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Chapter 3

Biology

Life histories

The Oecophorinae, which comprise more than 20 per cent of the named Australian species of Lepidoptera, have adapted to a wide variety of climates, ranging from those of the highrainfall areas of the north-east to the most arid inland localities, and from the tropical north to the temperate and subalpine and alpine areas of the mountains in south-eastern mainland Australia and Tasmania. Although 🥳 many species may be bivoltine, or even multivoltine, especially those inhabiting the warmer and moister coastal areas of eastern Australia, undoubtedly the majority are univoltine. There is little systematic information available on the phenology of Australian species, but label data of specimens in collections, and the results of surveys, suggest that the adults of most species are active during the spring and early summer months, irrespective of rainfall distribution. It is clear, of course, that the flight periods of species living in cool or cold climates occur later than those in more temperate areas or in the tropics, and the temperature regime in those areas would not normally permit the completion of more than one generation annually. However, it is interesting to note that in northern Australia, where there is a mid to late summer rainfall pattern, most species are apparently active at the driest time of the year, between August and December.

Host relationships

Perhaps the most clear-cut result of my many years' study of the biology of Australian Oecophorinae is their overwhelming dependence on the plant family Myrtaceae as larval food, especially the very large genus Eucalyptus. In striking contrast, only a small percentage of Australian Oecophorinae depend on the even larger genus Acacia (Mimosaceae). Within the Myrtaceae, all food-plant records are of the 'dry-fruit' genera, mainly *Eucalyptus*, but also Lophostemon, Angophora, Syncarpia, Melaleuca, Leptospermum and Kunzea. It is thought that these genera evolved within Australia from Gondwanan ancestors (White 1986), and have proliferated in this continent with the gradual onset of aridity. It is of

special significance that a high percentage of the Australian Oecophorinae feed as larvae on dead *Eucalyptus* leaves, a food source not exploited by most other Australian Lepidoptera, with the exception of the Epitymbiini (Tortricidae) and the Epipaschiinae (Pyralidae). It seems that the evolution of the Australian Oecophorinae has paralleled that of the 'dry-fruit' section of the Myrtaceae, mainly *Eucalyptus*, with an enormous multiplication of species adapted to a diversity of habitats, especially in sclerophyll forest, woodland, mallee and, in more arid areas, eucalypts growing along watercourses and on rocky outcrops.

Eucalypts produce considerable quantities of leaf and bark litter, shedding leaves freely for a variety of reasons, such as drought, wind, flushes of new growth, the effects of wild fire, insect attack, etc. The older leaves of most species are tough and leathery and, when relatively dry, are resistant to fungal breakdown and attacks from most invertebrates except termites. Here was a developing food source which was not seriously exploited by other organisms. In the Northern Hemisphere many Oecophorinae are known to utilise dead plant material as food, and the Gondwanan ancestors of the Australian representatives of the subfamily would also have had the capacity to exploit dead plant material. However, dead eucalypt leaves are especially poor in nitrogen and rich in phenolic compounds, including tannins, a potential disadvantage which has been overcome by many Australian oecophorines. It should be noted also that those species that feed on living eucalypt leaves exploit the mature leaves, not the soft new growth favoured by many other lepidopterous larvae. Mature living eucalypt leaves also have low levels of nitrogen and are rich in essential oils and phenolic compounds.

The few Australian families of flowering plants other than Myrtaceae, known to be utilised by occasional species of Oecophorinae include Mimosaceae (Acacia), Fabaceae (Dillwynia, Pultenaea), Epacridaceae (Monotoca, Brachyloma, Leucopogon), Proteaceae (Banksia), Lauraceae (Neolitsea), Euphorbiaceae (Drypetes) and Loranthaceae (mistletoes). Lichens have

been reported by Meyrick (1886) as the host of two Australian species (*Psaroxantha calligenes* and *Zonopetala decisana*), while dead sapwood is used by *Barea* Walker, *Machetis* Meyrick, and probably other related genera.

