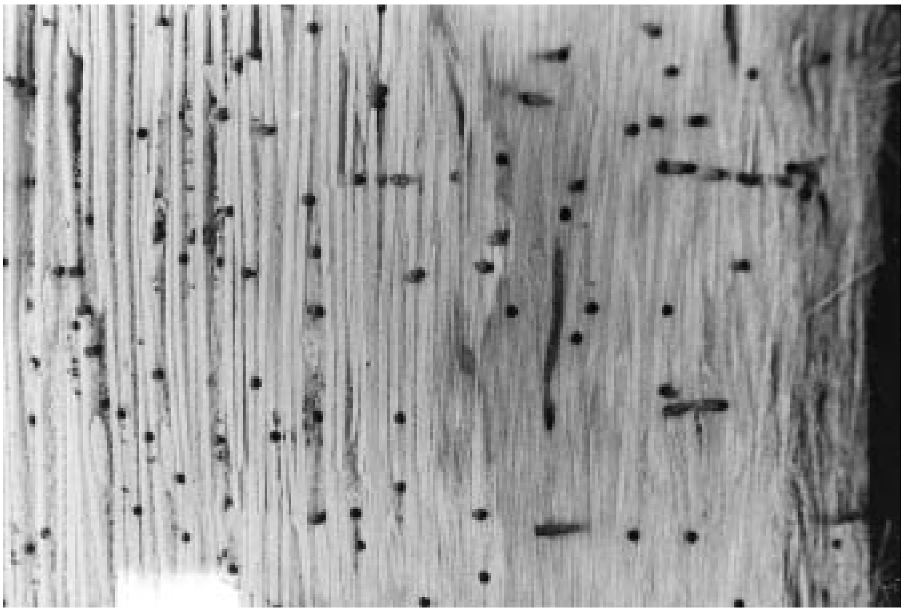


Fig. 5.16. Galleries of ambrosia beetles in stem of *Washingtonia robusta*. Photo by Forrest W. Howard.

ambrosia-beetle damage is seen in the stems, controlling the beetles would provide little, if any, benefit to the palm.

A cosmopolitan ambrosia beetle, *Xyleborus ferrugineus*, is one of the most widely distributed and economically important ambrosia beetles in the world. It occurs throughout much of North America, Mexico, Central and South America, tropical Africa, South-East Asia, the Hawaiian Islands, Micronesia and Australia. It attacks more than 180 species of dying, unthrifty, cut and broken trees, including palms in the tropics (Solomon, 1995). It is most damaging to logs left in the forest or in temporary storage. It is also an alleged pest of coconut palm and a vector for the wilt disease of cacao. *Xyleborus perforans*, widely distributed throughout warm regions, was recorded as a secondary pest of coconut palms in the Seychelles and Jamaica. Its alleged role as a primary pest in Fiji (Paine, 1934) may be questioned. The oak–hickory ambrosia beetle, *Xyleborus affinis*, is a cosmopolitan species that attacks more than 250 species of trees and palms (Solomon, 1995). *Platypus parallelus* is a tropical species that also attacks many kinds of trees. These latter two species are the most common beetles recovered from stems of dead or weakened palms in the records of the Florida State Collection of Arthropods (Michael Thomas, personal communication).

Ambrosia beetles probably use semiochemicals to find stressed palms that are suitable for colonization attempts. Detailed observations were made on an ambrosia-beetle attack on a palm (*Washingtonia robusta*) in Florida. Within days after being struck by lightning, *X. affinis* and *P. parallelus* attacked the lower section of the stem, the upper portions remaining free of beetle galleries. The lightning strike did no obvious physical damage that would facilitate the beetle attack, as the stem of the lightning-struck palm was as physically resistant to penetration (measured by a penetrometer) as nearby healthy palms. Stressed palms are not always attacked by ambrosia beetles. For example, ambrosia beetles have not been observed in stems of thousands of palms of different species that have died from lethal yellowing in Florida (F.W. Howard, R.M. Giblin-Davis and Michael Thomas, unpublished).

Because of the mostly secondary nature of attacks by ambrosia beetles, control should be focused on removing the primary stressing factors (e.g. disease, poor growing conditions).

Bostrychidae

Powder-post beetles (Bostrychidae) look like bark beetles but can be distinguished from them because the head and prothorax project downwards, the pronotum is tuberculate and they possess non-elbowed antennae, without a club, and have five visible tarsomeres, instead of four as in scolytines. The larvae are wood-borers, with mycetomes near the beginning of the gut. The microorganisms associated with the mycetomes are transmitted with the sperm to the eggs of the next generation. The larvae of bostrychids can be differentiated from larvae of weevils and ambrosia beetles by the presence of legs (Peterson, 1977). Bostrychids do not produce cellulase and therefore restrict their feeding to sugars and starch from stressed, moribund or recently dead wood.

The giant palm borer, *Dinapate wrighti*, is the largest bostrychid (30–52 mm long) in the world (Fig. 5.17). It attacks mature (> 20 years old) California fan palms, *Washingtonia filifera*, and the date palms in the south-western USA and Baja California, Mexico (Olson, 1991). *Dinapate hughleechi* occurs in eastern Mexico on *Sabal texana* (Cooper, 1986). Like palm weevils, the imagos probably emerge, fly to a suitable host palm, with transplanted palms being favoured (Wymore, 1928), harbour in or burrow into the crown area, mate and oviposit (Baker, 1971). Larvae feed on living tissue in the stem (Wymore, 1928) and have long developmental times, ranging from 3 to 9 years. They create galleries as they bore up and down the stem to a level 1.3–2 m above the ground. Mature larvae cut a pupal chamber near the stem

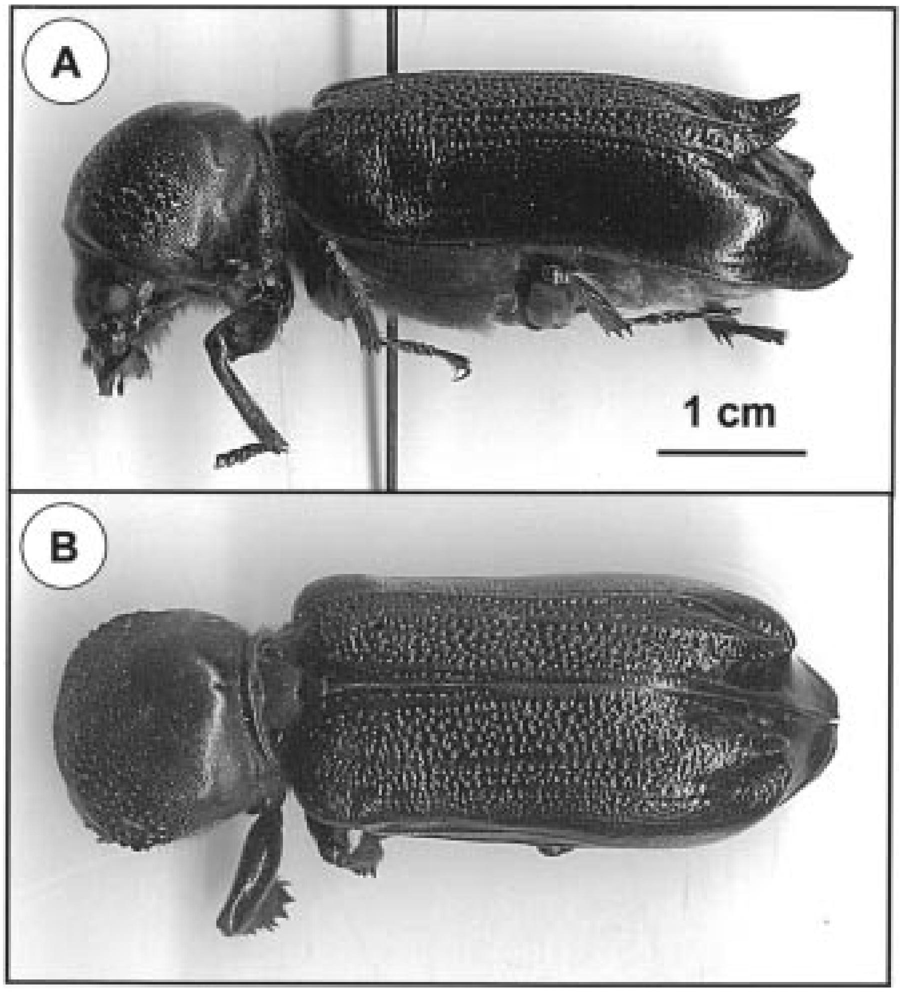


Fig. 5.17. *Dinapate wrighti* (Coleoptera: Bostrychidae). (A) Lateral view. (B) Dorsal view.

periphery, where they pupate, facing out. The imagos cut a 2–3 cm diameter hole and emerge. This hole can indicate the presence of the beetle, but may be hidden by fibres. The larval galleries eventually compromise the structural integrity of the palm and create a dangerous situation in the landscape, because the apparently healthy palm can suddenly fall over. Reliable detection and control methods are not currently available (Olson, 1991).

There are two minor bostrychid pests of date palm in the eastern hemisphere: *Apate monachus*, which is a pest in North Africa, and *Phonopate frontalis*, in North Africa and the Middle East (Carpenter and Elmer, 1978). The imagos of *A. monachus* oviposit in fronds and rachides and the larvae bore galleries up to 6–8 mm wide by 12 cm long, which weaken the rachis, resulting in breakage. This beetle can also reportedly bore into the trunks of weakened palms (Calcat, 1959). A forest pest in West Africa (Wagner *et al.*, 1991), it was introduced into Puerto Rico, where it normally attacks a variety of logs and dying trees; however, when populations are high, it will attack healthy plants, including coffee trees (Martorell, 1945). Control involves immediate pruning and burning of affected fronds to kill the beetles. The imagos of the frond borer, *P. frontalis*, damage the rachis of date palm.

Lymexylidae

Protomelittomma insulare (Lymexylidae) is known only from coconut and wild palms (*Sterensonia, Nephrosperma, Deckenia* and

Roscheria) in Madagascar and the Seychelles. Interestingly, certain native palms, e.g. *Lodoicea maldivica* and *Verschaffeltia*, are not attacked (Brown, 1954). Healthy, well-fertilized coconut palms, aged 7–20 years old, appear to be the most susceptible to infestation by *P. insulare* (Nye, 1961). Adult lymexylids live only a few days, whereas the larvae are borers and sometimes require more than 2 years to develop before pupating in a cell excavated in the wood (Wheeler, 1986). *Protomelittomma insulare* is an unusual beetle, with larvae that possess legs, and a sclerotized terminal segment or anal plate, which is used to push cores of frass out of feeding galleries at the stem base of infested palms. Lymexylids are generally fungus growers, cultivating ascomycete fungi in their tunnels. However, no mycosymbionts have been identified for *P. insulare*, even though a large number of fungi, yeasts and bacteria have been reported from their larval galleries (Wheeler, 1986). The non-feeding imagos of *P. insulare* are reddish brown in colour. The active males, are 6–13 mm long and live 6 days. The less active females are 9–18 mm long and live only 3–4 days (Lever, 1979). Females lay masses of about 100 white eggs in cracks in the stem, which hatch in about 11 days. Larvae enter the base of the stem where roots occur. The larvae bore into the stem, preferring the softer internal tissue, and then tunnel upwards. As many as 200 larvae, each attaining a length of about 20 mm just prior to pupation, can infest a single stem base and reduce the region to a dark pulpy mass. Larvae of *P. insulare* apparently extract the juices from the host tissue. The last abdominal segment is modified into a hoof-shaped, melanized plate with 18 or more small pits in the surface. The larvae use this plate to clean the gallery and push debris from it. The characteristic yellowish-brown pellets issuing from boreholes in the stem base are symptomatic of *P. insulare* infestations. Pupation occurs in a cell excavated in the stem.

Protomelittomma insulare is probably the most serious pest in the Lymexylidae, causing serious damage to coconut production in the Seychelles. On Praslin Island between 1953 and 1958, more than 77% (95,000) of the coconut palms were infested with *P. insulare*, causing a significant drop in coconut production. However, after excising necrotic tissue, exposing tunnel entrances (being careful not to remove any more tissue than necessary) and covering the damaged areas of the stems with a mixture of tar creosote, coke residue, water and an inert non-soluble material (60 : 9 : 3 : 29), the infestation was reduced to 18% (Nye, 1961). Tar was reapplied if larval excrement was still visible after a week.

Scarabaeidae: Dynastinae

A large number of rhinoceros beetles (Scarabaeidae: Dynastinae) are borers in palms (Fig. 5.18). Major males (well-nourished specimens) of many species of this subfamily (except *Strategus*) possess a dorsal horn on the head and an anteriorly directed pronotal concavity. Most of these beetles are large (30–60 mm) and black or dark brown, with a velvety reddish-brown pubescence on the ventral surface. The most important pest species to palms are members of the genus *Oryctes*, although there are pestiferous members in the genera *Strategus, Scapanes, Xylotrupes, Papuana* and *Chalsoma* (Lever, 1979; Bedford, 1980). Bedford (1980) provided an excellent review of the biology, ecology and control of these insects, with references to the taxonomic literature.

