

THE NATURAL HISTORY OF INSECT HERBIVORY ON MANGROVE TREES IN AND NEAR SINGAPORE

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ABSTRACT. - Concise notes are given on the biology of 102 insect herbivores attacking nine principal tree taxa (21 spp.) in Singapore mangroves. They are discriminated to species but not all are precisely named pending taxonomic treatment. The degree of stenophagy varies widely. *Avicennia* and *Sonneratia* support a more distinctive herbivore spectrum than others, which may reflect their relative taxonomic coherence and isolation. Although the insects have distinctive strategies, some show a surprising degree of niche plasticity which is discussed in context with host phenology. Prospects for damage assessment and host-plant management are also discussed. Illustrations are provided for many of the more important insect species.

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INTRODUCTION

Mangrove forest formerly covered an estimated 13% of Singapore's total area (Corlett, 1987). Today very little remains, but small areas are being considered for conservation. As part of a programme to optimise management, a study is being made of organisms that affect the growth and survival of mangrove trees.

There are two main reasons why this should be done. One is that to maintain an indigenous plant in healthy condition under local conditions one needs to know what level of natural damage is normal. Insects are rarely severely damaging to a healthy host but respond rapidly to declining resistance. Significant changes may well indicate stress from pollution or deteriorating soil or water regime, perhaps in time to take corrective action. A mature tree is a valuable investment that can take decades to replace. In addition of course, should pest control intervention be necessary for its own sake, a detailed knowledge of each insects natural history and host range is prerequisite.

The second reason concerns introduction of exotics. Very recently an area on the north coast of Singapore (Sungei Buloh estuary) has been proposed as a bird and mangrove reserve. A proposal (Murphy & Sigurdsson, 1989, 1990) to develop a mangrove arboretum at this site is being favourably received. While the re-introduction of species recently extinct, or the introduction of regional species only slightly outside their range poses no risk this is not necessarily so for major inter-continental translocations. Thus mangrove trees introduced to San Diego (southern California, U.S.A.) apparently threaten to overwhelm salt-marsh communities crucial to coastal bird populations.

Given adequate controls, there is much to be gained from judicious transfer of exotic plants, and mangroves may well offer valuable properties in coastal stabilisation, support of off-shore fisheries and novel forms of ornamental. It is precisely this aspect of adequate controls that is addressed in this paper. For many but not all the plants discussed here, it seems likely that we can offer agents that in the absence of their own natural enemies would virtually halt the propagation of their host as the need arose.

Herbivory, the direct exploitation of living plant tissue by animals, is known to involve crabs, molluscs and insects in the mangrove system. Crab damage is fairly well documented in general terms but very few papers go into detail. Mollusc attack is hardly documented at all, and is mainly superficial and perhaps incidental to epiphyte grazing. Insects are known to be important but have been much neglected in mangroves. The most important summary is that of Hutchings and Recher (1982) for Australia, partly quoted in Hutchings and Saenger (1987). Even so only a few examples of herbivorous species are mentioned.

This paper attempts a general account for the Singapore context but is to be regarded more as a progress report than a finished product. The first step is purely descriptive - collecting, rearing and matching pests to their host and damage type. This is a slow process and never complete, even for a single locality. Insects field-collected from the host plants have been offered host material in the laboratory to confirm feeding and nature of damage. It is thought useful to summarise results to date under the respective host plants, leaving detailed descriptive treatment until later. Since many of the insects are in taxonomically difficult areas and some are undescribed, this later treatment will have to be by taxonomic group. For non-specialist mangrove workers to whom this account is addressed this summary may provide some leads, even though the naming of insect taxa is provisional. For their benefit also, a short statement on insect herbivore strategies is given.

The major zonal mangrove angiosperm trees that occur in Singapore are dealt with, together with a few minor elements of special interest. Although *Hibiscus tiliaceus* is not strictly considered a true mangrove, it is a definitive element of the system in Singapore because of its association with mud-lobster mounds in back mangroves, and is included for that reason. Sometimes although an insect is known to occur in Singapore mangroves its host association has been made elsewhere. Some trees, although present in Singapore, have been too incompletely studied for mention (e.g. *Xylocarpus*) and the same is true for most mangrove plants normally treated as minor components of the ecosystem. It is hoped to devote a separate paper to some or all of these when our data is more complete.

Only a few species have been treated in any depth, these being the commonest representative of each major genus in Singapore. These species are *Avicennia alba*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Bruguiera cylindrica*, *Rhizophora apiculata* and *Sonneratia alba*. Other species are mentioned in comparison with the main representative of their genus, or briefly in isolation, the families being arranged in alphabetic order.

Each genus treated is briefly characterised emphasising features relevant to herbivory, and then such literature on plant phenology and insect attack as is known to me is summarised. This is not claimed to be comprehensive. The phytophagous insects are then informally discussed in relation to plant structure and mode of attack. I have tried to arrange them in order of appearance during the sequence of development of plant structures, first the foliage, then shoot development and finally the reproductive structures. Within this framework an attempt is made to separate species by mode of attack - edge and patch grazers, leaf miners, sap-flow ectoparasites (suctorial feeders) being treated separately as far as possible. It has not proved wholly successful since some species have proved far more plastic in their strategy than was anticipated - a point to be developed in more detail in the discussion.

INSECT HERBIVORE STRATEGIES AND DAMAGE TO THE HOST

Insect damage can be broadly classified into grazing (the destruction of whole tissue) and sapflow ectoparasitism (interception of transport by piercing sucking insects, often without significant structural damage). Some Hemiptera inject toxins and cause local lesions, and some are seed feeding and may totally destroy the propagule so the distinction is not clear. Foliage damage may be internal as with leaf miners, from the edge or from dorsal or ventral surfaces ("patch-grazing"). Some insects are structurally limited to one mode of attack but many are plastic or change strategy during development. Even so, when only a few herbivores attack a given host, particular damage types can often be assigned to a specific causal agent with some confidence.

The most important phytophagous groups are Lepidoptera and Coleoptera. Lepidoptera are grazers only in the larval stage and usually have to be reared to the adult for identification at present. Direct larval identification to species will become possible only as this project proceeds, although family criteria exist. These are usually too technical for non-specialists. Some phytophagous Coleoptera attack plants as larvae (e.g. Mordellidae and certain Chrysomelidae) but many do their most conspicuous damage as adults during a phase called "maturation feeding". After metamorphosing from the larva, which may also be phytophagous but not necessarily on the same host, adults may feed on foliage or bark for a prolonged period, especially while females are maturing eggs. This is especially common with Scarabaeoidea and Chrysomeloidea.

Of other groups, phytophagous Orthoptera feed in all stages but are difficult to rear and identification of immatures is speculative. Leaf-mining and flower or fruit boring Diptera have to be reared. In Hemiptera, host association is only confirmed if immatures are regularly found on the host. The same is true for mobile Homoptera. Field observation may be valuable but non-specific probing can occur on unacceptable hosts. Homoptera often have a non-toxic saliva and may cause little direct damage except as pathogen vectors, unless at high densities when there may be systemic phytotoxaemia. Some Heteroptera inject toxic saliva causing local necrosis which reduces their role as vectors but may cause significant direct damage, especially to shoots.

SECTION I: THE MANGROVE TREES AND THEIR INSECT HERBIVORES

Avicenniaceae (formerly included in Verbenaceae)

AVICENNIA Linn.

Leaf buds small, leaves opposite, thin, strongly dorsiventral with dense trichomes

below, smooth salt-secreting above. Twigs equipotent with narrow pith and timber with included phloem. Flowers small in terminal cymes, fruit waterdispersed with a single large viviparous embryo with thick, folded fleshy cotyledons. No dormancy period. There are four species in Singapore. *A. alba* Blume a common pioneer on mudbanks, seafronts and regenerating plots, *A. marina* (Forsk.) Vierh. normally a pioneer in more saline sites, now very rare in Singapore; *A. officinalis* L. and *A. lanata* Ridley on mature estuarine mangrove flats. A good anatomical account is given by Tan and Keng (1969) and Mathews and Rao (1986) have shown that the included phloem is developed from the first internode.

Insect defoliation has been reported by Ridley (1898, *Hyblaea* in Malaysia) and Piyakarnchana (1981, 1982, *Cleora* in Thailand). Robertson and Duke (1987) ranked *A. marina* in their high to intermediate category with area losses of 10.5 to 17.1% in Queensland. Arrow (1917) mentions *Adoretus lacustris* "feeding in great abundance" in India.

Other specific host records are few. In Florida a weevil *Stenobaris avicenniae* Linell was described from *A. nitida*. The minute plume-moth *Cenoloba oblitalis* was reared from fallen propagules of *A. marina* in Queensland (Common, 1970). The scale insects *Paralecanium neomaritimum* and *Halococcus formicarii* Takahashi (Coccidae) were described from *Avicennia* in Malaya. Williams and Watson (1988) list *Hemiberlesia lataniae* and *Lindingaspis rossi* (Diaspididae) and *Planococcus pacificus* (*Pseudococcidae*) from *Avicennia nitida* in the South Pacific where this Atlantic species is introduced. The only whitefly reported in the polyphagous *Trialeurodes vaporariorum* from *A. nitida* in the U.S.A. (Russell, 1963).

In Singapore the foliage pest complex on *Avicennia* seems to be largely stenophagous on the genus but not selective between species. There is however, a significant difference in the flower feeding assemblage on *A. officinalis* compared with all others. The following account refers principally to *A. alba* but since most herbivores attack all species, mention of others within the text on *A. alba* is necessary. The brief account given for other species is only to draw attention to striking differences.

***Avicennia alba* Bl.**

Easily recognised by the lanceolate leaves, small flowers in lax cymes and long mucronate fruit, this is the commonest species in Singapore.

Foliage damage. - The small vegetative buds seem to suffer little specialised insect attack although at times apical damage occurs from the earliest stages from some of the moths that later move to expanded leaves. Expanding young leaves can be heavily attacked by two species of the *Monolepta cavipennis* complex (Col. Chrysomelidae) (Colour Pl. 1). Both species produce small circular patch-grazed areas on the under surface, the result of maturation feeding by adults. Major outbreaks can occur during which young leaves may be totally destroyed and beetles will feed on older leaves. Ovipigerous females of both species have been taken flying over the ground below host trees and cemented eggs to pneumatophores when provided under laboratory conditions. Like many other galerucines the larvae of at least one is known to be a root feeder, boring the pneumatophores (see below). No other chrysomelids were seen and the otherwise rather polyphagous eumolpine *Rhyparida wallacei* does not accept *Avicennia* in vitro. The scarabaeid *Lepadoretus compressus* also seems not to attack *A. alba* even when growing together with *Sonneratia* suffering heavy damage, in contrast to the report of Arrow (1917).

Three species of Cryptorhynchine weevils, one species of *Rhadinomerus* and two of *Camptorhinus* (Col. Curculionidae) (Colour Pl. 2) are occasionally taken on foliage and all three do maturation feeding from mature foliage under laboratory conditions. They form distinctive pin-hole perforations and narrow grooves which are sometimes seen in the field, but rarely cause significant area loss. All three are known to be timber borers of inter-tidal *Avicennia* logs as larvae (a separate paper on mangrove timber beetles is in preparation, where these will be described).

Young leaves may be webbed by larvae of *Hyblaea puera* (Lep. Hyblaeidae) (Colour Pl. 8) which is an edge feeder and pupates in the rolled leaves. Apart from Ridley's old record (1898) this is known as a major defoliator of teak (*Tectona grandis*) in the related family Verbenaceae). *Avicennia* may play a role as reservoir host in teak growing countries, not necessarily negative if the population supports parasites. Present records are only from *A. alba*. The life history of this species is well documented on teak (Beeson, 1941) and is broadly similar on *Avicennia*. A distinctive feature is that the young larvae make a temporary case by notching the edge and folding in part of the margin. Similar folds have been seen occasionally due to species of *Odites* (Lep. Lethiceridae) and other species of this genus on other plants (*Rhizophora*, *Lumnitzera*) have this habit. Once its larva is beyond the second instar, *Hyblaea* ceases to make such folds and feeds between webbed leaves whereas *Odites* retains the fold throughout its development.

All species of *Avicennia* are regularly attacked by a leaf-mining moth *Phyllocnistis* (Lep. Gracillariidae) (Colour Pl. 13) which mines the upper surface of young expanded leaves and pupates in a fold at the edge which is characteristic of the genus. *A. lanata* seems to be more heavily attacked than other species.

Two exclusively edge-feeding geometrid species have been reared. *Cleora injectaria* (Colour Pl. 6) is a large ennomine with very variable colour pattern. The mature 3.5 cm larva is brown and descends the trunk to pupate in cells beneath inter-tidal algae at the base. This suggests that Piyakarnchana (1982) who refers to pupation in rolled leaves, may have had a mixed infestation with *Hyblaea*. The species is not host specific and has been also been reared from *Sonneratia alba*, *Aegiceras corniculatum*, *Bruguiera cylindrica* and *Allophylus cobbe*. Male genitalia of specimens from all these hosts were indistinguishable and conform with the figure given by Prout (1928).

The small pale green males of *Chloeres quantula* (Colour Pl. 6) are a regular feature in mangrove light traps. Its typical geometrine larvae are green at first becoming brown, 2.3 cm when mature and pupate exposed on the leaf. As far as known they feed exclusively on *Avicennia* spp.

Large, irregular patch grazing marks on the under surface are a common feature in *Avicennia*. Many of these are due to noctuid moths. The small tufted larvae of a species of *Nola* (Lep. Nolidae) (Colour Pl. 12) are involved but not often seen, even though the adults are very common at light. Species of this genus are said to be lichen feeders but whether this species also does so is unknown. Much more extensive patch grazing is done by the pale green pink spotted semi-looper caterpillars of *Erastroides* sp. (Lep. Noctuidae) (Colour Pl. 12). Larger semi-loopers belonging to at least two species of *Aucha* (*A. velans* and *A. villiana*) are edge-feeding (Colour Pl. 11). These noctuid larvae descend on threads when mature and pupate inter-tidally under rotting timber or algal mats. The large mottled blackish-grey adults of *Aucha* spp. are a very characteristic feature of *Avicennia* mangroves throughout Southeast Asia, perching head down on the tree trunks and flying freely in day time.

Several species of patch grazing phycitine Pyralids have been reared from *Avicennia* foliage and it is also attacked by one or more species of bag-worm moths (Lep. Psychidae). These groups are beyond my competence. They can be of major importance and extensive defoliation by bag-worms is a common feature during windy weather when larvae are dispersed. For the Phycitinae, although the species have not been identified, at least four are recognised and others attack flowers (see below). Most are chronic low-level elements of the fauna but one caused a short-lived local out-break at defoliating level. I have received a sample from Hong Kong (S. Y. Lee coll.) where possibly the same species "causes massive recurrent defoliation of *Avicennia marina*". An interesting point is that although so many Phycitinae attack *Avicennia*, no members of the group have yet been detected attacking any other mangrove genus as primary herbivores.

Two species of *Odites* (Lep. Lethococeridae) (Colour Pl. 9) make marginal leaf folds but are rare. The species are distinct from those discussed later on *Lummitzera* and Rhizophoraceae. Local attack by the large polyphagous caterpillars of *Attacus atlas* occurred once simultaneously with many other trees. Cases of foliage feeding by *Archips* and *Uliocnemis* were seen, the latter being better known as a flower feeder (see below); this larva attached leaf fragments to its tubercles instead of flowers.

There appear to be few sap-sucking insects attacking foliage, perhaps deterred by the salt excretion. The main exception is a very common shield bug *Antestiopsis* sp. (Hem. Pentatomidae) (Colour Pl. 4) whose adults are common everywhere and by no means only on *Avicennia*. However the juveniles appear to feed only on this genus and egg masses tend to be laid among its flowers where the youngest juveniles are commonly found in numbers.

Occasionally, mid-ribs can be heavily infested by the large mealy-bug *Crypicerya jacobsoni* (Hom. Margarodidae) which can attack many tree species. Insect and mite galls are a conspicuous feature of the genus. All of the insect galls seen seem to be due to Cecidomyiidae (Diptera) but none have been identified. *A. officinalis* is particularly susceptible (Colour Pl. 3). One species has been described in the literature as *Stephaniella falcaria* Felt from Java (Felt, 1919), but on gall morphology it is clear that many species exist (Docters van Leeuwen, 1919). Galls formed by mites (Acarida, Eriophyiidae) are present on all species and especially conspicuous on *A. alba*. *Eriophyes cheriana* Masee is described from Indonesia and two galls on *A. officinalis* recorded from India by Mani (1973). The identity of the Singapore material is not known at present.

Twigs and small branches can be infested by the scale insect *Ceroplastes rubens* (Hom. Coccidae). This is especially true of *A. lanata* and *A. officinalis*. Infestations leave the trees heavily contaminated with sooty mould fungi. At one site infestations appear to have been of very long standing, to the extent that layers of wax could be found in soil cores. Several other Coccidae are occasionally seen including species of *Coccus*, *Saissetia* and *Chloropulvinaria*. Trees are also occasionally heavily infested by the polyphagous lac-scale *Tachardina aurantiaca* (Hom. Tachardiidae).

Structural damage. - Twigs of all species are susceptible to borer attack by an undescribed genus of Mordellistenini (Col. Mordellidae) (Colour Pl. 3). The larva bores through the pith canal and causes nodular enlargement of nodes. The damage is widespread in Southeast Asia and apparently the same species is the commonest mordellid in light trap catches in southern Thailand where the main host is *A. officinalis*.

Lepidopterous twig boring also occurs and all larvae seen belong to Cossidae. Bole attack by Cossidae is common in *Avicennia* and young trees of *A. alba* at several sites have been killed. The only species reared was *Zeuzera conferta* Walker which is also known to attack *Sonneratia* and *Barringtonia* in mangroves as well as several non-mangrove hosts (Holloway, 1986). In light-trap collections, this is the only cossid taken in mangroves in Singapore, although in Brunei there is apparently a more diverse fauna (Holloway, loc. cit.). In heavily infested *Avicennia* saplings, the larvae are found in all sizes of twigs and branches. Very young shoots may be attacked from the first node behind the apex and die back. Older nodes may be girdled, with or without destruction. Several nodes on the same axis may be affected. Clearly, the larvae can leave their galleries and re-enter the plant at another node, much as described by Beeson (1941) for *Xyleutes ceramica* attacking teak. This is the classic "bee-hole borer" strategy so familiar to foresters.

Holloway speculates that the rich cossid fauna in Brunei mangroves is due to reduced competition from termites. Although termite attack has not been seen on living trees in Singapore, it is known to be significant in Australia (Hutchings & Saenger, 1987) and Sri Lanka (Jayewardene, 1987). Dead wood is, of course, subject to termite attack and several species of *Neotermes*, *Prorhinotermes flavus* and *Nasutitermes matangensisformis* have been taken from *Avicennia* timber but are not believed to be primary.

Dying trees can be infested by scolytid timber beetles from a very early stage. In Singapore *Xyleborus indicus*, *X. cognatus*, *Progenius bidentatus* and *P. costatomorphus* (Scolytidae) and *Platypus lineatus* (Platypodidae) have been seen to attack standing trees still partly or wholly alive but probably dying from other causes. Almost always such trees were affected by nearby reclamation which disturbed the drainage. Murphy and Meepol (1990) give a brief account of mangrove scolytids in Thailand.

Propagule attack. - Propagule mortality from insect attack is high in *Avicennia* and begins with destruction of unopened flower buds by a very complex assemblage of caterpillars. One of these is a larva constructing a portable case on which are threaded a chain of eaten buds. This has now been found to be a species of *Eupoicilia* (Lep. Tortricidae) (Colour Pl. 18) which also attacks buds of *Bruguiera cylindrica* (q.v.) and no doubt is polyphagous on many small-flowered trees.

Individual flower buds are also attacked internally by a minute eucosmine *Acroclita* sp. (Lep. Tortricidae) and by the larvae of *Cenoloba taprobana* (Lep. Tineodidae) (both on Colour Pl. 17). Apparently the same species also attacks the fruit, in which it resembles the larger Australian species *C. oblitalis*. *C. taprobana* larvae form frass-filled galleries in flower stalks and some of the larger basal buds are entered and eaten out from the base. The damage to the stalk causes die-back of all buds distal to the site of attack. This borer strategy is compatible with the known habits of *Cenoloba* in maturing fruit which it may invade from the fruit pedicel or enter directly from eggs laid on the surface. In fruit it bores entirely within the cotyledons, the frass packed into the gallery so that no large aperture to the outside exists. For this reason it can survive immersion in fallen fruit or rooted seedlings. The plumule is not attacked and thus not killed.

Buds and flowers are penetrated from outside by several larger caterpillars, including one or more species of *Autoba* (Lep. Noctuidae) which pupate in a cocoon of detached buds attached to the raceme, at least two unidentified species of Phycitinae (Lep. Pyralidae) (Colour Pl. 16) and by a remarkably procryptic looper caterpillar *Uliocnemis partita* (Lep. Geometridae) (Colour Pl. 7) which attaches loose buds to tubercles on its back so that it is

effectively concealed among the flowers. This pupates in loose webbing concealed among frass and detached bud scales. *Archips* (Tortricidae) and *Tatobotys janapalis* have been seen.

Also typically flower feeding are the early stages of another phycitine moth (Lep. Pyralidae) (Colour Pl. 16). This later moves to leaves where it feeds beneath a thin oval web, patch grazing the ventral surface. After moving from place to place, each time constructing a new web, it finally pupates again under the leaf and with a shielding web.

Flower rot associated with small acalypterate flies is common. Most common of these is a species of *Asteia* (Dip. Asteiidae) (Colour Pl. 3) - a family for which "practically nothing is known about their biology" (Hardy & Delfinado, 1980). A species of *Scaptodrosophila* (Dip. Drosophilidae) also occurs. Some of this fly attack may not be primary but follow from the distinctive die-back caused by *Cenoloba* larvae. However as documented under *Avicennia officinalis* there are reasons to exclude this for *Asteia*.

Oviposition directly into developing fruit by an unidentified baridine weevil provisionally called "*Limnobaris*" (Col. Curculionidae - not *Stenobaris*!) may occur from an early stage (Colour Pl. 2). Adults are commonly seen on flowers shortly after the corolla falls and some maturation feeding attack on the ovary has been seen. Oviposition normally occurs into the skin of partly grown fruit. Larvae mine internally in the cotyledons without damaging the embryo proper and the galleries, like those of *Cenoloba* are entirely internal, frass-filled and without external aperture. For the same reason, they do not seem to seriously affect survival and weevil attack persists in fallen fruit even long into water dispersal and into seedling life.

Much the most serious pest causing mortality of mature propagules of *A. alba* is *Autoba alabastrata* (Lep. Noctuidae) (Colour Pl. 11). Adults are hardly ever seen, but a high proportion of fruit of all species can be attacked by the larvae of *Autoba*. The larva of *Autoba* bores into a well grown fruit, webbing it to the nearby stem, and immediately destroys the embryo. The fruit soon falls free but is held by the silk while the larva hollows it out before moving on to penetrate another. Depending on size of fruit and host species, one larva may destroy up to seven or eight fruit before finally pupating inside the last one. An infested tree is conspicuously decorated with shrivelled dead fruit. This strategy seems necessary for a species which leaves large apertures into eaten fruit, extrudes its faeces, and pupates without a water-tight cocoon. *Autoba* cannot complete development from immersed propagules. *A. alabastrata* is consistent in appearance when reared from *A. alba* but material of the genus reared from other *Avicennia* species and from flowers varies greatly. It is not yet clear whether perhaps a complex of several closely related species may be involved.

In contrast, yet another phycitine is frequently reared from fruit, unlike *Autoba alabastrata* not killing the embryo and not attaching it to the tree but pupating inside in a dense silk cocoon. The cocoon apparently resists immersion and this species can emerge from fallen fruit. Thus among these fruit boring insects at least three independent strategies for coping with the problem of immersion in water dispersed propagules can be seen.

A significant loss of fruit which fall to the ground can be attributed to the opportunistic ground feeding larvae of the pyraustine moth *Hymenoptychis sordida* (Colour Pl. 15). These are very common intertidally, spinning silk galleries among algae and litter. They are very general feeders consuming green algae, decomposing litter and wet rotted timber on which they develop very slowly. If an *Avicennia* fruit falls into their territory it is preferentially attacked and they quickly complete development.

