

Morphology and behaviour of the larva of *Calindoea trifascialis* (Lepidoptera: Thyrididae), a chemically-defended retreat-building caterpillar from Vietnam

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Abstract

The final-instar larva of *Calindoea trifascialis* is described and illustrated for the first time, including chaetotaxy. All instars have paired fleshy lateral protuberances associated with large exocrine glands on the first abdominal segment. When disturbed, the larvae secrete defensive allomones that deter ants. The larvae construct tent-like feeding retreats and skeletonize the leaves of *Dipterocarpus tuberculatus* while concealed within the retreat; retreats of increasing size are constructed throughout larval development. When feeding is completed, the final-instar larva constructs a pupation retreat. This leaf roll falls from the plant and is capable of movement prior to pupation. The morphology and larval retreats of an unidentified species of thyridid from Queensland, Australia are also illustrated and discussed in the context of the new information concerning *C. trifascialis*.

Key words: abdominal protuberances, allomones, exocrine glands, defense, Dipterocarpaceae, weaver ants, Vietnam, Australia

Introduction

Thyrididae are mainly tropical and subtropical moths with about 760 described species currently classified in 4 subfamilies (Dugdale *et al.*, 1999). The biology and phylogenetic affinities of this family are poorly understood. Although thyridids are often associated with the Pyraloidea (e.g., Neunzig, 1987), no synapomorphies have been identified that support this assignment (Scoble, 1995; Dugdale *et al.*, 1999). Thyridid specimens are

rare in collections and usually seen in small numbers in the field (Whalley, 1976). It is therefore not surprising that very little is known about their life history and immature stages and that what is known is based on a few Palearctic and Nearctic species (Hasenfuss, 1979, 1980, Thiele, 1986, 1997). The paucity of information on immature stages of tropical thyridids was most recently highlighted by Li (1996). In his review of the biology of Oriental thyridids, Li noted that only seven species were represented in the larval collection of the Natural History Museum (London). Li (1996) provided ecological notes for eleven species (in eight genera) of thyridids in Hong Kong and recorded immature stages for eight species, although the morphology and chaetotaxy of the larvae were not discussed. He recorded regurgitation when disturbed in one species and also noted that another emitted a foul smell when disturbed. Furthermore, he observed that six species (in 5 genera) were leaf rollers. About 50 species of Thyrididae are known from Australia, and the few known larvae also feed in shelters on leaves (Common, 1990).

Given the rarity of thyridids in most habitats, it was therefore noteworthy to find large numbers of larvae of *Calindoea trifascialis* (Moore) in the dry dipterocarp forest of southern Vietnam. This provided the opportunity to describe and illustrate the final-instar larva and pupa of *C. trifascialis* and to provide detailed information on the construction of both feeding and pupation retreats in this species. The larvae of *C. trifascialis* are remarkable in both morphology and behaviour. All instars have lateral protuberances on the first abdominal segment and have associated exocrine glands that produce a cyanogenic defensive secretion (Darling *et al.*, 2001). All larval instars construct tent-shaped feeding retreats on the leaves of the host plant. Both of these traits are apparently unique in Lepidoptera, and will be discussed in the context of living in the dry dipterocarp forest of Southeast Asia.

Methods and materials

Field studies and collections were made in southern Vietnam, Yok Don National Park between 22 May and 1 June 1997 and 4-9 June 1999 (Dac Lac Province, ca. 2 km SE Ban Don, 12°53'N, 107°48'E; ROM 973601, 993601). The dominant vegetation is dry dipterocarp forest with widely spaced trees and extensive grass cover, including bamboos (Laurie *et al.*, 1989). The dominant tree species in these fire-climax savanna woodlands are fire-tolerant species of *Dipterocarpus* Gaertner and *Shorea* Roxb. ex Gaertner (Dipterocarpaceae). These dipterocarps often form single species or codominant stands that are deciduous for more or less prolonged periods during the dry season (Ashton, 1982). In both years field work was conducted at the beginning of the rainy season when the trees were fully leafed out. Although 1997 was much drier than 1999, the caterpillars were abundant in both years and were the most conspicuous herbivores in the dipterocarp forest.

Calindoea trifascialis is currently known only from Burma, Thailand, and the Andaman Islands and its only recorded host plant is *Dipterocarpus tuberculatus* Roxburgh (Tuck *et al.*, 1994). At Yok Don, larvae were collected only on the leaves of young plants or suckers of *D. tuberculatus* 0.5 to 1.5 m above the ground. Caterpillars were much rarer on mature trees of this species and were not observed on other trees or shrubs. Leaves were collected and returned to the park headquarters for observation, experimentation, and photography. Caterpillars were preserved in EtOH for morphological study and for possible isolation of glandular secretions; 12 were reared to adults and identified as *Calindoea trifascialis* (det. B. Landry, 1997; M. Shaffer, 2001). Voucher specimens of adults and larvae were deposited in the entomology collection of the Royal Ontario Museum (Toronto), the Canadian National Insect Collection (Ottawa), the Natural History Museum (London), and the Institute of Ecology and Biological Resources (Hanoi). Videotapes of retreat construction behaviour were made 23-27 June 2000 and are filed in the Royal Ontario Museum (DCD Vietnam 2000, videotapes 3, 5).

Natural history

Eggs and oviposition behaviour were not observed but are assumed to be on the young leaves of *D. tuberculatus*. High, conical retreats ('tents') were common on the leaves of *D. tuberculatus* (Figs. 1, 2, 6). Tents of various sizes were found, ranging in height from about 5 mm to 50 mm. There is a strong correlation between the size of the larva (length, head capsule width) and the size of the tent (height, surface area), but it is uncertain if there is a 1:1 correspondence between instar and tent size (K. Bailey, unpublished report). Caterpillars feed exclusively within the tents, methodically skeletonizing the enclosed upper leaf surfaces (Fig. 2), starting at the apex of the tent and working down to the base. Frass accumulates within the tent (Fig. 2) and when feeding is completed the larva cuts an exit hole near the base of the tent (Fig. 6, arrow) and constructs a new, larger retreat. The total number of feeding retreats constructed during the larval instars was not determined but must be greater than four based on the distribution of larval size and retreat size observed. No retreat construction was observed in the field during the day suggesting that this normally occurs at night. However, damaged tents (Fig. 2) were quickly repaired with silk during the day (Fig. 5) and new retreats were constructed during the day if the larvae were evicted from the retreat and/or transferred to another leaf. When feeding was completed the final-instar larva (Fig. 3) constructs a pupation retreat in the form of a leaf roll (Fig. 6, left; 7). The completed leaf roll detaches from the leaf and falls to the ground and the caterpillar remains active within the retreat for up to 5 days. Under ambient conditions, the adult moths (Fig. 8) emerged about 17 days later (K. Humphreys, unpublished report).