The coconut rhinoceros beetle, *Oryctes rhinoceros* (Colour Plate 15d), is one of the most damaging insects to coconut palm and African oil palm in southern and South-East Asia and the western Pacific islands. While in most endopterygote insects that are pests of economic plants it is the larval stage that causes the damage, in *O. rhinoceros* it is the imago. The larvae (Colour Plate 15e) develop in decaying wood and thus, as decomposers, could be considered beneficial. In general, it is young imagos of *O. rhinoceros* that do the

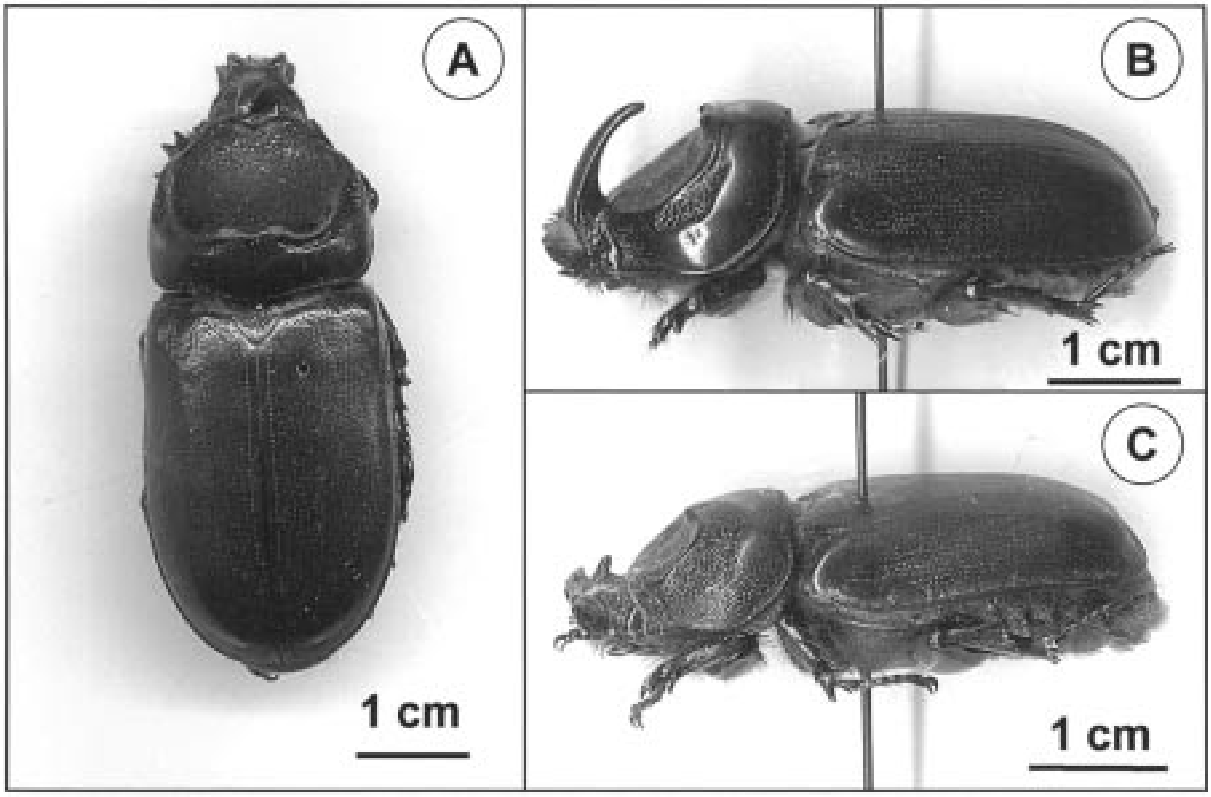


Fig. 5.18. *Oryctes monoceros* (Coleoptera: Scarabaeidae). (A) Dorsal aspect of a major male. (B) Lateral view of a major male. (C) Lateral view of female.

boring damage that affects the crowns of healthy palms. Females lay 70–140 eggs in rotting wood, manure and decaying vegetation in coconut plantations, where the larvae mature. The whitish-brown egg is 3–4 mm long and takes about 12 days to hatch. The larva develops during 72–130 days. The large (60–105 mm long) white mature larva is C-shaped, with a brown head capsule and legs. The posterior part of the abdomen is a bluish-grey colour. Although edible, they are not favoured, like palm weevil larvae, by humans (see Box 5.1). They can be found in decaying or dead standing palms killed by adult beetles, lightning, cadang-cadang or other causes. Pupation, which usually occurs in the soil but can occur in larval habitats, lasts about 20 days. The cocoon is usually composed of soil or plant tissue. The imagos remain in the cocoon for about 11–20 days, after which they remain mostly in the breeding sites, flying short distances (maximum recorded flight is 700 m) to the crowns for feeding (Lever, 1979). The life cycle lasts from 4 to 9 months, allowing more than one generation per year. Adult longevity is about 3 months. The burrow of the adult penetrates 10–50 cm down to near the centre of the spear cluster, where the beetle feeds on juice from host tissue. Crushed tissue pushed out of the entrance of the burrow indicates that the adult beetles are present. This feeding causes damage to the inflorescences and fronds, decreasing or delaying fruit production. Mature fronds that were attacked while in the developing stage often have patches of missing foliage, as if clipped by scissors (Colour Plate 15f). In healthy older palms the damage caused by the beetles can be tolerated, but in palms 1–3 years old it often results in death or severe malformation. In addition, the burrows may provide secondary access for palm weevils or pathogens that can kill the palm. Life-history data for *Oryctes, Scapanes* and *Strategus* are summarized by Bedford (1980).

Oryctes rhinoceros (30–57 mm long) is distributed throughout Asia and the western Pacific (for a historical account, see Bedford, 1980) and attacks coconut palm, African oil and date palms and a variety of palms grown for ornamental purposes, including *R. regia, Livistona chinensis, Corypha umbraculifera* and *Raphia ruffia* (Gressitt, 1953; Bedford, 1980). It also attacks pineapple, sugar cane, *Pandanus* and banana (Lever, 1979). *Oryctes monoceros* (Fig. 5.18) and *Oryctes boas* occur mostly in tropical Africa and attack coconut and date palms, among others. The fruit-stalk borer, *Oryctes elegans*, is a serious borer of fronds and fruit stalks of the date palm in Iran, Iraq and Saudi Arabia (Carpenter and Elmer, 1978). Minor pests of date palm include *Oryctes sahariensis* in Chad and Sudan, and *Oryctes agamemnon* (syn. *Oryctes sinaicus*) in Saudi Arabia, on the Sinai Peninsula and on the Arabian Gulf coast of Iran (Carpenter and Elmer, 1978; Bedford, 1980). In New Guinea, *Oryctes centaurus* (50–60 mm long) attacks the inflorescences of *Metroxylon* species after flowering (Lever, 1979). The four subspecies of *Scapanes australis* occur in different regions of the New Guinea archipelago, attacking young coconut palms, banana stems and Manila hemp (Bedford, 1980; Anon., 1991). In parts of the West Indies, *Strategus quadrifoveatus* adults tunnel 4–6 cm into soil and attack and kill coconut palm seedlings or coconut palms less than 3 years old, i.e. prior to trunk formation (Lever, 1979; Bedford, 1980). *Strategus aloeus* adults (40–58 mm long) burrow up to 50 cm in the soil just under the stem base of 1–3-year-old African oil palms and then tunnel up into the base of the plant, sometimes moving into the stem above the soil line. This beetle is distributed in northern South America and is mainly active at the beginning of the rainy season (Ahumada *et al.*, 1995). *Strategus julianus* attacks young date palms in Texas and Arizona (USA) (Carpenter and Elmer, 1978). The latter species also attacks coconut palms in Mexico, where it is known as the Mexican rhinoceros beetle, or *mayate* (Laura Sampedro and Humberto Carrillo Ramírez, personal communication). *Xylotrupes gideon* occurs throughout India, South-East Asia, New Guinea and northern Queensland, where it attacks newly opened coconut palm inflorescences and the abaxial surface of the frond midribs (Bedford, 1980).

The imagos of *Oryctes* and other palm rhinoceros beetles aggregate at palms and breeding sites. Recently, ethyl-4-methyloctanoate was identified as the male-produced aggregation pheromone of *O. monoceros* (Gries *et al.*, 1994b) and *O. rhinoceros* (Hallett *et al.*, 1995). *Oryctes rhinoceros* males also produce ethyl-4-methylheptanoate and 4-methyloctanoic acid, but these were significantly less attractive than ethyl-4-methyloctanoate and did not increase its attraction. Freshly milled, empty African oil palm fruit bunches enhanced the attraction of ethyl-4-methyloctanoate to *O. rhinoceros*, suggesting synergy between early fermentation products and aggregation pheromone (Hallett *et al.*, 1995). Semiochemical-baited vane bucket traps were more effective for capture of *O. rhinoceros* than pitfall or barrier traps (Hallett *et al.*, 1995). Further work is needed to determine if semiochemical-based mass trapping will be cost-effective and if semiochemicals can be employed for biorational pesticide or pathogen delivery systems.

The most important management option for *O. rhinoceros* is the elimination of breeding sites. This involves the removal, burial or destruction of dead or dying plant material (see Box 5.1). Shredding and burning of felled palm trunks is not cost-effective and has been banned in parts of South-East Asia to prevent air pollution in a region with over 4.5 million ha of African oil palm (Tajudin *et al.*, 1993). Insecticide drenches of breeding sites (Lever, 1979) and programmed application of granular insecticides, such as carbofuran, to young palms have been recommended (Ho and Toh, 1982), but are not very effective and pose risks to humans and the environment. A variety of biological control agents have been attempted for the control of palm rhinoceros beetles, including scoliid wasps and several predatory beetles, without much success (Lever, 1979). Pathogens, such as the fungus *Metarhizium anisopliae*, have been introduced into compost heaps for control of *O. rhinoceros.* This is a popular method in South-East Asia, because it is relatively cheap, and sometimes provides adequate control (Colour Plate 16a, b). An inundative biological control release using the baculovirus *Rhabdionvirus oryctes* was tried in the Philippines, resulting in reductions of *O. rhinoceros* populations to 10–20% of preinoculation levels (Zelazny and Alfiler, 1987, 1991).

Lucanidae

Lever (1979) reports that the imagos of several species of *Eurytrachelus* are borers in the stem just below the petioles of coconut palms in New Guinea and the Solomon Islands. Larvae apparently feed in rotting wood and humus.

Cerambycidae

The palm stem borer, *Jebusea hammerschmidti* (syn. *Pseudophilus testaceus*), is an important borer pest in date palm groves in the Middle East and India, especially in humid areas (Carpenter and Elmer, 1978; Al-Azawi, 1986). Infestation levels of up to 79% of date palm trunks in Iraq have been reported (Hussain, 1963b), and it was the most important date palm pest in Qatar (Al-Azawi, 1986). Palm stem borer exit holes expose the fronds and inner stem to opportunistic fungi and bacteria, causing stress, blockage of nutrient and water movement and breakage (Al-Azawi, 1986). The beetle weakens palms and occasionally causes mortality. This may attract the fruit-stalk borer, *O. elegans*, for breeding (Al-Azawi, 1986).

Jebusea hammerschmidti is univoltine, with imagos appearing from May to August, depending upon the location. Eggs are laid in the palm crown, where they hatch in 15 days. The larvae bore into the petioles. Larvae feed for about 3 months and then migrate and bore into the stem, causing a characteristic, dark brown, gummy exudate from entrance holes (Carpenter and Elmer, 1978). The larvae (up to 50 mm long) are apodous, white or pink-coloured, pubescent and posteriorly tapered (Al-Azawi, 1986). Larvae pupate and overwinter in a cell in the stem. The adult beetle bores its way out of the trunk in an oblique gallery 1–14 cm long, creating a symptomatic 1-cm-diameter emergence hole. The quantity of emergence holes and the presence or absence of live *J. hammerschmidti* affect the monetary value of date palm orchards in Iraq. Control methods involve insecticide applications to the crown for control of the imagos, prior to oviposition during June and July (Carpenter and Elmer, 1978).

Lepidoptera

Castniidae

There are several moth species that cause significant boring damage to palms as larvae. One of the largest insect boring pests of palms is *Castnia daedalus* (syn. *Castnia dedalus*, *Eupalamides daedalus*, *Eupalamides cyparissias, Lapaeumides daedalus*) (Fig. 5.19). This moth, distributed in northern South America and the Amazon basin, produces large whitish caterpillars (about 10 cm long), which attack coconut palm and palms in the genera *Euterpe*, *Pritchardia, Livistona, Mauritia, Maximiliana, Oenocarpus* and *Roystonea* (Lepesme, 1947; Lever, 1979; Ferreira *et al.*, 1994). The larvae of this and related species are a human food source in some localities of tropical America (see Box 5.1). Species of *Castnia* are also pests of other monocotyledons, including bananas, sugar cane and pineapples. The adult moth of *C. daedalus*, brown-coloured and with violet spangles, is unusually large (wing-span 14–18 cm). This conspicuous moth attracted the attention of early naturalists: the species was described in 1775 by Cramer. Female

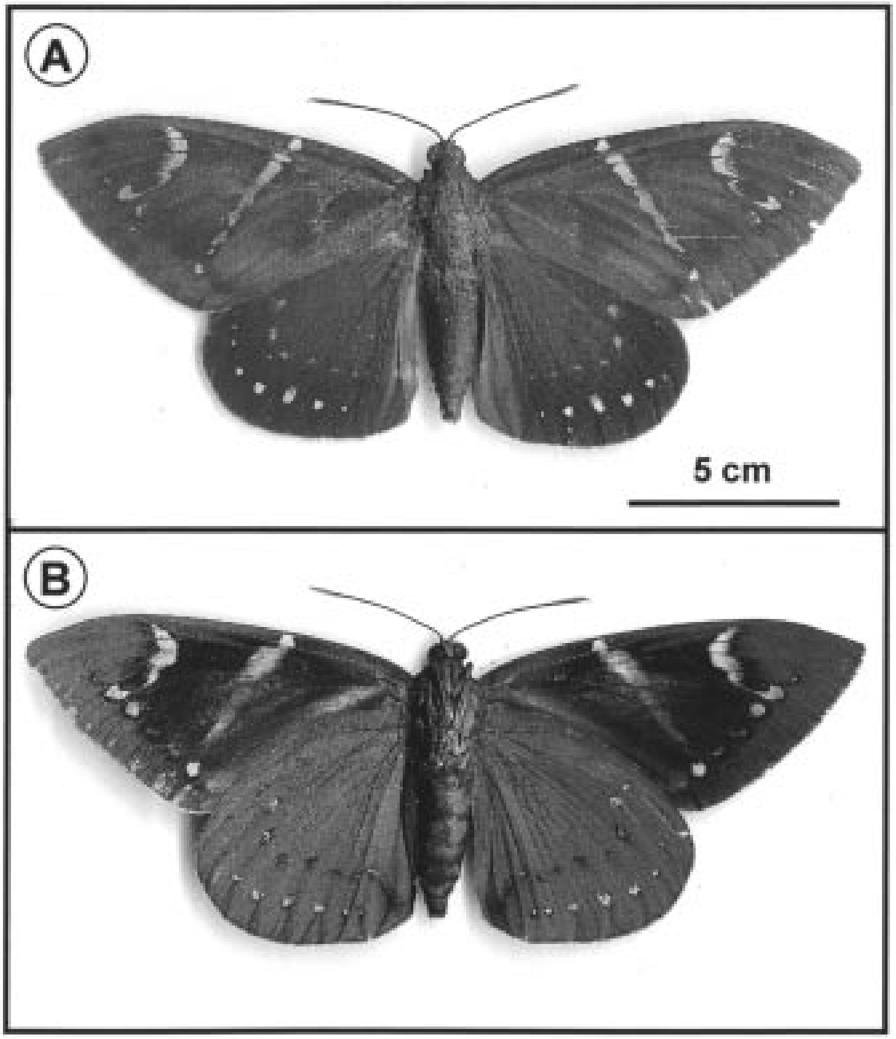


Fig. 5.19. Adult of *Castnia daedalus* (Lepidoptera: Castniidae). The larvae of this large butterfly are borers in trunks of palms. (A) Dorsal view. (B) Ventral view.

moths may lay about 265 pink eggs (4.3–4.7 mm long) in groups of two to eight at the base of the palm crown. They hatch in about 17 days. The larval stage, consisting of 14 instars, takes up to 1 year. The larvae pupate in a long cocoon, composed of fibre from the petioles. Pupation lasts about 35 days (Rai, 1973; Korytkowski and Ruiz, 1980).