Young inter-tidal seedlings, once established do not normally suffer much insect attack (c.f. *Sonneratia*) but a single instance has been seen of an unknown tortricid with similar attack mode to *Lasiognatha*. A major hazard at this stage seems to be overgrowth by green algae which attracts surface grazing by Littorinid gastropods. The faeces of these can be packed with the ventral trichomes of *Avicennia* and one might speculate that these, whose adaptive function has not been satisfactorily accounted for, might be a defence against damage to the true epidermis at this stage.

Root attack. - Little is known about root pests in *Avicennia*. The system is complex, consisting of thick primary roots with a woody medulla and spongy surrounding layer of aerenchyma with a thin superficial cortical layer, from which tufts of normal feeding rootlets and erect pneumatophores arise. A single species of *Oliarus* (Hem. Cixiidae) (Colour Pl. 4) attacks feeding rootlets at or above mean high water spring tide level, where pneumatophores penetrate the raised mounds formed by mud lobsters (*Thalassina*). They are gregarious in small chambers packed with wax filaments. The wax is provided by the female when laying egg batches, and supplemented by the growing larvae. This wax may provide sufficient water repellance to protect them from occasional tidal immersion. These habits are very similar to those described for *Oliarus felis* Kirk. by Hacker (1925), a species found in the high inter-tidal grassland just behind mangroves in Australia. The adults of the Singapore species can be swept in numbers from flower trusses of *A. alba*, and less often from vegetative shoots.

It is mentioned above that the two species of *Monolepta* have ovigerous females flying over mangrove soil at low tide and far from dry land, and since larvae of many Galerucinae are known to be root feeders (Jolivet, 1988), those of these were expected to be associated in some way. It has recently been confirmed that the larva of one (*M. aff. bicavipennis*) bores into the pneumatophores at or just below ground level, forming galleries in the aerophil layer but not attacking the woody medulla (Colour Pl. 1). The surface cortical layer is grazed from below but not perforated and the frass accumulates in the galleries. Occupied galleries are thus not penetrated by sea-water. Around heavily affected trees, many pneumatophores are reduced to thin, dead cortices as above the site of *Monolepta* attack the outer tissues rot and are attacked by larvae of Chloropid and Stratiomyiid flies among others. Pneumatophores are also attacked by *Sphaeroma* spp. (Crustacea, Isopoda), some of which attack may be primary, since *Sphaeroma* galleries certainly extend into healthy tissue. *Sphaeroma* however, is not a true herbivore, its galleries being for protection and opening to the exterior to admit the water current by which the animal is believed to feed.

***Avicennia lanata* Ridley**

A common tree on sandy soils, this species is easily recognised by its blunt, concave leaves, densely pilose shoots, small flowers in compact cymes and packed clusters of small quadrate fruit. Nothing has been traced in the literature on its phenology or pests. Many of the species attacking *A. alba* have been seen on *lanata* but it has not been studied intensively. It seems to suffer more attack by *Phyllocnistis* and by the scale insect *Ceroplastes rubens* but less damage from most foliage grazers. Very few insects attack the flowers but an unusual Phycitine was reared and *Autoba* has been reared from the fruit.

***Avicennia marina* (Forsk.) Vierh.**

Only a single locality (Sungai Pandan estuary) with very few mature trees is known

for this species in Singapore. When sterile it is difficult to discriminate from *A. alba* but the smaller quadrate fruit in which the plumule lacks hooked hairs are unmistakable. This is the most wide-ranging species of the genus and more is published on it than any other. Hutchings & Saenger (1987) summarise Australian data and references including information on phytophagous insects. Apart from some host specific species (e.g. *Melanagromyza avicenniae* (Dip. Agromyzidae) this is one of the few mangrove species for which termite attack on living trees is reported (Hutchings & Recher, 1982; Jayewardene, 1987). West and Thorogood (1985) report defoliation by an unknown pyralid moth in Australia, and an unidentified phycitine (Lep. Pyralidae) has been sent to me from Hong Kong where it is "responsible for massive, recurrent defoliation" (S. Y. Lee *in litt.*) Lin & Wei (1983) reported extensive damage by a tortricid moth in China.

Perhaps reflecting the marginal condition of our remaining population, leaves of this species are heavily grazed by many of the commoner insects in Singapore, and sometimes almost defoliated by bag-worms (Lep. Psychidae). The flower assemblage has not been studied, but fruit are attacked by *Autoba*.

Avicennia officinalis L.

Easily recognised by the larger flowers and fruit and the ovoid leaves with little hair-pile, this species is little mentioned in the literature but Williams and Watson (1988) record the scale insect *Lindingaspis rossi* in the south Pacific. The phenology is not reported but in Singapore flowering and fruiting is very seasonal, flowering beginning in March and fruit mature by August.

Almost all foliage feeding insects reported from *A. alba* also occur on *officinalis*. However a higher incidence of leaf galls and of mordellid shoot boring has been noted (above) in Thailand. The most striking differences concern herbivory on flowers. *A. officinalis* has conspicuously larger flowers and buds than any other species of the genus and this apparently influences the herbivore spectrum. *Autoba* sp. 2 which is rare on *alba* seems to be much more frequent on *officinalis* which is probably its primary host. Several species common on *alba* have never been seen on *officinalis*, notably the phycitine (species 2), *Uliocnemis*, and the very minute bud moth *Acroclita*. Much more common on flower buds of *officinalis* is the species of *Asteia* (Dip. Asteiidae), the larvae often abundant beneath the sheathing bracts of unopened, apparently healthy buds. In *officinalis* the buds secrete a copious mucilage, quite unlike the dry buds of other species of *Avicennia* and in this material the fly larvae are found. According to available literature, the immature stages of Asteiidae are unknown and this species therefore deserves detailed study.

The much larger fruit of *officinalis* can permit the complete development of an *Autoba* in a single fruit, but the biology on this host is otherwise identical to *A. alabastrata* on *A. alba*. Some variation suggests that a second fruit-feeding species of the same genus may be involved on this host and that the flower-feeding species may also develop in fruit.

Because *officinalis* grows higher in the tidal profile, it is probably more often the host of the root-feeding cixiid *Oliarus* than is *alba* though since the root systems of different species of *Avicennia* cannot be distinguished this remains uncertain.

Combretaceae

LUMNITZERA Willd.

Resting buds rather small, elongate. Leaves obovate, fleshy, isobilateral, spirally ar-

ranged, not salt secreting. Twigs with narrow pith. Wood dense, without included phloem. Flowers in terminal or axillary racemes, fruit a small woody drupe, water dispersed. Two species, both in Singapore. *L. littorea* (Jack.) Voight, found throughout the profile has red flowers in terminal racemes; *L. racemosa* Willd., with white flowers in axillary racemes is exclusively back mangrove. Hard to distinguish without flowers. The pest complex seems to be similar. Most of our work refers to *racemosa*. Phenology not well known but Wium-Andersen and Christensen (1978) give data for *littorea* from southern Thailand, mentioning that leaves were little affected but most fruit were destroyed by insects. Robertson and Duke (1987) ranked both in the low damage group with 3 to 4% leaf area loss in Australia. Similar rates seem to be current in Singapore. No reported outbreaks. Williams and Watson (1988, 1990) list two mealy-bugs, *Dysmicoccus nesophilus* and *Phenacoccus pacificus* (Pseudococcidae) from *L. littorea* (as *L. coccinea*) but no other pest records have been traced.

***Lumnitzera racemosa* Willd.**

In Singapore the small buds seem to have no attack. Expanding young leaves are regularly patch and edge-grazed by several Chrysomelidae (Coleoptera) (Colour Pl. 1). The polyphagous eumolpine *Rhyparida wallacei* is frequent, along with two unidentified species of *Tricliona*, the polyphagous galerucine *Monolepta bivittata* and a species of Alticinae.

These species continue feeding on expanded young leaves and are joined by *Lepadoretus compressus* (Col. Scarabaeidae) (Colour Pl. 3) which is much larger, strictly patch grazing and which makes extensive marks often zig-zag in shape. *A. compressus* is a very polyphagous nocturnally feeding pest inland. However there are a number of poorly known species of the genus which breed in mangroves (e.g. *A. ? lacustris*) including at least two in Singapore. How far these contribute to *Adoretus* type feeding marks is not known.

At this stage another chrysomelid, *Coenobius* sp. (Cryptocephalinae) (Colour Pl. 1) begins attack. This very small black beetle makes linear superficial grazing marks which penetrate the palisade layer but not the underlying enlarged water storage cells. Marks of this type are a characteristic feature of both species of *Lumnitzera* but have been seen on no other plant. The species is probably host specific and undescribed. The larvae have been reared in vitro and feed on decomposing litter. They construct tight fitting cases of faecal pellets as is usual in this subfamily. These larval habits probably account for the fact that while both species of *Lumnitzera* are attacked when growing at inland, high level sites, *L. littorea* when growing in fully inundated mangrove sites, is free of *Coenobius* damage.

Edge feeding by unidentified immature grasshoppers (Orth. Tettigoniidae) occurs occasionally. They may be attributable to a species of *Stylomolpa* of which adults have been seen.

Mature foliage of *L. racemosa* commonly bears subcircular holes six to eight mm in diameter. These result from leaf mining by a species of *Thiotricha* (Lep. Gelechiidae) (Colour Pl. 5). The larvae of this species first attack the fruit, penetrating and hollowing one which is then carried as a portable case. The growing larvae may feed on several fruit before moving to the foliage. There it penetrates the lamina, attaches the case with silk and excavates a mine to the radius it can reach. Heavily infested plants are conspicuous from the shriveled fruits attach to the foliage. The tiny white moths fly freely around the host in day-time.

Foliage is also attacked by unidentified bag-worm moths with smooth cases of *Dappula* type (Lep. Psychidae), by a species of *Odites* (Lep. Lethiceridae) which forms marginal leaf rolls and by the colourful, long-haired, gregarious larvae of *Trabala vishnou* (Lep. Lasiocampidae) (Colour Pl. 8), and a *Scopula* (Lep. Geometridae) (Colour Pl. 7).

When trees are populated by the pastoral ant *Oecophylla*, larvae of the lycaenid butterfly *Hypolycaena erylus* (Colour Pl. 13) may do considerable damage. Extensive defoliation of whole shoots has been seen, not certainly attributable to lycaenids but of similar damage type and on young trees containing abandoned *Oecophylla* nests.

Sap feeding Hemiptera include the polyphagous flatid *Salurnis marginellus* (Hom. Flatidae) and two leaf-hoppers *Dryadomorpha pallida* Kirk. (Colour Pl. 4) and *Parohinka longiseta* (Mel.) (Hom. Cicadellidae), all three having been reared from shoot feeding larvae. There is no apparent pathogenicity. Foliage is often characteristically deformed by an armoured scale insect *Aspidiotus* sp. (Hom. Diaspididae) which attacks the margin, causing deep notching and a chlorotic area about one cm across. Leaves are occasionally attacked by unidentified mealy-bugs (Hom. Pseudococcidae) without visible damage. Immatures and adults of a shield bug *Glaucias* sp. near *dorsalis* (Dohrn) (Het. Pentatomidae) (Colour Pl. 4) are found on shoots. Although adults may be found on many plants, larvae have only been found on *L. racemosa*.

Loss of developing fruit due to *Thiotricha* larvae (Lep. Gelechiidae) has already been mentioned in *L. racemosa*. The slightly larger fruit of *L. littorea* have not been seen to suffer this attack, but larvae transferred from *L. racemosa* accepted *L. littorea* foliage and completed development.

Under stands of this species, fallen fruit have been found to suffer losses from seed feeding lygaeid bugs. In this family, the subfamily Rhyparachrominae typically feeds on fallen seed and is suspected of being a major cause of propagule failure in many plants (Sweet, 1960). Large numbers of *Pamerana fulvomaculata* Malipatil (Colour Pl. 4) and *P. nigrifolia* Walker (Het. Lygaeidae) along with other rhyparachromines have been seen among *Lumnitzera* fruit where these accumulate, and a high proportion of the seeds show typical lygaeid damage. Post dispersal fruit are a component of marine strand litter far from the parent trees. There is a known assemblage of other rhyparachromine lygaeids in this habitat which may contribute to further loss.

***Lumnitzera littorea* (Jack.) Voight**

This larger tree which tends to grow more sea-wards than *L. racemosa* has been less studied. Foliage damage exists and no doubt many of the species recorded from *racemosa* attack it and some have been mentioned above. The fruit are not attacked by *Thiotricha*, probably because of their larger size, and in Singapore no fruit damage of any type has been detected. This is in striking contrast to the report of Wium-Andersen and Christensen (1978).

Euphorbiaceae

***Excoecaria agallocha* Linn.**

A dioecious tree with toxic latex throughout, small buds, spirally arranged simple thin dorsiventral leaves. Twigs with narrow pith. Flowers on both sexes in erect axillary catkins, the females maturing to trilocular dry fruit which split to release globular dry

seeds which are water-dispersed. The species is abundant in Singapore. The phenology is not documented in detail but foliage is very seasonal even in Singapore, the leaves flushing red and deciduous at least once a year, though never completely since young leaves are expanding by the time old ones drop. Corner (1952) states that this happens "after dry weather" and in Singapore there is usually such a spell following the northeast monsoon in February, but whether sporadic dry spells at other times also provoke leaf drop has not been reported.

For general herbivory, Robertson and Duke (1987) ranked this lowest with only 0.3% leaf area loss and only 8% of leaves showing any damage. Defoliation by the large caterpillars of *Ophiusa melicerta* (Lep. Noctuidae) is however reported from Indonesia by Whitten and Damanik (1986). This name is a synonym of *Achaea janata* mentioned below. Bole attack by the long-horn beetles *Aeolesthes holosericeus*, *Coptops aedificator* and *Dihammus rusticator* is mentioned by Beeson, (1941) though it is not certain that they attack living trees. Common (1970) mentions larvae of *Macrocyttara expressa* (Lep. Cossidae) tunnelling gregariously in the trunks of *E. agallocha* in Queensland. Williams and Watson (1988) record the scale insects *Pinnaspis stracheni* and *Selenaspis articulatus* (Diaspididae) and *Planococcus pacificus* (Pseudococcidae) in the Pacific area. The existence of an epipaschiine moth called *Cecidipta excaecariae* Berg (Lep. Pyralidae) may be mentioned, though as it came from Argentina and thus outside the known range of mangroves and of the plant genus this may prove irrelevant.

In Singapore, foliage herbivores are quite important and we have the impression of more loss than indicated by Robertson and Duke (1987) but that this involves the loss of whole leaves or stripping entire branches. This might be overlooked by sampling individual leaves for damage. The youngest leaves while still folded show crumpling associated with pink larvae of an unknown gall midge (Dip. Cecidomyiidae) feeding within the fold. This has not been successfully reared.

Opening leaves are also attacked by larvae of *Sauris* sp., (Lep. Geometridae) (Colour Pl. 7). Eggs laid singly on the margin of newly opened leaves hatch to tiny looper caterpillars which begin edge feeding immediately. They grow rapidly and complete development within a week, before the leaves have significantly hardened. The mature larvae drop to the ground to pupate and in another week the small, delicate adults emerge, beautifully marbled with green to resemble lichens on the tree trunks where they rest. Males of this genus group have bizarrely distorted wings that make them immediately recognisable. A cursory examination of genitalic preparations in the British Museum (Natural History) collection suggests that several genera are really involved.

Young leaves and tender shoots also have leaf mines from which a *Phyllocnistis* (Lep. Gracillariidae) has been reared, apparently the same species attacking many other plants including *Avicennia* and *Clerodendrum* in mangroves (Colour Pl. 13).

Older foliage is eaten by the large grey hairy caterpillars of ?*Paralebeda* sp. (Lep. Lasiocampidae) (Colour Pl. 8). These are most often seen gregariously on the trunk during day-time where the deflexed lateral hairs make them very procrustic, and they feed during the night. Pupation takes place in cocoons webbed with larval hairs inside hanging dead leaves and attack is more often recognised from persistent cocoons from old outbreaks than from finding larvae. *Gadirtha pulchra* (Noctuidae) was seen once.

Extensive local defoliation can occur from day-feeding gregarious caterpillars belonging to *Selepa discigera* (Lep. Noctuidae) (Colour Pl. 12). The species is treated as a synonym of *Selepa celtis* Moore by Hampson (1894), probably correctly and Moore described

the larvae from Ceylon (Sri Lanka). These larvae are surface patch grazers feeding in large clusters while young, becoming edge feeders when full grown, and are easily recognised by the long white hairs and yellow body colour with dorsal dark patches on abd. 2, 7 and 9. Moore's description as quoted by Hampson appears to match the Singapore material exactly. They pupate in typical sarrothripine cocoons among the foliage.

Although not seen in Singapore as major outbreaks such as that reported by Whitten and Damanik (1986), *Achaea janata* (Lep. Noctuidae) (Colour Pl. 11) occurs occasionally. The large brown mature larvae have reduced prolegs on abd. 3 and 4 and dorsal tubercles on abd. 8 and are edge feeders. Pupae are covered with a white bloom, typical of the subfamily Acontiinae (see Kitching, 1984) and are found in cocoons of webbed leaves. Interestingly, very young larvae, unlike the well grown one, are also bloomed with wax and look very different from the full-grown one. The species is fairly polyphagous though normally on Euphorbiaceae. A pupa has also been found on *Hibiscus tiliaceus* in mangroves but this may be no more than a larva migrating prior to pupation.

Excoecaria can be heavily grazed by phaneropterine nymphs (Orth. Tettigoniidae) of a species regularly seen on this host but rarely on any other. These immatures are distinctive but no adult has been matched to them.

Sap-flow ectoparasites are uncommon, but a species of *Chloropulvinaria* has been seen to attack foliage and immatures on new shoots caused substantial deformation. A major outbreak of larvae of the scutellarine bug *Calliphara nobilis* (Hem. Pentatomidae) (Colour Pl. 4) occurred on an isolated female tree in fruit. It seems likely that *Excoecaria* is the primary host of this species whose adults are seen widely throughout Singapore mangroves clustered on foliage, but whose larvae are very rarely seen.

Bole damage by the longicorn beetle *Aeolesthes holosericeus* (Col. Cerambycidae) (Colour Pl. 1) is very common in Singapore, the entire bark being loosened and with cut out discs, three to five cm in diameter at sites of emergence holes. Adult beetles sometime are found in large numbers under the loose bark. Whether healthy trees are attacked or only if weakened in other ways is not certain.

Young fruit are attacked by unidentified juveniles of a red bug (possibly *Dasynus laminatus* Hem. Coreidae) and mature fruits show holes caused by internal seed feeding insects. Usually only a single hole exists in each fruit but all three seeds are destroyed - a situation resulting from attack by larvae of at least two species of fruit-flies (Dip. Tephritidae) which when mature drop to the ground for pupation. *Elleipsa quadrifasciata* was only recently described from the Philippines and is illustrated by Hardy (1974). The other is an undescribed species of *Adrama* (Colour Pl. 3). The larvae can jump as is described for other tephritids. Adults of these species are occasionally seen on foliage of various mangrove plants along with another species of Adramini whose host has not yet been discovered. It is interesting that *Excoecaria* should support two very different tephritids with such similar habits, and raises the possibility that the third may also be involved - an extensive rearing programme is in progress to test this hypothesis. Also in fruit an unidentified pyralid caterpillar has yet to be reared. Immatures of *Calliphara nobilis* while capable of feeding on shoots definitely feed preferentially on mature seed capsules when available.

Lythraceae

Pemphis acidula Forster

Probably extinct in Singapore since loss of the few specimens formerly found near

Tanjong Gul when reclamation for the Jurong industrial estate took place. On the other side of the Straits of Singapore however, a small population still exists on Pulau Batam (Indonesia) where it has been studied. The species also exists in Malaysia (J. B. Sigurdsson pers. comm.), even though Burkill (1966) stated that the species had only been recorded from Singapore island. The phenology is undescribed though here it seems to flower continuously, and no pest outbreaks have been reported. In Pulau Batam, no significant foliage damage was seen, but a single moth pupa was found in rolled leaves which failed to emerge. The most interesting discovery was that flowers are infested by a bud-moth, apparently a species of *Thiotricha* (Lep. Gelechiidae) (Colour Pl. 5) distinct from that attacking *Lumnitzera racemosa* but whose biology is essentially similar.

An interesting feature of this plant is that maturing fruit secrete a massive plug of salt at the apex. While this may be its form of salt regulation (unreported in the literature) it is possibly also a deterrent to *Thiotricha* attack. This plug is visible on the figure in Colour Pl. 5.

Myrsinaceae

Aegiceras corniculatum (L.) Blanco

A shrub or small tree with small buds, rounded, salt-excreting, spirally arranged dorsiventral leaves and umbels of white flowers maturing to curved fruits superficially like those of Rhizophoraceae but actually a complete fruit which dehisces to release the propagule.

Nothing is reported on phenology, but trees in Singapore began flowering synchronously in the dry spell at the end of the northeast monsoon in late February. Fruit-fall began in late August and was complete by mid-September when the only crop of new leaves was put out.

No pest outbreaks reported. The only recorded herbivores known to me are Meyrick's (1866) citation of *Aegiceras* as foodplant of *Scorpiopsis pyrobola* Meyrick (Lep. Oecophoridae) in northern Australia, the larva feeding within a rolled tube formed from part of a leaf, and Hutchings and Recher (1982) mention the lycaenid *Nacaduba kurava*.

In Singapore the population is very low. On the main island I know of five mature trees at Sarimbun and single individuals in four other places. A few individuals at Mandai were heavily damaged by bag-worm attack in 1976 and died out at that site. At present significant damage by a bagworm (Lep. Psychidae) occurs at other sites. The damage caused by this species at first consists of circular marks very like those caused by *Pagodiella* on *Rhizophora* (q.v.) and then the larval cases are indistinguishable. However in this species the case is later transformed into a tubular one and larvae make irregular grazed patches.

Also attacking this plant are *Cleora injectaria* (Lep. Geometridae), *Archips* sp. (Tortricidae) a slug caterpillar *Darna trima* (Limacodidae), the gregarious lasiocampid *Paralebeda*, a very distinctive leaf-miner which forms a tight, helically coiled mine on the abaxial surface, and minor damage to young leaves by the chrysomelid beetle *Rhyparida wallacei*. The leaf miner was recently reared and proved to be a second species of *Phyllocnistis*, very different from the *citrella* type found on other plants. The larva has striking fluke-like appendages at the tail.

Sap-flow parasites include *Crypticerya*, *Chloropulvinaria* and one or more species of *Pseudococcus* (Coccoidea) and a species of *Aleurodicus* (Aleyrodidae). Most of the taxo-

onomic work on *Aegiceras* foliage pests remains to be done and no further detail can be given at this stage.

Although trees seem healthy, they suffer severe attack by *Zeuzera conferta* (Lep. Cossidae) and are prone to drop branches.

No sign of early bud or flower attack has been seen but mature propagules are bored by the larva of a moth apparently belonging to the genus *Anarsia* (Lep. Gelechiidae) (Colour Pl. 5). This habit is most unusual, all of the known larvae of Dichomeridini being leaf-tyers or rollers (Hodges, 1986). Like so many of these mangrove moths this is almost certainly undescribed. Although externally a typical *Anarsia*, unmistakable from the absence of the third palpal segment in the male, the male genitalia are complex, highly asymmetrical and like nothing I have seen anywhere in the Lepidoptera, although a tendency towards this asymmetry does exist in some of the Meyrick species of *Anarsia* illustrated by Clarke (1969).

Rhizophoraceae

Now regarded as a uniquely mangrove family, this is recognised by the elongate leaf buds enclosed in bracts which fall as the young leaves open to a loose funnel, the smooth leathery opposite dorsiventral leaves with long petioles; the flowers in axillary cymes and characteristic viviparous fruit in which the radicle develops precociously to a long spear-like shaft. Twigs have a characteristic wide pith cylinder and a distinctive growth form with alternation of long and short metamers (Rau & Murphy, 1990).

A very important paper by Onuf *et al.* (1977) gives both the natural history and much quantitative data on the impact of five identified foliage feeding Lepidoptera on *Rhizophora mangle* in the mangroves of Florida, U.S.A. This is the only paper known to me in which the contribution by different species to mangrove herbivory is discriminated. In Thailand, Chaiglom (1975, 1982) and Vaivanijskul (1976) have made mention of species attacking *Rhizophora mucronata* and Rau and Murphy (1990) list some from other Rhizophoraceae. Murphy (1990e) illustrates many of these Thai species, but the provisional names used there have been updated somewhat since. Thus the moth referred to as *Epagoge* sp. is here called *Capua endocypha* (*Capua* was treated as a synonym of *Epagoge* at one time, Diakonoff, 1939), and *Pleuroptya sabinusalis* is now known to be *P. balteata* or a member of its group. Otherwise the names used in the Thai papers, although still provisional, remain our current opinion.