FIGURES 1-8. *Calindoea trifascialis*. 1-7. Final-instar larvae and retreats. 1. Feeding retreat (tent) on leaf of *Dipterocarpus tuberculatus*. 2. Larva and feeding damage exposed by opening retreat. Note: accumulated frass (right) and partial cutting of leaf surface (arrow). 3. Habitus of final instar larva. Note: apices of forward-directed lateral protuberances with glandular secretions (arrow). 4. Oblique view of mid stage in construction of feeding retreat, caterpillar cutting fifth segment of leaf. Note: silk struts hold the leaf in an elevated position. 5. Repairing an opened retreat. 6. Comparison of feeding retreat (right) and pupation retreat (left). Note: exit hole in feeding retreat (arrow). 7. Posterior view of nearly completed pupation retreat, the bottom is not completely sealed. Note: Silken struts. 8. Newly emerged adult.

Immature stages

I was unable to determine the number of larval instars because oviposition was not observed and individual larvae were not reared to pupation. All larvae were similar in overall morphology and all had distinct lateral protuberances on the first abdominal segment (length 5-25mm, n=80). The descriptions and morphological illustrations are based on two larvae, length 21mm and 22mm. Both of these are near the maximum of the size range and are regarded as final-instars.

Final-instar larva (Figs. 2-5, 9, 10)

Head capsule orange-brown (amber) in color, body translucent yellow, appearing green due to ingested plant material (Figs. 2-4). Primary setae arranged on light brown pinacula; secondary setae absent. Maximum length 25mm.

Head (Fig. 9A, 10A-C): Hypognathus. Adfrontals extended two-thirds distance to epicranial notch. Frontoclypeus without a suture, extended about one-half distance to epicranial notch. Mandible 5-toothed, distal three stronger with distinct median ridges (Fig. 10C). Labrum with about 10 stout setae, smaller setae also present. Six stemmata present. Arrangement of setae and pores as in Figs. 10A, B.

Thorax (Fig. 9A): Prothorax (T1) with distinct shield; L-group bisetose on a single pinaculum, separate from prothoracic shield; SV group bisetose, SV1 about twice as long as SV2; spiracle large, oval. Segments T2 and T3 with D1, D2 and SD1, SD2 each on separate pinacula; L-group bisetose, L2 on a distinct pinaculum; SV bisetose.

Abdomen (Figs. 2-5, 9B-D, 10D-F): Segments A1-7 each with D1, D2, and SD1 each on separate pinacula. Segment A1 with SV bisetose, on a single pinaculum; A2 with SV trisetose, on a single pinaculum; A3-A6 with SV trisetose, associated with prolegs and not on pinacula; A7 with SV trisetose, with a bisetose pinaculum and a smaller ventral seta; A8 and A9 with a single SV seta, not associated with pinacula. Segment A1 with long, setose, club-shaped antero-lateral directed fleshy protuberance arising between the separate pinacula with L1 and L2 (Figs. 2-5, 9B); apex of protuberance bilobed with two distinct setal types (Fig. 10F) long and peg-like at apices and short and slender between lobes and on shaft. Internally, a large, folded exocrine gland is attached to the base of the protuberance (Fig. 10F), and the gland is closely associated with the A1 tracheae and spiracle (Fig. 10E). Prolegs with crochets arranged in a circle, multiserial, biordinal (Fig. 10D).

Remarks: The larva of *C. trifascialis* conforms to the diagnoses of Thyrididae provided by Neunzig (1987) and Common (1990); the L group is bisetose on T1 and the crochets on the ventral prolegs are irregularly biordinal and arranged in a circle. As is other Siculodinae, the larvae are fairly slender (Common, 1990).

The most remarkable feature of the *C. trifascialis* larva is the paired lateral protuberances on A1 and the associated glands. It is impossible to determine the distribution of these structures within the Siculodinae, which includes *Calindoea*, because of the paucity of information on morphology of thyridid caterpillars. Li (1996) presented natural history

information for 11 species (in 8 genera) of Hong Kong thyridids and mentioned the larvae for 8 species (in 6 genera), including *C. argentalis* (Walker). No mention was made of lateral protuberances on A1 and none are present in his published photographs. These structures appear to be unique in Thyrididae and no references can be found to similar structures in any other lepidopteran larvae.