The early-instar larvae bore in the fruits and peduncles. Infested African oil palm fruits and peduncles rot, and the larvae moved to higher fronds (Huguenot and Vera, 1981). Later instars make shallow galleries between the petioles and the stem, causing premature frond abscission. Galleries extend up to 1 m long on the trunk. In some areas of Guyana, characteristic stem galleries are absent, because larvae bore only the petioles and peduncles, rather than the stem (Rai, 1973). Significant reductions in fruit production have been reported in plantations infested with *C. daedalus* (Rai, 1973). In a few cases, palm death occurs when larvae bore the growing point of the palm. Coconut palm becomes susceptible to attack after trunk formation (about 4–5 years old) and remains so until stem height exceeds 7 m (Rai, 1973). African oil palms become susceptible when about 5 years old (Schuiling and Van Dinther, 1980).

An egg parasitoid, *Ooencyrtus* sp. (Hymenoptera: Encyrtidae), was isolated from eggs of *C. daedalus* in Peru (Ruiz and Korytkowski, 1979) and, under some conditions, is important in regulating its populations (Huguenot and Vera, 1981). Entomogenous nematodes have reduced larval populations of *C. daedalus* in the laboratory, but were not effective in a field trial (van den Segeren Oever *et al.*, 1984). IPM, relying mostly on natural enemies, has been highly successful against a similar species, *Castnia licus,* a pest of sugar cane, which is also known to attack palms, and this example should be studied by those concerned with *C. daedalus* (Esquivel, 1983). Scouting plantations, pruning and destroying infested fronds and rotted fruit stalks are considered to be good preventives (Genty *et al.*, 1978; Schuiling and Van Dinther, 1980).

Like stem borers in general, *C. daedalus* is difficult to control with chemicals, and chemical control is somewhat futile once borer damage is extensive. Control of incipient infestations is more likely to be successful. Several methods have been devised for scouting for incipient infestations, such as dissecting fruit stalks and examining them for early-instar larvae (Mariau and Huguenot, 1983). Several chemicals have been effective in killing the larvae when applied as sprays or trunk injections (Rai, 1973; Asgarali and Ramkalup, 1992; Asgarali *et al.*, 1992).

Tineidae

The banana moth, *Opogona sacchari*, is a primary pest of many plants, including palms in Florida and row crops in Europe, Africa, Madagascar and South and Central America. Davis and Peña (1990) described the morphology and biology of *O. sacchari* in detail. Their observations are summarized here. The imagos are small (length of forewing ranges from 7.3 to 12.5 mm), dark greyish-brown moths, with two small dark spots (Davis and Peña, 1990). Larvae are up to 30 mm long and are white, with small legs and prolegs and a dark brown head capsule and plates. It attacks nursery stock of *Dypsis lutescens*, *Chamaedorea* spp., *Syagrus* sp., *B. gasipaes* and *Wodyetia* sp. in Florida (Davis and Peña, 1990; Peña *et al.*, 1990a). *Opogona* and related tineids are typically detritus-feeders and scavengers. However, *O. sacchari* attacks damaged tissues and then begins feeding on living tissue. Generation time is about 50–70 days in the laboratory. Mating occurs between 1300 and 1600 h. Eggs are laid singly or in groups – sometimes exceeding 300 – on unexpanded fronds and stems, where they hatch in about 7 days (Davis and Peña, 1990). In young *Chamaedorea* palms, the larvae feed at the base of the plant, where aerial roots enter the soil. Larval feeding damage occurs in the petioles, stem and roots of the host palm. In seedlings, damage is often difficult to detect until the collapse of fronds or frass from larval feeding accumulates at the plant base (Heppner *et al.*, 1987). Newly emerging fronds may become necrotic and bleached (Davis and Peña, 1990). There appear to be seven larval instars and pupation lasts about 12 days. We have also observed *O. sacchari* associated with weevil borers, such as *M. hemipterus* and *R. cruentatus*, in ornamental palms in Florida.

Opogona sacchari populations can be reduced with single applications of carbaryl, chlorpyrifos, methomyl and several other insecticides (Peña *et al.*, 1990a). Also, the entomopathogenic nematodes *S. carpocapsae* and three species of *Heterorhabditis* are effective in controlling *O. sacchari* (Peña *et al.*, 1990a, b). Recently, we have done research with *O. sacchari*, demonstrating the presence of a female-produced sex pheromone attractive to males. These identified and synthesized semiochemicals may be useful for monitoring populations and the timing of applications of pesticides in the future (Jorge Peña, unpublished data).

Glyphipterigidae

The root borer of oil palm, *Sagalassa valida*, is a small, brown-banded moth in the family Glyphipterigidae. It causes significant damage to the roots of young (2–6-year-old) African oil palms in plantations in western and eastern Colombia. The biology is reviewed by Pinzon (1995). Initial oviposition involves between eight and 30 eggs per female, presumably deposited in moist areas near the base of the palm. Eggs hatch after about 8–9 days and the neonate larvae, which are very mobile, bore into primary roots and develop through six instars for 45–48 days. Larvae consume the entire central core of the roots they infest (total root mass consumed is about 2 g of roots per larva). Pupation takes 12–18 days. The imagos are short-lived (5–6 days) and come from the forest surrounding the plantation. Thus, in African oil palm plantations, the greatest damage is at the borders. The total life cycle takes about 78–81 days. Larvae can indiscriminately bore up to 81% of roots of young palms (Peña and Jimenez, 1994). The continuous damage caused by the root-boring larvae results in premature frond death and poor rooting, which, in Tumaco, Colombia, lead to yield decreases up to 70% (Ortiz *et al.*, 1994). *Sagalassa valida* infestations are most problematic in young oil palm plantations (Pinzon, 1995).

The entomopathogenic nematode *S. carpocapsae* was effective for controlling *S. valida* in the laboratory and in the field (1.5×10^6 nematodes per palm) (Ortiz *et al.*, 1994). Other methods for control include an endosulphan (Thiodan) drench of soil within an 80 cm radius of and including the base of the stem (Pinzon, 1995). Cultural control methods involve keeping and maintaining clean borders between the plantation and the surrounding forest.

Isoptera

Termites are polylectic consumers of cellulose that occasionally become pests to palms, especially during times of high termite population densities, plant stress, drought or dryness and/or when alternative sources of cellulose are unavailable. Termites may build up large populations where woody material has been buried, and then attack palms planted there (Mariau and Mallet, 1999). Boring damage caused by termite workers can occur in roots, stems or fronds, and can kill seedlings when populations are high. In Iraq, *Microcerotermes diversus* attacks the roots, fronds and stem of weak date palms and can kill offshoots (Hussain, 1963b). Species of *Odontotermes* can infest date- and coconut palms in Sudan and India (Carpenter and Elmer, 1978). *Macrotermes* (syn. *Bellicositermes*), *Coptotermes*, *Ibostoma* and *Psammotermes* were pests of date palms in Mauritania (Carpenter and Elmer, 1978).

Termites of the genus *Neotermes* (Isoptera: Kalotermitidae) attack living wood and thus are called ‘live-wood termites’. Many species of this genus attack dicotyledonous trees in tropical regions. One species, *Neotermes rainbowi*, called the coconut termite, is distributed on atoll islands of Tuvalu and the northern Cook Islands in the South Pacific. They hollow out and establish colonies in trunks of coconut palms, which are prevalent on these islands. They are believed to attack only palm ‘wood’.

Alates fly to palm stems to establish colonies, which can later spread to adjacent palms along roots in contact or through the soil, if not prevented by competition from other termites. The damage of this termite compromises the structure of the stem, so that it may snap even in light winds. When infested palms are felled by wind, the main colony, with the original queen and king (reproductive forms), may persist in the stump, while the portion of the colony in the broken stem may produce new reproductive forms and become independent.

Management consists of scouting for infested palm stems, removing and burning advanced infestations and treating incipient infestations with water suspensions of the entomopathogenic nematode *Heterorhabditis* sp. or dry spores of the fungus *M. anisopliae* (Lenz, 1996, 1997). For some termites, treatment of the base of individual palms with lindane and other insecticides was formerly recommended (Carpenter and Elmer, 1978), but new baiting systems for subterranean termites might be more effective (Su and Scheffrahn, 1998).

In the Caribbean, tunnels leading up palm trunks are sometimes seen. These are usually constructed by species of *Nasutotermes*, which forage on woody detritus that collects in the palm-leaf axils and on dried spathes. They are not pests of palms (Rudolf Scheffrahn, personal communication).

6

Population Regulation of Palm Pests

Dave Moore

> Is not disease the rule of existence? There is not a lily pad floating on the river but has been riddled by insects.
>
> (Henry David Thoreau (1817–1862), American philosopher and naturalist, *Journals*)

Population Regulation

All populations are regulated by biotic and abiotic factors, usually with marked interactions between many factors. There is a tendency to view population regulation in terms of control of arthropods. Those acting as pests of commercial palms attract more attention than insects of palms in the wild. In the wild, success depends on the survival of the populations and, if palms in a particular ecosystem maintain themselves over long periods, even with marked oscillations in numbers, they have passed the test. Considerable damage can be tolerated, and regulation of herbivore populations and of their enemies occurs at the ecologically sustainable rates. With commercial palms, a consistent surplus is required. Arthropods reducing this surplus may be controlled with an artificial strictness, with level and speed of control of prime importance.

However, much specific information on population regulation of palm arthropods comes, inevitably, from examples of commercial palms. Often they can relate to the natural situation, as many agricultural techniques build on what occurs in nature, but many of these are aimed at maximum production, not necessarily arthropod control. Chemical pesticides promised to make this irrelevant, but the problems related to chemicals ensure that biologically orientated arthropod regulation is paramount.

For convenience, arthropod population regulation can be viewed as natural control or agricultural pest management. Natural control in this context includes the abiotic (e.g. climate and soil type) and the biotic (e.g. host-plant resistance, natural enemies, host populations). The various features interact markedly. For example, drought may result in the elevation of soluble nitrogen levels in host plants. The degree of this will relate to the soil structure and its water-holding capacity. Elevation of soluble nitrogen levels may result in outbreaks of herbivores. The same drought in different soils may result in relatively high silica levels in plant tissues, providing protection against arthropods. The natural enemy complex will be more, or less, effective against the rates of population increase.

Agricultural pest management uses all the above, wittingly or otherwise. Knowledge of agronomy and horticulture enables healthy palms to be produced that are usually resistant or tolerant to most herbivore attack, but more attractive to a few species. Plant breeding has tended to increase vulnerability to some pests and diseases, but provides possible responses against certain pests. Planting densities and the composition of species in a planting (i.e. monocultures or mixed), the manipulation of ground cover, fertilizer use, irrigation and other factors influence arthropod numbers, very often via complex interactions with the natural enemies. Autochthonous (native) natural enemies may be effective by themselves, or may be manipulated to enhance their effectiveness. In some cases, natural enemies are artificially introduced for biological control.

Natural Enemies

Classically, natural enemies are grouped into predators, parasitoids and pathogens (usually pathogens include nematodes). In practice, many arthropods will also act as competitors and some as parasites, but their impact is often difficult to evaluate. Examples of the agents in use against arthropods are based around those attacking palms. Frequently, especially in biocontrol programmes, one or two agents are considered as major regulators, but often many agents are involved to apparently minor degrees. There may be extensive complexes. For example, *Oryctes rhinoceros* has 82 species of arthropod natural enemies, five nematode species, two protozoan, two fungal, one bacterial, one Rickettsiales and three virus species. Nineteen countries were cited as receiving arthropod agents during biological control programmes. The only reliable success with biological control against *O. rhinoceros* has been with a baculovirus (Waterhouse and Norris, 1987).

Waterhouse and Norris (1987) also gave detailed accounts of biological control and natural complexes for a number of palm pests, including *Brontispa longissima, Graeffea crouani, Aspidiotus destructor* and *Agonoxena argaula*. For *Tirathaba rufivena*, nine primary parasitoids (seven Hymenoptera and two Diptera), attacking various stages from egg to pupae, and three hymenopterous hyperparasitoids were recorded from Indonesia. These were the ones regarded as important and an equal number of anonymous species were considered unimportant.

The pattern is undoubtedly similar with arthropods on wild palms. Each individual herbivore may be assumed to be associated with a large number of natural enemies, with many complex interactions occurring. Two examples will be used to illustrate natural control: Limacodidae of South-East Asia (Cock *et al.*, 1987) and *Opisina arenosella*, a palm herbivore that receives much research attention (CAB *International*, 1996). Even these relatively well-understood examples are incomplete, but they do give indications of what might be expected to occur in arthropods of wild palms as well. The complexes that attack a single herbivore are usually vast. Similarly, parasitoids and predators will be attacked by intricate systems. A herbivore such as *O. arenosella* may be attacked by dozens of primary parasitoids, which may, in turn, themselves be parasitized. The herbivore is thus associated with many scores of parasitoids. Along with predators, the web becomes huge. In the same way that the herbivores of wild palms are neglected, so are their natural enemies.

Pathogens

Diseases of insects are caused by viruses, bacteria, fungi and protozoa, and are often important in the regulation of insect populations. Most information relates to viruses and fungi and relatively little work has been done on other groups of pathogens in the tropics in relation to palm herbivores.

Viruses

Six main families of viruses cause diseases in insects (Entwistle, 1983), of which the Baculoviridae, which include the nuclear polyhedrosis and granulosis viruses (NPVs and GVs), are generally considered the most suitable as control agents. In part, this reflects their wide host range in nature (over 1000 Baculoviridae–insect associations are known, including many species of Diptera, Hymenoptera and Lepidoptera) and the fact that they have never been found to occur in vertebrate animals or plants. Infection begins with digestion. The protein inclusion bodies of NPVs and GVs break down under the alkaline midgut conditions of the host and virion replication occurs in gut cells or elsewhere in the insect.

Virus dissemination occurs in many ways in nature. Dead and dying insects ooze or regurgitate infected fluids (Entwistle, 1983). Infected imagos of *O. rhinoceros* may excrete up to 1 mg of virus per day. Parasitoids from the Braconidae, Encyrtidae, Ichneumonidae and Tachinidae can transmit baculoviruses while attacking hosts and occluded viruses can survive passage through the guts of vertebrate and invertebrate predators.