Takahashi (1950) recorded the scale insect *Paralecanium vacuum* from *Rhizophora* sp. in Singapore, Malaya and Riau Is. The species is still to be found sparsely on most Rhizophoraceae.

An important category of herbivores unique to the family is an assemblage of scolytid beetles attacking radicles of propagules both before and after they drop. These have been documented by Beeson (1930), Kalshoven (1959) and Browne (1961) together with scattered notes in the taxonomic literature.

In Singapore, several insect herbivores appear to be common to all Rhizophoraceae and will be documented first, before dealing with those which on current evidence are apparently more host specific. These include the caterpillar of *Capua endocypha* Meyr. (Lep. Tortricidae) (Colour Pl. 17) which commonly attacks the leaf buds before opening and then extends attack to newly expanding leaves which are webbed together. Mature foliage is grazed by leaf webbing caterpillars of *Odites* spp. (Lep. Lethicoceridae) (Colour Pl. 9) and these, together with *Capua* appear to be the most consistently present of all insect

herbivores. There are low populations of at least three types which are provisionally treated here in *Odites*. This group formerly placed in Xylorictidae, is taxonomically difficult and there is still disagreement over its correct family and the discrimination of genera. I follow the opinion (and reservations) of Minet (1986) in using Lethicoceridae. One small form, certainly a separate species, completes development in marginal leaf folds while two larger ones feed between strongly webbed leaves and are suspected to be sexes of a single, highly dimorphic species. The larvae of these "*Odites*" are very distinctive with broad, heavily pigmented head and shield, and a characteristic pattern on the last three abdominal segments. All are very similar and no way to discriminate species on larvae has yet been found, although the adults are very distinct. These comments also apply to the quite different species found on *Avicennia* and *Lumnitzera*. Larvae of "*Odites*" are very slow growing, do relatively little damage and have never reached epidemic densities so they may not need to be studied quantitatively.

Occasional individuals of the small nettle caterpillars of *Darna* aff. *trima* (Lep. Limacodidae) are seen. These edge-feed transversely across the width of the mature leaf lamina of spp. of *Rhizophora* and *Bruguiera*, much as described by Onuf *et al.* (1977) for *Alarodia slossoniae* in Florida. This species is heavily parasitised and has never appeared in numbers.

The maturation feeding by *Monolepta longitarsis* and *Rhyparida wallacei* (Col. Chrysomelidae) on newly expanding foliage which Rau and Murphy (1990) found to be important in Thailand, exists in Singapore but is of very minor significance.

Flower and propagule damage varies significantly between species and will be discussed individually.

BRUGUIERA

Leaf buds elongate cylindrical enclosed in dehiscent bracts and opening to a loose funnel; leaves opposite, moderately thick, strongly dorsiventral, the under surface without black spots, only the midrib defined, strongly protruding beneath and continuing to a long cylindrical petiole. Twigs with broad pith cylinder, fleshy at first; timber dense; Flowers and fruit typical of Rhizophoraceae. There are two widely different facies within the genus, one small flowered with slender fruit, represented in the area by *B. cylindrica* and *B. parviflora*; one with large fleshy flowers and stout fruit represented by *B. gymnorhiza* and *B. sexangula*. Since the two groups are so different the species are treated separately. *B. sexangula* no longer exists in Singapore but is mentioned by Nakahara (1981) as the host of the scale insects *Coccus longulus*, *Saissetia coffeae*, *Crysomphalus aonidum* and *Nipaecoccus vastator* in Hawaii.

***Bruguiera cylindrica* (L.) Bl.**

The commonest species in Singapore, this belongs to the small flowered group with slender fruit radicles and is easily recognised by its triadic cymes when flowering, large trunk lenticels and relatively small leaves.

Phenology has been studied in southern Thailand by Wium-Andersen and Christensen (1978). Major defoliation have been reported in Indonesia by a bag-worm *Acanthopsyche* sp. (Lep. Psychidae) by Intari (1984). Robertson and Duke (1987) did not include this species in their study. Rau and Murphy (in press) recorded 6% mean area loss in southern Thailand which would place it in their intermediate to low damage category.

Literature records exist (following Meyrick, 1925) of damage to radicles of propagules by the tortricid moth "*Argyroploce lasiandra*", a species currently treated as a synonym of *Cryptophlebia ombrodelta* in Inoue *et. al.* (1982). Takahashi (1952) reported the scale insect *Coccus punctuliferus* from *B. cylindrica*. Williams and Watson (1988-90) record no Coccoidea since this species hardly reaches the Pacific.

Foliage damage begins as usual with *Capua* attack upon the bud and young leaves. At the time of bud unrolling, young leaves may be susceptible to *Rhyparida* and *Monolepta* damage but to a much lower level than in *Rhizophora*. Both beetles are relatively uncommon in Singapore at present. In addition to *Capua* attack, the expanding foliage is commonly edge-grazed by the large larvae of *Dysphania* aff. *subrepleta* (Lep. Geometridae) (Colour Pl. 6) which, on present evidence, seems to be entirely restricted to this host. On mature foliage, both species of *Odites* are relatively common. Other Tortricidae occur rarely (*Archips*, *Homona*).

Less common but still widespread, larvae of *Polyura schreiber* (Lep. Nymphalidae) (Colour Pl. 13) have mainly been seen on *B. cylindrica* and were once reared from eggs being laid on *Rhizophora apiculata*, though since this butterfly occurs widely inland where it has been bred from *Nephelium* (d'Abrera, 1958) it may yet prove to have other mangrove hosts. The ornamentation of the larval head bears a striking resemblance to the mature flower head of *B. cylindrica* and may be procryptic on this host.

Sapflow parasitism seems very limited. Larvae of the scutellarine bug *Calliphara nobilis* (Hem. Pentatomidae) whose metallic adults cluster gregariously in large numbers beneath leaves of most species of *Bruguiera* and *Rhizophora*, have so far only been collected on *B. cylindrica* among Rhizophoraceae. Even then only single individuals were seen, in striking contrast to the situation on *Excoecaria* (q.v.) which is probably its main mangrove host. The species is certainly not host specific since it is common in inland forest as well as mangrove. Occasional plants have been seen with foliage infested by *Crypticerya* (Hom. Margarodidae) and the very flat *Paralecanium vacuum* (Hom. Coccidae) is occasionally seen as single individuals on the upper leaf surface.

No twig or stem borers have yet been recorded.

Propagule predation in *B. cylindrica* begins, as usual, with flower attack. The flower buds, normally produced in axillary triads, show very high survival in Singapore and a high productivity of mature fruit is the norm. Nevertheless both bud and fruit do suffer some loss. The flower attack is by a small tortricoid moth *Eupoicilia* sp. (Lep. Tortricidae) (Colour Pl. 18) whose biology is somewhat similar to the *Thiotricha* spp. known from *Lumnitzera* and *Pemphis* but without the leaf-mining phase. The Cochyliini to which it belongs are well known to be flower feeders and are probably common in Southeast Asia though few species have yet been described. The *Eupoicilia* larvae enter the flower bud, web it to the host and after it detaches, carry it as a portable case. Other buds are attacked, with or without transfer and the original case may be carried throughout larval life. It shrivels to form a longitudinally ribbed case, quite unlike the original flower bud (which is smooth). Sometimes however, the larva transfers to a second bud, leaving the old one still attached to the side. Attack may be at the open flower stage also. At pupation, these cases may be found on foliage, but their origin was not recognised until the rearing programme from flowers was carried out. There may be no foliage feeding but some larvae did make minor patch grazing. Unlike *Thiotricha* spp. with otherwise similar biology, this was not done by leaf mining. As mentioned before, this species also feeds on *Avicennia* flowers and may well be more polyphagous. However it is none of the species previously described from the region (see e.g. Kawabe, 1987) and is probably undescribed.

Mature propagules are attacked by larvae of a small graptolithine moth provisionally placed in *Cydia* s. lat. (Lep. Tortricidae) (Colour Pl. 17). Larvae tunnel the radicle and, when mature, create a circular window sealed by a silken membrane through which the adult ecdyses. Several larvae can develop in a single radicle. The damage is very local and sporadic, and larvae suffer a high rate of parasitism. No scolytid beetles have been reported as boring the radicles. Both bud and fruit attack evidently have very little impact on fruit production by *B. cylindrica*.

***Bruguiera parviflora* Wight & Arnold ex Griff.**

Now very rare in Singapore, only a few trees remaining in the Pasir Ris park which however fruit profusely and it will be possible to replant more widely. The species is easily distinguished from *cylindrica* by the papery calyx persistent on the very slender radicles. It is considered a rather short lived, opportunistic species. Its phenology does not seem to have been documented, but the impression from our small population is that fruiting is very seasonal, in marked contrast to *B. cylindrica*. Robertson and Duke (1987) placed it in the low damage category in Queensland with 3.3% leaf area loss. Rau and Murphy (in press) found about 13% loss in southern Thailand or well into the high to intermediate damage category. Much of this damage was traced to crab attack rather than insects. They reported the usual attack by *Capua*, *Adoretus* and *Rhyparida* and also reared *Glyphodes ernalis* (Lep. Pyralidae) from leaf-webbing larvae. It is to be expected that there will be a wider variety than this, possibly including flower and propagule attack similar to that on *B. cylindrica*.

Flower attack was not detected in Singapore, but in addition to *Capua* and *Odites* damage, trees are known to suffer from bag-worms, *Pagodiella* sp. (Lep. Psychidae) and heavy attack by a *Chloropulvinaria* (Hom. Coccidae) leading to extensive sooty mould coating on foliage. No propagule attack has yet been detected.

***Bruguiera gymnorhiza* (L.) Lamk.**

This species, ultimately the largest of all mangrove trees, is common in Singapore but only as relatively young plants, which however flower and fruit freely from small size. The larger leaves and often red bud-bracts usually distinguish it, and of course it is unmistakable in flower or fruit. Phenology is not documented, but it does not seem to be seasonal in Singapore.

The scolytid beetles *Coccotrypes fallax* and *Cryphalus borneensis* have been reported as attacking radicles (Browne, 1961).

Although a common species in Singapore, relatively little foliage damage has been seen on *B. gymnorhiza*. There is a low level of attack by *Capua*, one or more of the *Odites* spp., and some polyphagous forms including *Attacus*, *Cleora* and *Gonodontis*. The large flowers show no signs of damage, though they commonly carry populations of mites when open. The thick radicles of rooted propagules have been seen with infestations of *Coccotrypes fallax* (Col. Scolytidae) as has been previously reported by Browne (1961).

***CERIOPS* Arn.**

Immediately recognisable by the flattened buds, broadly obovate leaves and ridged radicles of the propagule, *Ceriops* has two species, *C. decandra* and *C. tagal* in the region. The phenology does not seem to have been studied for *C. decandra* but that of *C. tagal*

was studied in southern Thailand by Wium-Andersen and Christensen (1978). Robertson and Duke (1987) recorded 6.3 to 6.8% leaf area loss for two varieties of *C. tagal* in Queensland while Rau and Murphy (in press) found 9.3 to 11.8% in *C. decandra* in Thailand. They reported shoot attack by *Capua* and leaf grazing by *Rhyparida* and *Adoretus* in Thailand, but much more damage was due to crab attack. Damage to radicles of propagules by scolytid beetles has been occasionally reported. *Coccotrypes fallax* was implicated by Beeson (1941) in India, and "*Cryphalus negrosensis*" by Cabahug *et al.* (1987) in the Philippines (I have not traced a description of this species).

Ceriops tagal recognised by pendant fruit and monopodial growth form is a common species in Singapore whereas *C. decandra* appears to be extinct.

Reports of insect attack appear to be limited to those summarised by Hutchings and Recher (1982) of *Procalyptis parooptera* (Lep. Tortricidae) *Hypochrysops apollo* and *H. appeles* (Lep. Lycaenidae) as foliage feeding in Australia.

In Singapore, general damage levels are low in *tagal* but the species receives some attack by *Capua*, and an *Odites* sp. Unlike the situation in *Bruguiera* and *Rhizophora*, *Capua* very rarely attacks the leaf buds, which in *Ceriops* are protected by relatively hard bracts with a varnish-like coating. The species is however, common on both young and almost mature foliage and seems to be the main cause of leaf area loss. No flower damage has been reported and fruit set is high. A single case of propagule damage by a tortricoid moth boring the radicle has been reared but no cases of scolytid damage have been seen.

RHIZOPHORA L.

Immediately distinguished from *Bruguiera* by the stilt roots and the stippling of the under-surface of leaves with black "cork-warts", this genus contains the most important economic timber trees in mangroves and has been most intensively studied. Of the three species found in Singapore, *R. apiculata* is so different in floral structure (1986) and architecture (Rau & Murphy, 1990) that it could arguably be treated as a distinct genus *Aerope* Blume. This is not done since it is said to cross with *R. stylosa* in the south Pacific. There is no indication that the insect pests discriminate between the sections.

Most records identify the host to species except for the scolytids attacking radicles. The species recorded from the genus are *Coccotrypes fallax*, *C. litoralis*, *C. nephelii*, *C. rhizophorae*, *Cryphalus littoralis* and *Ernoporus inermis*. (These names have been updated from the recent generic revision by Wood (1986) and do not necessarily appear in those combinations in the original records). Hutchings and Recher (1982) report termite and lycaenid attack in Australia.

***Rhizophora apiculata* Bl.**

Phenology was studied in southern Thailand by Christensen and Wium-Andersen (1977). Leaf area loss in Queensland was reported at 4 to 6% by Robertson and Duke (1987) and in Thailand at between 6 and 8% by Rau and Murphy (in press). These authors also give a preliminary account of herbivore attack. The most damaging pest was gregarious larvae of a pyraustine moth *Pleuroptya balteata* which destroyed whole branch terminals, but there was significant bud boring and young leaf attack by *Capua*, leaf-mining by a fly *Tropicomia* sp. extensive young leaf damage from *Hypolycaena erylus*, and extensive damage to newly unrolling leaves by two chrysomelids *Monolepta longitarsis* and

Rhyparida wallacei (Colour Pl. 1) which led to anthracnose leaf spotting. Older foliage was grazed by a lasiocampid moth, probably *Suana concolor*. Root and propagule damage by *Coccotrypes* spp. (Col. Scolytidae) was mentioned and several, probably non-specific Homoptera recorded as sap sucking.

In Singapore, several of the species reported from Thailand have not yet been found, notably the *Pleuroptya*, *Suana* and *Parasa*, (illustrated by Murphy, 1990e) although the species are widespread polyphagous forms and almost certainly occur. *Hypolycaena* was never seen on *Rhizophora* although common on some other mangroves (*Lumnitzera racemosa* and *Scyphiphora hydrophyllacea*). Damage levels from *Monolepta* and *Rhyparida* were very low. The most significant attack on buds and young leaves was from *Capua*. As leaves mature, low levels of *Odites* spp. occur. One small stand of stressed trees of *R. apiculata* has shown long standing attack by the bag-worm *Pagodiella* sp. (Lep. Psychidae) restricted to the same few trees over a period of 3 years. Other trees within and near the stand, including *R. mucronata* and *R. stylosa* as well as other mangrove genera were not or hardly damaged. Similar very local attack was seen at other mangrove sites not regularly visited (Pulau Semakau, Lim Chu Kang). The only other mangrove species seen to be attacked by this pest was *B. parviflora* but apparently the same bag-worm species appears sporadically on inland trees of several unrelated species with the same extremely localised, chronic etiology.

Twig borers are not normally significant on *Rhizophora* except that in areas where *Avicennia* and *Sonneratia* are heavily attacked by *Zeuzera conferta*, shoot die-back from young larval attack can be conspicuous. The damage does not extend to branch or bole and these are considered to be strays from other hosts.

A few scale insects and related Homoptera are occasionally seen. In Coccidae, species of *Saissetia*, *Coccus*, *Inglesia*, *Paralecanium*, and *Chloropulvinaria* occur, usually very locally. A species of *Lecanodiaspis* attacked young saplings at damaging level at one site. Leaves occasionally carry aggregations of *Pseudaulacaspis* sp. (Hom. Diaspididae). An undescribed species of the whitefly genus *Aleurolobus* (Hom. Aleyrodidae) exists but is very rare.

No organisms damaging flowers are known. Developed and fallen propagules can be attacked by *Coccotrypes fallax*. In spite of reports by other authors (e.g. Browne, Kalshoven, Onuf *et al.*) *C. rhizophorae* has never been seen in Singapore to attack propagules although it is a widespread and major cause of damage to young stilt roots (Colour Pl. 2).

***Rhizophora mucronata* Lamk.**

Some information of phenology in southern Thailand is given by Sukwong *et al.* (1975) and by Wium-Andersen (1981). In Singapore it seems to bear flower and fruit year round. Robertson and Duke (1987) gave low levels of damage (1.4 to 2.6%) in Queensland. Defoliation by the geometrid moth *Cleora injectaria* was reported from Thailand by Chaiglom (1975). One case of damage by gregarious nettle caterpillars *Parasa sundalepida* occurred (Rau & Murphy, in press). The pest complex in Singapore is essentially as in *R. apiculata*. Heavy infestation of propagules by *Coccus* sp. (Hom. Coccidae) has been seen leading to conspicuous deformation of the radicle. Fruit are often heavily infested with *Coccotrypes fallax* (Col. Scolytidae) without damaging the developing propagule, although once these are dropped the radicles are subject to infestation.

***Rhizophora stylosa* Griff.**

Uncommon on the Singapore mainland but abundant on Pulau Semakau and across the strait in the Indonesian island of Pulau Batam, this species is here at the extreme western limit of its range. In the small population at Pasir Ris park it flowers and fruits continuously throughout the year. No reports of pest outbreaks have been traced. In the Pacific, Williams and Watson (1990) report *Kilifia acuminata* and *Paralecanium* sp. (Coccidae) from this species. Casual observation suggests that in Singapore *R. stylosa* may carry the same pest complex as other species of the genus. However the trees seem very free from damage of any sort.

Sonneratiaceae (formerly included in Lythraceae)

SONNERATIA Linn. f. (Blatti. Adans.)

Apical leaf buds small and partly protected by apposed petioles, but flushing synchronously and then very susceptible to attack. Broad, rather fleshy opposite leaves, usually isobilateral. Nodes below petiole with nectaries characteristic of the genus. These are functional on very young shoots and may attract ants, bees and other flying insects in large numbers. Shoots fleshy with wide pith cylinder. Wood dense. Flowers large, in apical cymes, opening at night, bat pollinated. Fruit are apple-like, many seeded and water-dispersed. There are three species in Singapore, *S. alba* J. Sm., a common pioneer on soft muds at HW neap levels but seedlings found everywhere when mangroves are cleared; *S. ovata* Backer, a moderately common small back mangrove species; *S. caseolaris* (L.) Engl., typical of up-river, only weakly brackish areas, now very rare in Singapore.

Phenological studies do not seem to have been done on any species but in Singapore it appears that flowering and fruiting is highly seasonal in *S. alba*. Mass flowering began in the dry period following the northeast monsoon in early February and fruit from this crop were falling by early April and thereafter flowering and fruiting continued widespread until October. There is hardly any during the November to January wet season. Seedlings of *S. alba* often form dense stands on newly exposed mud banks but few survive. Murphy and Lee (in press) speculate that the species has a pre-emptive strategy adapted to mobile substrates. *S. ovata* also seems to flower seasonally but *S. caseolaris* is said to flower continuously.

Robertson and Duke (1987) found *S. alba* to have over 10% leaf area loss at one site and only 1.2% at another, while *S. caseolaris* had 10% at one site. They thus just fell into their intermediate to low damage category. The only report of serious defoliation traced is by Kalshoven (1953) who implicated *Lymantria ? galinari* (Lep. Lymantriidae) "... on a small island in the estuary of the Barito river in South East Borneo - all specimens of *Sonneratia acida* were defoliated ...". The scale insect *Halococcus formicarii* Takahashi is described from ant occupied cavities in twigs of *S. alba* and *S. caseolaris* in Malaya. No records of Coccoidea from this genus were made by Williams and Watson (1988-90).

Foliage grazing. - *Sonneratia* appears to be relatively free of attack by the chrysomelid beetles that are conspicuous on most other mangrove species, and no comparable damage has been seen. A species of *Monolepta* does occur but in insignificant densities and a species of Clytrinae (Col. Chrysomelidae) has been collected but did not feed in vitro and was possibly from another nearby host (Colour Pl. 1). Very much more conspicuous on

Sonneratia than on any other host are the distinctive large zig-zag patch-grazed holes made by the nocturnal ruteline beetle *Lepadoretus compressus* (Col. Scarabaeidae) (Colour Pl. 3). This very polyphagous pest of inland trees breeds inland. Where stands of *Sonneratia* border grassland, it is very noticeable that land-ward trees receive heavy attack but those to the sea-wards are untouched. A rather wide range of other nocturnal scarabaeids (*Holotrichia*, *Anomala* and *Apogonia* spp.) have been occasionally seen but only on land-ward trees near extensive parkland. They are not considered a normal element of the mangrove fauna.

In the Singapore area, although specific attack on resting leaf buds has not been detected, attack on expanding leaves by the pyraustine moth *Taurometopa pyrometalla* (Lep. Pyralidae) (Colour Pl. 14) begins very early and involves growing point destruction. The *Taurometopa* larva binds the two apposed apical leaves into a closed purse-like case and feeds entirely within it, all frass remaining within this case. Sometimes it moves to further shoot apices, but it can complete development within a single apex. This suggests the apical shoot of *Sonneratia* may be unusually nutritious and an analysis is desirable. When mature, the larva leaves the destroyed shoot and pupates in a cocoon on a nearby twig. Although *Taurometopa* is considered a rare moth by museum taxonomists, it is widespread in Southeast Asian mangroves and has been seen in Pulau Batam (Indonesia), Pulau Tioman (Malaysia), Phuket and Ranong (Thailand). At the last site, specimens have been collected year-round in light traps. Damage typical of *Taurometopa* is extremely common on old trees of *S. alba* at many sites and the apical die-back of leading shoots leads to a characteristic twiggy development with frequent diversion of growth to lateral shoots. There are indications that other insects may cause similar damage, and this effect may not always be due to *Taurometopa*. The species also attacks *S. ovata* and may well accept all species of *Sonneratia* but is not known from any other genus.

A second, apparently undescribed species of the same genus group (actually a *Balaenifrons*) has also been found in Singapore (Colour Pl. 14). This species exists in the British Museum collection as part of the series of *Balaenifrons homopteridea*, but is quite distinct and accounts for the peculiarly disjunct distribution attributed to this species by Hampson (1917). This was very common in light trap catches at one site (along with *T. pyrometalla*) and was reared from *Sonneratia alba* damaged in much the same way. The difference lay in the mode of pupation. Whereas *pyrometalla* leaves the destroyed shoot apex to make a cocoon on the stem, this second species pupates within the shrivelled remains. Interestingly, the larva leaves the leaf fold briefly and spends some time webbing it to the undamaged part of the stem. Thus while shoots damaged by *pyrometalla* soon fall off, those attacked by this other species can be recognised by dead, dry leaders dangling from the branches within which the pupae are found.

Leaves at this stage are also attacked by larvae of *Boeotarcha crassicornis* (Lep. Pyralidae) (Colour Pl. 15) which while young, patch-graze in gregarious assemblages of 5 to 10 individuals between leaves webbed together. Older larvae disperse and patch-graze on the open surface of mature leaves beneath loose webbing which retains some frass, finally pupating in a dense silk cocoon within a rolled leaf which is firmly webbed to adjacent foliage or stem. *B. crassicornis* is common in light trap catches and has previously been reported from mangroves in Thailand by Vaivanijkul (1976). It has reached local outbreak levels in Singapore (Pasir Ris, coastal plots immediately following the northeast monsoon) with extensive loss of leaf area.