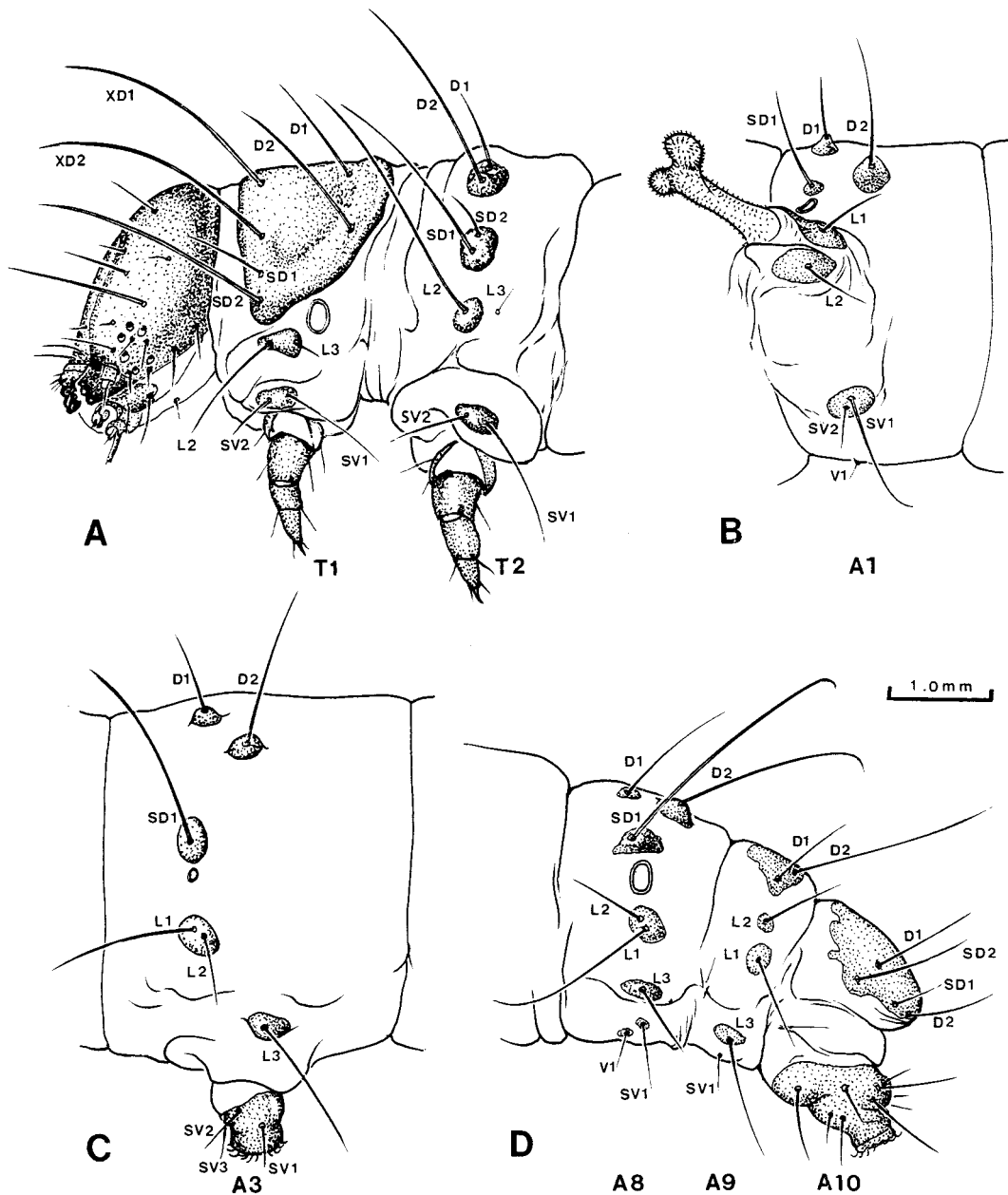


FIGURE 9. Structure and chaetotaxy of final-instar larva of *Calindoea trifascialis*. A. Head, T1, T2; B. A1; lateral. C. A3; lateral. D. A8-A10; lateral.

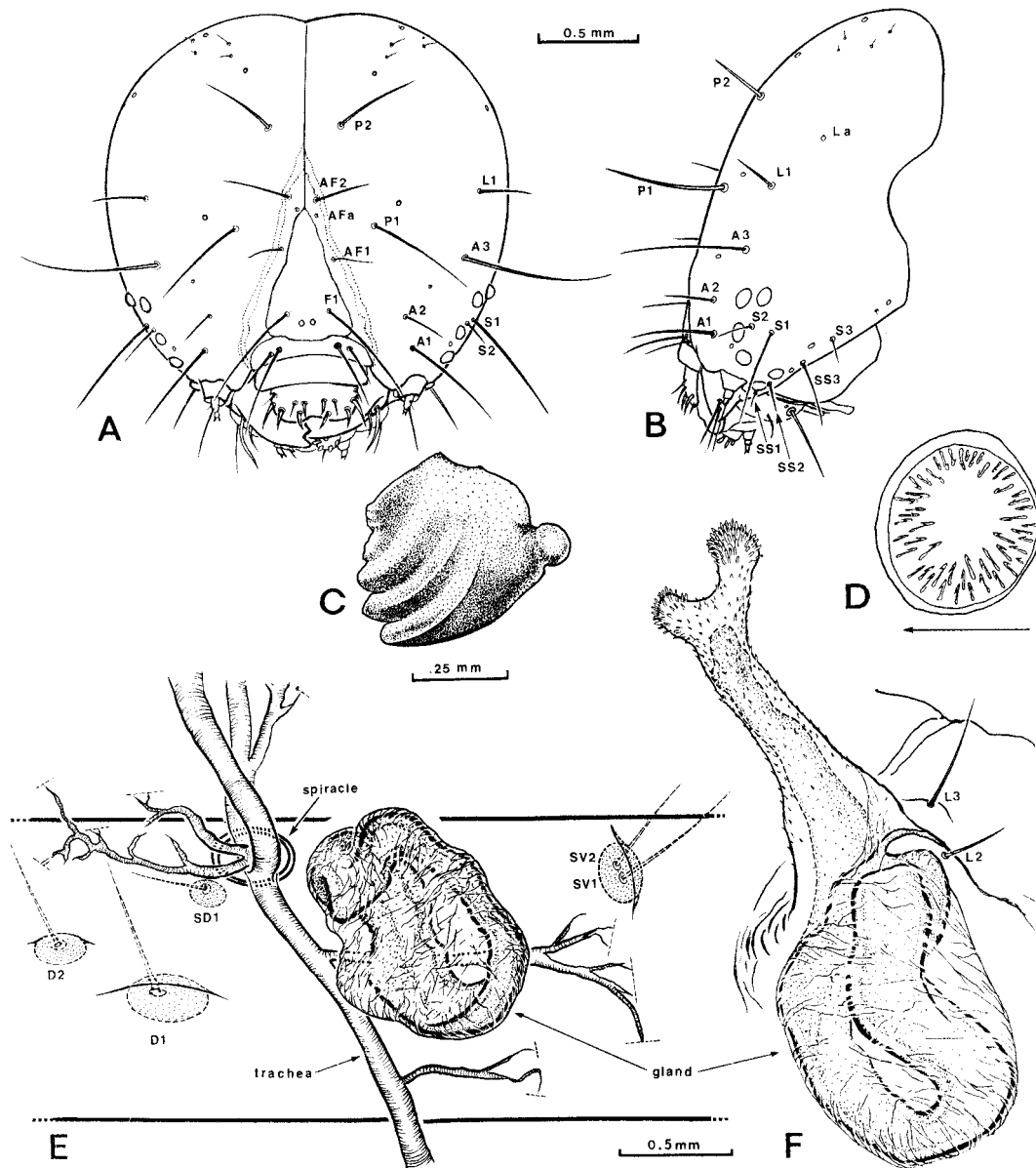


FIGURE 10. Structure and chaetotaxy of final-instar larva of *Calindoea trifascialis*. A. Head; frontal. B. Head; lateral. C. Mandible. D. Crochets; arrow pointing to meson. E. Gland associated with abdominal protuberances; internal structure. F. Gland and A1 protuberance, lateral view.