Members of six families of viruses are known to cause disease in larvae of around 40 species of Limacodidae (Entwistle, 1987). They have been associated with spectacular epizootics, often occurring when wet weather begins. This indicates the high persistency of inoculum within ecosystems, despite adverse environmental aspects, such as sunlight.

Natural levels of virus infection may be high. Around 20% of populations of *Parasa lepida* in Indonesia contained two different types of virus, including a baculovirus (Desmier de Chenon *et al.*, 1988). In addition, three types of virus were noted from *Darna trima* at a natural level of 24% and two types of virus were found from *Setothosea asigna*. The speed at which epizootics occur can be understood with such high levels of natural occurrence.

An NPV that caused widespread mortality was recorded from *O. arenosella* in Kerala, India (Philip *et al.*, 1982). Death occurred 3–8 days after infection. Symptoms included sluggishness, reduced feeding, a pink coloration and a rapid darkening to black after death.

Probably the most notable biocontrol successes with pathogens against palm insects is that of the rhinoceros beetle *O. rhinoceros*. The use of viruses, sometimes in conjunction with *Metarhizium anisopliae*, has achieved significant population regulation in managed palms.

Fungi

Over 700 species of fungi, mostly mitosporic fungi and Entomophthorales from about 90 genera, are known to be pathogenic to insects and mites (Colour Plate 16a, b, c). Unlike other pathogens, such as viruses and bacteria, fungi do not have to be ingested to infect their hosts. The infective unit, the conidia, adheres to the host cuticle and germinates. The resultant germ tube penetrates the cuticle by combined physical and chemical activity and the fungus proliferates and develops inside the host. After death, the fungus may break through the cuticle and sporulate externally, allowing secondary infections to establish. Some fungi are very restricted in their host range; for example, *Aschersonia aleyrodis* infects only whiteflies and soft scale insects. Other species have a wide host range at the species level, although individual isolates may be selective. *Beauveria bassiana* has over 700 recorded host species and *M. anisopliae* has been recorded from over 300 species of Coleoptera, Lepidoptera, Orthoptera and Hemiptera. Other genera frequently found include *Verticillium*, *Aspergillus*, *Hirsutella*, *Nomuraea* and *Paecilomyces*. There are relatively few authenticated records of fungal pathogens from Limacodidae, but those that occur are from the usual genera (Evans, 1987). *Aspergillus flavus* has been identified from *Thosea* sp. and *Parasa* *philepida*, but is probably an opportunistic pathogen. This may be fortunate, because the *A. flavus* group produces aflotoxins, which can be harmful to humans. *Beauveria bassiana* has been recorded from *P. philepida* and, as *Isaria sphaerocephala*, from *Aphendala recta*. There are surprisingly few records of *M. anisopliae*, *Paecilomyces javanicus*, *Paecilomyces lilicanus* and *Verticillium lecanii.*

Cordyceps spp. are probably the most common pathogens on limacodids. Unfortunately, this genus is poorly understood. Taxonomy is one problem, as Evans (1987) suggests that the disparate species previously claimed may be a single species. However, *Cordyceps* is probably an endemic and highly specific pathogen of limacodids and probably an important cause of mortality in general populations, even without considering epizootics.

Laboratory trials have demonstrated the efficacy of, for example, *Paecilomyces farinosus* against *O. arenosella* and *B. bassiana* against *Metisa plana*. Recent advances in insect pathology have demonstrated the importance of formulation and application of insect control products containing fungi.

Other pathogens

Entomopathogenic nematodes are widespread but have rarely been recorded from even the well-known pests of palms. This is not surprising, since most of the insect pests of palms occupy arboreal niches, while the entomopathogenic nematodes inhabit soil. The genera *Steinernema* and *Heterorhabditis* have been of major interest for biocontrol purposes. They are symbiotically associated with bacterial species of the *Xenorhabdus* and *Photorhabdus* genera. The nematodes have an infective third stage, which searches out its host (with varying degrees of success) and enters it before releasing the bacteria, which proliferate and kill the host. Mermithid nematodes are found, usually infrequently, in many species of insects, but rarely in epizootics. *Steinernema carpocapsae* controls *Sagalassa valida* (Glyphipterigidae), a root pest of palms.

Although the delta endotoxin (protein) of the spore-forming bacterium, *Bacillus thuringiensis*, is the active ingredient in most of the commercially successful biopesticides, bacteria have been rarely recorded in herbivores of palm ecosystems. Protozoa are also noticeable mainly by their apparent absence, although a cephaline gregarine, *Leidyana* sp., has been recorded from the midgut of larval *O. arenosella* (Rabindra, 1981). *Rickettsia* is virtually unrecorded. Cock *et al.* (1987) refer only to viruses and fungi in relation to Limacodidae and only the former in any real detail. This seems to be a fair reflection of the current state of knowledge. However, other avenues for pathogens in biocontrol have been opened in recent years and are discussed under biological pesticides.

Predators

Predators eat many prey during their lifetime and are significant regulating agents, both in biocontrol programmes and as indigenous members of an ecosystem. Some of the more notable insect predators are found among the Coleoptera (e.g. Carabidae, Staphylinidae, Coccinellidae), Neuroptera (Chrysopidae), Diptera (Syrphidae) and Heteroptera (Pentatomidae, Anthocoridae and Miridae). Spiders and mites are also important predators, often with greater selectivity against pest populations than was formerly suspected.

Among mites, those of the genus *Hemisarcoptes* (Hemisarcoptidae) are non-specific predators on armoured scale insects (Hemiptera: Diaspididae). *Hemisarcoptes coccophagus* is recorded as effective in controlling *Parlatoria blanchardi* on date palms (Gerson and Smiley, 1990). A number of predatory mites are recorded as enemies of the coconut mite, *Aceria guerreronis*, with apparently little impact on populations.

More commonly recognized predators include many coccinellids. These are the major predators used in biological control programmes. For example, *Chilocorus* spp. have been employed against *Aspidiotus* spp. scales. *Stethorus utilis* (Fig. 6.1) is often associated with tetranichid mites on palms and presumably preys on them. A predatory thrips, *Aleurodothrips fasciapennis*, also feeds on *A. destructor*. In Florida and probably elsewhere, coccinellids are important predators of introduced palm aphids, *Cerataphis* spp., although these beetles are native or were introduced for control of other target pests (Colour Plate 16d).

Ant complexes play vital roles in many herbivore situations, most elegantly illustrated in studies with coreid pests of coconuts. *Oecophylla smaragdina* is an effective control agent against *Amblypelta cocophaga*, unless it is in turn attacked by other ant species, such as *Pheidole megacephala*. A similar ecological web occurs with *Pseudotheraptus wayi* in Africa. *Tapinoma melanocephalum* is an important egg predator of the stick insect *G. crouani*.

Twenty-six species of spiders of six families were assessed as predators of *O. arenosella* in Kerala, India (Sathiamma *et al.*, 1987). The spiders, all occurring naturally in coconuts, were year-round predators, and four species – *Rhene indicus*, *Marpissa tigrina*, *Sparassus* sp. and *Cheiracanthium* sp. – were considered important predators. *Rhene khandalaensis* is also recorded as a valuable predator. Although spiders are considered generalist predators, they may often have a major, and unnoticed, influence on natural populations of insect species on palms (Howard and Edwards, 1984).

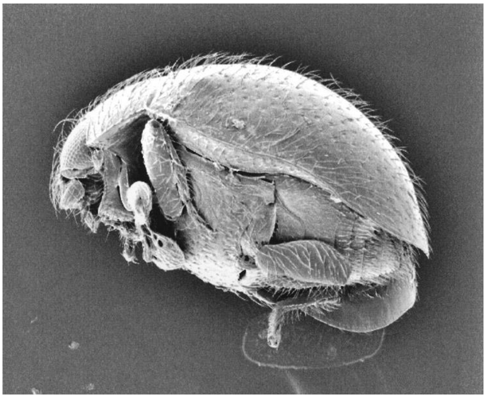


Fig. 6.1. *Stethorus utilis* (Coleoptera: Coccinellidae), identified by M.C. Thomas. This tiny black beetle (1.5 mm long) apparently preys on tetranychid mites. It is common on foliage of palms infested with mites in Florida.

All the Hemiptera recorded as predators of larval limacodids are considered generalists. Dolling (1987) recorded 11 species as predators of eight different species of Limacodidae from South-East Asia. Predacious shield-bugs of the Pentatomidae are considered to be ‘timid’ (Dolling, 1987). Their prey consists of larval Lepidoptera. *Cantheconidea* spp. are the main predators recorded. *Dindymus rubiginosus* (Pyrrhocoridae) feeds on Hemiptera and Lepidoptera, including the limacodid *S. asigna*. The predatory species in the family Reduviidae are more aggressive. *Cosmolestes picticeps*, *Syndus heros* and *Sycanus* spp. are important species.

Among the less well-studied groups of predators, those attacking *O. arenosella* include a chrysopid, *Ankylopteryx octopunctata* (Neuroptera), which preys on the eggs and early larvae (Sathiamma *et al.*, 1985). Larval *Chrysopa scelestes* also consumes *O. arenosella*. *Cardiastethus exigius*, *Cardiastethus affinis* and *Alofa sodalis* (syn. *Buchananiella sodalis*) (Hemiptera: Anthocoridae) attack the eggs and early larval stages. The carabids *Parena nigrolineata* and *Calleida splendidula* consume larvae and pupae.

Predators useful as biological control agents often have common attributes (Ehler, 1990). They usually have a good colonizing ability, even in temporary and changing agroecosystems. They can persist even in the absence of the target host (implying a lack of specificity) and show opportunistic feeding habits, enabling them to exploit a large pest population. Hardiness in the laboratory is of critical importance, because, beyond the theoretical qualities required, there is the need to rear and study the target natural enemy before use. Many biocontrol programmes have used second- or third-choice agents mainly because they can be reared and studied in the laboratory.

Parasitoids

Parasitoids are insects whose larvae develop by feeding on or within an arthropod host, which is almost always killed by the process (Gauld and Bolton, 1988). The parasitoid lifestyle is found in members of the Hymenoptera, Diptera, Strepsiptera and Lepidoptera. The first two orders are by far the richest in parasitoid species. There are less than 600 known species of Strepsiptera worldwide, but *Coriophagus* (*Halictophagus*) *zanzibarae* is a strepsipteran parasitoid of the later stages of *P. wayi* (Coreidae), and *Stichotrema dallatorreanum* is a strepsipteran parasitoid that has successfully controlled *Sexava* spp. (Acrididae: Tettigoniidae) on coconut palms (Lever, 1979).

The term parasitoid covers a vast number of species. Perhaps 10–15% of metazoan organisms are parasitoids, with probably at least 250,000 species included in the Hymenoptera. Parasitoids differ from predators in that all are insects. Surprisingly, some authorities classify mermithid nematodes as parasitoids. The adults of insect parasitoids are free-living, obtaining much of their nutrition from plant substances, while the larval stage is responsible for the actual parasitism of the host. It has been known since the early 1800s that parasitoids that attack egg and larval stages are common, pupal parasitism less so and parasitism of the adult host very rare (Kirby and Spence, 1826). A negative-feedback situation probably exists with the last. Because parasitoids of the adult stage are rare, they are rarely sought and even less frequently found (see *Phymastichus coffea*).

Many hymenopteran and dipteran parasitoids are ectoparasitoids, with eggs or larvae being laid, and subsequently developing, outside the body of the host. In contrast, endoparasitoids, which are more frequent, develop inside the body of their host. This requires a specialized ovipositor to pierce the host's cuticle. Primary parasitoids are those that attack an unparasitized insect. These parasitoids can, in turn, be parasitized by hyperparasitoids. Solitary parasitoids, whether ecto- or endoparasitoids, lay a single egg in or on the host, while gregarious parasitoids lay many. Superparasitism and multiparasitism refer to parasitism of a host already parasitized by a member of the same or a different parasitoid species, respectively.

Female parasitoids have to locate their host, overcome any physical defences, assess the host's suitability and successfully oviposit. Over the range of hymenopterous parasitoids, an amazing array of activities are displayed to achieve parasitism. Host location is usually considered to be a process of finding the host habitat in broad terms and then homing in on a myriad of cues to reach the potential host. (For example, *Apanteles taragamae* (Hymenoptera: Braconidae) is strongly attracted to the frass of *O. arenosella*.) Once the female has located its host, it may assay its size and physiological state and determine if it is already parasitized. Gregarious parasitoids adjust the number of eggs that they lay according to conditions. The female often stings the host to achieve permanent or temporary paralysis.

The hosts are usually not defenceless and protection may be provided by behavioural aspects of the female and young alike. *Microtylopteryx hebardi* (Acrididae) was observed to feed on a range of plants in a rainforest habitat in Costa Rica, where *Chamaedorea exorrhiza* was one of the hosts. The grasshopper has a serrated ovipositor for boring into and ovipositing in plant tissue (Braker, 1989). This may have a number of purposes, but avoidance of parasitoids is likely to be one. Various other types of host defences against parasitism are known.

Parasitism is normally assessed in terms of the percentage of the hosts sampled that are parasitized. This vastly underestimates the effects of parasitoids on host populations. Sampling to give an accurate assessment is difficult and usually does not take host age and parasitoid preference into account. A parasitoid that attacks a third instar of its host will not be found in a second instar. To consider the second instar as free of parasitism reduces the estimated effect of the parasitoid because a portion of these will become parasitized. Usually of far more significance are the actions that result in host mortality but not in parasitism. One of the most significant of these is host feeding. Although the adult usually obtains much nutrition from plants, many female parasitoids feed on individuals of the species that form its host, obtaining lipids and proteins especially. This action usually results in the death of the host. Parasitoids may probe with their ovipositor into the body of a potential host to determine whether it is suitable for parasitism and this also can result in death. The presence of a parasitoid may induce defensive actions, such as scattering or dropping from plants, which may result in mortality. Parasitoids have also been associated with the spread of insect diseases, for example with viruses. The sum of these and other actions is usually greater than successful parasitism.

The qualities sought of a parasitoid required for a biological control programme have been discussed by many authors, but can be broadly summarized by the views of Huffaker *et al.* (1977). They include fitness, adaptability and a high searching capacity for hosts, with density-dependent parasitism. Of critical importance is host specificity. The parasitoid should usually be specific to a single host or a few closely related species. Too wide a host range carries danger of damage to non-target organisms and insufficient control of the intended target. Whether parasitoids selected for their ability to regulate a pest population during an outbreak will have the qualities necessary to maintain their hosts at a sufficiently low level is difficult to determine. In reality, biological control relies heavily on practicalities. Often the parasitoid selected is either the one found soonest or the easiest to rear or transport, rather than that with the finest qualities.