Few Australian oecophorine larvae are known to be coprophagous. Those of an undescribed species of Telanepsia Turner feed on possum droppings, living in vertical tunnels in the soil below a dung pellet and tunnelling into the pellet to feed. Two other species of Telanepsia have been reared recently from koala droppings (M. Horak pers. comm.). Unusual feeding behaviour is exhibited by the larvae of Trisyntopa, which occur in the nests of parrots. The larvae live in silk galleries spun in the floor of the nest chamber and feed on the freshly ejected faecal material of the nestlings, keeping the nest and nestlings clean. The larvae of T. scatophaga White live in the nest chambers of the golden-shouldered parrot Psephotus chrysopterygius in Cape York Peninsula (Turner 1923), and the hooded parrot P. c. dissimilis in the Northern Territory; the nest chambers are excavated from termite mounds. The larvae of T. euryspoda Lower have been found in the nests of rosella parrots (Platycercus) in tree hollows, and appear to have habits similar to those of T. scatophaga.

In the Wingia group of genera some information is available on the host relationships of 38 of the 91 genera recognised in this revision. Twenty-one of the genera have larvae feeding on living foliage, a much higher proportion than in known genera of other groups of Australian Oecophorinae. Seventeen of those genera use living leaves of Myrtaceae, usually Eucalyptus, but occasionally Leptospermum, Melaleuca, Kunzea, Lophostemon, Angophora and Syncarpia. The larvae of 14 genera feed. at least during part of their development, on dead Eucalyptus leaves and occasionally on dead Angophora or Syncarpia leaves. A total of 29 genera (76 per cent) are dependent on Myrtaceae. Only three genera (Epicurica, Parocystola and Sclerocheta), and a few species of Chrysonoma, are restricted to living phyllodes of Acacia, and only a single species, Tortricopsis pyroptis, regularly feeds on dead phyllodes of Acacia, but has also been recorded on the live foliage of Exocarpos (Santalaceae) and even the introduced gymnosperm Pinus radiata. There is a single record of Enoplidia simplex feeding on dead Acacia phyllodes, whereas this species usually uses dead Eucalyptus leaves. Three species of Tanyzancla have been reared from Epacridaceae (Monotoca, Brachyloma, Leucopogon), Endeolena xanthiella and Tortricopsis uncinella

from Pultenaea and Dillwynia (Fabaceae) respectively, Eochrois epidesma from mistletoes (Loranthaceae), E. callianassa and Acmotoma magniferella from Banksia (Proteaceae), Lophopepla asteropa from Drypetes australasica (Euphorbiaceae) and Callimima lophoptera from Neolitsea (Lauraceae).

It is a matter of interest to know how Australian oecophorine larvae are able to digest dead Eucalyptus leaf material, which is of such low nutritive value. Although there is no direct evidence, it is possible that these larvae, like termites, have a gut flora which assists in breaking down the dead material. This is a subject deserving attention. In some cases, of course, especially in moist situations, fungal mycelia are probably responsible for breaking down the dead leaves or may provide nutriment directly. Fungi are very likely to be involved in the utilisation of moist sapwood by the larvae of Barea and other genera, but many Australian oecophorines feed on dead leaves under humidity conditions too low to permit fungal growth.

Adult

The adults of Australian Oecophorinae at rest fold their wings in a characteristic way. Many arrange the wings in a steeply roofwise fashion, while others fold them more or less flat above the body. The antennae in the fully resting posture are pressed back along or beneath the fore wing close to the costa, whereas in a settled position prior to complete rest, or in an alert position, the antennae are held out at a broad angle in front of the head. Resting adults usually extend the fore legs in front at a fairly broad angle to one another, but some species, in which the fore tibiae and tarsi are dilated with scales (e.g. Callimima) (Fig. 403), or have a bright pattern matching that of the head, thorax and fore wings (e.g. Lophopepla) (Fig. 112), extend them in front and press them close together.

Although Australian Oecophorinae often have the fore wings cryptically patterned and coloured, many are relatively brightly coloured. In the Wingia group, pink or red colours appear in many genera, especially in Garrha, Euchaetis, Wingia, Prionocris, Eochrois and Lophopepla. Several genera, notably those which occur in dry sclerophyll forest, woodland and mallee, have yellow or orange-yellow fore wings, patterned in dark brown or black; this may well have an aposematic function. Outstanding examples are found in Chrysonoma, Mionolena, Endeolena, Echinobasis, Heteroteucha, Plectobela, Psaroxantha, Saphezona and

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the eggs are inserted in the tissues of the flower spikes. As the immature stages of *Phytotrypa* have not so far been discovered, the oviposition behaviour of the adults remains unknown.