Pupa (Fig. 11)

Known known only from exuvia. Length about 12 mm. Dark brown, heavily sclerotized. Distribution of setae and spiracles as in Fig. 11. Labial palpi not visible. Mesothoracic spiracular opening large, semicircular, surrounded anteriorad by band of dense golden-yellow pustules and posteriorad with deep indentation in the cuticle; the cuticle

and pustules are invaginated cephalad to form a hollow ball-shaped chamber (Fig. 11D). T3 spiracle also in a deep indentation of the cuticle. Apparently functional spiracles visible on segments A2-7, with A7 distinctly the largest; vestigial spiracle present on A8. A8 and A9 separated dorsad by a distinct crenulate furrow, extended laterad to a large, deeply impressed fovea (Fig. 11A, B). Cremaster present ventrad, with 2 rows of strong, apically curled (fiddlehead-shaped) setae, anterior row with 6 setae, posterior with 4 setae.

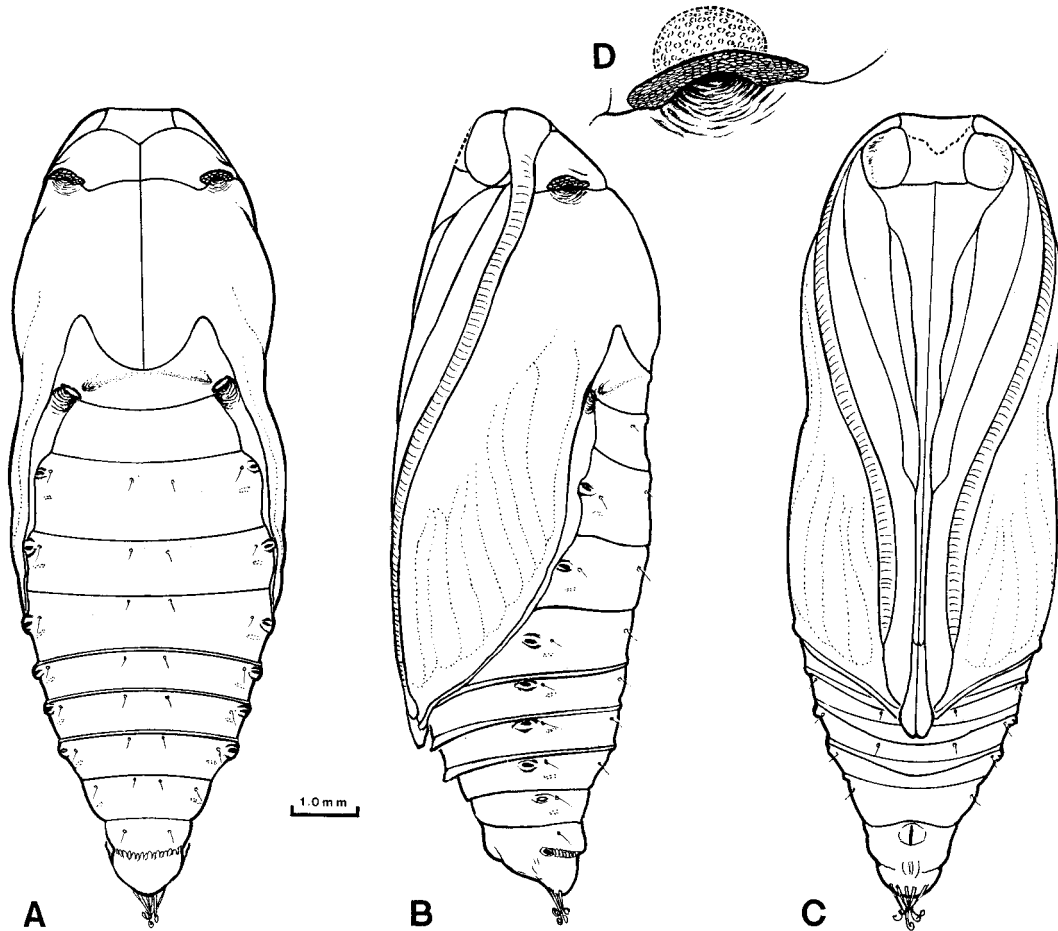


FIGURE 11. Structure of pupa of *Calindoea trifascialis*. A. Dorsal. B. Lateral. C. Ventral. D. Detail of spiracular area, internal chamber indicated by broken line.

Retreat Construction

Larval or feeding retreat (Fig. 12a-d)

The larva begins construction of the larval retreat in an exposed position on the upper surface of the leaf. The mouthparts are moved in broad arcs over the leaf surface and a

thin layer of silk is laid down. Next, a broad semi-circular arc is cut in the leaf surface, starting at an approximately 60 degree angle to the leaf margin (Fig. 12a; see also Fig. 2). A heavy strut of silk (1) is attached to the leaf surface and midway along the cut edge, pulling the cut portion of the leaf above the leaf surface. The larva remains within the folded leaf, only partially exposing itself while cutting the leaf and attaching silk (Fig. 12b; see also Fig. 4). Subsequent cuts form a deep arc into the interior of the leaf; and cutting alternates with attaching silk struts. Subsequent silk attachment points shift inward on the cut portion of the leaf and the subsequent attachment points on the leaf surface shift toward the leaf margin (2, 3, etc; see also Fig. 4). The result is the folding of the leaf margin back on itself and these edges are sealed with silk (Fig. 12c; see also Fig. 5) to form what will eventually be the apex (X) and vertical surface of the cone. Cutting continues until the caterpillar can pull the retreat into a vertical position (Fig. 12c) with the cut edges resting on the leaf surface (dotted line). To facilitate erection of the cone, the larva partially cuts or scores the final one-third of the semi-circular arc (Fig. 2, arrow). Silk is then used to secure the cone-shaped retreat firmly to the leaf surface (Fig. 12d). The construction of a feeding retreat takes about 3 hours. Figure 13 provides a template and step-by-step directions for construction of a feeding retreat.

