

3. Biology

Life histories

The Olethreutinae have by far their greatest diversity in the warmer and wetter parts of Australia, where rain or monsoon forests are their dominant habitats. Interpretation of label data in collections suggests that the great majority of species have several generations per year, especially in the moist tropics and subtropics. Species with a wide distribution and clearly several generations in the north are nevertheless rarely collected during winter in the temperate region, suggesting a slowing of their development during the cooler months. However, there may well be univoltine species in cooler and drier regions, especially among the Eucosmini in temperate southern latitudes or higher altitudes and possibly among the Grapholitini in seasonally dry habitats. No work has been done to establish whether any of the Australian Olethreutinae have a strict diapause to accommodate a seasonal food supply, such as availability of suitable fruit or seeds for some of the borers.

The flat tortricid ovipositor lobes are characteristic for the family and possibly an adaptation for a specific egg-laying mode. Nearly all tortricid eggs are round to oval, strongly flattened, dome-shaped to scale-like. In contrast to the Australian Tortricinae (Powell and Common 1985), there is very little information about olethreutine oviposition. Olethreutine eggs are usually deposited singly on the host plant, rarely in small, irregular clusters (Peterson 1965; van der Geest and Evenhuis 1991). In some species and genera with modified, telescopic ovipositors, the eggs are inserted into crevices in the host plant. None of the Australian species have ovipositors that would suggest a piercing mode of oviposition.

Feeding habits within the Olethreutinae are very diverse, ranging from leaf rolling and spinning foliage together to boring in shoots, fruit, seeds, stems, roots and woody branches. Some produce blister mines in leaves. The larvae of a few Australian species including *Spilonota constrictana* (Meyrick) live in a portable case made of hollowed flower buds or seed capsules spun together to form a tube (Fig. 730). Unlike some Tortricinae, none of the Australian Olethreutinae have been reared from dead plant tissue, i.e. leaf litter.

The ancestral tortricid larva is presumed to have been an external feeder, given the presence of an anal fork in all three tortricid subfamilies (Horak 1989). This structure serves to eject faeces from the feeding shelter and has frequently been lost in groups with internally feeding (i.e. boring) larvae. Had an internally feeding larva without the anal fork been ancestral, it would be very unlikely that later derived external feeders in all three subfamilies would have developed exactly the same type of anal fork. A considerable proportion of Australian olethreutine larvae are borers, often in seeds and fruit: one of the main reasons for their economic importance. However, both feeding modes, leaf rolling and boring, are found in several olethreutine tribes, and parallel shifts from one mode to the other have obviously occurred. It had been hoped that mapping internal and external feeding onto the cladogram resulting from this study would provide an indication of the shifts in feeding modes, but the cladistic analysis turned out to be too flawed to expect critical insights in this respect. However, the trends within tribes strongly suggest that: 1, external feeding is the more ancestral state within those tribes using both feeding modes, except possibly for the Grapholitini, and 2, switches between the two feeding modes have happened repeatedly, even within a tribe. In both the Microcorsini and Bactrini all larvae are borers, the former endosperm feeders in fruit and nuts and the latter predominantly in stems, often of monocotyledons. The known larvae of the Australian Olethreutini are nearly all leaf rollers or leaf tiers except for some species within *Lobesia* Guenée, *Ophiorrhada* Diakonoff, *Gnathmocerodes* Diakonoff, and *Gatesclarkeana* Diakonoff, genera from four different genus-groups. The feeding mode is known for only a few enarmoniine genera, but it ranges from leaf rolling to fruit boring, and in *Loboschiza koenigiana* (Fabricius) both feeding modes occur in the same species. The larvae of *Ancylis* Hübner, probably the sister group to the remaining Enarmoniini, are usually leaf rollers, but one Australian species produces blotch mines in *Banksia* leaves. The Eucosmini also include external as well as internal feeders, with the more ancestral groups (*Epinotia* Hübner) predominantly leaf