A very common but relatively minor patch-grazing caterpillar that webs old leaves

firmly together is the small mottled red and white larva of a species related to *Epiphractis* (Lep. Oecophoridae) (Colour Pl. 10). The genus is now regarded as a synonym of *Orygocera* Wals. but I use the Meyrick name as better describing my material. Much less common but usually with similar habits are the smaller, red-banded larvae of a species of *Hypatima* (better known as *Chelaria*) (Lep. Gelechiidae) (Colour Pl. 5).

Young seedlings and saplings often have the apex including the meristem attacked by leaf webbing larvae of *Lasiognatha leveri* (Lep. Tortricidae) (Colour Pl. 18). The larvae freely attack inter-tidal seedlings and saplings, the dense silk trapping air while the larvae are submerged. This has been described by Lever (1952, 1955) under the name *Olethreutes leveri* Bradley. This name was overlooked by Diakonoff (1973) when he revised the regional Olethreutini and he considered *Lasiognatha* to be monospecific. The species also attacks higher shoots on mature trees but has not been seen as a major outbreak, whereas on inter-tidal seedlings it can be devastating and cause considerable mortality. Its attack is recognised by the very strong silk webbing, usually involving several apical leaves, and the strong, white silk cocoon from which the pupal pelt protrudes on eclosion.

Young expanded leaves are attacked by several specific and polyphagous Lepidoptera. *Arhopala pseudocentaurus* (Lep. Lycaenidae) (Colour Pl. 13) is an edge feeder attended by weaver ants (*Oecophylla smaragdina*). This species is known to attack species of Lythraceae (to which *Sonneratia* has been assigned), Combretaceae and a *Quercus* (Corbett & Pendlebury, 1978: 286). Many lycaenids are more dependant upon ant attendance than on strict host specificity. Unlike most other butterflies, lycaenids tend to include phylogenetically and chemically very different plants in their host range, perhaps for this reason (Gilbert, 1979). *Dasychira* (Colour Pl. 10), *Archips* (Colour Pl. 17), a phycitine (Colour Pl. 16) and a *Scopula* (Colour Pl. 7) also occur. Large hairy larvae of *Trabala krishna* can defoliate whole branches and cocoons are commonly seen.

Edge feeding by several caterpillars can be common at some times of the year. The commonest species reared in Singapore is *Eretmopus discissa* (Lep. Geometridae) (Colour Pl. 7). Its slender green looper caterpillars have a dark line along the back when young. This looks very like the edge of a bitten leaf and makes them hard to see. When full grown they lose this pattern and appear to mimic a fallen *Rhizophora* bud bract. They leave the tree to pupate in the ground.

Localised major defoliation by the epipaschiine moth *Heminomistis flagellalis* (Lep. Pyralidae) (Colour Pl. 15) is very common. This species is also reported by Vaivanijkul (loc. cit.) As is typical of this subfamily, the larvae are gregarious and destroy both young and old leaves. Extensive webbing with included frass, dead leaf fragments and detached twigs attached to the branches is distinctive. The larvae leave these nests to graze at night. They pupate in communal clusters on the branches. Three out of 12 saplings at one site died as a result of an outbreak. The species occurs regularly in small numbers at other sites and is suspected of heavy attack on high trees on which defoliation is associated with typical "nests" visible with binoculars.

Bag-worms (Lep. Psychidae) have been seen only rarely on *Sonneratia* and in Singapore they seem to be much less important on this host than on *Avicennia*.

As regards leaf miners, one species that may cause damage superficially resembling that of *Taurometopa* is a species of *Lyonetia* (Lep. Lyonetiidae) (Colour Pl. 10). This is a gregarious leaf-miner sometimes attacking at the same stage of early leaf expansion, but

more commonly is slightly older expanded leaves. In contrast to *Taurometopa*, faeces are extruded from the leaf and in dry weather these adhere in coiling wiry strings through perforations in the laminar cuticle which are distinctive. As a leaf miner, *Lyonetia* does not damage the meristem even when mining young leaves. The larvae leave the mine to pupate gregariously in typical hammocks of silk very like those formed by European species of the genus. The mines of *Lyonetia* are at times among the commonest damage seen on recently expanded leaves. This is certainly an undescribed species since adults lack the head tuft so characteristic of the genus.

The commonest of all leaf miners on *Sonneratia* is *Caloptilia (Sphyrophora) scaeodesma* (Lep. Gracilariidae) (Colour Pl. 10). Larvae commence life in a normal leaf mine on the upper leaf surface and when full grown make a marginal leaf fold, much like the pupal fold of a *Lithocolletis*. However the larva normally leaves this chamber and on the same or an adjacent leaf it cuts a slot and rolls one margin to form a conical, spirally enrolled case. Although galls are rare on *Sonneratia*, one appears as a swollen fold with hypertrophied nutrient tissue inside. From this the same species of *Caloptilia* has been reared several times and it is now believed to be no more than an aberrant reaction to its normal leaf-coiling habit. It is apparently host specific. This is evidently an important species and in mangrove light trap catches it sometimes constitutes almost 50% of the total microlepidoptera fraction.

Structural damage. - Occasional destruction of new shoots by *Zeuzera conferta* (Lep. Cossidae) larvae has been seen, but much die-back in young plants is caused by the large bug *Mictis* sp. (Hem. Coreidae) (Colour Pl. 4). This is a suctorial feeder on shoots which apparently injects toxic saliva causing lesions which kill the shoot. The species is possibly restricted to mangrove since material in the British Museum (Natural History) from Penang (classified as *Mictis* "species 3") came from this habitat. It is clearly different from the well-known *M. longicornis* which is a major pest of leguminous and other trees inland. However *Zeuzera* is certainly the most important timber pest, a high proportion of saplings being infected and grown trees showing evidence of former attack or even of current infection.

Sap feeders. - *Sonneratia* carries a relatively wide range of sap-flow ectoparasites. Most conspicuous on foliage is the jumping plant-louse *Boreioglycaspis forcipata* (Hom. Psyllidae). Its larvae, covered in curling wax filaments are common and sometimes almost smother whole trees. A very distinctive large species of *Macropulvinaria maxima* gp. (Hom. Coccidae) occasionally reaches local outbreak levels, being found in large numbers on old foliage and twigs. Both species seem to be host specific. Several species of *Tricentrus* (Hom. Membracidae) and also *Nilautama* in the same family attack the twigs. *Salurnis* (Hom. Flatidae), *Andes* sp. (Hom. Cixiidae) and several species of Coelidiinae and Tartessinae (Hom. Cicadellidae) are regularly seen. Locally, individual plants can be densely infested with a species of *Egropa* (Hom. Tettigometridae) which is gregarious and attended by ants (*Anoplolepis longipes*) (Colour Pl. 4).

Propagule damage. - Propagule loss begins with damage to the developing flower buds. An unidentified weevil (Col. Attelabidae, Rhynchitinae) (Colour Pl. 2) causes death of large buds which are fully eaten out and, when dry contain 5 to 20 cells. The weevils emerge to the foliage and attack small to medium buds while maturation feeding, causing extensive loss of flowers. In laboratory culture, the weevils will also perforate *Sonneratia* foliage if offered no buds, but reject other mangrove foliage offered. The foliage damage has not been detected in the field. During the flowering season in Singapore (1990) a very

high loss of buds occurred, commonly almost the whole crop in the upper part of certain trees, with successful fruit set occurring only on one or two low branches. It had already been noticed that fruit set in this species is commonly confined to part of a tree and in retrospect one wonders how often this may be due to pest attack. In a number of cases buds were also attacked by larvae of *Hypatima* which apparently gain access through weevil feeding perforations. Pedicels of buds attacked by weevils are very occasionally bored by an ambrosia beetle, possibly *Hypothenemus* sp. (Col. Scolytidae) but this is presumed to be secondary and is not known to attack healthy pedicels or twigs.

Flower buds are also subject to attack by the caterpillar of *Balaenifrons ochrochroa* (Hamps.) (Lep. Pyralidae) (Colour Pl. 14) which bores into them and webs them to the stem to prevent premature drop. This large larva destroys several buds during its protracted development and can sometimes be responsible for great losses in production. Attack extends to open flowers and fruit in all stages of development. On buds or flowers, the larva pupates inside the last one attacked, leaving it hanging from a tough thread. These hanging buds and flowers dry soon afterwards and in this state may be occupied by a phycitine feeding on the remnants, which also pupates inside. This aetiology is easily discriminated from weevil damage where the buds are not webbed to the plant and tend to dry out in situ without breaking free. How the weevils suppress abscission is not known.

Mature fruit are often heavily attacked by an unidentified species of *Eucosma* s. lat. (Lep. Tortricidae) (Colour Pl. 18) which causes damage similar to the well known "codling moth" of apples. Vaivaniukul (1976) mentions the oriental fruit moth *Rhyacionia "cristata"* (presumably *cristana*) from mangrove in Thailand but gives no details of host. My material is certainly not *cristana* (redescribed by Diakonoff, 1939: 231) but is in Eucosmini and might prove to be the species referred to. Half grown fruit have also been found infested with a minute lepidopterous larva that feeds inside individual seeds. Unfortunately it has not yet been successfully reared. A high proportion of seeds can sometimes be destroyed by a seed feeding chalcidoid wasp *Megastigmus* sp. (Hym. Torymidae) and mature fruit may be peppered with its emergence holes. This species is not in the British Museum (Natural History) collection and no named species have been associated with *Sonneratia* (J. la Salle, pers. comm.). The pulp is sometimes mined by a presumed weevil larva (Col. Curculionidae) that does not attack the seeds.

Sterculiaceae

HERITIERA LITTORALIS Dryand in Aiton

Not yet studied in detail, this tree is noteworthy as host of the psyllid plant-louse *Tyora ornata* (Kirkaldy) (Hom. Carsidaridae) which can infest young shoots and flower fascicles in large numbers. The psyllid is now recorded from Singapore to the Pacific and probably occurs throughout the natural range of its host. Attack by *Adoretus gemmifer* (Col. Scarabaeidae) in the Sundarbans is mentioned by Arrow (1917).

Tiliaceae

HIBISCUS TILIACEUS L.

This common and widespread coastal tree is an important component of back mangroves in Singapore though not restricted to the habitat and often excluded from the strict mangrove flora. Perhaps because of the association with mud-lobster mounds which in this country form a well developed part of the system, it must be treated as a mangrove

component here. The large bracts, alternate leaves with long petiole and heart-shaped lamina on which three main veins bear slit-like extrafloral nectaries make it unmistakable. Flowers and buds large; fruit globular, dehiscent shedding numerous small spherical seeds.

Nothing quantitative appears to have been published on its phenology or on levels of herbivore attack. However there are many casual records of insects known to attack it. Coccoidea reported by Williams and Watson (1988, 1990) from the Pacific include *Icerya seychellarum* (Margarodidae), *Ceroplastes rubens*, *Coccus hesperidum*, *C. longulus*, *Parasaissetia nigrum*, *Saissetia coffeae*, *S. mirandus* and a species of *Cerococcus* (Coccidae), *Crisicoccus chalepus*, *Dysmicoccus nesophilus*, *Maconellicoccus hirsutus*, *Planococcus pacificus* and *Pseudococcus longispinus* (Pseudococcidae), *Hemiberlesia palmae* and *Pinnaspis stracheni* (Diaspididae). Defoliation by *Acontia intersepta* (Lep. Noctuidae) and seed attack by *Decadarchis minuscula* (Lep. Lyonetiidae) is mentioned by Beeson (1941).

In Singapore, young shoots and leaves are heavily attacked by an alticine beetle *Erystus ? saundersi* (Col. Chrysomelidae) (Colour Pl. 1) which causes extensive skeletonisation. A number of moths attack young foliage, including *Halitalodes* (formerly *Sylepta*) *derogata* (Lep. Pyralidae) which is a widespread pest of all Malvaceae; a small nymphuline *Ambia poritialis* (Lep. Pyralidae), and several other unidentified species.

Sapflow ectoparasites include the psyllid *Mesohomotoma hibisci* (Froggatt) (Hom. Carsidaridae) whose larvae are gregarious under bracts and secrete copious wax filaments. Old leaves are commonly infested with a range of whiteflies including *Singhius hibisci*, *Aleurotuberculatus* sp., *Tetraleyrodes* spp. and *Bemisia* aff. *tabaci* (Hom. Aleyrodidae).

Leaves are commonly galled by the mite *Eriophyes hibiscitillus* Nalepa (Acarida, Eriophyiidae).

Flower buds are attacked by species of *Acidoxantha* (Dip. Tephritidae), a genus wholly associated with *H. tiliaceus* as far as known. Apparently different species occur in different parts of its range and in Singapore by an undescribed species near *A. totoflava* Hardy. Fruit, especially when splitting to expose the seeds are heavily infested with the strictly host-specific seed feeding bug *Dysdercus decussatus* (Het. Pyrrhocoridae) (Pl. 4) whose crimson immatures are conspicuous. Adults are often gregarious in large numbers under foliage.

Hibiscus has not yet been studied intensively and undoubtedly supports a much wider range of herbivores.

THESPESIA POPULNEA (L.) Solander

Not studied in detail, *T. populnea* is most remarkable as host of the psyllid *Haplaphalara dahli* (Hom. Aphalaridae) which causes distinctive marginal leaf galls throughout its range. *Macropulvinaria thespesiae* (Green, 1909) was described from this host in Sri Lanka.

SECTION II: ILLUSTRATIONS, TAXONOMIC COMMENTARY AND INDEX TO THE PRINCIPAL HERBIVOROUS INSECT SPECIES

Content and Arrangement

The preceding section, intended mainly for the benefit of people involved in the management of specific mangrove trees, is likely to be confusing for workers interested in specific insects. Because of the complexity of host associations, information may be scattered in several places. For that reason an index to those species discussed at length is incorporated in the captions to the illustrations. The many names quoted from literature, and Singapore records that are no more than casually mentioned are excluded from this list and neither illustrated nor indexed. This mainly concerns the Coccoidea.

Colour Plates and text have been arranged in a rather inconsistent but basically alphabetic sequence of higher taxa, followed by species alphabetically under genus name. Inconsistencies are partly for economy in cost of colour plates, partly because of current problems in classification or naming, and partly because of an attempt to sort taxa recognisable to non-entomologists. The first order of alphabetic listing of higher taxa is highlighted in **bold print**. In the "outline" (below), a more rigid alphabetic sequence is adopted and this section is keyed to the plates.

The outline of higher taxa is for the benefit of mangrove field workers who actually attempt a herbivore survey. In it, I have given short non-technical notes on recognition of these higher groups. They are not reliable outside the limited regional fauna, and even there should be used only as a hint.

Species level taxonomy is only discussed in the captions to the plates and is necessarily more technical. As has been emphasised before, most of the species identifications are provisional and will have to be revised or elaborated in time. The opportunity is taken to summarise the current taxonomic situation for each, to provide the full name and authorship if known, and to acknowledge help from specialists. Identifications by the author indicated "det. DHM" are less reliable unless so qualified. I am only too aware that serious errors are likely and both captions and figures may help more experienced taxonomists to correct them in due course. Some of those species whose taxonomy is suspect are being given more formal taxonomic treatment in work currently in progress.

With reared material of Lepidoptera, some recognition features of larvae may also be summarised in the captions even though this may have been mentioned in the preceding text.

Because of extreme condensation, especially in pls. 1- 4, plant taxa are referred to by codes wherever space is limiting. These are standard among mangrove workers and consist of initial letters of genus and species names. Thus *Avicennia officinalis* is coded **Ao**.

Reference insect specimens will be deposited in the Zoological Reference Collection of the National University of Singapore.

Outline of Orders and Families of Phytophagous Insects Studied

Because I expect this article to be used by mangrove field workers, some very elementary entomology is included here. At the other extreme, the individual captions may make statements about technicalities of interest only to systematists. For lack of space it was not

possible to discuss major groups in the text facing the plates and still preserve a direct match between captions and figures.

Order COLEOPTERA (Beetles). Colour Pls. 1-3

The beetles do not need formal definition, even for non-zoologists. Adults are only likely to be confused with a few cockroaches (which have tail cerci) and Hemiptera (which have a piercing proboscis). They constitute the largest order of insects and identification can be difficult. The "Insects of Australia" (CSIRO, 1970) is a useful guide to families for the oriental region. Typical members of many families have a distinctive appearance easily learnt with practice (e.g. "weevils" (colour plate 2) or Mordellidae (colour plate 3). The first step in rough identification of less obvious groups is finding the "tarsal formula" (TF), - counting the tarsal segments on each pair of legs.

The biggest assemblage of phytophagous forms have tarsi adapted for walking on leaves, apparently with TF=444 and the 3rd. joint forming a large hairy pad. Actually there is a tiny 4th. joint, exposed and the pad missing in a few wood-boring groups (e.g. Scolytidae) or aquatics (e.g. *Bagous*). This group includes the Cerambycoidea, Chrysomeloidea and Curculionoidea.

Family **Cerambycidae** (Long-horn beetles). **Colour Pl. 1.** Elongate beetles with long antennae and legless wood-boring larvae. Only likely to be confused with Oedemeridae in the mangrove fauna. These have TF=554 and larvae with legs.

Family **Chrysomelidae** (Leaf-beetles). **Colour Pl. 1.** Usually small to medium sized, rounded or oval in shape, often colourful. The larvae usually in soil. There are about 12 distinctive subfamilies, those in mangroves treated sequentially in Colour Pl. 1. Useful recent key works to oriental forms are by Gressitt and Kimoto (1961) and Kimoto & Gressitt (1981, 1983) but serious workers will find the fine anatomical work of Chen more informative.

Alticinae. Easily recognised by the enlarged hind femora and jumping habit, the flea beetles are not to be confused with other Chrysomelids. However the genus *Scirtes* (Helodidae) is superficially similar and common in mangroves. Apart from the diagnostic tarsal structure, *Scirtes* has prominent spurs on the hind tibiae. Good genus key in Scherer (1969).

Clytrinae. Usually cylindrical, with abdominal sternites narrowed medially as is Cryptocephalinae, but with antennae serrate and without the toothed hind border of the pronotum. Medvedyev (1984) supplements other references.

Cryptocephalinae. The species involved (*Coenobius* sp.) has a distinctive, deeply serrulate hind margin to the pronotum which on all material available to me seems to be characteristic of the whole subfamily. If so, this character which is not mentioned in the literature makes recognition of Cryptocephalinae very easy.

Eumolpinae. Hard bodied chrysomelids with antennae widely separated, this is one of the largest subfamilies.

Galerucinae. Soft bodied chrysomelids with the antennal insertions close together, this is also a very large group. In addition to other literature, the key by Shute (1983) is useful. Only the genus *Monolepta* is represented in our mangroves. It belongs to the Luperini in which the male hypopygium has paired slits in the margin through which the slender parameres can be protruded. The genus is recognised by the elongate hind basitarsus.

Curculionoidea (Weevils). Colour Pl. 2. The "weevils" are a group of beetles easily recognised by the head produced into a more or less long snout bearing mandibles at the tip. They are the largest single group of living things with about 40,000 described species in over 3500 genera, and their classification is in chaos. Even the status of the superfamily is uncertain, some workers including them in the Chrysomeloidea, others separating out the Scolytidae in a distinct superfamily. Classification of this vast group has not significantly advanced since the last century and the oriental fauna has never been comprehensively surveyed. Not surprisingly we are unable to give precise names to any of the mangrove species described here. For convenience the genus name of that taxon to which the species has been most nearly traced with available literature, usually a subfamily or tribe, is used.

Family Attelabidae. Recognised by the antennae lacking a scape.

Family Curculionidae. Recognised by elbowed antennae - the long basal joint (scape) present. A vast group divided into many subfamilies among which the Cryptorhynchinae have a deep ventral groove to receive the rostrum, while the Barinae do not (these are the only subfamilies mentioned here).

Family Scolytidae. Cylindrical wood-borers with snout reduced.

Family Mordellidae. Colour Pl. 3 The unique body shape is diagnostic. The subfamily Mordellisteninae have multiple comb-ridges on the posterior tibiae. Several Mordellisteninae have been seen in light catches, but the species in plate 3A is much the commonest. Keys by Ermisch (1950, 1969) will be found a useful introduction to the group.

Family Scarabaeidae. Colour Pl. 3 Recognised by the lamellate antennal club. TF=555, no ventral pad. This large family includes many well known nocturnally feeding species in the subfamilies Dynastinae, Melolonthinae (equal claws) and Rutelinae (unequal claws), which are major defoliating pests of inland trees. Well-known polyphagous pest species of *Apogonia*, *Aprosterna*, *Serica*, *Holotrichia*, *Anomala* and *Adoretus* s. lat. do attack landward mangroves but only the latter group are of any importance. The Adoretini are rutelines with very specialised mouthparts, the labrum forming a sclerotised shelf against which the widely separated mandibles operate through circular openings on each side. This restricts them to surface patch grazing and they make a very distinctive, usually zig-zag bite mark (Colour Pl. 3G) which is easily recognised.

Order DIPTERA (Two-winged Flies). Colour Pl. 3.

Only fore-wings functional for flight, the hind pair reduced to "halteres"; the larvae of phytophagous forms usually leg-less "maggots"). Includes Nematocera with long, many-jointed antennae of which Tipulidae may have root-feeding larvae, but although this family is common in mangroves, none have yet been implicated. Gall midges belong here. Brachycera (antenna short, 3-segmented) include some Dolichopodidae known to have phytophagous larvae - a common family in mangrove but larvae unknown, adults predatory. The phytophagous families discussed below are "acalypterates" which have no lobe behind the wing to shield the haltere.

Family Agromyzidae. Small often black flies with pointed ovipositor, the larvae mining leaves. Much work published by Spencer.

Family Asteiidae. Small acalypterates with reduced venation have received much attention recently, notably from Hardy and Papp. The main reference for Asteiidae is still

that of Sabrosky (1956) who gives a key to world genera. See also Hardy and Delfinado (1980).

Family **Tephritidae** (True fruit-flies recognised by the interrupted vein Sc, patterned wings and conical ovipositor). Excellent keys to the oriental species of the group have been published by Hardy (1973, 1974, 1986).

Order HEMIPTERA (True Bugs). Colour Pl. 4

(Recognised by the jointed piercing proboscis).

Suborder **Heteroptera** (recognised by distinct separation of corium and membrane in the forewing). Many are predators but a large group of phytophagous forms exist, adults mostly with lateral stink-glands before the hind-legs, larvae with them dorsally on the abdomen. The structure of these are important in classification.

Family **Coreidae** (recognised by close parallel venation in the membrane).

Family **Lygaeidae** (usually small, dull-coloured bugs, mainly seed feeders, with ocelli present). See warning below under Pyrrhocoridae.

Family **Miridae** ("capsid-bugs", recognised by open, loop-like cells in membrane). None are illustrated here but an unidentified species attacks *Avicennia* in Thailand.

Family **Pentatomidae** ("Shield-bugs", the enlarged scutellum and 5-jointed antennae are distinctive).

Family **Pyrrhocoridae**. A family of usually red and black bugs distinguished from Lygaeidae and Coreidae by the absence of ocelli. Seed feeding red bugs exist in several other families including Lygaeidae and Coreidae. Some of these can be found in mangroves, notably a species of *Leptocoris* (Coreidae) attacking fruit of *Finlaysonia obovata* and *Dasynus laminatus* (Coreidae) attacking *Allophylus cobbe*. These can easily be mistaken for Pyrrhocorids by a beginner, and a true pyrrhocorid *Antilochus* sp. may be associated with them as a predator. Only one true pyrrhocorid is regularly herbivorous in our mangroves.

Suborder **Homoptera** (distinguished by lacking hemelytra and having a posterior rostrum). All are plant feeding and many are important plant pests.

The active group (**Auchenorrhyncha**) include the "leaf-hoppers" for which the most recent and reliable family key appears to be that in O'Brian and Wilson (1985).

Family **Cicadellidae**. Easily discriminated from other leaf-hoppers by the hind tibia with a continuous row of mobile spines.

Family **Cixiidae**. The family is not easily definable for amateurs, but can be recognised as a fulgoroid group by the keeled frons, flaps covering the wing base and copious production of wax filaments.

Family **Tettigometridae**. All species of Tettigometridae look very alike, including all details of colour pattern, so the photograph (4N) is diagnostic. Apart from a species of *Megaloplastinx* which is larger with an acute head and extremely rare, only species of *Egropa* occur in Singapore. There are about five species present but can only be discrimi-

nated on male genitalia. Most often seen infesting pods of legumes, the gregarious habit and extensive sheets of communally laid eggs are characteristic. There is little variation in size.