The role of hyperparasitoids is the subject of debate. Intuitively, they would appear to reduce the efficacy of parasitoids. Obligate hyperparasitoids are always screened out of introductions made for biological control. However, facultative hyperparasitoids, those that develop at the expense of either a non-parasitic host or a primary parasitoid, can be important agents (Ehler, 1990). A facultative hyperparasitoid could be of positive value in biological control if the collective impact of primary and secondary parasitoids is greater than that of the primary alone and does not have a significant negative effect outside the target system (Ehler, 1990). However, two of the most notable classical biological control projects of recent years, against the mealybugs *Phenacoccus manihoti* and *Rastrococcus invadens*, were achieved despite very high levels of hyperparasitism (Agricola and Fischer, 1991).

Natural-control parasitoids

The majority of the species of Hymenoptera are parasitoids. This is an ecological role of nearly all of the superfamilies Ichneumonoidea, Proctotrupoidea, Stephanoidea, Ceraphronidea, Trigonaloidea, Megalyroidea and Orussoidea (Gauld and Bolton, 1988). Many in the Chalcidoidea, Cynipoidea, Evanoidea and Chrysidoidea are also parasitoids.

A few arachnid groups are attacked, but the usual hosts are insects, mainly in the endopterygote orders Lepidoptera, Coleoptera, Diptera and Hymenoptera and the exopterygote Hemiptera (Gauld and Bolton, 1988). Insects with aquatic or highly active young stages have fewer associated parasitoids. The great complexity of the Hymenoptera is such that, despite degrees of specificity of hosts within groups, trying to describe them is beyond the scope of this section. Gauld and Bolton (1988) provide detailed and readable information.

The Diptera are the second most important order in terms of parasitoids. Several families are exclusively parasitic and tend to have clearly defined host ranges (Askew, 1971). Exceptions showing greater diversity of hosts or feeding habits include the Tachinidae and the Calliphoridae, probably the most successful dipteran families in biological control. Few dipteran parasitoids hyperparasitize other Diptera. Another difference from the Hymenoptera is that, in a greater proportion of dipteran parasitoids, the first-instar larvae, rather than the adults, locate the host. Some parasitoids of Diptera are known but, again the majority attack other insects. The Bombyliidae are mainly parasitoids of Hymenoptera, but some species attack beetle larvae and others attack pupae of Diptera or Lepidoptera. Nemestrinidae attack beetle larvae or pupae and some species attack locusts. Phoridae, as a group, have cosmopolitan tastes, with millipedes, coccinellid beetles, Diptera, ants, Lepidoptera and bees numbering among their hosts. In contrast, the Pipunculidae are solitary endoparasitoids of Cicadellidae, Cercopidae and Delphacidae. The Tachinidae are of major importance, with hosts mainly among the Lepidoptera and Coleoptera, but also among Acrididae, Dermaptera and larval Tipulidae (Diptera).

Parasitoids used in classical biological control

In practical biological control, three taxa, Ichneumonoidea, Chalcidoidea and Tachinidae, have been the major source of agents. Greathead (1986) gave a detailed account of the characteristics of agents used. Their use does not imply that other groups do not play a significant part in natural ecosystems. Parasitoids attack many non-pest species; some groups are exclusively or predominantly hyperparasitic and others are species that attack a restricted range of hosts. The following brief descriptions of the major sources of biological control agents are from Greathead (1986). They give an indication of levels of specificity, useful for biocontrol practitioners. Although spectacular successes have been achieved with one or two species of natural enemies, often control is by complexes and with interactions with abiotic factors (Waterhouse and Norris, 1987).

Ichneumonoidea

The Braconidae and Ichneumonidae are large and varied families, but successful agents have been derived from relatively few genera. In the Braconidae, the predominant genera in biocontrol are *Apanteles*, *Bracon* and *Opius*. They have been most successful in controlling Lepidoptera. The Ichneumonidae are solitary parasitoids of larvae or pupae of endopterygote insects, especially Lepidoptera, but have been particularly successful against larvae of the phytophagous suborder Symphyta of the Hymenoptera (Gauld and Bolton, 1988), which is not represented on palms. Species of the subfamily Aphidiinae exclusively attack aphids.

Chalcidoidea

The most frequently used and successful superfamily is Chalcidoidea, with the Eulophidae, Pteromalidae, Encyrtidae and Aphelinidae being the most important families. Notable eulophids include *Pediobius parvulus*, used against *Promocotheca coerulipennis* (see Box 2.2), *P. coffea* (q.v.), and *Phymasticus xylebori*, which attacks the imago of *Xyleborus perforans* (q.v., Chapter 5). Pteromalidae have been successfully used against dipteran and lepidopteran pests, while the Encyrtidae are very successful agents against Pseudococcidae and Coccidae. Diaspididae, Aleyrodidae and Aphidoidea pests have been controlled on a number of occasions by parasitoids in the family Aphelinidae.

Diptera

The successful control agents have come from the Cryptochetidae and Tachinidae, with the latter of more significance, ranking alongside the more important families of Hymenoptera in terms of classical biological control. The Tachinidae exhibit a diversity of oviposition or larviposition strategies, all of which appear capable of exerting significant control.

Tachinids have been involved in some of the most important successes, such as control of the coconut moth, *Levuana iridescens* in Fiji by *Bessa remota* (Fig. 6.2; see Box 2.1). They have also been considered important against other palm pests, such as Phasmida (e.g. the defoliators *Ophicrania leveri* and *Megacrania phelaus*), Lepidoptera (e.g. *Brassolis astyra, Omiodes blackburni*) and Coleoptera (e.g. *Parabillaea rhynchoporae* is a pupal parasitoid of *Rhynchophorus palmarum*). The calliphorid *Sarcophaga fuscicauda* is a minor parasitoid of the weevil *Rhynchophorus ferrugineus*. Flies of the Calliphoridae, Conopidae and Phoridae are occasional parasitoids of *Neotermes rainbowi*.

Harmful Effects of Biocontrol

Although biological control is generally an environmentally benign form of arthropod control, it has ecological consequences. Insect population regulation by natural enemies is occurring continuously in nature, but human activity has been responsible for major transfers of species throughout the world. Classical biocontrol is usually in response to an exotic insect proving to be an economic pest. Both the pest outbreak and any other form of control are also going to have ecological consequences. Biocontrol, if successful, is irreversible and possible disadvantages have to

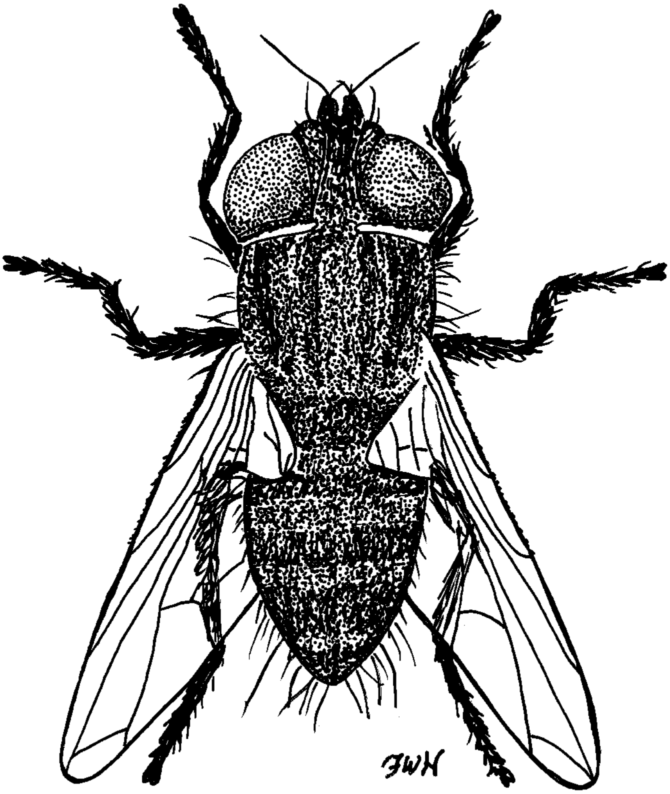


Fig. 6.2. *Bessa remota* (Diptera: Tachinidae), imago. This parasitoid was imported from the Malay Archipelago to Fiji in the famous biological control campaign against *Levuana iridescens* (Zygaenidae), a pest of coconut palms. After Puan Hamidah Suhaimi and Encik Ng Beng Cheng, in Ooi (1977).

be weighed in advance, but the record with classical biological control, especially of insect pests, is very good.

There are legitimate concerns that introduced predators and parasitoids may attack non-target organisms. Specificity is one of the main characteristics required in a biocontrol agent, but this specificity may not be complete. Howarth (1983) considered that the introduction of many parasitoid species into the Hawaiian Islands has depressed populations of indigenous species. Whether they would have been depressed even further by high populations of exotic pest species or by other forms of pest control is impossible to determine.

Biopesticides

The practice of spreading diseased insects through crops may have been practised thousands of years ago. Although in modern times there has been interest in using insect pathogens for biological control purposes, success has been limited. In the commercial context, pathogens represent only a tiny proportion of products sold. In 1991, the world agrochemical market was estimated at nearly $27,000 million. Biopesticides constituted a little over 2% of this value. Over 90% of biopesticide sales were based on the toxin of *B. thuringiensis* as the active agent (Rodgers, 1993).

Bacteria, fungi, viruses, protozoa and nematodes are the active ingredients of a range of commercial biopesticide products. They have been used against major and minor pests of crops, ranging from grass to forestry. At their best, they provide control equal to or better than that of chemical pesticides but with fewer disadvantages. All too frequently, however, the promise has far exceeded the reality.

Biopesticides potentially have many advantages over chemical pesticides. Because they are much safer to operators, producers and consumers as well as non-target organisms, registration costs are low. Resistance management should be easier with the flexibility offered by the products. Secondary cycling from cadavers sometimes ensures a long persistence of the active ingredient in practical terms (Thomas *et al.*, 1995).

However, success for biopesticides is slow in coming. In part, this has been due to a misplaced emphasis on the active ingredient, the pathogen, and only relatively recently has equal emphasis been placed on formulation and application. The first commercial *B. thuringiensis* product was marketed in France in 1938, but it is really only during the past 20 years or so that products have been reliable enough for practical agricultural purposes.

Many of the perceived and actual disadvantages of biopesticides are being resolved. A product shelf-life of 12–24 months at ambient temperature (depending on location) is feasible for many products. Some biopesticides appear to be too specific, but continued research results in new isolates, which expand the potential targets. The original isolates of *B. thuringiensis* were active against Lepidoptera, but isolates active against Coleoptera and Diptera have been found and used in commercial products. Isolates active against flukes, nematodes and mites have also been found (Rodgers, 1993). The results of research are stimulating. There is now evidence that some fungi may be highly suitable for use in biopesticides in hot climates. Morley-Davies *et al.* (1996) maintained over 80% viability in conidia of a range of *Metarhizium* and *Beauveria* spp. for more than 10 days at 50°C. One isolate of *M. anisopliae* maintained this level of viability for over 60 days at 50°C. Other examples of progress are given by Feng *et al.* (1994), who also describe pest control programmes using *B. bassiana* in China. A number of these were against pests of trees. Commercial palm plantations have used *B. thuringiensis* against lepidopteran pests and there has been much, and often duplicated, research on viruses and fungi for use as biopesticides. As the products and strategies for biologically orientated control develop, they are likely to become of increasing significance.

7

Principles of Insect Pest Control on Palms

Forrest W. Howard

> As for the necessity of this art, it is evident enough, since this can live without all others, and no one other without this.
>
> (Abraham Cowley (1618–1667), English doctor of medicine, poet and farmer, in *Of Agriculture*)

Insect control can be divided into seven different categories: natural, physical, cultural, host-plant resistance, biological, chemical and miscellaneous. Integrated pest management involves combining multiple methods of the same or different categories.

Natural Control

In their natural environments, insects are under natural control by biotic factors, including predators, parasitoids and microbial agents, and by abiotic factors, such as those related to weather. The effect of these agents on palm-associated insects is to maintain low population levels, so that, although damage may be present, it is usually slight.

When palms are brought into cultivation in their native regions, natural control may continue working to keep the palms relatively free of insect pests. For example, in Florida, the native *Sabal palmetto* grows in extensive stands in wild areas and is also planted throughout the urban areas. The same insect species attack it in both wild and urban areas, and in both areas usually these species occur in low population levels due to natural control.

Natural control does not always achieve a high enough degree of control to satisfy human interests. It is natural for many kinds of insects living in their native habitats to undergo periodic population explosions, which may cause extensive damage to their host plants. This is most likely to happen when there is some disturbance in the natural factors that normally keep their populations low. Similarly, outbreaks of native insects may occur on native palms in cultivation, and may even be aggravated by factors associated with urban areas, such as synthetic fertilizers, excessive irrigation, pesticides, poor soil structure, transplant shock, dense planting of a single species, etc.

Physical Control

Physical control involves the use of any physical means of controlling insects or preventing their damage. Window-screens and fly-swatters are familiar examples. A common method of physical control of palm pests is hand-collecting to remove caterpillars and other insects. This technique is obviously highly labour-intensive and may often be cost-prohibitive for large-scale agriculture, as was shown experimentally for control of a coffee pest in Kenya (Pelley, 1935). However, it may be effective in palm nurseries or on small properties, especially for controlling a species such as *Brassolis sophorae*, whose caterpillars congregate in 'nests' by day. Using brooms to remove caterpillars from taller palms has been used in plantations in Asia. Mealybugs, aphids and other insects may be removed from fronds or leaf axils with a strong spray of a garden hose. This may be an option for a limited number of small palms. Sticky barriers around trunks are used to control some insects, e.g. Phasmida, which climb into palms from the ground. A more spectacular form of physical control involved the eradication of the white date scale insect, *Parlatoria blanchardi*, from the south-western USA by dousing the palms with kerosene and setting them ablaze (Boyden, 1941).

Cultural Control

Cultural control is control of insects via agricultural or horticultural practices. Crop rotation is one of the familiar examples in agriculture.

In palm culture, keeping palms healthy generally protects them from borers and certain other kinds of insects. Conversely, a borer attack is generally taken as symptomatic of a horticultural problem. This is a delicate thing to have to explain to a grower who invested efforts in horticultural care, only to be rewarded by the arrival of ambrosia beetles. In fact, the horticultural requirements of many palms are not well known. For example, a horticultural practice known to promote vigour in palms in general (e.g. abundant irrigation) may be a stress-causing factor for certain species (e.g. those native to dry savannahs). Some palms are grown in regions with conditions so different from those of their natural environments that it is doubtful whether horticultural practices can completely correct this. For example, *Phoenix canariensis*, which is adapted to the Mediterranean (Cs) climate of the Canary Islands (Colour Plate 2c), is a popular ornamental palm in many humid tropical countries (tropical wet (Af) and tropical wet and dry (Aw) climates) (see Box 1.1). Many of the lesser-known palm species may have very fine-tuned (and unknown) requirements. To complicate matters, the lush foliage of healthy palms may be relatively attractive to some defoliators and sap-sucking insects.