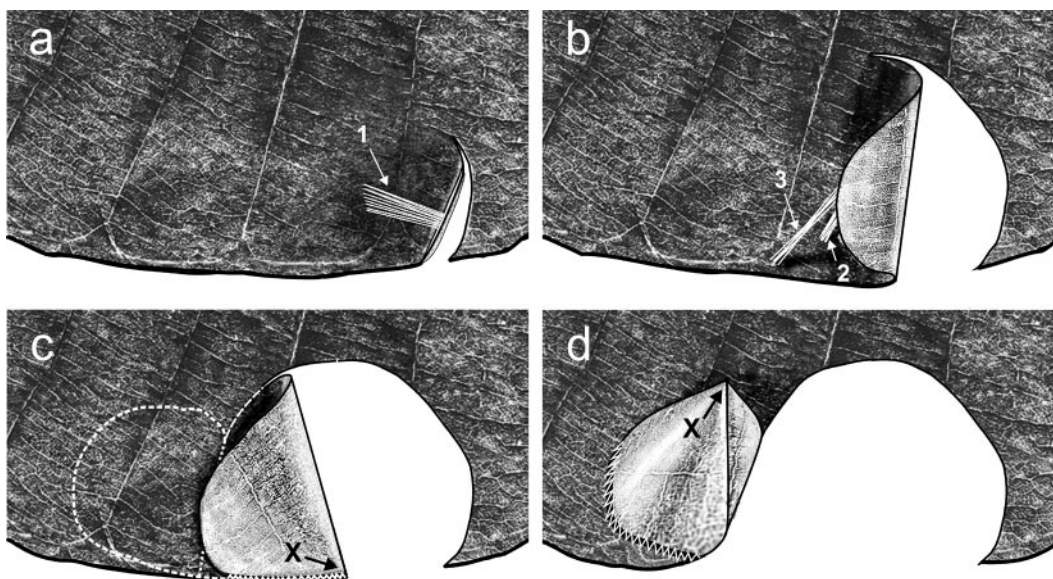


FIGURE 12. Steps in retreat construction. a-d. Feeding retreat. See text for discussion. 1-3 successive silk struts; X, apex of retreat. e-h. Pupation retreat. See text for discussion.

The larva feed by skeletonizing the inside of the retreat (i.e., the upper leaf surface). Feeding is usually restricted to the raised surfaces (Fig. 2); feeding damage was not observed on the 'floor' of the retreat. Frass accumulates on this horizontal surface and is

not removed from the tent (Fig. 2). When the vertical surfaces are consumed a exit hole is made (Fig. 6, arrow) and either a larger feeding retreat, or a pupal retreat, is constructed.

When feeding retreats are opened, the larvae either quickly repair the damage by sealing the leaf margin to re-erect the tent (Fig. 5), or immediately begin construction of new retreat. Retreat construction must normally occur at night; it was never observed in the field during the daylight hours.

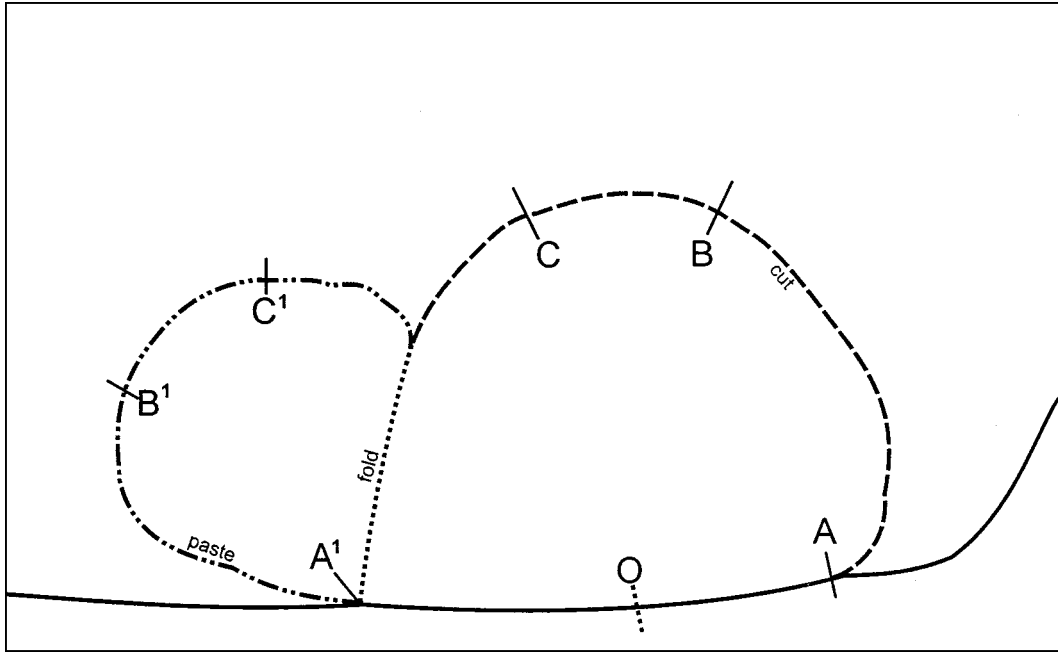


FIGURE 13. Template for construction of feeding retreat. Photocopy and follow these steps. 1. Cut out leaf margin. 2. Cut leaf from A to B to C to midpoint between C and C'. 3. Fold A to A' and seal from O to A/A'. 4. Raise cut portion and attach to leaf surface with C to C', and B to B'.