Sternorrhyncha. These Homoptera includes the semi-sessile plant-lice (Sternorrhyncha) which for reasons of cost are not illustrated or fully indexed here. Most of my identifications are unreliable and should be treated with caution.

Order HYMENOPTERA (not illustrated)

Only one genus of Torymidae (Chalcidoidea) is mentioned in the text, *Megastigmus* (det. J. La Salle, NHM London) [p. 145]. This is rather large for the family, yellow with black markings on the body and with a very conspicuous stigmal vein. The species is seed feeding on *Sonneratia*. Females, as usual in the family, have a very long ovipositor. Care is needed to discriminate truly herbivorous wasps from the many parasitic forms that may appear when rearing.

Order LEPIDOPTERA (Butterflies and Moths). Colour Pls. 5-18.

Recognised by scaled wings and coiled proboscis.

Moths and butterflies are too familiar to need defining even for laymen. Mangrove workers will want guidance mainly in recognising larvae since these are the herbivorous stage, and this is the main purpose of providing these illustrations. It cannot be too strongly emphasised however, that any serious work should include rearing at least some material to adult for a professional check. Many of the genera mentioned are represented by distinct if related species as one moves to parts of S.E. Asia remote from Singapore.

It should also be emphasised that one should never assume that adults commonly seen in flight are necessarily those responsible for conspicuous damage to the trees. Many conspicuous species breed in litter, dead wood or inter-tidal algae, while some very common grazers are hardly ever seen as adults even during an outbreak. Direct identification from larvae or rearing is mandatory.

Finally never trust a host record based on finding a pupa or pupating larva without strong circumstantial evidence of feeding. Many larvae migrate some distance before pupation and can easily be found on the wrong host. I have made many errors in this way.

Family Cossidae. Large moths with long abdomen, narrow wings, proboscis short or absent; the larvae wood-boring.

Family Gelechiidae. Colour Pl. 5. All mangrove species seen are typical members of the family, easily recognised small species combining a scaled proboscis, lack of tympanal organs and an emarginate apex of the hind wing. This feature is due to a characteristic way of folding the wing along the discal cell. Old key in Meyrick (1925b) works well. The known species are very host specific.

Family Geometridae. Colour Pls. 6-7. Adults of this family are recognised by the combination of unscaled proboscis with presence of abdominal tympanal organs. Typical larvae are unmistakable being true "loopers" with only the posterior pair of abdominal prolegs in addition to the anal claspers.

Family Gracilariidae. Colour Pl. 10. Small moths with unscaled proboscis, no

tympanal organs, usually resting head up with front legs displayed; larvae leaf-miners with only 3 pairs of ventral prolegs.

Family Hyblaeidae. Colour Pl. 8. A small family of doubtful affinities (see Minet, 1982), noctuid like but venation distinctive and without tympanal organs. The very short porrect palps are distinctive in the mangrove fauna.

Family Lasiocampidae. Colour Pl. 8. Often very large moths with feathery antennae and proboscis absent. Larvae hairy, often gregarious.

Family Lethiceridae. Colour Pl. 9. Medium sized white or grey moths that rest flat; the larvae webbing or rolling leaves. A problem group (see text to Colour Pl. 8 for details).

Family Limacodidae (not illustrated). Slug and nettle caterpillars, the adults stocky. The best account is by Holloway (1986).

Family Lycaenidae. Colour Pl. 13. Unusually rather small "blue" butterflies with forelegs functional in both sexes. Larvae slug-like, commonly with ants.

Family Lymantriidae. Colour Pl. 10. Feathery antennae, no proboscis, thoracic tympanal organs; the larvae with tufts of setae.

Family Lyonetiidae. Colour Pl. 10. Small moths with base of antenna broadened by scales to form an "eye-cap"; the larvae miners and, in *Lyonetia* pupating in quite unmistakable hammock-like slings.

Family Noctuidae. Colour Pls. 11-12. A large and very common family with scaleless proboscis and thoracic tympanal organs; the larvae usually smooth short-haired with at least two pairs of ventral prolegs, usually 4, the crochets arranged in a longitudinal band. However many mangrove species have hairy larvae. In general a "semilooper" is likely to be a noctuid.

Family Nymphalidae. Colour Pl. 13. Nymphalid butterflies. Usually large butterflies with forelegs reduced in both sexes.

Family Oecophoridae. Colour Pl. 10. Small moths with scaled proboscis but no tympanal organs, differing from Gelechiidae in venation and hind wing not notched.

Family Psychidae (not illustrated). Moths all male - with genitalia characteristically protruded (females remain like larvae). Larvae are "bag-worms".

Family Pyralidae. Colour Pls. 14-16. Large family group unique in combining scaled proboscis with abdominal tympanal organs.

Family Tineodidae (= Oxychirotidae). Colour Pl. 17. Only known mangrove species a tiny "plume moth".

Family Tortricidae. Colour Pls. 17-18. Small moths, often "bell-shaped" at rest, but also including very small forms not "typical" in appearance. Proboscis without scales. No tympanal organs. Palps short, porrect, thick.

Order ORTHOPTERA (not illustrated). (Grasshoppers and their allies, recognised in all stages by the jumping hind legs).

Family **Acrididae** (short-horn grasshoppers). A few species enter mangroves, notably *Valanga nigricornis*, *Patanga succinta* and *Xenocatantops humilis*. *Eucoptacra cingulatipes* is quite common on vegetation just outside. No feeding on any trees mentioned here has been recorded.

Family **Tettigoniidae** (long-horn grasshoppers). Larvae have been regularly encountered feeding on several mangrove trees but immatures cannot be identified at present. It is my impression that they play a significant role as foliage grazers and this is one of the most important gaps in our knowledge of mangrove herbivory.

Order PHASMATODEA (not illustrated) (Stick and leaf insects). Two species are known from mangrove in Singapore. *Lonchodes brevipes* is a large stick insect occasionally seen on *Hibiscus tiliaceus*. Workers should be warned that much of the literature is confused as the generic names in this group were wrongly applied in early work. A larva of *Phyllium* sp. has been taken on *Bruguiera cylindrica*.

COLOUR PLATE 1. COLEOPTERA: CERAMBYCIDAE AND CHRYSOMELIDAE

Family Cerambycidae

Fig. A. *Aeolesthes holosericeus* Fabr. (det. DHM) [p.133]
 Adult body length up to 2.5 cm. Only recorded mangrove host *Ea*, larvae boring dead trunks. Beeson (1953: 105-108) lists it from 44 tree species including *Ea* in India, and gives life history. Not known to attack healthy trees but can establish in weakened ones. Maturation feeding not documented but species of this family normally do so from bark of young shoots.

Family Chrysomelidae

Subfamily Alticinae

Fig. B. *Erystus* aff. *saundersi* Brian (det. DHM) [p. 146]
 Body length 3 mm. Skeletonising young foliage of *Ht*, sometimes in enormous numbers. The species is diurnal. Larvae not traced but probably root-feeding on the same host.

Fig. C. Alticinae sp. indet. [p. 130]
 Body length 4 mm. Collected once night feeding on young foliage of *Lr*.

Clytrinae

Fig. D. *Smaragdina* sp. (det. DHM) [p. 141]
 Body length 2.2 mm. Attracted in numbers to young foliage of *Sa* on one occasion only (Pulau Batam). Did not feed in lab. Status uncertain. The species seems close to *atrocincta* Pic.

Cryptocephalinae

Figs. E-G. *Coenobius* sp. (det. DHM) [p. 130]
 Adult (F) body length 1.7 mm. Minute with deeply recessed head and eyes almost in contact. No described species match exactly and probably new. Feeds only on *Lr* making linear feeding marks (G). Larvae (E) in ovoid cases of faecal pellets, feed on decaying leaves beneath infested trees.

Eumolpinae

Figs. H-I. *Rhyparida wallacei* Baly (det. DHM) [pp. 123, 130, 134, 136, 137, 138, 139, 140]
 Adult (H) length 4mm. One of the commonest chrysomelids in mangroves, *R. wallacei* rejects *Avicennia* and *Sonneratia*. It is recorded from *Aegiceras*, *Ct*, *Bc*, *Bg*, *Bp*, *Ll*, *Lr*, *Ra*, *Rm* and *Rs*. Recorded on *Bruguiera* in Palau (Gressitt, 1955) and *Rhizophora* seedlings in Thailand (Rau & Murphy, 1990). The genus has the lateral plates of propleuron straight (cf. *Tricliona*).

Figs. J-K. *Tricliona* sp. 1. length 3.4 mm. (det. DHM) [p. 130]
 Fig. L. *Tricliona* sp. 2. length 4.2 mm. (det. DHM) [p. 130]
 The genus recognised by strongly arched side plates of propleura overlapping back of eye. Both species night feeding on *Lr* and nothing known of their immatures.

Galerucinae

Fig. M. *Monolepta bivittata* Jacoby (det. DHM) [p. 130]
 Adult (M) length 3.2 mm, collected regularly, feeding on young leaves of *Lr* in back mangroves at night (along with *Rhyparida*, *Tricliona* and *Lepadoretus*). The species is widespread in S.E.Asia and common in Singapore, inland as well as on the coast, and is evidently polyphagous on a wide range of hosts. Its presence in mangroves seems restricted to the land-ward margin.

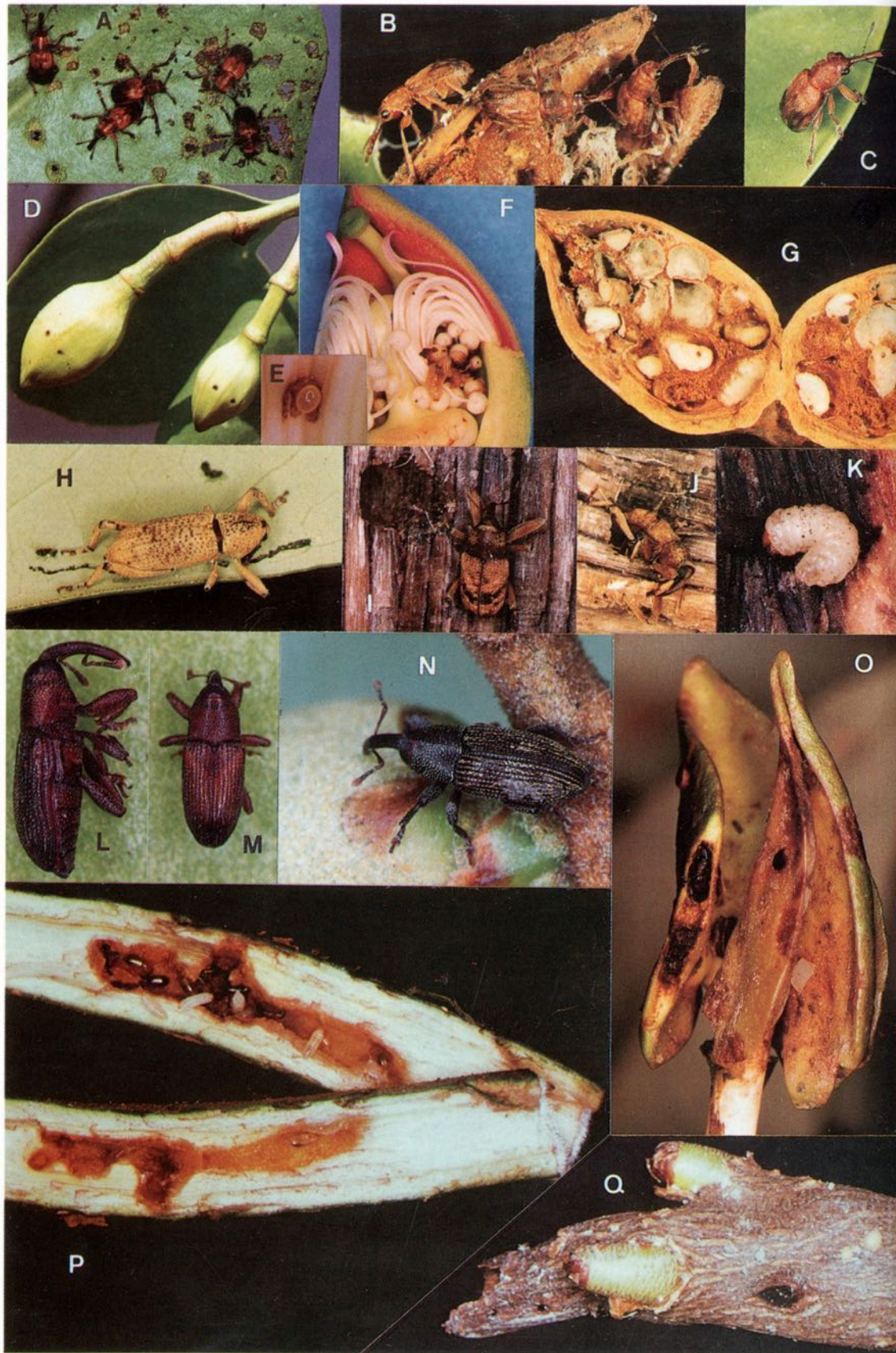
Fig. N. *Monolepta* sp. 2 near *bivittata* (det. DHM) [p. 141]
 Adult (N) length 4 mm, rarely seen feeding on *Sa*, common in light trap catches at Pasir Ris. No other hosts known. Superficially resembles that illustrated as *cavipennis* by Kimoto but not of that group. Provisionally placed near *bivittata*.

Fig. O. *Monolepta* sp. 3 aff. *cavipennis* (det. DHM) [pp. 123, 128]
 Adult (O) length 6 mm. Pattern distinctive and consistent for the Singapore population. Feeds exclusively on *Avicennia*. An outbreak affected young *Aa* some years ago at a site since reclaimed. An allied form illustrated by Murphy (1990e) severely attacked *Aa* in Thailand.

Figs. P-U. *Monolepta* sp. 4 aff. *bicavipennis* Chen (det. DHM) [pp. 123, 128]
 Adult female (P) length 6 mm, brown, male (Q) red, slightly smaller. Formerly called *M. aff. bifoveolata* by Rau & Murphy (1990). Having recently seen Kimoto's illustrations of the Galerucinae of Vietnam, I now think *bicavipennis* a more likely attribution. Mature larva (R) bores pneumatophores and has a prominent anal proleg not seen on the first instar (T). Eggs (S,T) glued to surfaces, strongly sculptured.

Fig. V. *Monolepta* sp. 5 aff. *longitarsis* Jacoby (det. DHM) [pp. 136, 137, 139, 140]
 Body length 4 mm. Keys to *longitarsis* in Maulik (1936) and no more likely attribution has been found in other literature. The species appears restricted to *Rhizophoraceae*. Very rare in Singapore but in Thailand, along with *Rhyparida wallacei* apparently a major pest.





COLOUR PLATE 2, COLEOPTERA: CURCULIONOIDEA

Family *Attelabidae*. Recognised by the antennae lacking a scape.

Figs. A-G. "*Rhynchites*" sp. [pp. 144, 145]
 Body length 4-5 mm. A weevil attacking flower buds of *Sa* spp. and probably host specific. The species was not traced in either the Paris or London Museums, but Voss' collections, presumably somewhere in Germany, need to be examined. The species is confirmed in *Attelabidae*, *Rhynchitinae* but no closer (C. Lyal). Adults apparently do maturation feeding both from foliage (A) and young flower buds. Eggs are laid singly into buds (D, E) and the whole life history is (G) inside the bud, the number developing depending on its size. Adults (B, C) are common on foliage.

Family *Curculionidae*. Prominent rostrum and elbowed antennae.

Fig. H. *Camptorhinus* sp. (det. C. Lyal) [p. 124]
 Body length (photographed specimen) 7.5 mm. but very variable. Males larger than females with dense scopa of long hair on fore tibia in this species. Larvae bore into inter-tidal *Avicennia* timber waterlogged and infected with a foul-smelling, blue-coloured bacterial rot. These larvae have 6 long curved anal appendages not reported for the group. *Camptorhinini* have the sternal groove ending in the prosternum as a closed cup, and *Camptorhinus* is the only genus of the group with free claws, both true for this species. This genus determination is therefore reasonably close.

Figs. I-K. "*Rhadinomerus*" sp. [p. 124]
 Body length 5.5 mm. Also reared from inter-tidal *Avicennia* timber and known to maturation feed on *Avicennia* foliage, this species has normal larvae. The species is a cryptorhynchine in *Mecistocerini* in which the sternal groove extends back to the metasternum. It is not certainly in *Rhadinomerus* and should properly be referred to as "genus near". Several species have been described in *Rhadinomerus* attacking *Rhizophora* timber (Marshall, 1933). It is none of these. Again the identification is due to C. Lyal.

Figs. L-O. "*Limnobaris*" sp. (det. DHM) [p. 127]
 Body length 2.8 mm. This species, a monophagous feeder in cotyledons of *Avicennia* propagules (O) is confirmed in *Barinae* by C. Lyal but no valid genus assignment could be made. The species was compared with *Stenobaris avicenniae* and is certainly not that (american) species. It is not in the British Museum collection. I personally ran it through Arnett's (1968) key to north american genera, the only text available to me. The name *Limnobaris* is thus an amateur statement that it conforms to the key characters used in that publication, and should be given no authoritative credence. The genus *Limnobaris* is said to be widespread, but whether it occurs in the oriental region is not known to me.

Family *Scolytidae*. Cylindrical wood-borers with snout reduced.

Figs. P-Q. *Coccotrypes rhizophorae* (det. DHM) [pp. 139, 140]
 Body length 2.6mm. In Singapore, only found attacking the apices of young prop roots of *Rhizophora* spp., it has been widely reported from seedlings, which habit is here exclusive to the supposedly related *C. fallax* (not illustrated). *C. rhizophorae* causes apical dieback of the prop root which then produces one or more laterals to replace the dead apex (Q). Trees subject to heavy infestation have a characteristic "stepped" type of prop root resulting from this. *Coccotrypes fallax*, in my opinion is misplaced in the genus. It has a well developed prosternal tubercle such as is found in the related genus *Dryocoetiops*, but differs in the elongate pygidium. See key in Wood (1986). The older literature usually cites these species in the synonymous genus *Poecilips*.

COLOUR PLATE 3. COLEOPTERA (MORDELLIDAE, SCARABAEIDAE) AND DIPTERA

Family Mordellidae.

Figs. A-C. "*Mordellistena*" sp. (det. DHM) [pp. 125, 129]
 Adult (A,C) length 3 mm. Adults of this species have the penultimate segment of anterior tarsi simple but produced beneath into a long process. This excludes the *Falsomordellistena* group but is aberrant in *Mordellistena* and it probably requires a new genus. The larva (B) is a twig borer of *Avicennia* and is recognised by a sclerotised, conical tail spine characteristic of the group.

Family Scarabaeidae. Recognised by the lamellate antennal club.

Figs. D-E. *Chaetadoretus* aff. *lacustris* Arrow (det. DHM) [pp. 130, 138, 139]
 Body length 12 mm. Adoretine larvae are common in drier mangrove soils, especially in *Thalassina* mounds. The illustrated species has been reared and is a member of *Chaetadoretus* which is definitely not the widespread pest species *C. borneensis* Kraatz which is well known to me. Although common in Singapore *borneensis* has not been known to enter mangroves. Only *lacustris* Arrow has actually been described from mangroves and Arrow (1917) says "larvae were found at the roots of an aquatic shrub, *Acanthus ilicifolius*, ... and the adults were feeding in great abundance upon the leaves of *Avicennia*." The Singapore species has genitalia quite different from a species feeding in Thai mangroves (illustrated by Murphy 1990e) and neither is true *lacustris*. The mangrove Adoretini need a professional revision.

Figs. F-G. *Lepadoretus compressus* (det. DHM) [pp. 123, 130, 142]
 Body length 11 mm. This very common, polyphagous pest species enters mangrove from the landward edge but does not breed there. Attacks Sa and Lr but not *Avicennia*. Fig. G compares samples of Sa foliage from landward, mid-mangrove and seaward sites, showing how intensity of damage declines away from land. Adoretine damage has not been seen on Rhizophoraceae in Singapore, but in Thailand was associated with their species of the *lacustris* complex.

Order DIPTERA

Family Agromyzidae (leaf mining flies)

Figs. H-I. *Tropicomyia* sp. (det. DHM) [p. 139]
 Adult (not illustrated) shiny black, wing length 1.5 mm. Leaf mine in dorsal surface of Ra leaf (H) and closeup of puparium (I). *Tropicomyia* (see Spencer, 1973: 180) are small species formerly included in *Melanagromyza* and commonly still so treated. All my adult material is slide-mounted and cannot be figured here but male genitalia do not correspond to any I have seen described.

Family Asteiidae (small flies with reduced venation)

Fig. J. "*Asteia*" sp. (det. DHM) [pp. 127, 129]
 Wing length 1.5 mm. Photograph of freshly emerged specimens arbitrarily mounted on young buds of *Avicennia alba* to show approx. size. It in no way indicates any natural habit. Reared larvae leave the buds when full grown and climb upwards to pupate on the cap of the vial. Puparia not seen in nature. Main host Ao. Venation and chaetotaxy very similar to typical *Asteia* spp. but with aberrant features. The wing has incipient costal breaks and the female genitalia are distinctive, with large and complex accessory glands suggestive of possible larvipary. On emergence, females have very reduced abdomen with undeveloped ovaries and a protracted period of maturation feeding is clearly necessary. They have never been collected by light-trapping or sweeping, and until recently never seen as adults on the host plant. A single individual found resting on foliage at dawn had half developed eggs. The biology of this species is being actively pursued.

Family Cecidomyiidae (gall midges)

Fig. K. Leaf galls of ? *Stephaniella falcaria* Felt (det. DHM) [p. 125]
 Leaf galls possibly corresponding to this species are widespread on *Avicennia*, especially on Ao.

Family Tephritidae (True fruit-flies)

Figs. N. *Adrama* aff. *rufithorax* Malloch (det. DHM) [p. 133]
 Wing length 6 mm. Rather commonly seen on mangrove foliage, this species and the following have both been reared from mature fruit capsules of Ea. The species keys in Hardy (1986) to *rufithorax* but has pollinose stripes on the thorax not mentioned by the author.

Figs. L-M. *Elleipsa quadrifasciata* Hardy (det. DHM) [p. 133]
 Wing length 5 mm. Also reared from fruit of Ea.





COLOUR PLATE 4. HEMIPTERA

Suborder Heteroptera (corium and membrane in forewing)

Family Coreidae (close parallel venation in membrane)

Fig. A. *Mictis* sp. (det. DHM) [p. 144]
 Adult length 25 mm. These large brown bugs used to be common on Sa saplings and did significant damage to shoots. Recently uncommon but immatures with striking flanges on fore-legs are still seen, (see Distant, 1902).

Dasyneus laminatus (not illustrated) (det. DHM) [p. 133]
 Adult length 20mm. A large red and black bug known to attack *Allophylus cobbe* and suspected (from immatures only) to feed on seeds of *Excoecaria*. Easily mistaken for a pyrrhocorid.

Family Lygaeidae

Fig. B. *Pamerana fulvomaculata* Malipatil (det. Malipatil) [p. 131]
 Adult length 7 mm. One of several ground dwelling lygaeids found under stands of *Lumnitzera* where the fruit are mainly dead and with shrivelled contents. Empty fruit due to *Thiotricha* attack are quite different in appearance.

Family Pentatomidae (Shield-bugs)

Figs. C-E. *Antestiopsis* sp. (det. DHM) [p. 125]
 Adult length 10 mm on Aa, doubtfully on other *Avicennia* spp., adults on other trees thought to be casuals. The species is much duller in colour than the related *Antestia anchora* which occurs on *Wedelia triflora*.

Figs. F-G. *Calliphara nobilis* Linn. (det. DHM) [pp. 133, 137]
 Adult (F) length 15 mm, dull metallic green with pattern of spots as illustrated. The reddish sheen which is over-emphasised here exists but is less conspicuous. Adults can be abundant in gregarious swarms beneath large leaves such as *Rhizophora* and disperse with loud buzzing when disturbed. Main larval host Ea (G).

Figs. H-I. *Glaucias* aff. *dorsalis* (Dohrn) (det. DHM) [p. 131]
 Adult (H) length 14 mm. *Glaucias* is a replacement name for *Zangis* which is preoccupied, but may be only a species group in *Gastraulax*. Larvae and eggs (I) found on Lr.