Stem borers are usually not detected in palms until they have damaged them. Growers often attempt to correct the problem by applying an insecticide against the beetles. Of course, borer damage in stems of palms does not heal. In an active infestation, the beetle larvae are inside the stem and not affected by the insecticide, and killing the adult beetles may do little to prevent further damage. In summary, it is more important to identify and correct the adverse growing conditions, of which the beetle attack is merely symptomatic.

Stressed palms may be relatively attractive to some insects other than borers. Where the coconut scale insect, *Aspidiotus destructor*, is a pest on coconut palms in a coastal area of Côte d'Ivoire, the scale insects were slightly less abundant on palms around villages. This was attributed to higher levels of minerals from village wastes, in contrast to the sterile sandy soil of the beaches (Mariau and Mallet, 1999).

Horticultural practices that minimize injury to palms may prevent the attack of some insects. For example, wounds in palms caused by tractors, pruning equipment, etc. may provide oviposition sites for *Rhynchophorus* weevils (Mariau and Mallet, 1999).

Insect and mite problems are often related to higher planting density. For example, the prevalence of damage due to coconut mite, *Aceria guerreronis*, seems to be at least partly related to the planting density of coconut palms (Howard *et al.*, 1990). Monocultures, i.e. plantations, nurseries, landscaped areas and glasshouses containing single species of palms (Colour Plates 1b, c and 2a, d, Fig. 7.1), provide abundant food for particular pests and thus encourage the development of dense pest populations. Where applicable, planting ornamental palms interspersed with other kinds of plants or with a diversity of palm species tends to curtail insect attack.

A ground cover of a selected herbaceous plant species is often maintained in coconut palm and African oil palm plantations for preventing soil erosion, adding organic matter, reducing competition of noxious weeds and providing forage for livestock. Leguminous ground covers improve the nitrogen content of soils. Additionally, a degree of cultural control can be provided by some ground covers. Leguminous ground covers, e.g. *Arachis pintoi* and *Pueraria phaseoloides*, which are already used in plantations in many countries, are poor hosts of the lethal-yellowing vector, *Myndus crudus*, and thus would be advantageous in plantations in the Caribbean and Central America (Howard, 1999a). In Asia and the Pacific, a creeping ground cover, e.g. *P. phaseoloides*, may cover dead logs and other larval habitats of *Oryctes rhinoceros*. The ground cover tends to reduce the number of beetles that find and oviposit in these sites. Whether this is because the odours of the ground cover mask those of decaying vegetation, the decaying material becomes unsuitable for the larvae because of a change in its moisture level or the vines simply hide these sites from view is not known (Mariau and Mallet, 1999). Ground cover may provide nectaries, which serve as a food source for hymenopterous species that help control pests of palms. In Ghana, *P. phaseoloides* as a ground cover supported a hispine leaf-miner, *Platypria coronata*, which served as an alternate host for parasitoids of a leaf-miner pest of African oil palms (Bernon and Graves, 1979).

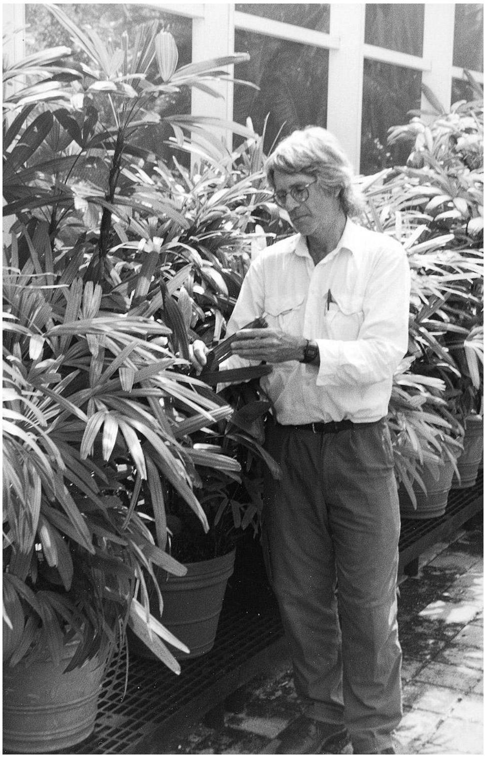


Fig. 7.1. Examining *Rhapis excelsa* in a glasshouse for scale insects.

Sanitation (e.g. removing dead stumps) is a form of cultural control that is often effective in reducing populations of insects such as *O. rhinoceros*, which pass their larval stage in decaying trunks and similar materials. However, where such practices do not reduce pest problems, allowing vegetation to decay naturally is a way of recycling nutrients.

Host-plant Resistance

Host-plant resistance is a method of control that utilizes varieties or species of plants that are resistant to certain pests. Sometimes, naturally resistant plants are discovered fortuitously. In many cases, they are developed through long, difficult breeding programmes. The method has been particularly well developed for protection of annual crop plants, because the relatively brief life cycle of such plants facilitates the breeding of new varieties.

Economic palms (coconut, date, etc.) are bred for disease resistance, productivity, etc. (Harries, 1973), but there has been almost no breeding of palm varieties for insect resistance. Some palm species used for ornamental purposes are seldom attacked by insects. This is obviously an advantage, but is probably seldom considered when selecting species for landscaping. The fact that such species as coconut palm, *P. canariensis, Roystonea regia* and *Washingtonia robusta* may be attacked by serious insect pests has not seemed to diminish their popularity.

Biological Control

Biological control involves introducing predators and parasites into an environment to control a target pest. It differs from natural control in that it relies on human intervention. Some of the most famous examples of successful biological control have been programmes against pests of economic palms. These include successful campaigns against the coconut moth (*Levuana iridescens*) (Box 2.1), a hispine leaf-mining beetle (*Promecotheca coeruleipennis*) (Box 2.2) and the coconut scale insect (*A. destructor*), all on coconut palms in Fiji, and the introduction of beetles that controlled *Parlatoria blanchardi* on date palms in several countries of North Africa, the Middle East and India (Gaillot, 1967; Iperti *et al.*, 1970; Laudého *et al.*, 1970; Kaufmann, 1977; Stansly, 1984; Muralidharan, 1994).

Once established successfully, biological control is one of the most effective, long-lasting and environmentally compatible methods of insect control. But often programmes are successful only after numerous attempts at introducing the same or different natural enemies. More often than might be expected, programmes have been unsuccessful because of the natural enemy's failure to become established where it is introduced, or for a variety of other reasons (Taylor, 1955; Shreiner, 1989). A further concern is that concerted efforts must be made to prevent 'side-effects', such as a predator attacking beneficial native insects. In modern times, biological control programmes are done carefully and with a great deal of research to try to ensure success. Thus, research and development of biological control for any particular pest constitute a long and expensive undertaking. Due to the expense of this method, research and development of biological control tend to be concentrated on pests of extraordinary economic importance. Pests of ornamental palms rarely fall into this category.

Chemical Control

Chemical control is control of insects with insecticides, repellents, feeding inhibitors and other biologically active chemicals. In the 1800s and early 1900s, simple non-organic substances, such as sulphur dust and lead arsenate, were used for crop protection against insects. Beginning in the 1940s, synthetic organic compounds were developed as powerful insecticides. Although generally highly effective against pests, they are toxic to a broad array of other organisms. Pesticides classified as chlorinated hydrocarbons tend to be highly persistent. While this was an advantage for insect control, persistent chemicals can travel through the food-chain and affect many organisms far removed from the target pest. Thus, since the 1970s, chlorinated hydrocarbons have been largely phased out of use as insecticides. Synthetic organic insecticides still in use include organophosphates (e.g. dimethoate, malathion) and carbamates (e.g. carbaryl). The toxicity of different chemicals in these groups varies from highly to slightly toxic. Pyrethroids (e.g. permethrin) are chemically similar to pyrethrins, which are natural plant derivatives.

Recently, chemical companies have been highly successful in discovering and developing insecticides whose toxicity is much more specific to insects than those previously available. These include insect growth regulators (e.g. dimethynonane, fenoxycarb, methoprene), which are compounds chemically similar to hormones produced by insects themselves, but which are lethal to the insect at the dosages applied. Diflubenzuron and lufenuron are insect growth regulators that interfere with larval moults by disrupting the synthesis of chitin. Abamectin is a natural substance that is toxic to insects, but has a low toxicity to higher organisms. Since it can penetrate several layers of plant cells, it has been useful for control of leaf-miners, and is highly effective against spider mites. Imidacloprid is a unique chloronicotinyl compound, which, when drenched into the root zone of plants, is taken up systemically. It tends to concentrate in new growth, the feeding site of many insect pests. Since it is taken up very slowly into the plant, there is a lag, usually of many weeks, between application and insect control, but, once it becomes active in the plant, it protects it for a relatively long period.

Bacillus thuringiensis is a bacterium that produces substances that are highly toxic to certain insects. These toxins are the active ingredient in Bt, a product that can be mixed with water and sprayed on plants for controlling such insects. Recently, there has been a renewed interest in botanicals (compounds found in plants) that are toxic to insects. Natural products often have low or negligible toxicity to vertebrates, in which case they are sometimes referred to as biorationals. Some of these have been used for centuries for insect control. An example is azadirachtin, which is an extract of the seed of the neem tree, *Azadirachta indica* (Meliaceae), which, when applied to leaves, acts as a feeding inhibitor to defoliators. Additional botanicals are pyrethrum, which is extracted from *Chrysanthemum cinerariaefolium* (Compositae), and methanolic extracts from the bitterwood tree, *Quassia amara* (Simaroubaceae). Biorationals have obvious environmental and safety advantages. However, their effective use often requires better knowledge of the target insect and more skill in timing applications than is necessary for the more broadly toxic synthetic organic insecticides. For example, both azadirachtin and Bt are most effective against lepidopterous larvae when they are in early instars. Thus, knowledge of the insect's seasonal history and conscientious scouting to determine when its early instars are present are necessary to ensure good control with biorational products.

Insecticides may be classified according to their mode of activity on insects. Contact insecticides are effective when applied directly to the insects or to sites where the insect will come into contact with them. Some contact insecticides can be applied to foliage or other plant parts, so that insects that feed on them acquire a lethal dosage. The latter class of insecticides is appropriate for controlling externally feeding defoliators, such as many caterpillars. Some can also be sprayed on buds to protect them from borers, although borers are best controlled by cultural control, i.e. by keeping palms healthy.

Systemic insecticides are absorbed into the plant's system either when applied to the leaves, injected into the trunk or injected or fed into the roots. Because they circulate within the plant and thus are not exposed to direct sunlight or rainfall and are maintained under relatively even temperatures, systemic insecticides are generally effective for longer periods than contact insecticides. Trunk injections of systemic insecticides have been used to control many pest species, including defoliators and sap-suckers. The general method was originally developed for use on dicotyledonous trees, which normally heal the injection holes. The method has the disadvantage when used on palms that they do not heal holes in their trunks; thus injection holes may be infection sites for fungi and other pathogens. Plugging the holes after injection may prevent infection.

Root injections are a way of applying systemic insecticides to palms without damaging the trunk. In this method, the insecticide is contained in a small bag or other container, from which a tube extends. The soil is removed from a live root, the tube fitted over the cut end of a root and the material fed by gravity into the root (Ginting and Desmier de Chenon, 1987). Applications can be made to multiple root ends simultaneously. This is a slow method when numerous palms are involved (Philippe *et al.*, 1999).

Root drenches involve the pouring of

insecticides into the root zone. An example is an imidacloprid drench for controlling *Xylastodoris luteolus* (Hemiptera) (q.v.). A small amount of imidacloprid is mixed in a 20 l bucket and the contents poured very slowly on the soil near the base of the trunk (Howard and Stopek, 1998, 1999). The method is very simple and requires no special equipment. The drench may be applied by mechanized equipment if a large number of palms are to be treated. Some of the insecticide is leached through the soil without being adsorbed by the plant, a disadvantage avoided by root injections.

Systemic insecticides are used against defoliators, but are particularly effective against piercing–sucking insects that feed in the sap stream, all of which are in the order Hemiptera. Whiteflies, palm aphids, mealybugs and soft and armoured scale insects are the most common hemipterans on palms. Systemics are an important tool for control of armoured scale insects, because they are protected from contact insecticides by their hard, waxy scale.

Oils are often effective against scale insects. They work by sealing off the insect's air supply. Some petroleum-based oils may be toxic to some palms, especially during hot weather, mostly because of the organic solvents that they contain. However, some light oils (summer oils) are less likely to damage plant tissue. Fish-oil products are apparently rarely, if ever, phytotoxic to palms, probably because they do not contain petroleum distillates. An advantage of oils is that it is unlikely that any insect species can develop resistance to them.

Water solutions of insecticidal soaps are effective against some insects, such as aphids and spider mites. Soap solutions are sometimes phytotoxic to palms, causing a 'burn'. This can be avoided on some palms by leaving the soap solution on the palm for not more than an hour, during which time it may be expected to kill the target insects, and then washing the palm with clear water from a garden hose.

A desirable objective in chemical control of insects is to achieve acceptable control with minimal use of insecticides. Thus, one should use the lowest rate and the lowest number of applications that will control the insect. Reducing insecticide use reduces hazards to humans and the environment, saves resources and money and helps keep insect pest species from evolving resistance to pesticides.

Plants have many defensive chemicals, and it has sometimes been suggested that applying insecticides is merely a way of supplementing them. But this is an oversimplification. Many synthetic insecticides are much more toxic than the defensive chemicals of plants. And, since insecticides are not manufactured internally in the plant but must be applied externally, a large portion of the chemicals applied usually 'misses the target', ending up on nearby trees and other objects, on or in the ground or, by drifting on air currents, at distant terrestrial or aquatic sites. A portion of the compounds applied as root drenches may enter the groundwater. Fortunately, safer insecticides are being developed, and modern horticulturists are aware of the importance of using insecticides judiciously and safely and with minimal effects on the environment.

Miscellaneous

In addition to the six general categories of control already discussed, a seventh category contains miscellaneous methods that are applicable to particular situations. An example is the sterile-male release technique, which has been an extremely effective method of solving some insect pest problems. Briefly, the method involves swamping the pest population with sterile males, so that females do not lay viable eggs. An expensive endeavour requiring much research for any given target, it has been most effective against certain flies (Diptera), an insect order that contains few, if any, pests of palms.