Larva

The larvae of Oecophorinae all live in some kind of a shelter, which protects them from desiccation, extremes of temperature, and often from predators. Most of the Australian species which utilise living foliage form a shelter by joining one or more adjacent leaves with silk, and construct a cell or gallery of silk within. When many eggs are deposited together, the first-instar larvae are often semi-gregarious; the larvae of Ageletha are gregarious throughout larval life, living in silk galleries spun amongst a bunch of several living and dead eucalypt? leaves. Some species keep their shelters free of faecal pellets, while others incorporate their taecal pellets into the silk structure. The larvae of certain species of Philobota Meyrick, and a few other species, feed on the foliage of grasses, Including cereal crops. They live in vertical tunnels in the soil, coming to the surface at night to feed, and finally pupate in the gallery some five centimetres beneath the surface.

The majority of those species which feed on dead foliage also live in silk shelters spun between adjacent leaves, sometimes in the drier leaf litter on the ground, but more frequently in slightly moister situations. These include accumulations of dead leaves in the crevices or hollows of tree-forks, stumps, logs or rocks, close to the base of trees, stumps, stones or logs on the ground, behind loose bark on tree trunks, on palm or cycad fronds, on epiphytes, and beneath fallen branches. Certain species are very resistant to desiccation and are found between joined dead leaves still adhering to fallen twigs or branches, ceasing to feed when the foliage becomes too dry, and resuming when the leaves absorb moisture from dew or rain. A few species spin tubular silk galleries on the ground beneath the leaf litter, the gallery gradually increasing in diameter as the larva grows; pupation occurs in a much broader, loose section at the end of the gallery.

The construction of portable cases is a behaviour pattern occurring widely in the larvae of Oecophorinae, and is found both in species which feed on living and on dead foliage. In those larvae feeding on living foliage the cases range in form from the crude flat cases of *Chrysonoma fascialis*, to the cylindrical or

slightly flattened cases of Myrascia (Figs 677, 678), the short, hollowed out lengths of twig in Hemibela (Fig. 610), and the snail-like helical case of overlapping leaf fragments in Aristeis Meyrick, Provision for increasing the size of the case as the larva grows has been achieved in various ways. In Myrascia bracteatella, for example, the case, which is constructed of faecal pellets firmly fixed in position with silk, is enlarged by the larva cutting along one side and incorporating its larger droppings. The successive additions are clearly visible on the outside of the case by the various sizes of the faecal pellets used. In Hemibela progressively larger pieces of twig are cut off and hollowed out by the larva as it grows. In Aristeis the silk helical gallery is gradually increased in length and diameter and additional, progressively larger pieces of leaf are added to the outside.

Portable cases of those species which feed on dead leaves are commonly constructed by folding over or rolling a piece of leaf or bark and lining it with silk. In *Chezala* Walker, for example, the first-instar larvae feed between joined leaves in small galleries incorporating their faecal pellets. After the first ecdysis they cut out tiny pieces of leaf and fold it over, joining the edges with silk, and forming a roughly cylindrical case. It is then lined with silk. As the larvae grow, progressively larger pieces of leaf are cut out to form similar, larger cases. Pupation occurs within the final case after a firm silk cocoon is spun. In Garrha the first-instar larvae also feed between joined leaves, spinning small silk galleries. Soon after ecdysis they cut out tiny, irregular fragments of leaf, joining pairs of them at the edges with silk to form lenticular cases. To enlarge the case the larva discards one half of its case before attaching the other half to another leaf and cutting out a similar but larger piece to complete the case. At the next stage the smaller piece of the case is discarded and an even larger piece cut in the same way from another leaf to form the larger case. This procedure is repeated until the larva reaches maturity, when it pupates within its final case without a cocoon, the pupa being attached by the cremaster to the silk lining.

Feeding on dead plant material is usually regarded as a plesiomorphic trait and this may well be so in some genera of Australian Oecophorinae. However, there is evidence that the utilisation of dead eucalypt leaves by certain genera of the *Wingia* group is a specialisation, developed in response to the tendency of *Eucalyptus* to shed its older leaves in response to adverse weather or other factors.