Family Pyrrhocoridae

Fig. J. *Dysdercus decussatus* Bois. (det. DHM) [p. 146]
 Adult length 12 mm. A distinctive and widespread species always found on Ht as a seed feeder. I have not followed the taxonomy of the genus beyond the old revision by Freeman (1947) but doubt if any changes will have been made.

Suborder Homoptera

Family Cicadellidae

Fig. K. *Dryadomorpha pallida* Kirkaldy (det. M. D. Webb) [p. 131]
 Length 6.5 mm. This and the related *Parohinka longiseta* can be common at light. Immatures of both have been seen on *Lumnitzera* but probably not host specific. Both species widespread and not confined to mangroves. In the small subfamily Paraboloponinae for which the acute head is rather characteristic, recently revised by Webb (1981).

Family Cixiidae

Figs. L-M. *Oliarius* sp. (det. DHM) [pp. 128, 129]
 Adult (L) length 12 mm, with shallowly tectate wings and 5 longitudinal keels on pronotum, found on Aa. Presence of the soil-dwelling larvae is detected by the masses of filamentous wax (M). The only other common cixiid in mangroves is a species of *Andes* with the wings very steeply held so that the animal seems laterally compressed. Nothing is known of the life history of *Andes* but it feeds on Sa [p. 144].

Family Psyllidae s. lat. (not illustrated)

- Boreioglycaspis forcipata* (Crawf.) on Sa (det. DHM) [p. 144]
- Haplaphalara dahli* Rübbsaamen on Tp (det. DHM) [p. 146]
- Mesohomotoma hibisci* (Froggatt) on Ht (det. DHM) [p. 146]
- Tyora ornata* (Kirkaldy) on Ht (det. DHM) [p. 145]

Other Sternorrhyncha not illustrated or indexed

Family Tettigometridae

Fig. N. *Egropa* sp. (det. DHM) [p. 144]
 Adult length 3.8 mm, quite common on Sa but patchy in distribution. Less brightly coloured than most species seen but the pattern is the same. Always attended by *Anoplolepis longipes*. Larvae have a spine on the head.

Order HYMENOPTERA: Family Torymidae

The account by Bouček (1988) is useful.

Megastigmus sp. (det. LaSalle) (not illustrated) [p. 145]

COLOUR PLATE 5. LEPIDOPTERA. COSSIDAE, GELECHIIDAE

Family Cossidae [not illustrated]

Zeuzera conferta Walker (det. DHM)

[pp. 126, 135, 140, 144]

Wing span 30-45 mm. This species is well established to be the principal lepidopterous timber borer in mangroves throughout S.E.Asia. I am told it is a major problem in Burma where it affects new plantings for coastal stabilization. The adult is illustrated by Holloway (1986) who compares it with other species of *Zeuzera*, and by Murphy (1990c). The larva is easily recognised in all sizes by the strongly tuberculate hind border of the prothoracic shield. Space prevents me from illustrating the life history here. The species has been recorded from Aa, Ao, Al, Ra, Rm, Aeg, Sa, So.

Family Gelechiidae

Figs. A-C. *Anarsia* sp. (det. DHM)

[p. 135]

Wing span 14.5 mm. A fruit borer of *Aegiceras* easily recognised to genus by the heavily tufted labial palps which, in the male, lack the apical segment (visible in A which has the head turned). Attacked fruit always develop a large oval hole at the base (B).

Figs. D-F. *Hypatima* sp. (det. DHM)

[pp. 143, 145]

Wing span 12.5 mm. Better known in the old literature as *Chelaria*, this genus is characterised by a fan of erect bristly scales on the underside of the second palpal segment (just visible in fig. E). This species is a widespread but minor leaf grazer on Sa, very occasionally entering flower buds following other damage. The larva with dull red transverse bands and dark head and tail plates is easily recognised. Several species of *Hypatima* seem to be present in light catches.

Figs. G-J. *Thiotricha* sp. 1 (det. DHM)

[pp. 130, 131, 137]

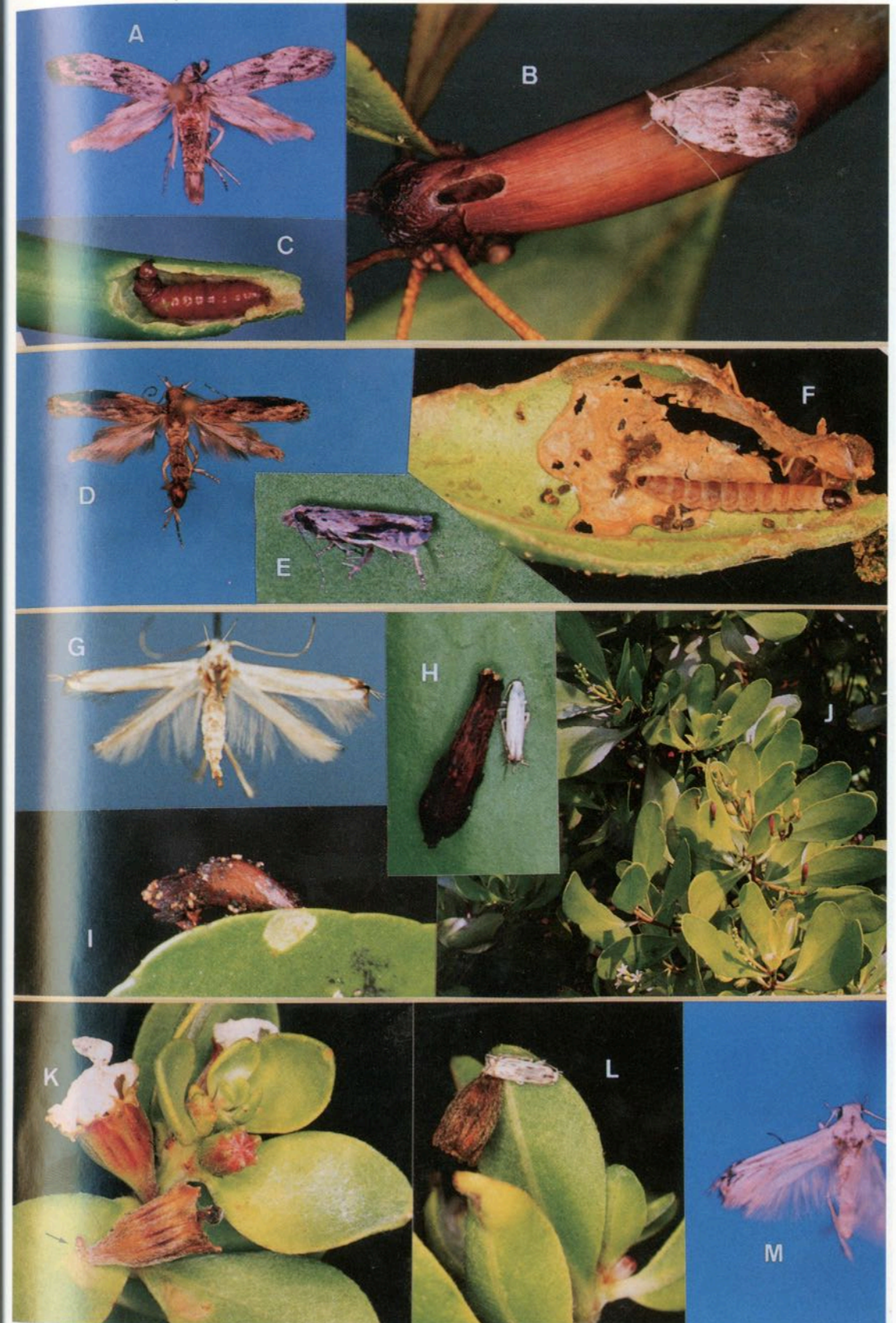
Wing span 8 mm. The adult (G, H) has a distinctive acute apex to the fore-wing which protrudes at an angle. These tiny silvery moths fly in numbers around the host plant Lr during the day time. The larva at first bores flower buds and carries one as a case, later blotch mining the leaves (I). The anterior end of the larva has sclerotised plates but not the abdominal segments behind A1.

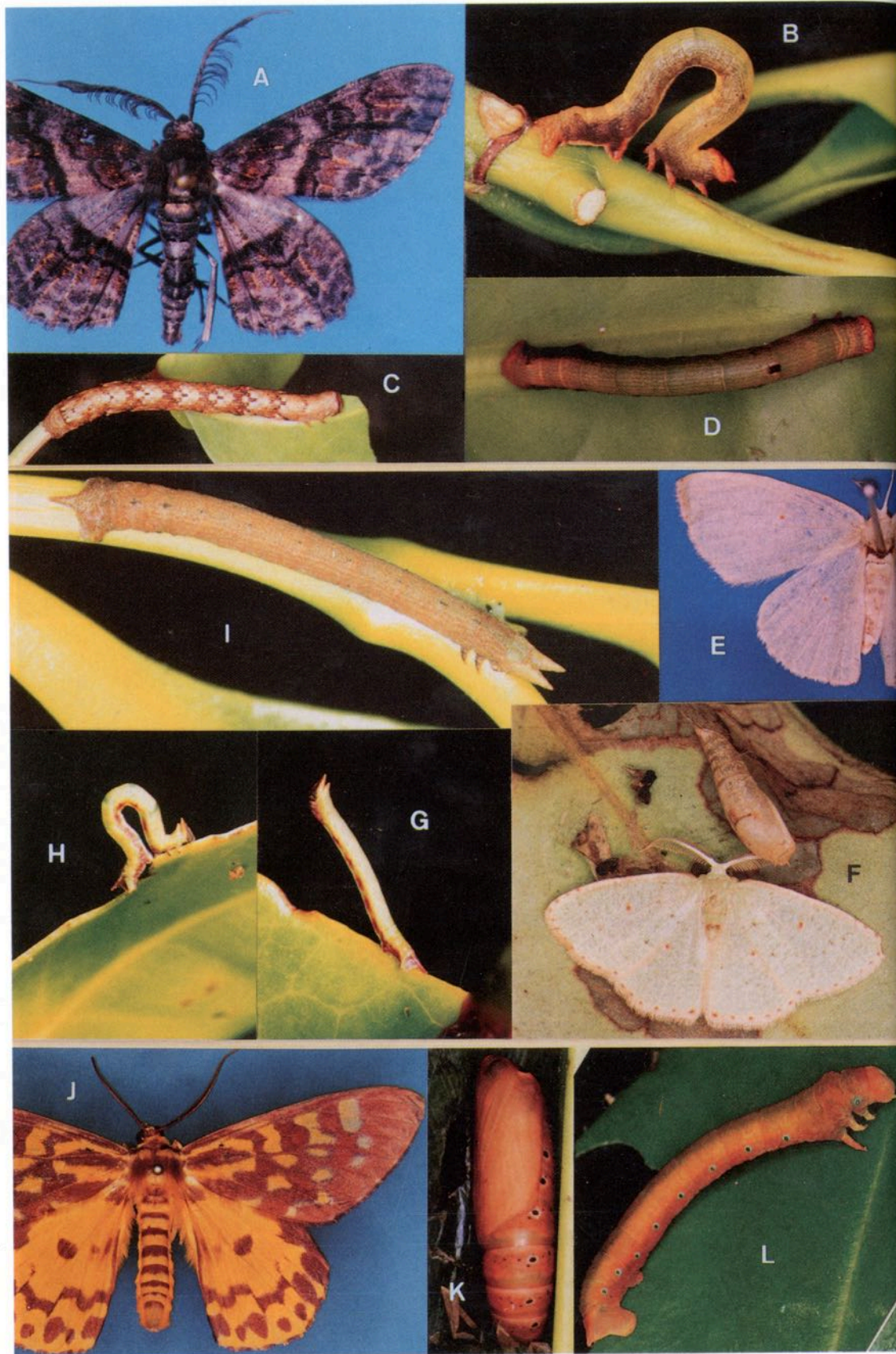
Thiotricha sp. 2 (det. DHM)

[p. 134]

Wing span 8 mm. Very similar to the preceding species in both appearance and habits, but distinguishable by slight colour differences (L, M) and its host association with *Pemphis*. The larva (arrowed on K) is also similar. Fig. K also shows the conspicuous salt plug which develops on the apex of fertilised flowers in this plant.

Colour Plate 5





COLOUR PLATE 6. LEPIDOPTERA: GEOMETRIDAE

Figs. A-D. *Cleora injectaria* (Walker) (det. DHM) [pp. 123, 124, 134, 138]
 Adult male moth (A) wing span 34 mm. The adult colour pattern rather variable especially between sexes. Male genitalia absolutely diagnostic, Prout (1928) illustrates from a Singapore specimen. The larva (B-D) very variable in colour pattern but generally grey to brown, very commonly with a dorsal mark on abd. 3 which is not necessarily as clear as shown on D but usually detectable on close inspection. Head blunt and tail with two short, blunt tubercles, typical of Ennominae. It has been reared from a wide range of mangrove hosts (*Avicennia*, *Rhizophoraceae*, *Aegiceras*, *Allophyllus* and will no doubt be found on non-mangroves as well. The larva descends the trunk to pupate in an oval, silken cocoon at the base of the tree, usually under algae or in soil.

Figs. E-I. *Chloeres quantula* (Swinhoe) (det. DHM) [p. 124]
 Female (E) wing span 24 mm, male (F) wing span 22 mm., the male pale green with brownish spots extending onto costa distinctive (Prout, 1934). The antenna with apical antennal segments not pectinate. Pupa exposed on the leaf typical of Geometrinae, not distinctive and similar pupae have yielded a *Scopula* though *Chloeres* is much the commonest species on *Avicennia*. The larva with cleft head and produced tail spine is characteristic but a common type in Geometrinae. The species has never been reared from any host but *Avicennia*.

Figs. J-L. *Dysphania* aff. ^A~~subreperta~~ Walker (det. DHM) [p. 137]
 Wing span 60 mm. Identification is based on the characteristic shape of the spot in cell (Prout, 1932). The genus is a large one and badly in need of revision. This large and colourful species has only been reared from Bc but records under the same name exist from non-mangrove localities. Larvae are similar to others described in the genus, see e.g. Barlow (1982) figure of *Dysphania transducta* (plate 50 no. 3).

COLOUR PLATE 7. LEPIDOPTERA: GEOMETRIDAE (CONTINUED)

Figs. A-C. *Eretmopus discissa* (Walker) (det. DHM) [p. 143]
 Adult male (A) wing span 38 mm. Material was compared with *E. marinaria* by J. Weintraub and is presumably under this name in the NHM (London) collection. However Prout (1931) reviews the genus and claims a clear separation into 3 species. Since my males have thickly tufted hind tarsi I provisionally adopt Prout's name. Young larva (C) with dorsal red stripe mimicing bitten leaf margin. Old larva (B) loses this pattern. The bluntly cleft head is typical of Geometrinae. The larva is common at some times of year and only known from Sa.

Figs. D-F. *Gonodontis clelia* (Cramer) (det. DHM) [p. 138]
 Adult male (D, E) wing span 40 mm. Female larger. The species is unmistakable and keys to *Orsonoba* in Hampson (1895). Dr. Holloway assures me it should be treated in *Gonodontis*. The larva (F) with conspicuous tubercles on abd. 2 and 3 and is polyphagous on a wide range of hosts, in mangroves including Aa, Sa, *Aegiceras* and *Allophyllus* but always rare.

Figs. G-I. *Sauris* aff. *remodesaria* Walker (det. DHM) [p. 132]
 Adult male (G) wing span 28 mm. has bizarrely modified wings. *Sauris* s. lat. is a rather large genus with about 15 subgenera proposed, and related genera with similar wings exist. The whole group must be revised. The type of *remodesaria* has a male valva very like mine but is badly dissected and I cannot tell whether it shares a peculiar feature - the saccus very deep and holding two fascicles of very long hairs arising from the valvae apices. Other named species in the NHM (London) collection do have such genitalia, but there are several very different types within the "genus" which must be decomposed. Larvae (H) are incredibly procryptic and recorded exclusively on Ea, once as an island wide outbreak. Eggs laid on edges of very young leaves (I) are the easiest way to detect the species.

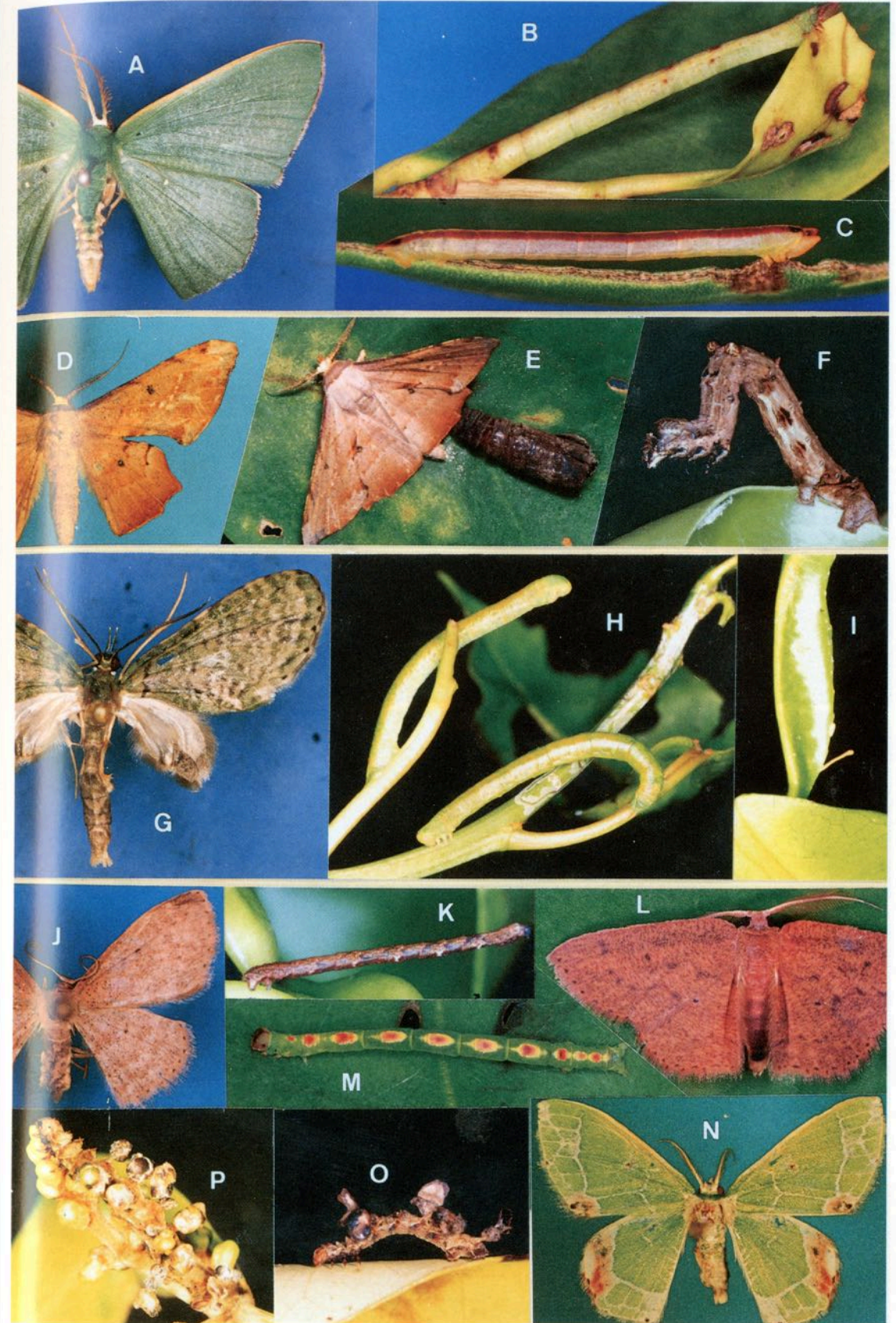
Scopula spp. One of the largest genera in the Geometridae with over 400 described species this appears as *Acidalia* in the older literature such as Hampson. The species are very similar, slight differences in face colour, shape of modified male hind legs and male genitalia being the main characters. Banzinger (1973) has been finding species attracted to eyes of cattle in Thailand. Banzinger & Fletcher (1985) have described some new species but most in the genus are poorly known. Differences between larvae may prove more striking than adults (c.f. figs. K, M). Several other species are known in mangroves than those illustrated, one reared from pupae found on Aa, one with larva strictly intertidal, black, feeding on algae and decomposing leaves; others as adults only. The larvae are rarely seen.

Figs. J-K. *Scopula* sp. 1 (det. DHM) [p. 131]
 Adult male (J) wing span 17 mm. Larva (K) dull grey brown, so far reared only on Lr.

Figs. L-M. *Scopula* sp. 2 (det. DHM) [p. 143]
 Adult male (L) wingspan 20 mm. Larva (M) green with dorsal row of red centred yellow spots, so far found only on Sa.

Figs. N-P. *Uliocnemis* aff. *partita* Walker (det. DHM) [pp. 125, 126, 129]
 Adult male (N) wing span 22 mm. The striking wing pattern is common to the genus but differs in details between species. This species is certainly not the common and widespread *U. biplagiata* figured in Barlow (1982) and of which Holloway (1979) illustrates the male genitalia. Larva (O, P) with lateral thoracic flanges, and dorsal abdominal tubercles to which fragments of plant material are attached. Only known from Aa, usually on flowers.

(Family Gracilariidae *Caloptilia* see colour pl. 10, *Phyllocnistis* see colour pl. 13)





COLOUR PLATE 8. LEPIDOPTERA: HYBLAEIDAE, LASIOCAMPIDAE)

Family Hyblaeidae

Figs. A-D. *Hyblaea* aff. *puera* Cramer (det. DHM) [pp. 123, 124]
 Adult male (A) wing span 35 mm. Some members of the species group have been discussed by Berio (1967) but more work is needed before our material can be confirmed. A larva attributed to *puera* is described by Singh (1956) and that of the Japanese species *fortissima* by Nakamura & Iwata (1969) and Sugi (1987). In Singapore the larva (B,C) varies in depth of colour and a totally black specimen has been seen. Normally the spotting pattern of the posterior segments is distinctive. A leaf webber of *Aa* which starts larval life in edge notches (D), *Hyblaea* appears as small sporadic outbreaks and is known to have caused extensive defoliation (Ridley, 1898).

Family Lasiocampidae. Often large, heavy bodied moths without tympanal organs, both sexes usually with a conspicuous tail tuft. Sexes may be very different in appearance. Larvae hairy and usually gregarious at first sometimes reaching enormous size (e.g. *Suana* not illustrated but see Murphy, 1990c). Very difficult to rear - one usually finds too many specimens, does not know when to separate them, and during their slow development has difficulty in keeping up the food supply.

Figs. E-H. ?*Paralebeda* sp. (det. DHM) [pp. 132, 134]
 Adult not figured. Eggs in clusters (E). Larvae (F,G) have been found on *Ea* and *Aegiceris*. Pupation in hanging rolled leaf (H). Can cause massive local defoliation. This was first thought to be *Paralebeda lucifuga* (Swinhoe) which it closely resembles (Plate 13 no. 2 in Barlow, 1982). A good series from *Aegiceris* shows males with genitalia significantly different from description (Holloway, 1982 p. 168).

Figs. I-K. *Trabala* aff. *krishna* Holloway (det. J. D. Holloway) [p.143]
 Adult female (I) wing span 55 mm. Larvae change colour on reaching last instar (cf. J and K). Only known from Sa, probably common since empty cocoons associated with extensive defoliation are widespread, but heavily parasitised and we have not yet reared males. Holloway (pers. comm.) thinks this may be "a pale mangrove race" of *krishna* but without males we cannot tell whether perhaps a distinct species is involved. For *Trabala* the paper of Owada & Kishida (1989) is useful.

Figs. L-M. *Trabala vishnou* Lef. (det. DHM) [p. 131]
 Adult female (L) wing span 49 mm. reared from gregarious larvae found in Pulau Tioman on *Lr*. Males are smaller and pale green. Larva also seen in Singapore but rare. The larva (M) differs from *krishna* in the more extensive black banding and does not change colour on maturing.

Murphy: Mangrove Insect Herbivory

XYLORICTIDAE
LETHICOCERIDAE
 COLOUR PLATE 9. LEPIDOPTERA: ~~LETHICOCERIDAE~~

Family **Lethicoceridae**. A family with distinctive male genitalia recently separated from ~~Xylorictidae~~ by Clarke (1955) under the name Stenomidae, but later found to include a group already given a higher taxon name. From the first it was known that the *Odites* group of genera superficially resembled Lethicocerids in genitalia but there is still disagreement as to placement. No-one currently works the group which involves many genus names of doubtful value - wing venation varies greatly, sometimes between sexes and the male genitalia are very uniform. Workers on Lethicoceridae reject them from the group (Sattler), but workers on Xylorictidae will not accept them there. That the *Odites* genus group is a coherent assemblage is clear, perhaps no more than a tribe, but in which family they truly belong is quite unsettled.