Integrated Pest Management

Integrated management is the most economical and environmentally compatible approach to controlling plant pests. In its simplest form, combining two or more methods to control the population of a single pest constitutes integrated management. For example, growing a palm species that is resistant to a particularly damaging pest, avoiding overwatering (cultural control) and occasionally applying a pesticide would be an integrated pest management approach. This approach reduces the pressure on the pest to develop resistance to particular control measures. For example, if an insect is controlled solely by a particular chemical, it may be expected that a strain resistant to this chemical may develop. But, if the population is already controlled to some extent by host-plant resistance and perhaps a cultural method, less chemical control is needed and there will be less selective pressure on the insect for a resistant strain.

Alternating insecticides is another way of reducing selective pressure. If a pest can be controlled by insecticides in more than one class of chemicals (e.g. a carbamate and a biorational product), the different chemicals should be used alternately, so that the insect is not repeatedly exposed to the same chemical.

A key question in pest management is at what point insecticides or other control measures should be applied. Integrated pest management in some agricultural systems has become quite sophisticated, so that insecticides are applied only when impending economic loss is indicated by a certain number of insect pests per unit (e.g. the number of leaf beetles per leaflet). This number is known as the ‘economic’ or ‘treatment threshold’. Economic thresholds have been published for some pests of crop palms. In protection of ornamental palms, the more subjective threshold employed in shade-tree entomology may be more appropriate: control measures should be employed at the point when insects interfere with the use of the plant (Barbosa and Wagner, 1989).

The term pest ‘management’ as opposed to ‘control’ has been widely adopted to emphasize that insect pests cannot be eliminated and therefore must be ‘lived with’, i.e. managed so as to cause minimal damage. It is not usually necessary to completely eliminate insects from palms. Light damage to palms due to insect feeding may be tolerated in plantations and urban landscapes, as it is in natural areas. Insects are an important part of the environment. For example, insectivorous birds and many other forms of wildlife depend upon insects as their sole food source.

8

Field Techniques for Studies of Palm Insects

Forrest W. Howard

Come forth into the light of things,
Let Nature be your teacher.
(William Wordsworth (1770–1850), English poet. *The Tables Turned*)

As research on insects has expanded and intensified during the past two centuries, legions of entomologists have assembled a vast array of techniques for studying diverse taxa in myriad situations. Even the byword of entomological tools, the net, identified with Victorian naturalists capturing specimens of flying insects, currently comes in different models for sampling specific insect taxa in a variety of habitats. A comprehensive review of entomological techniques would fill many volumes. In this brief chapter, we wish to present a synopsis of techniques and approaches to fieldwork that are unique to the study of insects on palms.

In his classic book on the natural history of palms, Corner (1966) placed importance on methods and equipment that enabled palm scientists to ascend palm stems. Many of the methods he described were developed by harvesters of coconuts and other palm fruits.

The art of ambling up the stems of palms has been an integral part of the culture of many tropical countries since ancient times. Adroit climbing of coconut palms by people of Oceania, without any devices and dependent only on human strength and agility, is a well-known example. Skilled climbers are said to climb an average of 25–45 palms day^{-1} throughout the year (Piggot, 1964). These sturdy people are rated a notch above most tree climbers, because they scale a vertical column without the ‘ladder rungs’ that branches of dicotyledonous and coniferous trees provide.

Rope loops, encircling the stem and engaging the shoulder area or the feet are also very old methods. Hanging loops, which are employed in what Corner (1966) referred to as a modification of an African method, consist of a pair of ropes that loop around the palm stem, and which are attached to other loops that act as stirrups. One stirrup cradles the thigh, while the other supports the opposite foot. The climber alternately loosens each loop and moves it upward. This device, widely used by palm workers in the Americas (Corner, 1966), is clearly illustrated in Hodge (1958) and Rosengarten (1986).

Fronds and fruits of coconut palms are regularly trimmed as a safety measure in areas of frequent human activity, such as along the streets and beaches of Florida. Here, thousands of palms were formerly climbed with tree spikes, a technique borrowed from logging and utility pole climbing. Palms do not overgrow wounds in their stems, so the holes and gashes made by the spikes are permanent. Such wounds would be unacceptable in stems of, for example, *Roystonea regia*, grown as ornamental palms, because the smooth, grey, columnar stem of this palm is part of its appeal. Spikes result in less aesthetic damage to coconut palms, because with time the holes become eroded and blend somewhat with the rough, fissured texture of the stem. Climbers with spikes could potentially spread palm diseases in some regions, but in Florida this seems to have rarely, if ever, occurred. Wounds may attract borers in some regions. In regard to the safety of the climber, spikes were developed for poles and the straight trunks of conifers. Setting the spikes at the proper angle, which is critical, is difficult on the highly sinuous stems of some palms, such as coconut palm. Spikes are hard to drive into the exceptionally hard stems of some palm species, and the toughness of an individual stem may vary over its length. Spikes become stuck in highly fibrous areas of the stem and have to be pulled out by yanking the foot, thus upsetting the climber's balance. A spike set into an old spike wound or other soft area may suddenly slip out.

Samples of the inflorescence and fronds of an extremely rare palm, *Halmoorea trispatha*, in a remote area of Madagascar provided an incentive for a botanist (Beentje, 1994) to climb its smooth, swaying, 24.5 m stem with spikes. His account of this ascent is told with good humour, but it is nevertheless chilling.

An apparatus dubbed the 'palm bicycle', described by Davis (1961), consists of a framework and rollers that can be operated up and down palm stems. The idea has not caught on much. Such a device would have to be built in local machine shops, since it is unlikely that they will ever be mass-produced. Some coconut researchers have used a similar device, known as the 'baumvelo', 'tree grips' or 'Swiss tree bicycle', developed mostly for climbing tall conifers with clear boles. They are available from forestry equipment companies. The mechanics of the device are somewhat similar to that of the African method with loops, described above, but with adjustable steel straps instead of rope loops. A method involving a harness, with a safety line and climbing techniques borrowed from mountaineering, is described by a coconut breeder (Harries, 1977). Upon reaching the base of the crown, a hook attached to a safety line is slipped over one of the younger leaf bases to provide security for further ascent. Biologists use somewhat similar lines for hauling themselves into the canopies of tropical forests, but they attach the lines to tree branches, a structure lacking in palms.

Straight or extension ladders, of the type used in building construction and maintenance, are widely used by palm workers. Lightweight aluminium or wood ladders are preferred, so that they can be easily carried from one palm to the next, but the lighter the ladder the less its reach. An exceptionally light ladder used in the Philippines consists of a single pole with the rungs on both sides (Fig. 8.1). A ladder is usually placed so that the top rung rests solidly against the crown and is stabilized by its position against or among leaf bases. Securing the ladder to the stem and perhaps to the crown with chains or strong cords adds to its stability. There is some risk in relying entirely on a leaf base for supporting a ladder. Although normally strong and persistent, under pressure petioles of even young fronds will sometimes suddenly snap or shear from the stem. We have experienced this after prolonged cold periods in Florida, and conceivably drought and other conditions could also induce partial abscission.

A type of aluminium ladder developed for forestry and known as a Swedish sectional cone-picking ladder combines high reach and transportability. With the 3 m sections disassembled, the ladder can be easily transported in a small truck. The sections are connected at the study site.

Fig. 8.1. Ladder of type often used in coconut studies in the Philippines. Companion steadies ladder while observer climbs, then takes notes on observations made by climber. Photo courtesy of Philippine Coconut Authority.

The ladders are equipped with brackets, which are curved to rest against the stems of conifers. To press the bracket firmly against the stem, a chain is passed around it and secured with a clip. However, the braces do not conform to the shape of some palm stems, in which case it may be used without brackets as a straight ladder.

Additional methods used in different cultures include cutting steps about 0.5 m apart in stems of palms, which are climbed periodically (Piggot, 1964), which has disadvantages similar to those imposed by spike climbing, i.e. risk of injury to the climber and damage to the stem; stringing ropes from one palm to the next to make a high catwalk, so that two or more palms can be visited after a single trip from the ground; and training monkeys to harvest coconuts (Corner, 1966).

As a botanist, Corner (1966) emphasized techniques for climbing the stem, because it is the route to the base of the crown. This is the site from which the inflorescences, infructescences and fronds, which are the plant parts of greatest botanical interest, can be sampled. Here interests of harvesters, botanists and entomologists coincide, for it is also the site for studying and sampling insects and mites of the flowers, fruits and meristematic bud.

But much of the insect life on palms takes place out on the fronds. Petioles or the fronds themselves of some palms are short enough for them to be at least partially examined or for insect traps to be placed on them from the base of the crown. The problem is greatest with long pinnate fronds. Those of African oil palm, coconut palm, date palm and *Roystonea* extend 3–6 m from the stem (Hoyos Fernández and Braun, 1984), and those of *Raphia*, the longest leaves in the plant kingdom, extend 25 m (Uhl and Dransfield, 1987). One cannot climb out on a palm petiole, as is done on sturdy tree branches to reach the leaves. A route other than the stem is needed to reach the frond from the ground.

Platforms constructed on towers reaching among tree canopies have long been used by biologists of various disciplines, particularly for long-term studies in particular trees. A chief advantage is their stability. They might be an option for some studies of insects on palm fronds, but we know of only a few instances in which palm entomologists have tried them. Although multiple towers are an option, fixed observation towers would usually not be replicated enough for insect surveys or most entomological studies. Mobile towers are needed.

A device known as a 'bucket truck', 'aerial lift' or 'aerial platform' is used in the construction industry, by utility companies and by urban arborists (Fig. 8.2). It is, in fact, a 'mobile tower'. In Florida, such trucks have made climbing with spikes obsolete. The platform or bucket is lifted and lowered by a hydraulically operated, truck-mounted boom. In some models, the boom reaches 60 m and thus could hypothetically reach the tallest palms known (*Ceroxylon* spp.) (Fig. 1.4f; Anderson, 1976). In practice, boom lengths of 10–15 m reach the crowns of most palms in urban areas. They are expensive to purchase and costly to operate. Local park and street departments sometimes assist entomologists by making their bucket trucks available for conducting observations of palm pests in their communities.

Fig. 8.2. A truck-mounted hydraulic-lift 'bucket' used in tree maintenance is useful for studies of palm insects. In Florida, city parks and streets departments have assisted research entomologists by making this type of equipment available to them.

The simplest and most inexpensive portable 'tower' from which to examine palm fronds is the stepladder. Four-legged stepladders, the most common type available, should be avoided. They were designed for carpentry and related work on relatively even surfaces, where the four legs rest at approximately the same level, with the weight distributed equally between them. On the uneven surfaces of natural ground, the two pairs of legs usually have to be placed at different levels or, worse, three legs balance and the fourth hangs over a depression. As the climber mounts the ladder, the fourth leg drops lower and the weight shifts to it, causing the ladder to tilt. A rock or stick may then be placed in the depression as a precarious remedy.

Tripod orchard ladders are better for working on natural ground (Fig. 8.3). There are two fixed legs, which straddle a wide span. These should be placed on the ground at the same level. The third leg is swung back on its hinge and may be placed a little above or below the level of the fixed legs. More important is the inclination of the ladder, which should be about 15–20° from the vertical. Because all three legs find support, the weight on the ladder is about equally distributed on them, regardless of the angle of the hinged leg, resulting in remarkable stability.

From a tripod ladder 3.6 m tall, one can closely examine foliage that is about 4.6 m from the ground. An aluminium ladder of this size weighs about 15 kg and can easily be folded and carried repeatedly from palm to palm throughout a plantation for hours.

Among the foremost hazards in climbing palms are falling debris, armature of the petioles and stems and encounters with rats, poisonous snakes and nests of stinging hymenopterans and other creatures best not disturbed at dangerous heights. The use of hard hats and safety goggles is thus advisable. Tough leather gloves are often an appreciated item. Goggles are critically important when working with date palms, because of their long spines. Date palms that are visited frequently can be despined periodically.

Fig. 8.3. Aluminium tripod orchard ladder used for examining insects on palms, in this case, *Dypsis cabadae*, Florida. Photo by Martha Howard.

For most climbing, light, flexible shoes, which allow deft footwork, are worn. Plimsolls, with deep-treaded rubber soles to prevent slipping, are a good choice. Although leather boots are recommendable for most fieldwork, they are less suitable for climbing, except with spikes, in which case they are indispensable. Short trousers are preferred to long trousers for some climbing, because they give greater freedom for bending the knees, but of course the protection that long trousers provide is thus sacrificed (Box 8.1).

When hiring a local person to do the climbing, scientists should use good judgement to ensure that the climber has the necessary experience and skills. Poor rural men, through misplaced personal pride and the promise of some needed cash, could be induced to take on climbing challenges beyond their capabilities.

Reaching the foliage with poles is sometimes an alternative to climbing. A pole saw or pruner can be used to bring down fronds to examine and quantify sessile insects or the damage of chewing insects. Foliage as high as 15 m may be reached in this way (Frémond *et al.*, 1966). Since pruning often results in a shower of fibres and detritus that has collected in leaf axils, safety goggles should be worn. Insect traps can be raised and hung in palms and later lowered for inspection using poles with a hook on one end (Meyerdirk and Hart, 1982).

Biologists sometimes fell palms in order to obtain samples. Whether a palm is in a valuable landscape, on a plantation or in the wild, destroying it is a drastic measure. Botanists often fell palms as the most expedient method of obtaining herbarium

Box 8.1. On top of the world.

> We hug the earth, – how rarely we mount! Methinks we might elevate ourselves a little more. We might climb a tree, at least.
>
> (Henry David Thoreau, American philosopher and naturalist. *Walking*)

Whether one ascends into the crown of a tall palm riding the boom of a hydraulic aerial lift or climbs a ladder or the stem itself, the trip to the top can be exhilarating. We seem to have some natural inclination to get into the tops of things. Arriving high in the crown of a palm, one is in the dim light of a secluded theatre, where birds, lizards, insects and other creatures play out their eternal, nameless, intriguing dramas. It is fascinating to peer from the crown of a palm, to look down at nearby trees and other natural features from above, to see over the treetops to the cattle in an adjacent field or to the ocean or a mountain.

It was inspiring to meet a Señor Nazario, who with his son had a contract to regularly climb and trim the tall coconut palms on several public beaches in Puerto Rico. Using the 'African method', he had been climbing since boyhood, was 75 years old and had just reached the crown of a tall coconut palm when I had the privilege of looking up and being introduced to him by his son – who was climbing a nearby palm with the ease of a circus star.

