Table 2. -(continued)

Species and instar	Honey-gland	Tubercles	Perforated cupolas
3rd instar	+	+	+
4th instar	+	+	+
5th instar	+	+	+
6th instar	+	+	+
Subfamily Lampidinae			
Anthene definita (Butler)			
1st instar	-	-	+
2nd instar	+	-	+
3rd instar	+	+	+
4th instar	+	+	+
Euchrysops dolorosa (Trimen)			
1st instar	-	-	+
2nd instar	+	-	+
3rd instar	+	+	+
4th instar	+	+	+
Lepidochrysops ignota (Trimen)			
1st instar	-	-	+
2nd instar	+	-	+
3rd instar	+	-	+

+ = Present

- = Absent

different lycaenids.

Clark and Dickson (1956) reported that when extended the less highly developed form of the tubercles, such as that of *Anthene definita* (fig.8), remained erect throughout their movement and were held in this position momentarily or they worked in a series of flashes, a "rosette" of fine hair-like spines being extended from the crown as they attained their full length. In the genera of the subfamily Aphnaeinae the tubercles were much longer and had long hair-like processes; there was a protective chitinised spined casing in all instars except the first, through which each tubercle was extended. They also reported that in most of the larvae with this type of tubercle, each tubercle, in the process of extension, curved over strongly towards the honey-gland, and that during their full extension the tubercles' long hairs, as these spread out, brushed the vicinity of the honey-gland. The normal action of these tubercles was very rapid, with a number of successive quick beats, when the tubercles came into full play.

In many larvae in which the honey-gland first appears in the second instar, the tubercles appear in the third, e.g. *E. dolorosa* (see Table 2). In others, e.g. *P. lycegenes*, the tubercles appear in the first instar although the honey-gland appears in the second instar. In *Anthene amarah* Guérin both honey-gland and tubercles appear in the second instar (Clark and Dickson, 1971). In *Aloeides dentatis*, which has no honey-gland, the tubercles are functional in the second instar. From the above, there does not appear to be any significant relationship between the first appearance of the tubercles and the first appearance of the honey-gland.

Ehrhardt (1914) reported that at the base of each spiculate seta there is a large pyriform secreting cell which has a chitinous duct extending into a lumen formed as shown in fig. 10. This duct probably opens to the outer surface of the base of the seta, but its outer oriface, if any, was not observed. Malicky (1969, 1970) though did not find any glandular structures, in, on or near the tubercles of any of the species he examined. No glandular structures could be identified on the tubercles from the serial sections made of the larvae in this study. The tubercles should have been dissected out and sectioned separately from the rest of the larva, but unfortunately insufficient

specimens were available for this to be done.

Thomann (1901), Ehrhardt (1914) and others believed that the pyriform cells at the base of the setae secreted an odoriferous substance. Hinton (1951) on the basis of the histology of these cells, and in particular their internal cuticular ducts, supported the view that they are actively secreting after the formation of their respective setae.

In this study it was discovered that the tubercles of *A. dentatis* produced a volatile secretion that appeared to mimic the alarm pheromone of its host ant *A. capensis* (see Chap. 4.). This volatile substance is probably produced by secreting cells at the base of the setae similar to the one described above, but this will have to be confirmed when further *A. dentatis* larvae become available for study.

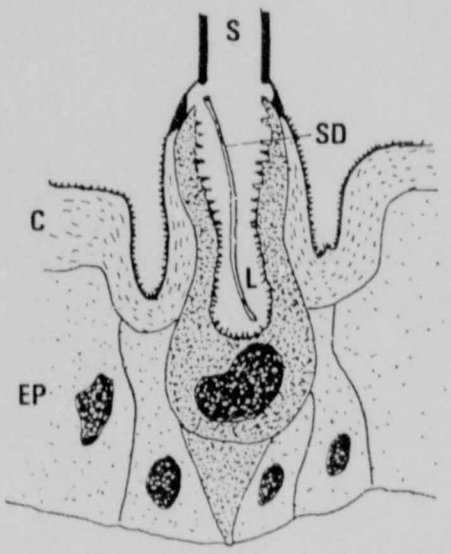

Fig. 10. Section through a pyriform secreting cell of one of the spiculate setae (S) of *Scolitantides orion* Pall. showing the sclerotised duct (SD) extending into the lumen (L); (C) cuticle; (EP) epidermis. (After Ehrhardt, 1914)

2.3.3 Perforated cupolas

These small epidermal glandular organs appear to have been first recorded by Hinton (1951) who suggested that they may produce an ant attractant substance. Malicky (1969, 1970) gave a detailed description of these glands and also suggested that they produced a volatile substance that attracted the ants. In this study it was found that these glands produce a volatile secretion that appears to mimic the brood pheromone of the host ant (see Chap. 4).

Malicky (1970) believed that these organs, like the honey-glands, are homologous with setae. The inner cell which is interlaced by longitudinal cavities which enclose the large nucleus and produces the volatile secretion is homologous with the trichogen cell. The second cell forms a plasmatic tube which serves as a duct for the secretion and is homologous with the tormogen cell.

2.3.4 Cuticle

The cuticle of lycaenid larvae is soft, but tough, and extremely thick. Malicky (1969, 1970) found that larvae of lepidopterous families other than lycaenids of the same size (± 20mm long) have cuticles about 5-10µm, but in final instar lycaenid larvae, 200-300um thicknesses are usual. The thicknesses of the cuticles of the final instar lycaenid larvae measured in this study confirm this observation (see Table 1.). The cuticles of early instar lycaenid larvae are proportionally just as thick (see Table 1.). A third instar *L. ignota* larva only 3.5mm long has a cuticle 5 times as thick as that of a larva from another family 6 times as long.