Larvae of all species are completely uniform in appearance including details of colour pattern - laterodorsal stripes involving the last three abdominal segments, but mature at different sizes. Pupation is between webbed leaves or inside a larval edge roll, and the cocoon is open at each end. A major difficulty with this group is that the larval pelt is usually expelled from the cocoon after pupation and very difficult to recover. Fletcher (1932) has described a life history in the group.

Figs. A-D. "*Odites*" sp. 1 (det. DHM) [pp. 136, 137, 139, 140]
 Adult female (A, C) wing span 34 mm, much larger than the male (B) wing span 21 mm which is suffused with grey and looks very different. We have reared much material and I am convinced this a single, highly dimorphic species common on all Rhizophoraceae. The female larva reaches 3 cm., the male pupates at much smaller size. A female reared from a pupa on *Xylocarpus* may or may not be the same - perhaps a migrant larva.

Fig. E. "*Odites*" sp. 2 (det. DHM) [pp. 125, 131]
 Wing span (both sexes) 21 mm. This species has been positively reared from Ao. The larva is typical of the group and pupates in a leaf-edge roll, usually hanging by one end. Although larvae are rarely seen, this can be the commonest *Odites* in light trap catches. The wing pattern closely resembles *O. perrisopsis* from Japan. It or a related species in which wing spots are slightly smaller but similarly arranged has been reared on Lr. We may have to deal with a difficult complex.

Fig. F. "*Odites*" sp. 3 (det. DHM) [pp. 124, 125]
 Male wing span 22.5 mm. A rare species reared from Aa, possibly related to *Odites* sp. 1 but certainly distinct.

Figs. G-J. "*Odites*" sp. 4 (det. DHM) [pp. 136, 137]
 Male (J, K) wing span 12.5 mm. This very small species (much magnified in figs. - note size of pin head) is occasional on Bc and suspected from larval rolls (G) on other Rhizophoraceae. Possibly more related to sp. 2 than sp. 1. Note that apart from its tiny size when full grown, the larva (H) is identical in appearance to sp. 1 (D).

Family **Limacodidae** (not illustrated) [pp. 134, 136]
Darna trima Moore (det. DHM) [p. 140]
Parasa sundalepida Holloway (det. DHM)

(Family **Lycaenidae** see colour pl. 13)
 (Family **Lymantriidae** see colour pl. 10)





COLOUR PLATE 10. LEPIDOPTERA: GRACILARIIDAE, OECOPHORIDAE, LYONETIIDAE, LYMANTRIIDAE

Family **Gracilariidae**. A large family of leaf-miners also commonly known as Lithocolletidae under which name a key to world genera is given by Vari (1961). Valuable details on genitalia are found in Kuznetsov (1979) but this is less complete. Living adults tend to have a characteristic posture displaying the front legs (fig. B) and the long antennae rapidly vibrating.

Caloptilia scaeodesma Meyrick (det. Yuan Decheng) [p. 144]
 Adult (A, B) wing span 10 mm. This species was described by Meyrick (1928) from material collected by Buxton almost certainly in mangroves. Buxton was one of the few workers who seriously collected in this habitat and he kept detailed notes, though Meyrick does not reproduce them. Several of the few known mangrove insects stem from his work (e.g. *Capua endocypha* below and the cricket *Apteronomobius* Chopard). The larva (C, arrowed) typically makes a coiled pupation roll on the edge of its host leaf (Sa). This is very characteristic of *Caloptilia* subgenus *Sphyrophora* to which it belongs. However at some times of the year much of the population forms galls (D-F) instead. Possibly it depends on age of leaf infected.

Family **Lymantriidae**. The familiar "tussock-moth" larvae with median dorsal tufts are unmistakable (R, Q at bottom of plate). Although very rarely seen in Singapore, members of this family have been reported as important in mangroves (Kalshoven, 1953; and M. Rau pers. comm. finds a species attacking *Rhizophora* in Papua-New Guinea) Literature on the family is scattered and largely outdated. The most commonly reported genus in mangroves is *Lymantria*.

Figs. O-R. ? *Dasychira* sp. (det. DHM) [p. 143]
 Male (O) wing span 22 mm. Larva (R, Q) pupating among foliage in a loose cocoon (P). The female should be much larger, paler and perhaps more conspicuously patterned. In this family the sexes are often very dimorphic.

Family **Lyonetiidae**. Mostly leaf-miners but *Decadarchis* [p. 146]
 in seeds. A useful but incomplete reference is Kuroko (1964). The pupal hammocks are very typical of *Lyonetia* s. str. (see fig. J).

Figs. G-J. *Lyonetia* sp. (det. DHM) [pp. 143, 144]
 Adult (G, H) wing span 7 mm, the antennae conspicuously longer than wings. This is certainly an undescribed species since all known members of the genus have a characteristic tuft of erect scales on the head, absent in this species which is completely smooth-scaled. Undescribed material in NHM (London) collection and in material of D. C. Yuan from China agree. The genitalia are simpler than most of the family but this tendency exists among Japanese species described by Kuroko (1964) so that I do not think a new genus would be justified.

Family "**Oecophoridae**". Close to Gelechiidae with which it shares the scaled proboscis and absence of tympanal organs but differs in wing venation. My limited experience with this family is restricted to using Meyrick's old genus key in *Genera Insectorum* (1922). Once one detects a misprint in this key (p. 14 couplet 242 should lead to 248) the only mangrove species so far seen in Singapore runs directly to *Epiphractis*. However *Scorpiopsis* should be expected [p.134]. The current situation however is that the mainly African *Orygocera* group with which *Epiphractis* has been synonymised (Viette, 1987) probably does not belong in that family (see Minet, 1986).

Figs. K-N. "*Epiphractis*" sp. (det. DHM) [p. 143]
 Adult male (K) wing span 12 mm, female 15 mm. The steeply tectate stance (L) is rather characteristic. The larva (M) a host specific leaf webber of Sa feeding on mature leaves, and has a distinctive red and white colour pattern. It pupates between strongly webbed leaves held together by strong pillar-like supports (N). The pupa is white. The male genitalia differ significantly from *Orygocera* as figured by Viette (1987) and I suspect this species requires a separate genus.

COLOUR PLATE 11. LEPIDOPTERA: NOCTUIDAE

Family Noctuidae. Often but by no means always, rather heavy bodied moths, most easily recognised by the bare proboscis and thoracic tympana usually with basal counter-tympana (lateral ridges on the abdomen). An enormous family whose taxonomy is in confusion (Kitchings, 1984). The old and virtually unobtainable monograph of Hampson (1898-1913) is still the only way to determine material without access to a major collection in spite of its deficiencies. Hampson (1894, 1895) is also useful though less comprehensive and includes many of the mangrove genera, though too often under synonymous names.

Figs. A-D. *Achaea janata* L. (det. DHM)

[pp. 132, 133]

Adult (A) wing span 57 mm. A large and well known species (the "castor semi-looper") polyphagous on Euphorbs and some other plants. Also in the literature as *Ophiusa melicerta*. Species of *Achaea* are not easily separated but Holloway (1982) gives an excellent synopsis of the current situation in Southeast Asian forms. The large larva (C, D) feeds on Ea in mangroves, is white pollinose when small, humped above the tail. The powdery pupa (B) is typical of Acontiinae.

Figs. E-G. *Aucha velans* Walker (det. M. Honey)

[p. 124]

Adult (E) wing span 34-39 mm, recognised by the yellow mark on the hind wing. Males have a tract of spines below the retinaculum and a "plectrum" of modified scales on upperside of base of hind wing that apparently scrape across them. The valvae are simple. The larva (F,G) is a semi-looper without black spotting feeding exclusively on *Avicennia*.

Figs. H-J. *Aucha villiana* Swinhoe (det. M. Honey)

[p. 124]

Adult (H) wing span 28-35 mm the small specimens once suspected of being a different species; now I think not. Hind wing uniformly dark. Males have retinacular patch scaled and no "plectrum", the valvae cleft. Females are suffused with pink beneath in all *Aucha* spp., and *Aucha aetha* Prout described from Penang is a female of *villiana*. The larva (I, J) has small black spots not seen on *velans* but is a similar semi-looper. The photograph is staged on a "foreign" leaf but the larva is, like other *Aucha*, restricted to *Avicennia*.

Figs. K-O. *Autoba alabastrata* Warren (det. DHM)

[pp. 126, 127, 128, 129]

Adult wingspan 18 mm. The female (K) is greyer than the male (L), the latter exactly matches Warren's original illustration which was mislabelled female (but correctly stated to be male in the description). Larvae have only the two posterior pairs of abdominal prolegs and are internal borers in fruit of *Avicennia alba*. Specimens from Aa are very consistent in appearance, but a bewildering variety of patterns and sizes appear when *Autoba* s.p. are reared from fruit of other species, or from flowers of the same genus. I reserve opinion on how many species are involved pending further study.

Colour Plate 11



COLOUR PLATE 13. LEPIDOPTERA: PAPILIONOIDEA AND PHYLLOCNISTIS

The **Papilionoidea**. "Butterflies" - diurnal forms with clubbed antennae said to assist in judging distance by sight. Contains several related families which, for convenience of organising the plates are treated together here. For Malaysia the fauna is comprehensively treated by Corbett & Pendlebury (1978). Several other species are known mangrove associates, but where hosts are known these are minor plants not treated here.

Family **Lycaenidae**. "Blues" In this family the underside marking (A, E) are important in discriminating species. Larvae usually attended by ants.

Figs. A-D. *Arhopala pseudocentaurus* (Doubleday) (det. DHM) [p. 143]
 Adult female (A, B) wing span 49 mm. The male has brown upperside border reduced to a narrow line. Pupa (C) is protected by silk baffles above and below. Larva (D) is distinctive by colour pattern and the stiff black setae, and has only been seen on Sa in mangroves but is known to be polyphagous.

Figs. E-H. *Hypolycaena erylus* (Godart) (det. DHM) [pp. 131, 140]
 Adult female (E, F) wing span 30 mm. The male more extensively blue above. The larva (H) has pale setae and has been found on Ra Rm Bc Lr and *Scyphiphora*. Male genitalia of mangrove material is as described by Shirozu & Saigusa (1962).

Family **Nymphalidae**. Large butterflies with 4 legs in both sexes, the larvae very varied, important in establishing major groupings. The peculiar larval head of *Polyura* is characteristic of the *Charaxes* complex.

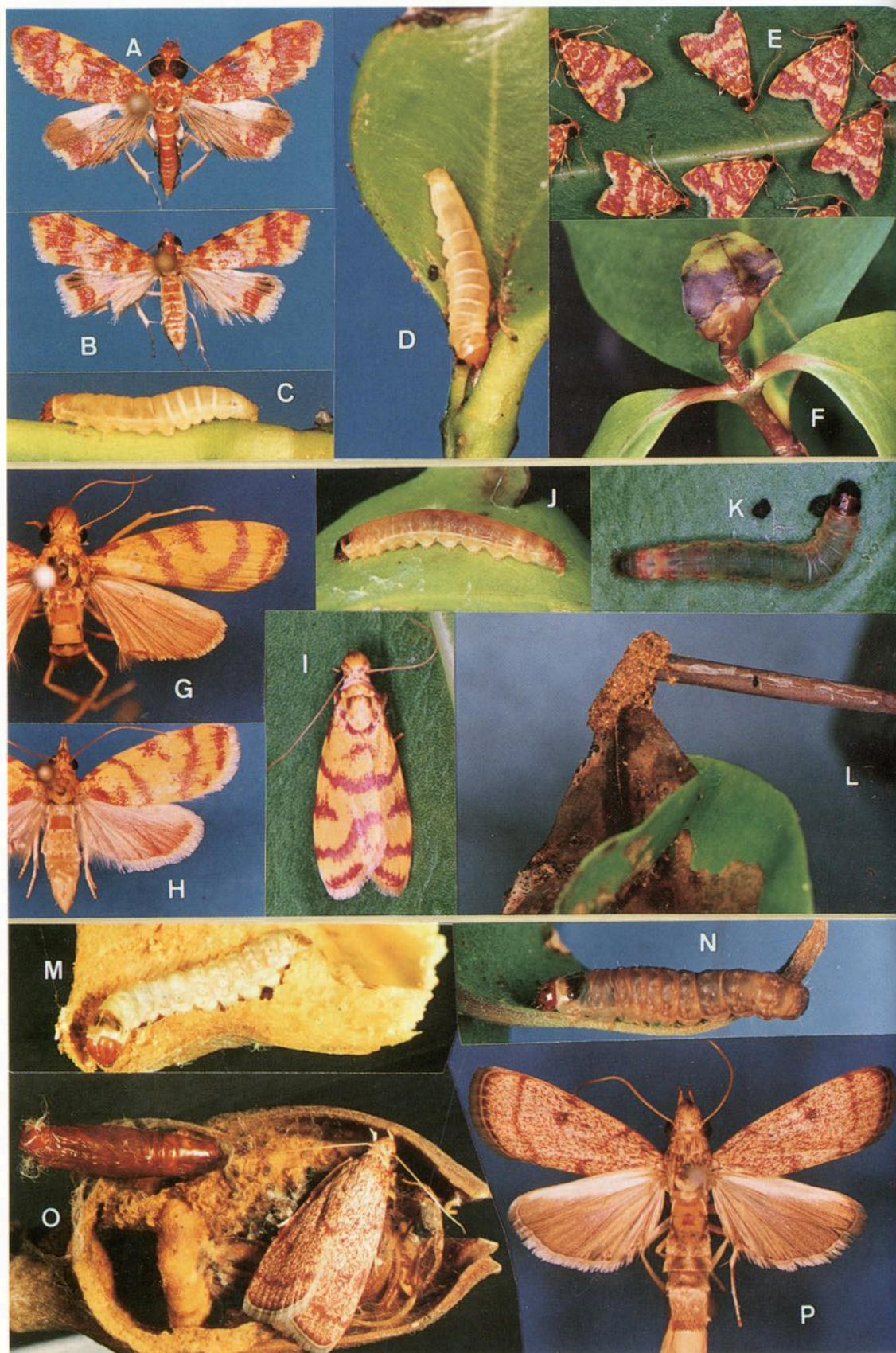
Figs. I-L. *Polyura schreiber* (Godart) (det. DHM) [p. 137]
 Adult (I) wing span 75 mm. quite commonly seen flying in Singapore mangroves. It is said to be commoner in Singapore than elsewhere, perhaps no more than a reflection of Singapore losing most of its lowland forest except mangrove by the time collecting was done. Larva (J,K) until recently only seen on Bc, but since then a female was found laying eggs (L) on Ra, on which the larvae are currently feeding.

Family "**Phyllocnistidae**". A very distinctive group of tiny leaf miners now generally included as a subfamily in Gracilariidae. The male genitalia are very simple and uniform in type but I am told even the slightest differences can be significant (Clarke pers. comm.). Specialists make drawings first and compare them minutely before concluding identity. Many species have virtually identical wing markings.

Figs. M-Q. *Phyllocnistis* spp. (det. DHM) [pp. 124, 128, 132, 134]
 Adults reared from *Avicennia* (M,N) and *Clerodendrum* (P) wing span 6 mm. Those from Ea (Q) seem to have slightly shorter and broader wings but identical pattern. Note that the apparent distribution of golden scaling varies with angle of illumination. Larva leg-less and changes morphology in the last, non-feeding instar, makes silvery mines usually in the upper surface of the leaf (O) and pupates in a marginal fold. A species (not illustrated) from *Aegiceras* is very different in colour pattern and makes a mine significantly different in appearance.

Family **Psychidae** ("bag-worms" - not illustrated or identified). [pp. 125, 129, 131, 134, 136, 138, 140, 143]





COLOUR PLATE 14. LEPIDOPTERA: PYRALIDAE

Family "Pyralidae". A well defined group recognisable by the combination of scaled proboscis and abdominal tympanal organs, but recently divided into two families (Minet, 1982) differing in the structure of the tympanal organs. The distinction is not always easy, but one difference is that Crambidae have a prominent median appendage before the the tympana - the "praecinctorium" which true Pyralidae lack. Unless specimens are set with the abdomen pushed up (which makes it easy to knock off when handling the fragile dry specimens), it can be very difficult to tell. I recommend non-specialists to stick to the old system, which at least makes the older and more familiar (and more comprehensive) literature usable. The long accepted arrangement of sub-families is also changing, mainly by separating out some peculiar groups as new ones.

Subfamily *Odontiinae* (recognised mainly by peculiar genitalia with membranous uncus - the monograph of American species by Munroe (1961) is a useful reference.)

The "genera" *Balaenifrons* (Hampson, 1917) and *Taurometopa* (Meyrick, 1933) were described in different subfamilies by their authors on the basis of the presence of absence of dorsal hairs on the cubital vein of the hind wing, a character then given much substance. In fact species belonging to these genera vary in the character and some specimens of *T. pyrometalla* have more extensive hairing than do the *Balaenifrons*. These species share a unique and striking character, an enormously inflated head in the male. In at least *T. pyrometalla*, the males gather in small assemblages called "leks" - from which females are presumed to choose the most "handsome" mate; one imagines they must prefer big heads. The genera are certainly very close and I suspect synonymous, though the large eyes in *pyrometalla* and some Australian species may justify separation. Both, together with *Boeotarcha* (next plate) belong to *Odontiinae*.

Figs. A-F. *Taurometopa pyrometalla* Meyrick (det. M. Shaffer) [pp. 142, 143, 144]
 Adult male (A) 16 mm, somewhat variable, sometimes "lekking" (E). Female (B) smaller (14 mm) but similar in pattern. Larva (C,D) feeding between apical young leaves of *Sonneratia*, pale with a pale brown head. It turns red just before pupation, leaves the bud and constructs a hard cocoon. In the lab. it scrapes material such as polythene to incorporate in the cocoon and larvae are often lost because of ability to bore through the vial cap.

Figs. G-L. *Balaenifrons* n. sp. (det. DHM) [p. 142]
 Adult male (G,I) wingspan 22 mm, female (H) slightly smaller at 19 mm. Larva (J,F) similar to *pyrometalla* when young except for darker head, but develops a distinctly different pattern of red pigment prior to pupation. Habits like *pyrometalla*, also on opening leaves of *Sonneratia*, but tends to pupate near or in the fed leaves (L). Larvae of this group have very short, blunt setation, (cf. *Boeotarcha*, q.v.). Two females of this species from Sarawak are included in the NHM London series of *Balaenifrons homopteridea* Hamps. - type species of the genus. They are not con-specific with the holotype male from Burma (Hampson, 1896a).

Figs. M-P. *Balaenifrons ochrochroa* Hampson (det. DHM) [p. 145]
 Adult male (P) wing span 23 mm. Larva (M, N) a borer of *Sonneratia* buds, flowers and fruit, pale except redder at maturity. In fruit it often bores the receptacle (M) especially when the fruit is also attacked by *Eucosma*. Pupation is inside the fed fruit or bud (O) without a strong cocoon. Like others the larval setation is short and blunt.

COLOUR PLATE 15. LEPIDOPTERA: PYRALIDAE (CONTINUED)

Figs. A-E. *Boeotarcha crassicornis* (Walker) (det. DHM) [p. 142]
 Adult male (A) wing span 21 mm. Female (B, C) substantially larger at 26 mm (*c.f. Balaenifrons* spp.). Larva (D, E) strongly pigmented and patterned throughout life, with long setation, an external surface grazer on expanded leaves of *Sonneratia* under loose silk webbing. The species has been treated as a synonym of *B. martinis* and is so arranged in the NHM London collection. However, the male holotype of *martinis* (figured in Hampson, 1896a) stands out in the series as very differently patterned to the rest and I reserve opinion on this synonymy pending revision.

The subfamily *Epipaschiinae*. Both the male antennal process and the gregarious habits of the larvae described below are features common in the subfamily (Hampson, 1896b).

Figs. F-I. *Heminomistis flagellalis* (Hampson) (det. DHM) [p. 143]
 Adult male (F) wing span 21 mm. Males have a prominent plumed appendage from antennal base which arched back over the thorax. Female similar but without antennal appendage. Larvae (G,H) dark, gregarious in webbed clusters of dead leaves during day-time, feeding at night; pupating in gregarious cocoons (I). Feed only on *Sonneratia*. Previously known from Borneo and Thailand. The pectinate antennae discriminate *Heminomistis* from *Lepidogma* in which the species was originally described (Hampson, 1906).

The subfamily *Pyraustinae* (recognised by the bilobed praecinctorium; in the mangrove species, males often with very elongate abdomen.)

Figs. J-K. *Hymenoptychis sordida* Zeller (det. DHM) [p. 127]
 Adult male (K) wing span 25 mm. Female larger with shorter abdomen. The moths are very common resting on pneumatophores and under leaves of intertidal seedlings. Larva (J) very common on tidally inundated ground, where they feed indiscriminately on decaying wood, leaves and green algae. Also attack seedlings of *Avicennia*. It is dull brown with heavily sclerotised small plates (pinacula) at the setal bases and keys in Hasenfuss (1960) to the vicinity of *Udea*. The species is extremely wide spread, from East Africa to Japan and north to the Himalayan foothills (Hampson, 1897).

Figs. L-N. *Tatobotys janapalis* (Walker) (det. M. Shaffer) [p. 127]
 Adult female (L) wing-span 20 mm. The wing pattern distinctive. Males with long abdomen as in *Hymenoptychis*. The moths are almost as common in mangroves as the previous species, but unlike it have not been reared from wild caught larvae on the ground. This is surprising since in the laboratory both species lay eggs freely and the larvae can be easily reared on decaying leaves of many mangrove species. Both thrive under very poor conditions and show promise of being useful laboratory animals. The larva is virtually indistinguishable from *Hymenoptychis* in all details of chaetotaxy except some head micropores (Cordeiro, 1987).





COLOUR PLATE 16. LEPIDOPTERA: PYRALIDAE (CONTINUED) PHYCITINAE

The subfamily **Phycitinae**. A large group, with characteristically wedge-shaped wings, usually dull coloured. Males of many but not all have the base of the antenna distorted at the base and with a scale tuft (see fig. B). Larvae usually with a ring-like sclerite surrounding base of dorsolateral seta on Th.2 and Abd.8. Many new genera were recently described from Sumatra by Roesler (1983), but the book lacks keys and is difficult to use, though very well illustrated. I have been unable to place any of the mangrove species.

Phycitinae sp. 1 [p. 127]
 Adult female (A) wing span 18 mm, male (B) slightly smaller, antenna with sinus and scale tuft. Larva (D,E) feeding on *Avicennia*, at first on flowers (F), later patch-grazing undersurface of leaves under a characteristic bubble-like web, within which it later pupates (C). Ring sclerites present but unpigmented and hardly visible; the larva pale green and easily recognised by small black lateral spots on Th. 1 and Th. 2, the latter associated with the ring sclerite of SD1. Apparently an undescribed genus of sub-tribe Phycitina to which sp. 3 also belongs.

Figs. G-I. Phycitinae sp. 2 (det. DHM) [pp. 127, 129]
 Adult male (G) wing span 17 mm, antennae with sinus and scale tuft. Larva (H,I) only known as a primary borer in fruit of *Avicennia* which does not attack the plumule, does not provoke fruit drop, and does not web the fruit to nearby parts (cf. *Autoba alabastrata* q.v.). Simple maxillary palps and culcita suggest this is in *Acrobasiina*.

Figs. J-K. Phycitinae sp. 3 (det. DHM) [p. 127]
 Adult male (J) wing span 13 mm, antennae with sinus and scale tuft. Female slightly larger with identical coloration. Larva pale green, with ring sclerites present but unpigmented, entirely without the black spots of species 1, but otherwise very similar. Habits also similar, feeding first on flowers and later on foliage under bubble-like webs.

Figs. L-N. Phycitinae sp. 4 (det. DHM) [p. 128]
 Adult male (L) wing span 11.5 mm. Antenna simple, without sinus or scale tuft. Larva (M, N) long-haired, dark above with pigmented ring sclerites, so far found only on flowers of *Avicennia lanata*.