Whatever method is used, palm climbers should be well trained in the art, constantly practise it, use reliable equipment and climb and descend carefully. Sir Edmund Hillary, perhaps the most famous mountain climber in history, expressed a thought that would seem to apply well to palm climbing: 'There are two aspects to achievement – reaching your goal and getting safely back home again. One is incomplete without the other!' (Hillary, 1997, in *The Most Important Thing I Know*, edited by Lorne Adrian, Cader Books, New York).

material, but it would be preferable to remove these materials without sacrificing the palm. Felling palms is more appropriate for sampling palms with irreversible damage by pests or diseases. Prior to the development of DNA technology for diagnosing phytoplasma-associated diseases (e.g. lethal yellowing), diagnoses were confirmed by verifying the presence of phytoplasmas in phloem tissue by electron microscopy (see Box 3.2). Thus, symptomatic palms were felled and bud tissue sampled. Felling of palms may sometimes have application in studies of stem borers and diseases such as red ring (see Box 5.2).

Palm stem tissue is relatively dense near the exterior, forming a 'core', which, in some species, is extremely hard. The density decreases towards the interior. The stem tissue at the centre is typically soft and moist, but interspersed with very strong fibres. Cutting tools used for felling palms dull rapidly. Saws tend to bind in the fibres and get stuck part way into a cut. Some palm species are more difficult than others in this regard. An axe is often the best felling tool, because it is less likely to bind and can be sharpened more easily that a saw. Axes should be kept sharp. The forester's adage that 'A dull axe is a dangerous axe' refers to the tendency for blunt axes to glance off the objects being cut. Saws should be cleaned immediately after use and before storage, because acids in palm tissue can build up and damage the metal parts.

Because most of the strength of the stem of a palm is in the outer 'rind', palms may fall before the cut extends completely through the stem. Thus, the first cut should be a large notch in the desired direction of the fall. A palm may fall when the back cut extends through the rind, snapping off through the softer centre.

It is sometimes said that the machete can do almost any job, but can do nothing perfectly. An exception might be that it has no equal for pruning palm fronds (Fig. 8.4). The petiole of even a large palm species may be severed with a single slanted cut. Cuts perpendicular to the petiole axis require more chopping, probably because the cut passes through a higher fibre density.

Binoculars were used to identify damage to coconuts by mites (*Aceria guerreronis*)

Fig. 8.4. Use of machete to sample frond of coconut palm. A cut at an angle is the most efficient. Photo courtesy of Philippine Coconut Authority.

in a survey of the distribution of this species in Florida and Puerto Rico (Howard *et al.*, 1990) and to appraise damage to fronds of *R. regia* by the bug *Xylastodoris luteolus* (Howard and Stopek, 1998). The validity of such observations is highly dependent on the entomologist's familiarity with the damage, best gained through close examination. With experience, some large insects, such as palm weevils, high in foliage can be identified with binoculars.

Binoculars with the specifications 7×, 35 (a magnification power of seven with a lens diameter of 35 mm) are recommended for field ornithology, partly because birds can be viewed in the reduced light of tree canopies; we find them adequate for entomological work in palms. At this magnification, foliage that is 21 m above the viewer (the height of taller palms in Florida) appears to be at a distance of 3 m. The advantage of a higher magnification, e.g. 10×, would be slight and might be offset by reduced brightness, clarity, breadth and depth of field. A larger lens diameter, e.g. 50, would provide a clearer image in low light conditions, e.g. in a dense forest.

Much entomological work can be accomplished on palm foliage that can be reached while standing on the ground. Although some insects (e.g. *X. luteolus*) are found only on taller palms, many insect species on foliage are probably adequately represented on younger, shorter palms. Examination of small palms is especially suitable for a preliminary survey of the insect fauna of palms in a particular area. For example, Howard *et al.* (1981) surveyed the auchenorrhynchous insects on palms in the Dominican Republic by travelling throughout the country during a 10-day period and collecting insects from palm foliage that they could reach from the ground. However, many of the insects on smaller palms may be strays from nearby grass and other low vegetation.

Containerized palms (Fig. 7.1) are particularly appropriate host plants for studying larvae that infest palms and sessile insects, such as palm aphids, scale insects and mealybugs, because they tend to remain on the same host plant even if it is moved around. Even excised plant parts (e.g. pinnae with cut ends in a vessel of water) are suitable as temporary hosts for many kinds of insects. However, *X. luteolus* did not survive on excised leaves in water, even when they were changed daily (Baranowski, 1958).

The feeding behaviour of palm insects may be considered in developing sampling methods for them. Most species either attack both palms and other plants or, if restricted to palms, attack multiple species of palms. Thus, in sampling populations of a palmivorous planthopper, *Myndus crudus*, on palms in different areas of Florida during a lethal-yellowing epidemic (Howard, 1980b), coconut palms and other lethal-yellowing-susceptible species contracted lethal yellowing at such a high rate that they often died during sampling periods, resulting in missing samples. It was thus decided to sample from the foliage of *Sabal palmetto*, because this species was known to attract this insect but was not susceptible to lethal yellowing.

Most palm research centres focus on a particular economic species. In some cases, it may be advantageous to maintain additional species that serve as hosts of the insects under study, either interplanted with the principal research species or in separate blocks. For example, coconut palm is the principal research palm at the Fort Lauderdale Research and Education Centre of the University of Florida. *Washingtonia robusta* is interplanted with it in one grove at the Centre. Because *W. robusta* is attractive to many of the same insects that attack coconut palm and is relatively cold-hardy, this palm may be counted on to provide foliage following frosts, a phenomenon expected about every 5 years in this region.

A hand-lens is standard equipment in field entomology, often worn on a leather thong or nylon cord around the neck so that it can be found easily. But climbing trees or palms with what amounts to a noose around one's neck seems inadvisable. One solution is to cut the thong and then sew it together again with just a few threads, which will break if the thong gets caught on something. A better idea is to carry the lens in the pocket of a jacket fastened with a cord, in the manner of pocket watches. A jacket with plenty of pockets makes it easy to carry note pads, pencils, vials, insect repellents, etc. Plastic vials carried in pockets are safer than glass vials. Any sharp instruments, such as probes or fine forceps, carried in pockets should be secured in some way – for example, by keeping them in capped plastic vials.

Most detailed examinations of scale insects and other minute arthropods have been done with a microscope inside a laboratory. We have often found it convenient to examine specimens in the field. For a light source, a small mirror can be used to focus sunlight on the microscope stage (Fig. 8.5).

Fig. 8.5. A mirror used to focus sunlight on a specimen serves as a portable microscope lamp for examining scale insects in the field.

For marking and labelling palms that are visited periodically for observations of insects or designating different treatments, we have adapted methods from forestry, taking into account the special nature of palms (Fig. 8.6). Fronds, leaflets and petioles can be written upon with a felt-tipped pen with waterproof ink, resulting in labels that last outdoors for more than a year. Paint sticks, which are similar to crayons but which contain oil-based paint, can be used for making highly visible labels on palm stems that last for about a year. A timber scribe is a tool used in forestry for quickly making grooves that serve as permanent labels in logs or other woody material. These are ideally designed with a bent blade for inscribing straight grooves and with a central pivot so that the scribe can be rotated to make circles or curved grooves, as with a drawing compass. We have used this method for marking African

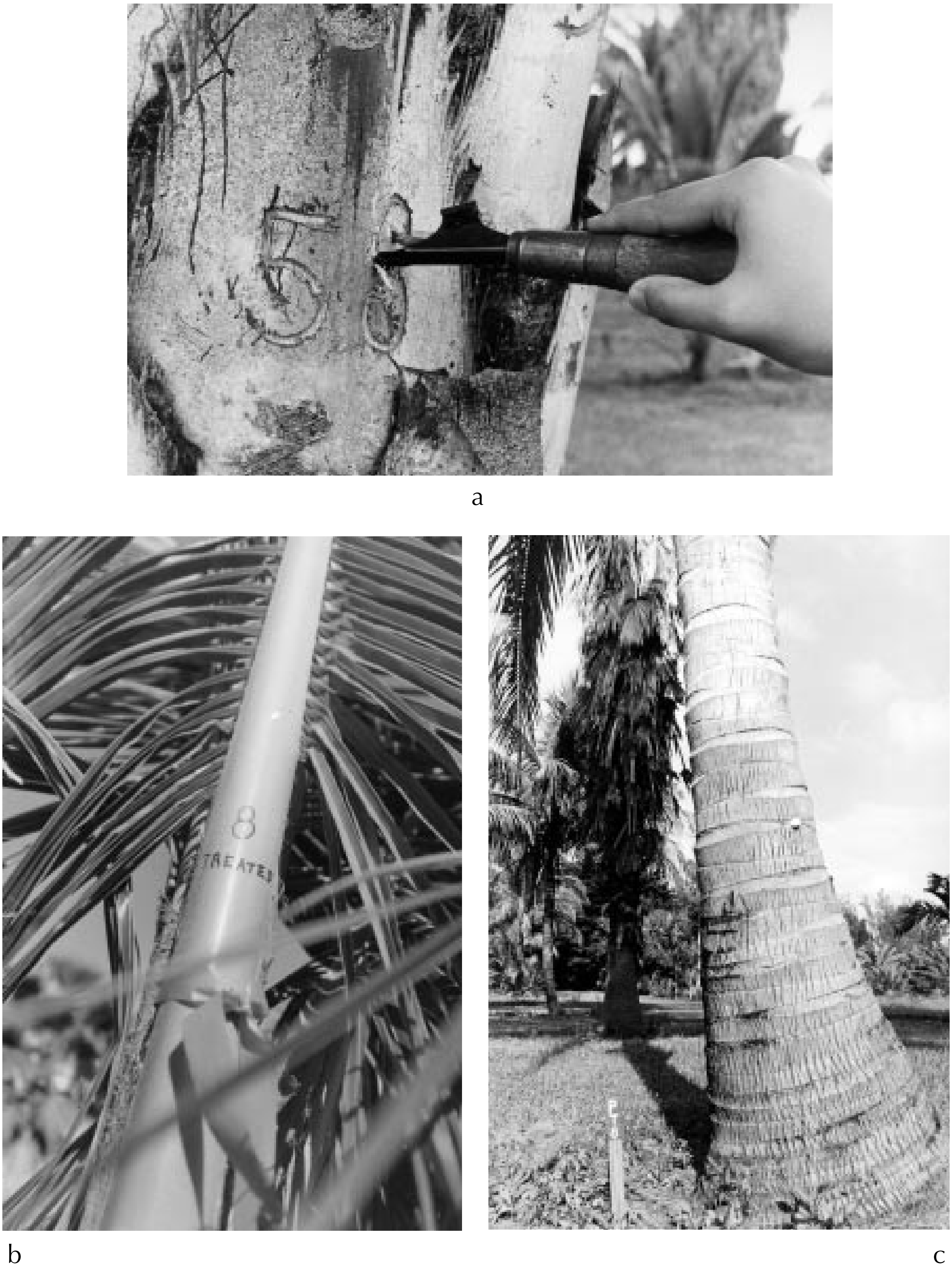
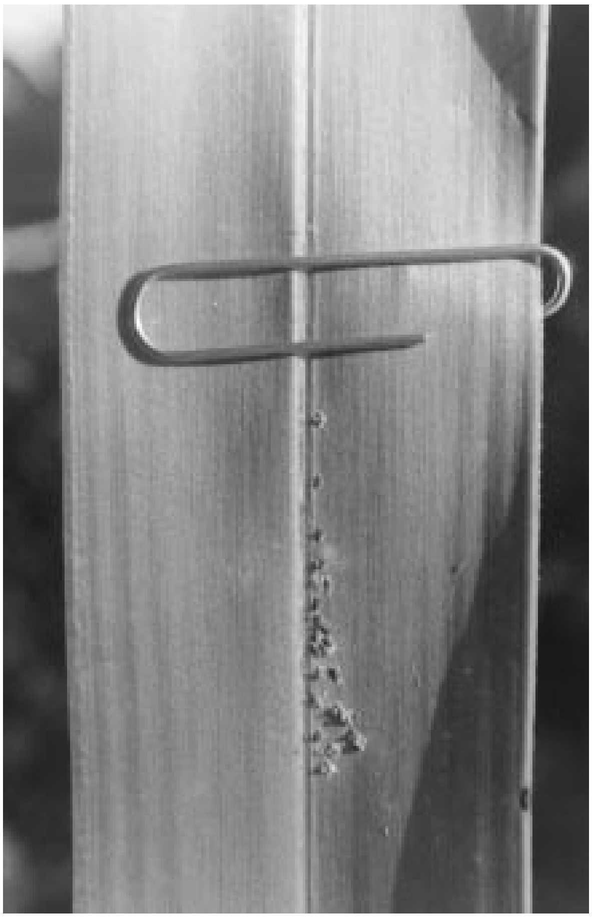


Fig. 8.6. (*and opposite*) Techniques for labelling palms in studies. (a) Timber scribe for marking petiole base of African oil palm. (b) Coconut palm petiole labelled with indelible marker. (c) Wooden stake and aluminium tag, two methods of marking coconut palms. (d) Paper-clip for marking location of aleyrodids on coconut leaflet.



oil palms, the stems of which are covered with very hard, persistent, leaf bases; this method would not be appropriate for many situations, such as for marking smooth-stemmed ornamental palms. As with the use of climbing spikes, in some regions the method may involve some risk of transmitting disease organisms. An aluminium tag attached to a wire loop around the palm stem is another way of providing a highly permanent label. The loop does not have to be widened or removed as the palm grows, because, although palm stems may expand slightly as they grow, they do not undergo annual lateral increments as in dicotyledonous trees. Prior to the formation of a stem, the label can be positioned temporarily by looping the wire around a few fronds. Wooden or bamboo stakes can be pounded into the ground adjacent to palms. They are easy to make and can be made highly visible by painting them bright colours, but, if made of untreated wood, they do not last long under tropical conditions. Palms or their parts selected for study are easier to spot if coloured flags are attached to them. Bright orange is visible at greater distances than other colours and contrasts with most outdoor environments. Where a second colour is needed, bright blue is easily distinguished from orange, although it does not contrast sharply against some tropical environments. Red is more conspicuous but, at long distances and under certain light conditions, is not easily distinguished from orange. Yellow or white flags are the least desirable, as they are not easily distinguished from a distance under tropical field conditions. Researchers who remove flagging when a study is completed demonstrate tidiness and may prevent confusion should flagging be used at the same site in a future study.

Among the tools and instruments borrowed from allied fields of agriculture and forestry and adapted to palm entomology are cant-hooks (Fig. 8.7), peaveys and pulp hooks, useful for moving and examining palm logs and organic debris for insects.

Field entomologists working with palms should be aware of the proper and safe use of machetes, various kinds of saws, axes, pruning shears and other cutting tools common in horticulture and forestry. This is perhaps best learnt from experienced workers.

Fig. 8.7. Cant-hook used in rolling rotting coconut logs in searches for beetles.

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