In Heliocausta, for example, the eggs are apparently laid in the eucalypt canopy where the young larvae must feed during the first couple of instars. At that stage each larva moves to a pair of adjacent undamaged leaves, joining them weakly with silk before severing the two petioles close to the leaf blades, and allowing the pair of leaves enclosing the larva to fall to the ground (Fig. 507). The larva then completes its development feeding on the pair of wilting or dead leaves. A somewhat similar but less spectacular behaviour pattern is exhibited by Antipterna enanthes (Figs 581, 582), in which the young larva folds over the tip of a living Eucalyptus leaf in the tree canopy, beneath which it remains and continues to develop after the leaf is shed. In Ocystola the larva makes a very roomy shelter by joining two living eucalypt leaves with silk; one half of the shelter carries a characteristic longitudinal ridge along an inner groove cut by the larva (Fig. 667). Within the shelter it constructs a small, flattened, elliptical case of faecal pellets and silk, with an opening slit at each end through which the larva protrudes to feed (Fig. 668), eroding the inner surfaces of the shelter. Late in its development the larva cuts off the outer half of the two leaves incorporating the shelter, allowing it to fall to the ground. It then continues to feed on the wilting and dead leaf material and finally pupates in the inner case. Such complex behaviour patterns apparently ensure that larvae feeding on mature living leaves in the tree canopy are able to complete their development should the leaves be shed.

By living in shelters, oecophorine larvae frequently avoid predators but, should they be exposed, few attempt to avoid capture by wriggling rapidly or dropping to the ground on a strand of silk. If disturbed a few of those which feed on living leaves of Myrtaceae regurgitate gut contents containing the pungent essential oils from the food plants on to the source of irritation. The larvae of Myrascia have refined this means of defence by evolving a diverticulum of the fore gut (Fig. 27), in which are stored the pure Melaleuca or Leptospermum oils ingested with their food (Common and Bellas 1977). The oil is not only regurgitated on to the source of disturbance but spreads over the body of the larva. M. megalocentra, which feeds during its early life in a rather flimsy web, is also aposematically coloured dull red with yellow pinacula. Late in larval life it constructs a portable case from strips of Melaleuca leaves joined with silk, whereas in M. bracteatella the larva spends most of its life in a case formed

from faecal pellets and silk. At intermediate ecdyses these larvae moult the cuticular lining of the diverticulum as well as the remainder of the fore gut, and at the final ecdysis the entire diverticulum, replete with oil, is moulted along with the remaining cuticle. The sac of oil remains attached to the exuviae alongside the pupa within the case (Fig. 680).

Pupa

Whether or not the pupa is contained in a cocoon, it is usually fastened by the cremaster or anal hooked setae to the silk lining the cocoon or shelter. It is often so securely fixed that it is difficult to remove it from its cocoon without breaking off the distal spikes of a specialised cremaster. The shrivelled finalinstar cuticle of the larva remains in the cocoon and, in Myrascia, the moulted diverticulum of the fore gut, replete with essential oil from the food plant, forms part of the exuviae. Clearly a tough-walled cocoon. shelter or case affords the pupa a high degree of protection from potential predators. In Myrascia, however, the presence of the sac of pungent oil is thought to have an additional protective function: should a predator succeed in opening the case it would be likely to rupture the sac and be repelled by its contents.

As adult eclosion in the Oecophorinae and most other Gelechioidea occurs within the cocoon or shelter, provision has to be made by the larva to enable the freshly emerged adult to escape promptly. Often a slit-like opening at one end of the cocoon, not easily penetrated from without, is provided during cocoon construction. Occasionally, as in some species of Ocystola, in which the adults have to escape not only from the inner case but also from the outer shelter formed by the joined leaves, a small hole is made by the larva in one of the leaves forming the shelter and covered by a thin septum of silk. It is remarkable that the scale vestiture of adults in which eclosion occurs within the cocoon or shelter is not damaged during their escape. No doubt the soft, unexpanded condition of the appendages ensures this. Soon after the adult escapes from the cocoon or shelter the wings are held back to back until they are fully expanded, when they very soon assume the normal folded position while the wings continue to harden.

Pests and synanthropes

Few Australian Oecophorinae have been implicated in economic damage to agricultural crops, pastures, forests or stored products. However, *Philobota productella* and related