Pupal retreat (Figs. 14e-h)

The larva also begins construction of the pupal retreat on the upper surface of the leaf. The mouthparts are moved in broad arcs over the leaf surface and thin layer of silk is laid down. Next, a tight semi-circular arc is cut in the leaf surface, starting at an approximately 45 degree angle to the leaf margin; thick struts of silk are used to raise and secure the cut portion of the leaf (Fig. 14e). Subsequent cuts form a gradual arc roughly parallel to, but eventually converging on the leaf edge; the alteration of cutting, rolling, and adding silk struts encloses the larva in a complete tube (Fig. 14f). The cutting stops when the leaf roll is about its own diameter from the leaf margin; the larva is now inside about two complete rolls of leaf (Fig. 14g). The larva then moves partially out of the leaf roll and makes a cut at the nearby leaf margin (Fig. 14g; dotted line). An inverted J-shaped cut is made from

the margin to the interior and a semi-circular cap is cut above the top end of the leaf roll; the leaf roll is now attached by only 1-2mm of leaf. Then, using its mandibles and silk, the larva folds the cap in place over the end of the tube and secures it in place by adding silk from the inside (Fig. 14h). Finally, the larva turns around in the leaf roll and seals the distal end with silk (Fig. 7). The larva switches position within the leaf roll a number of times, adding silk and securely sealing the tube. The construction of a pupal retreat takes between 2-3 hours. After construction is complete the larvae 'jump' inside the leaf roll and which eventually detaches the pupal retreat from the leaf.

In one construction event observed in detail (larva #4, length = 21mm, retreat height = 37mm), 7 individual cuts were made (13, 10, 14, 14, 22, 19, 18mm). The total time taken to construct the retreat was 2:50 hrs.

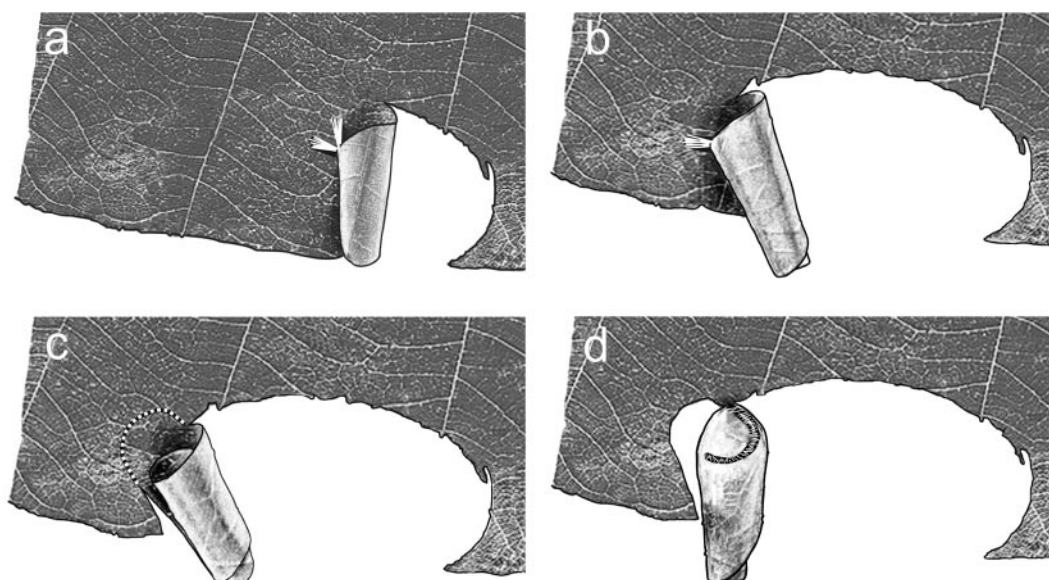


FIGURE 14. Steps in pupal retreat construction., a-d. See text for discussion.

Larval behaviour

Allomones and defense

The larvae have a strong lemony odour, particularly when disturbed. When pinched on the distal abdominal segments with forceps, the larvae raise backwards and place the apex of one of the abdominal protuberances in contact with the forceps. At the same time a clear liquid quickly spreads along the length of the protuberances (Fig. 3). There is also a noticeable increase in the intensity of the odour. A 'taste test', using either contacted forceps or a larva, results in a localized numbing of the human tongue which last for 10-15 seconds (n=3 observers). Weaver ants (*Oecophylla smaragdina* Fabricius) are very com-

mon in the study site and were used to assay the effectiveness of the defensive chemicals. Feeding retreats, both opened and intact, were avoided when placed on an ant foraging column (n=3, videotape 5) and even larvae removed from the tent and placed on the foraging trail were able to move with impunity among the ants (n=2, videotape 5). However, when dropped directly on the ants, the larvae were attacked and bitten (n=4). The response by the caterpillar was immediate and similar to the trials with forceps; the lateral protuberances were deftly moved to contact the ants, most of which immediately backed off and began grooming. On three occasions an ant was immobilized on contact with a lateral protuberance. Another bioassay, using an unidentified earthworm, also suggests chemical defense. A 15 mm piece of earthworm dabbed repeatedly on a *C. trifascialis* larva was avoided by the foraging weaver ants but an undabbed control was immediately attacked and carried away (n=1; videotape 5). These observations are consistent with a protective function by the glandular secretions and suggest that they are defensive allomones.

Pre-pupation behaviour

Activity does not stop when the leaf roll reaches the ground and the larvae were active within the leaf rolls for 3-5 days. They cause the leaf rolls to jump repeatedly, with both a vertical and horizontal displacement. Individual jumps are about one-third of the length of the pupal retreat and are the result of the larvae explosively recoiling backwards while attached to the inside of the retreat by the crochets on the last pair of prolegs (videotape 5). Movement can be forward or backward as a result of the larva switching its orientation within the retreat. The average distance traversed (i.e., displacement) per unit time is 83.5 cm in 315 seconds (n= 21), or about 1 metre in 6 minutes (K. Humphreys, unpublished report.). Pupation occurs within the retreats, almost certainly in leaf litter beneath the host tree.