Figs. O-P. Phycitinae sp. 5 (det. DHM) [p. 125]
 Adult male (P) wing span 15 mm, antennae with long basal sinuation and low scale ridge; female wing span 16 mm. Larva dull grey dorsally with pinacula and ring sclerites strongly pigmented; a gregarious patch-grazer on underside leaves of *Aa* which are loosely webbed with silk in which frass accumulates (O). Very young larvae may start attack at the apical bud. A minor local outbreak of this species occurred but was heavily parasitised and quickly came under control. We had a low success rate in rearing.

Figs. Q-R. Phycitinae sp. 6 near *Cryptoblabe* (det. DHM) [p. 143]
 Adult male (Q) wing span 15 mm, antennae with deep basal sinus containing a scale tuft and beyond it a long, hook on flagellar seg. 5 - the position typical of *Cryptoblabini* but much more developed. Larva a solitary patch grazer on foliage of *Sa*. Very uncommon.

Figs. S-U. Phycitinae sp. 7 near *Euzophera* (det. DHM)
 Adult female (S) wing-span 16.5 mm. The white costal bar is distinctive. ?Male (U), if correctly associated, quite different in colour. Larva (T) reared from various situations, always secondary to other species and presumably feeding on dead residual material. Has been reared from *Avicennia* fruit following *Autoba*; *Sonneratia* fruit following *Eucosma*; "nests" of *Heminomistis*; and shrivelled propagules of *Ceriops*. Although no primary attack is yet documented on *Ceriops* radicles, the whole aetiology of this species suggests it was secondary to some other cause of death.

COLOUR PLATE 17. LEPIDOPTERA: TINEODIDAE (OXYCHIROTIDAE),
TORTRICIDAE

The family **Tineodidae**. One of several families whose affinities and composition has puzzled systematists for decades. That *Cenoloba* is superficially a "plume-moth" is obvious, but the term includes several unrelated groups, and fundamental resemblances to moths with simple wings like *Oxychirotia* led to its inclusion in *Oxychirotidae*. New characters have led recent workers to merge this family with Tineodidae and include it in Alucitoidea (Both J. Minet and M Shaffer independently expressed this opinion).

Figs. A-E. *Cenoloba* aff. *taprobana* Hampson (det. DHM) [p. 126]
Adult (A) wing span 7 mm, unmistakable from the deeply divided wings. Larvae bore in *Avicennia* flowerbuds, their stalks (causing apical dieback - B) and fruit (D). Pale but with head barred with longitudinal dark stripes when boring, mature larvae develop distinctive colour pattern (C) before pupation, which may be internal (E, also shows a parasite cocoon) or in an external cocoon. SEM studies are being made of the larva which has a finely shagreened and intensely water-repellant cuticle. I am not sure that only one species is involved, but the Southeast Asian material is not *obliteralis* and resembles the type series in NHM (London) of *C. taprobana* (Hampson, 1912).

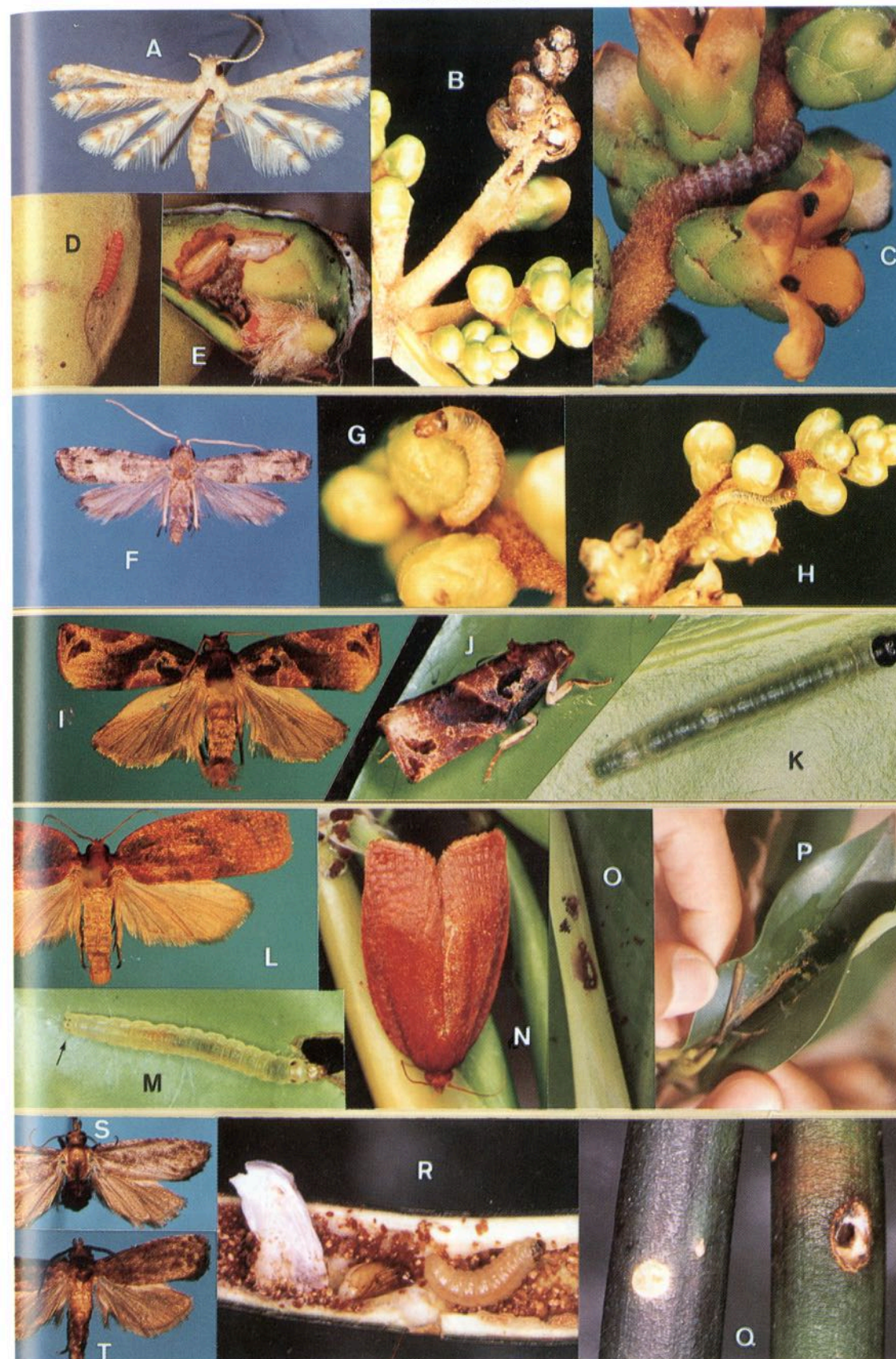
The family **Tortricidae**. Considered an archaic group, many tortricids have a distinctive "bell" shape when resting (J), and short porrect palps. They have bare proboscis and no tympanal organ. Larvae may have a distinctive anal comb (but absent in borers) and pupal skin protrudes from the cocoon on emergence.

Acroclita sp. (det. K. Tuck) [pp. 126, 129]
Adult (F) wing span 7.5 mm. Larva (G,H) with yellow head lacking black bars (*cf. Cenoloba* which is found in same habitat). Bores individual flower buds of *Avicennia* and emerges to pupate in a tiny cocoon on the peduncle which is covered with the brown scales and very procrustic. The larva has an anal fork with 4 teeth. This tiny moth belongs to *Olethreutinae* (with cubital pecten) which subfamily contains some of the smallest of all Tortricidae. Most of these very small forms are "dumped" provisionally into *Acroclita* but the group needs revision (K. Tuck pers. comm.).

Figs. I-K. *Archips* new species (det. K. Tuck) [pp. 125, 127, 134, 143]
Adult (I, J) wing span 20 mm. Larva (K) green with black head, a rare but widespread leaf webber polyphagous on several hosts (Aa, Aeg, Bc, Ea, Sa and *Acanthus*) and on Aa also attacks flowers. Apparently undescribed (K. Tuck pers. comm.).

Figs. L-P. *Capua endocypha* Meyrick (det. K. Tuck) [pp. 135-140]
Adult male (L) wing span 24 mm, not always as clearly patterned as this specimen, but this is a basic pattern type for the group and not distinctive. Female (N) substantially larger and unmarked. Larva polyphagous on Rhizophoraceae, often begins life by boring apical bud (O), later webs young leaves (P). Easily recognised by black patches as sides of prothoracic shield and characteristic pattern of 5 spots on anal shield (M, arrowed). Anal comb present. An extremely active larva which wriggles violently when disturbed and often drops to the ground. *C. endocypha* was described by Meyrick (1931) from material collected in Fiji where it has since been taken again in mangroves (G. Robinson pers. comm.) and is not truly a member of the genus *Capua* or of *Epagoge* (to which it was assigned by me in earlier papers). On genitalia it is clearly a member of the *Adoxophyes* complex, but broadly arched costa of hind wing suggests it requires a new genus (K. Tuck pers. comm.). A second species of this genus may co-occur in Australia.

Figs. Q-T. *Cydia* sp. (det. K. Tuck) [p. 138]
Adult male (T) wing span 13 mm, female (S) slightly larger. Larva (R) an internal borer of the radicle of propagules of *Bruguiera cylindrica* still hanging on the tree, often several in one fruit. Infected fruit identified by circular windows sealed by silk (Q). The larva has no anal fork.



COLOUR PLATE 18. LEPIDOPTERA: TORTRICIDAE (CONTINUED)



Figs. A-C. *Eucosma* sp. (det. K. Tuck) [p. 145]
 Adult male (A, B) wing span 18 mm. (female 21 mm) The larva is of typical borer type for the family, without anal fork, infesting mature fruit of *Sonneratia* (Sa,So), often 5 - 6 or more in a fruit. They tunnel widely, attacking the developing seeds, pupate inside the fruit and on eclosion the pupa is protruded (C).

Figs. D-H. *Eupoicilia* sp. (det. DHM) [pp. 126, 137]
 Adult male (H) wing span 10 mm. Female identical. Larva case-bearing, the case formed from the flower bud or flowers on which it feeds. On Bc a single hollowed bud forms the case (F) carried with it as it moves around. If too small a bud or flower forms its first case it may transfer to a second (E). The case is webbed to a leaf for pupation and the pupal pelt is exerted at eclosion (E,G). The species also feeds on Aa (D) when the case is assembled from a chain of eaten buds (arrowed). This genus, better known as *Clysiana* is a typical member of the Cochyliini now regarded as no more than a tribe of the Tortricinae although until very recently treated as an independent family Cochyliidae (or Phaloniidae). It is necessary to know these names if searching the literature (e.g. Diakonoff, 1941). The species has a very prominent appendix beyond the frenulum at base of hind wing. Such an appendix but usually much smaller, is a common feature in the group.

Figs. I-J. ? *Homona eductana* Walker (det. K. Tuck) [p. 137]
 Two adults presumed to be the same species but significantly different in appearance were reared, one (I) from Bc the other from *Allophyllus*. The specimens are in the NHM (London) pending further study.

Lasiognatha leveri (Bradley) (det. M. Horak) [pp. 128, 143]
 Adult male (K, N) wing span 15 mm. Female much less strongly patterned (L). Larva (O) dull green with dark head, webs very strongly the apical leaves of Sa seedlings and low saplings in inundated situations. The pupa (M) is protected by an elaborate system of silken baffles, presumably to protect it from immersion. Its biology was earlier discussed by Lever (1952, 1955). Using the monograph of Diakonoff (1953) I considered this a synonym of *Lasiognatha celligera* (see Murphy, 1990e) but the latest information is that Dr. Horak examined my material deposited in NHM (London) who agrees it is in *Lasiognatha* but considers the species distinct. The genus name *Lasiognatha* may prove to be pre-empted by an earlier one.

Order ORTHOPTERA [pp. 130, 133]
 Family Tettigoniidae (not illustrated or identified)

DISCUSSION

Although some work exists on general levels of foliage damage, little is available on the specific agents of herbivore attack in mangroves. The fine paper by Onuf *et al.* (1977) seems to be the single exception. There have been scattered reports of outbreaks and taxonomic literature sometimes indicates a mangrove host but no attempt has been made to synthesize the two. This paper attempts a beginning but although it includes records known to me from elsewhere than Southeast Asia, this is certainly incomplete and especially defective for the western hemisphere.

Phytophagous insects represent only a small part of the whole insect fauna in mangroves and, reflecting the depauperate flora, are relatively few in number compared with the situation in inland forest. Even so there are far more herbivores than listed here, many that have already been associated with minor elements of the phanerogam flora (e.g. those on *Clerodendrum* mentioned by Murphy, 1989b) or algae (Murphy, 1989a), or remaining untreated in our files. Many others that are known to be abundant and apparently restricted to mangroves have yet to be traced to host-plants.

Direct dependants of these primary herbivores such as parasitic Hymenoptera and Diptera have not been treated, though some predators of Sternorhynchous Homoptera are known. Thus my preliminary catalogue published as an appendix to Murphy & Tan (1980) lists the Neuroptera *Chrysopa ruficeps*, *Glenochrysa splendida* and an undescribed genus allied to *Chrysocerca*, and also the syrphid fly *Allobaccha amphithoe*, all now known to be predators of *Boreioglycaspis forcipata* an abundant psyllid attacking *Sonneratia*.

The most interesting components of the system are those that live intertidally and may be considered to some extent truly marine. The characteristics of this fauna have been briefly summarised by Murphy (1986b, 1990a, 1990b). The more intensively studied fauna associated with human disease transmission is discussed in Murphy (1990d). The interplay between the compartments is discussed by Murphy (1986a, 1990c).

Host Specificity

The association of a given phytophagous insect with a particular plant host, however consistent the results may be, is never more than proof that this is part of the host range. When dealing with a zonal system such as mangroves, frequently a narrow belt bordering other vegetation, one can never be sure that the herbivores are monophagous, even though evidence from within the system sampled is strong.

Nevertheless there are 14 species of Lepidoptera apparently monophagous on *Avicennia* and 13 on *Sonneratia* whereas Rhizophoraceae as a whole and *Lumnitzera* have 4 each and others have less. This probably reflects a real isolation in the first two plant taxa. In Coleoptera the Chrysomeloidea show a rather high incidence of monophagy at host genus or family level. The Hemiptera Heteroptera are normally identifiable only as adults which disperse widely from the host. Only consistent association of immatures can be taken as strong evidence. Such evidence as we have suggest that the few mangrove species have strong host preferences. Thus *Mictis* on *Sonneratia*, *Glaucias* on *Lumnitzera*, *Calliphara*

on *Excoecaria*, *Antestiopsis* on *Avicennia* are now considered to be established as primary host associations although occasional records of immatures from other hosts exist. This is rare enough to suggest they may be strays, but the possibility of a degree of polyphagy exists.

In spite of the above caveat, there is no doubt that host specificity is a real phenomenon. The Psyllodea are well known for extremely close host specificity (Eastop, 1979). In mangroves we have the association of particular species of *Tyora* with *Heritiera*, *Epipsylla* with *Derris*, *Mesohomotoma* with *Hibiscus*, *Haplaphalara* with *Thespesia* which seems to be species for species with no known exceptions.

An association between *Sonneratia* and a rather closely knit assemblage of odontine crambid moths seems to be emerging. One is the extraordinary genus *Taurometopa* (and/or *Balaenifrons*). Of the very few species in the genus group (8), three are now shown to be host specific to this plant. The distribution of most other described species is coastal and in potentially mangrove areas, so that more may yet be added to the list. That the only other odontine recorded, *Boeotarcha*, should be on the same host may also be significant.

The emergence of a higher taxon argues for a long isolation and supports botanical treatment of *Sonneratia* as an independent family. Whether other insects on the same host such as the *Caloptilia*, *Lyonetia*, *Heminomistis*, *Eretmopus* and the Rhynchitine weevil, all apparently monophagous on present evidence, support this view remains to be seen. All appear to be in small genera, subgenera or morphologically distinctive groups, that as far as known range closely with the plant genus.

Similarly with *Avicennia* it is noticeable that host specific noctuid groups exist in *Aucha* and *Autoba* (the latter probably a smaller taxon than the name implies), and only this plant genus supports a wide range of directly phytophagous Phycitinae. Again, the high incidence of apparently genus specific Coleoptera supports this view.

"Niche Plasticity"

Host range is one aspect only of a much more complex phenomenon - the animals "niche" - its place in the ecosystem and the overall strategy by which it maintains that place. As we have seen, each species not only has a characteristic host range, but also distinctive sites of attack, modes of feeding and defense which may or may not change as it grows.

It is easy to assume that first results are representative of the whole biology of a species, especially when they seem highly distinctive. Thus *Cenoloba* was "well known" to be a borer into *Avicennia* fruit and that its use of its host should include the apparently different strategy of flower bud and stalk boring came as a surprise.

Eupoicilia as a flower feeder on *Bruguiera cylindrica* appears quite different to its aspect when feeding on buds of *Avicennia alba*. In both cases the first assumption was that different, if closely related species must be involved, but as sufficient material accumulated for an adequate check, no evidence for this could be found. When

experimentally transferred from one host to another, the larvae continued feeding and completed development.

Many examples can be cited where first impressions of extreme specialisation were soon to be qualified. Thus *Uliocnemis*, and several phycitines, originally found as flower feeders on *Avicennia* were found to include foliage grazing or fruit boring either as occasional alternatives or as a normal change of strategy during development. The *Caloptilia* on *Sonneratia* conforms to its group when forming a leaf roll as pupal chamber, but its involvement in gall formation, at certain times of year its principal mode, also seems to be completely normal. Under laboratory conditions, even the apparently very host specific *Thiotricha* associated with *Lumnitzera racemosa* could foliage feed on *L. littorea*. Even rare and aberrant events may well be significant to species survival under difficult circumstances.

I am satisfied that these species do have considerable flexibility in using available resources and that it may well prove true of other species which on present evidence seem highly specialised. If so the apparent restriction of some species to mangroves may well be spurious. A *Cenoloba* adult has been taken at light in inland forest, remote from the coast, although as yet it has never been reared from any host plant other than *Avicennia* spp. There seems no particular reason why *Eupoicilia*, feeding on only remotely related hosts, should not include a variety of inland plants in its host range.

The adaptive value of polyphagy to species feeding on seasonally variable resources and the disadvantages of a narrow niche, either of habits or of host range are evident. If the susceptible host or structure is periodic in any way, either the insect must diapause (a common solution in strictly seasonal latitudes) or else the niche breadth must include alternative resources in which part of the population can persist.

Evidence for seasonality in Singapore is slim. Our records span almost two years but apparent changes in insect densities may not be repeated annually. Some plants are apparently seasonal in flowering - notably *Avicennia officinalis* and *Sonneratia alba*. It is not surprising to find that most flower and fruit attack in these hosts involves species accepting, as far as is known, all species of the plant genus and in both cases non-seasonal hosts exist. Thus *Avicennia alba* flowers continuously, and *Sonneratia caseolaris* is said to do so (the population is now extinct in Singapore as the last two trees died this year but it is abundant in Johore only a few kilometers away). Even so, although there may be conspicuous seasonality in flowering, in most plants immature and even odd mature trees are often out of synchrony. Thus even highly specialised insect associates suffer little real risk from vagaries of host-plant phenology.

The abundance of some species appear to be climatically coordinated. Thus major outbreaks of bag-worms tend to be after the northeast monsoon season (usually February to April) when higher wind speeds presumably aid dispersal of wind-borne larvae.

The Recognition of Foliage Damage

One of the hypotheses being tested was that feeding and/or other marks might enable damage to be assigned to its causal agent even after the event.

This can be done with some confidence for some Coleoptera since only a single morph (the adult) is involved. Thus *Coenobius* attack on *Lumnitzera* is unique in Singapore, though if other species of its group should be found this may have to be qualified. *Lepadoretus* (or at least Adoretini as a group) produce a quite unmistakable damage determined by the unique architecture of their mouthparts. The galerucine chrysomelids (*Monolepta* spp.) have a consistent strategy and, when host specific can usually be recognised. For the eumolpines *Rhyparida* and *Tricliona* the site of attack (very young leaves) is distinctive but there is some plasticity in damage which can involve both edge and surface feeding. Perhaps because *Tricliona* has broad lateral flanges on the sides of the thorax which constrain head movement they tend to be edge feeders, but *Rhyparida* is more commonly patch grazing and leaves marks much like those of *Monolepta* where its host-range overlaps (most Rhizophoraceae).

With Lepidoptera it is unusual to be able to discriminate species by damage alone except for a few special cases such as the leaf-miners or the perforation of *Lumnitzera* by *Thiotricha*. The crude classification into edge-feeding and patch-feeding proved unsatisfactory for two reasons. Many species change strategy as they grow, very young larvae commencing as patch-feeders or in axillae before changing to edge-feeding when partly grown. Sometimes the complete syndrome following a major attack is distinctive but this demands considerable experience and may be unreliable. Thus a *Hyblaea* outbreak would be recognisable from the limited host range (*Avicennia*) and the combination of juvenile edge-rolls, mature leaf-webbing and pupation in the foliage. Even so, *Odites* attack (currently very rare on this host) strongly resembles the first phase of *Hyblaea* attack.

Patch grazers do often produce distinctive patterns, and at a site where the herbivore spectrum for each host is known an experienced worker could probably make a good guess. Most species that pupate in the foliage have characteristic leaf-tying strategies or other features that help identification when an outbreak has been sufficiently extensive for a range of traces to remain. Thus all Tortricidae have pupal skins exserted from the cocoon after eclosion. *Epiphractis* makes distinctive pillar-like supports between the leaves. Nevertheless there remain many species which, on present evidence, can only be recognised during a current infestation.

Edge feeding is an even more intractable problem, and unfortunately this is precisely the kind of damage at which assessment of leaf area loss has usually been aimed. Crab attack, at least by unspecialised feeders such as the sesarmine Grapsids can usually be distinguished by the rough tearing, but apart from host data there seems little to distinguish the various kinds of insect damage. No clear distinction has been detected between even such remotely related forms as the tettigoniid Orthoptera and the edge-feeding caterpillars. Thus old damage from *Sauris*, *Paralebeda* or *Achaea* on *Excoecaria* is not certainly distinguishable from tettigoniid attack unless other evidence can be invoked. In practice the powdered pupal cases of *Achaea*, the hanging cocoons of *Paralebeda* and the empty eggshells laid by *Sauris* on leaf margins would probably enable recognition of a major attack. Similarly the association of characteristic cocoons with totally stripped shoots identifies *Trabala* spp. on appropriate hosts.

With species like *Cleora* and *Aucha* which leave the host entirely for pupation the prospect for sure recognition becomes remote though since tettigoniid attack on *Avicennia* is relatively low, these are presumed to account for most edge feeding on this host. Under normal circumstances these and the patch grazing *Erastroides* probably account for most chronic leaf area loss on *Avicennia*, but apart from collecting larvae (e.g. by beating) the evidence remains circumstantial.

Prospects for Foliage Damage Assessment

One of the big problems with assessing damage levels is that some very important attack leads to total loss. Thus *Sauris* on *Excoecaria* can destroy entire shoots, large or gregarious caterpillars such as *Paralebda* and *Selepa* on *Excoecaria*, and *Trabala krishna* on *Sonneratia* strip entire branches. How one is to incorporate such losses from simply assessing percentage loss from collected mature leaves is uncertain. Again those species that do not completely penetrate the lamina are hard to assess. Any species destroying the apical bud e.g. *Balaenifrons* on *Sonneratia* may reduce leaf production, but may do no more than divert leafing to laterals. An interesting feature of this last type of damage is its effect on the architecture of the plant. *Sonneratia* subject to chronic *Balaenifrons* attack has a distinctive "twiggy" growth form quite different from its appearance at apparently uninfested sites or during periods when the species are rare.

Prospects for Management

The general level of insect damage in Singapore is acceptable for normal maintenance purposes provided that environmental disturbance does not damage the plants. Enough is now known about the insects natural history for control therapy to be rationally planned should it become necessary. Replanting from propagules is probably the stage at which careful attention to pests will be necessary. Propagation normally starts in special beds where control can be centralised. After planting out, the main insect problem is probably *Zeuzera*, but even here the interesting possibility of biocontrol by entomo-pathogenic nematodes exists. Perhaps the greatest management problem is not an insect one but the parasitic plant *Cassytha filiformis* L. (Lauraceae). In Singapore this dodder-like parasite affects back mangroves severely in several places, especially those adjoining reclaimed land.

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