Note on an Australian species of Thyrididae

A single caterpillar was collected from a conical leaf roll on a sapling of *Dysoxylum pettigrewianum* F.M. Bailey (Meliaceae) in a complex mesophyll vine forest in north Queensland on January 28, 2000 (Coconut Beach Rainforest Resort, Cape Tribulation, 16°06'30"S, 145°27'12"E; ROM 2000017). The leaf roll was on the underside of the leaf and similar in shape and orientation to fig. 23B in Li (1996). No other larvae were found on the sapling and a 45 minute survey of the canopy of an emergent *D. pettigrewianum* using the crane at the nearby Australian Canopy Crane Research Facility was unsuccessful in locating additional specimens. Many leaves had the characteristic leaf damage caused by *Calindoea* larva, but apparently had already completed their larval feeding. The habitus of the larva (i.e., shape, colour) suggested *Calindoea trifascialis* and closer examination revealed lateral protuberances on the abdomen. However, these protuberances were eversible (Figs. 14, 15) and only visible only when contact was made with the larva; a exu-

date was clearly visible at the apex of the protuberances. The larva produced only a faint odour, much weaker than the Vietnamese species, and did not numb the human tongue. The larva was removed from the leaf roll and the construction of a new retreat was videotaped (DCD Australia 2000, videotape 1). This videotape and photographs of retreat construction are archived at the Royal Ontario Museum. Construction of the leaf roll followed the initial steps described above for the construction of the pupation retreat (Figs. 11e-f), except that the leaf edge formed a tight cone (Fig. 16). When completed, the cut edge was attached to the undersurface of the leaf with silk (Fig. 17). Three similar retreats were constructed before the larva was preserved. Opening the retreats revealed that the larva was feeding on the first cut surface of the leaf, not by skeletonizing but by consuming the entire leaf. The chaetotaxy of the preserved larva is almost identical to that described above for *C. trifascialis*, the only differences are the shapes of the pinaculae and the position of seta L3 on segment T2 (more dorsal in the Australian species). In addition, the cranium is white (cf. amber in the Vietnamese species). Three species of *Calindoea* are recorded from Australia (Shaffer and Nielsen, 1996) and all three are known from the Cape York Peninsula (N. Queensland) and may also occur in Cape Tribulation (E. S. Neilson, pers. comm.). Rearing studies will be needed to associate these larvae with any of the described species.

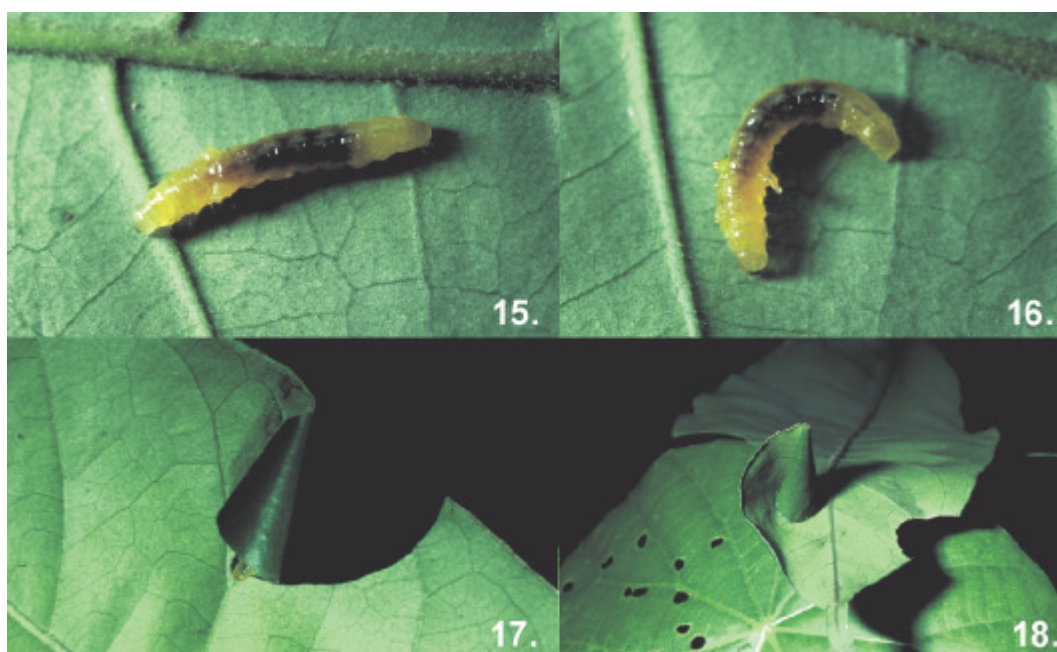


FIGURE 15-18. Larvae and larval retreat of unidentified species of Thyrididae from Queensland, Australia. 15. Habitus of larva with abdominal protuberances concealed. 16. Habitus of larva with abdominal protuberances everted. 17. Mid-stage in the construction of larval retreat. 18. Completed larval retreat. Note: retreat is on underside of leaf.

Discussion

Although there is relatively little information concerning the behaviour of thyridid larvae, it is almost certain that the tent-like feeding retreat of *Calindoea trifascialis* is an evolutionary novelty. All known larval retreats are leaf rolls, either conical or cylindrical (Common, 1990, fig. 6 and Li, 1996, figs. 5-7, 12, 14-23) and similar to the pupal retreats constructed by *C. trifascialis*. High tent-like retreats, enclosing a large, open chamber, have not been reported. There are also no previous illustrations or descriptions of the abdominal processes in Thyrididae. Li (1996) discussed 8 species and provided excellent habitus photographs of 6 of these, which would have shown these structures if they are present and permanently everted as in *C. trifascialis*. The eversible processes of the Australian species may provide an explanation. Protuberances may be more widely distributed in Thyrididae but unreported if they are everted only when disturbed. This would also provide an explanation for the frequent remarks about the possibility of chemical defense in thyridids (Li, 1996). There are species that "emit a foul smell resembling a stinking bug" and another that "emitted a choking smell so strong that it was still quite pungent at a distance of one metre" (Li, 1996). These odours may be associated with allomones produced by homologous abdominal glands. Defensive glands are rare in Lepidoptera larvae, except for the well-known case of prothoracic osmeterium in Papilionidae (Scoble, 1995). In moth larvae, the best studied cases are in Notodontidae where formic acid is released from glands in the prothoracic region (Eisner *et al.*, 1972; Weatherston *et al.*, 1979, 1986), although there is some uncertainty about the function of the secretions in various species. The discovery of abdominal glands and defensive allomones in Thyrididae adds considerably to the defensive repertoire of the Lepidoptera.

It is interesting to speculate whether the two extraordinary features of the larval biology of *Calindoea trifascialis*, tent-like feeding retreats and abdominal processes with associated glands, are adaptations to living in the dry, dipterocarp forests of southeast Asia. As evolutionary novelties, such speculation is appropriate. Dipterocarp forests are open habitats with direct sunlight and high temperatures and contrast markedly with the more mesic collecting localities of Li (1996). This begs the question of the function of the feeding retreats or tents. There are at least three possible reasons to make a concealed feeding retreat: protection from natural enemies, predators and parasitoids; protection from abiotic factors, including temperature and humidity; and protection from the defences of the host plant. Concealment from natural enemies seems unlikely given the potent defensive allomones produced by the larvae. If the tent is an effective defence, why bother producing the allomones? One possibility is that the retreat enhances the effectiveness of the chemical defence, producing an envelope of volatiles around the caterpillar. Abiotic factors cannot be ruled out. The tent would almost certainly reduce desiccation and would also shield the larvae from direct exposure to the sun. In addition to preventing desiccation of the larva directly, moisture from the frass, which accumulates in the retreat, and any moisture escaping from the plant during feeding would accumulate within the

retreat. Direct sunlight may also be a factor. It is the upper leaf surface that is skeletonized and the feeding retreats shield the larvae from prolonged exposure to unfiltered sunlight. Finally, the retreats might also interfere with the plants chemical defence against herbivores. One of the documented advantages of the leaf-rolling habit is to prevent the induction of photoactive chemicals by the host plant (Sandberg and Berenbaun, 1989; Sagers, 1992). The phytochemistry of *Dipterocarpus tuberculatus* is very poorly known (Gibbs, 1974) and until more information is available on the defensive responses of dipterocarps to herbivory, this will remain as an intriguing possibility.

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References

- Ashton, P.S. (1982) Dipterocarpaceae. *In: Flora Malesiana, Series I - Spermatophyta (Flowering Plants)*, Vol. 9(2). Martinus Nijhoff, The Hague, pp. 237-552.
- Common, I.F.B. (1990) *Moths of Australia*. Melbourne University Press, Carleton, 519 pp.
- Darling, D.C., Schroeder, F.C., Meinwald, J., Eisner, M. & Eisner, T. (2001) Production of cyanogenic secretion by a thyrnid caterpillar (*Calindoea trifascialis*, Thyrididae, Lepidoptera). *Naturwissenschaften (Berlin)*, 88, 306-309.
- Dugdale, J.S., Kristensen, N.P, Robinson, G.S. & Scoble, M.J. (1999) The Smaller Microlepidopteran-grade Superfamilies. *In: Kristensen, N.P. (ed), Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography. Handbook of Zoology*, 35. Walter de Gruyter, Berlin, 217-232.
- Eisner, T., Kluge, A.F., Carrel, J.C., & Meinwald, J. (1972) Defence mechanisms of Arthropods. XXXIV. Formic acid and acyclic ketones in the spray of a caterpillar. *Annals of the Entomological Society of America*, 65, 765-766.

- Gibbs, R.D. (1974) *Chemotaxonomy of Flowering Plants*. Volume III, Orders. McGill-Queen's University Press, Montreal. 698 pp.
- Hasenfuss, I. (1979) Zur evolutionsbiologie der Larven der Thyrididae (Lepidoptera). *Zoologische Bietrage (Bonn)*, 30, 195-203.
- Hasenfuss, I. (1980) Die Präimaginalstadien von *Thyris fenestrella* Scopoli (Thyrididae, Lepidoptera). *Zoologische Bietrage (Bonn)*, 31, 168-190.
- Laurie, A., Duc, H.A. & Anh, P.T. (1989) Survey for kouprey (*Bos sauveli*) in Western Daklak Province, Vietnam. The Kouprey Conservation Trust. Unpublished. 34 pp. Original not seen, but available from <http://www.wcmc.org.uk/infoserv/countrysp/vietnam/app7new.html#YOKDON> (accessed October 8, 2001)
- Li, K.H.K. (1996) Ecological notes on Hong Kong Thyrididae (Lepidoptera) including the immature stages of eight species. *Transactions of the Lepidopterological Society of Japan*, 47, 125-143.
- Neunzig, H.H. (1987) Thyrididae (Pyraloidea), In: Stehr, F.W. (ed.), *Immature Insects* [1], Kendall/Hunt Publishers, Debuque, pp. 495-496.
- Robinson, G.S., Tuck, K.R. & Shaffer, M. (1994) *A Field Guide to the Smaller Moths of South-East Asia*. Natural History Museum, London, 311 pp.
- Sagers, C.L. (1992) Manipulation of host plant quality: herbivores keep leaves in the dark. *Functional Ecology*, 6, 741-743.
- Sandberg, S.L. & Berenbaum, M.R. (1989) Leaf-tying by tortricid larvae as an adaptation for feeding on phototoxic *Hypericum perforatum*. *Journal of Chemical Ecology*, 15, 875-885.
- Scoble, M. J. (1995) *The Lepidoptera: Form, Function and Diversity*. Oxford University Press, Oxford, 404 pp.
- Shaffer, M., & Nielsen, E.S. (1996) Thyrididae. In: Nielsen, E.S., Edwards, E.D. & Rangsi R.V. (eds), *Checklist of the Lepidoptera of Australia*. CSIRO, Canberra, pp. 161-163.
- Thiele, J.H.R. (1986) Die Gattung *Thyris* Hoffmannsegg, 1803. Über die Ergebnisse der Untersuchungen für eine Monographie (Lep., Thyridae). *Atalanta (München)*, 17, 105-146.
- Thiele, J.H.R. (1997) Anmerkungen zur Biologie und Verbreitung von *Pseudothyris sepulchralis* (Lepidoptera: Thyrididae). *Holarctic Lepidoptera*, 4, 55-58.
- Weatherston, I, MacDonald, J.A., Miller, D., Riere, G., Percy-Cunningham, J.E. & Benn, M.H. (1986) Ultrastructure of exocrine prothoracic gland of *Datana ministra* (Drury) (Lepidoptera: Notodontidae) and the nature of its secretion. *Journal of Chemical Ecology*, 12, 2039-2050.
- Weatherston, I, Percy, J.E., MacDonald, L.M. & MacDonald, J.A. (1979) Morphology of the prothoracic defense gland of *Schizura concinna* (J.E. Smith) (Lepidoptera: Notodontidae) and the nature of its secretion. *Journal of Chemical Ecology*, 5, 165-177.
- Whalley, P.E.S. (1976) *Tropical Leaf Moths: A Monograph of the Subfamily Striglininae (Lepidoptera: Thyrididae)*. British Museum of Natural History, London. 192 pp.