Malicky (1970) pointed out that when lycaenid larvae were attacked by ants they were not damaged due to a combination of the particular construction of the ants' mandibles and the thick cuticles of the lycaenids. He observed that this mandibular construction was unique within predaceous arthropods. The molar part, a ledge with a row of small teeth prevented the penetration of the sharp elongate part through the thick cuticle. Thin cuticles of caterpillars other than Lycaenidae may be easily penetrated. He pointed out though that the thickness and plasticity of lycaenid cuticle did not protect it from the attacks of

other predators which have different mandibular construction. Ant mandibles without this molar ledge exist in the Dorylinae, but they are never lycaenid associated.

Malicky also found that in addition to its thickness, the lycaenid cuticle was folded in a particular manner so as to protect vulnerable organs such as the dorsal blood vessel and ventral nerve cor These organs were protected under concavities while the prominent protrusions contained less important structures such as fat bodies. He said that a biting ant is forced to crush one of the prominent cuticular ledges or protrusions between its mandibles, thus giving additional protection to the caterpillar, because its important organs become folded inward and not damaged. He pointed out that the size of the ledges corresponds well with the size of the mandibles of medium sized ants, but not with those of other predators of lepidopterous larvae, which are much larger.

The above observations by Malicky are not always true, during the course of this study several known host ants killed lycaenid larvae they did not normally associate with. For example, when trying to establish the identity of the host ant of *L. ignota* several larvae were offered to ant species known to attend other lycaenid larvae. *Camponotus maculatus* Mayr killed abd consumed *L. ignota* larvae on several occasions, but this may be due to the fact that the larvae were weak and dying from lack of food. In the case of *Anoplolepis custodiens* though the *L. ignota* larvae were nearly always killed immediately when discovered by this ant.

Third instar *L. ignota* larvae are very small (only about 3mm long) and are completely encircled by the jaws of the above mentioned two species of ants. Possibly the outcome would have been different if final instar larvae had been used as Malicky appeared to have been doing, although an early final instar *E. dolorosa* was killed by the ant *Camponotus niveosetosus* during the course of the study. On the whole, Malicky's observations appear to be valid as a number of lycaenid larvae of different species dealt with during the course of the study came through encounters with aggressive ants unscathed.

3. BIOLOGICAL GROUPS WITHIN THE LYCAENIDAE

The two symbiotic relationships to be studied in detail represent only a small part of the great variety of associations and feeding habits found within the Lycaenidae. To understand how these two symbioses could have arisen they have to be considered in the context of the life histories of other Lycaenidae. Also important is to see how the presence or absence of glands effect ant/lycaenid associations.

Hinton (1951) divided the Lycaenidae into a number of biological groups depending on their feeding habits and their associations with ants. As these groupings give a concise summary of the feeding habits and relationships with ants, a slightly revised version is discussed here with some examples of lycaenid species bred during the course of the study.

Table 3. The biological groupings of the Lycaenidae based on their feeding habits and their association with ants.

Feeding Preference		Myrmecophilous		Independent
		Facultative	obligatory	
Phytophagous	A.			+
	B.	+	+	
Phyto-predaceous		+	+ (from 3rd instar)	
Predaceous				
A. On Homoptera				+
B. On Homoptera and ant brood		+	+ (from 4th instar	
C. On ant brood			+	
Secretion feeders				
A. Ants			+	
B. Homoptera		+		
C. Both		+		

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Predaceous				
	A. On Homoptera			+
	B. On Homoptera and ant brood	+	+ (from 4th instar)	
	C. On ant brood		+	
Secretion feeders				
	A. Ants		+	
	B. Homoptera	+		
	C. Both	+		

3.1 Materials and Methods

The early stages of the species studied were collected at a number of different localities as indicated in the descriptions. When they were found the presence or absence of ants was noted. If there were ants present these were collected and housed with the larvae so that the interaction between them could be studied in detail. Some of the myrmecophilous larvae of each species were kept without the ants to see if they were dependent on them or not.

The phytophagous larvae were housed separately in small airtight plastic pots with the foodplant and a few ants if they were myrmecophilous. Airtight pots were used to prevent the foodplant from drying out too rapidly. The larvae of *Durbania amakosa natalensis* van Son were kept together on the lichen covered rocks on which they were found. These rocks were placed in a large plastic airtight container so that the larvae could not escape.

The larvae predaceous on ant brood were kept in formicaria with their host ants (see page 60).

The larvae were studied under a dissecting microscope to establish whether the honey-gland and tubercles were present. When under observation the larvae and ants were studied with a hand lens.

3.2 Results

3.2.1 Phytophagous

A. Independent

The species in this group feed only on plant material and are usually not found associated with ants in any way.

Durbania amakosa natalensis van Son

This species was bred from specimens collected at Karkloof in Natal. The eggs are laid singly or in small batches among lichen on rocks or in crevices. The larvae appear to feed on the strands of blue-green algae (Cyanophyta) which are found amongst the lichen, not on the lichen

itself as recorded by Clark and Dickson (1971) for the nominate subspecies. The duration of the instars is very variable. There are neither tubercles nor honey-gland in this species. The body markings match the lichen on the rocks and the lateral hairs act as shadow-breakers, both rendering the larva inconspicuous. When moulting the larva merely crawls out of the old skin. The larvae do not appear to be ant associated in any way.

The pupa is attached to the partially discarded larval skin which is itself attached to the rock in a concealed spot, usually a rock overhang.

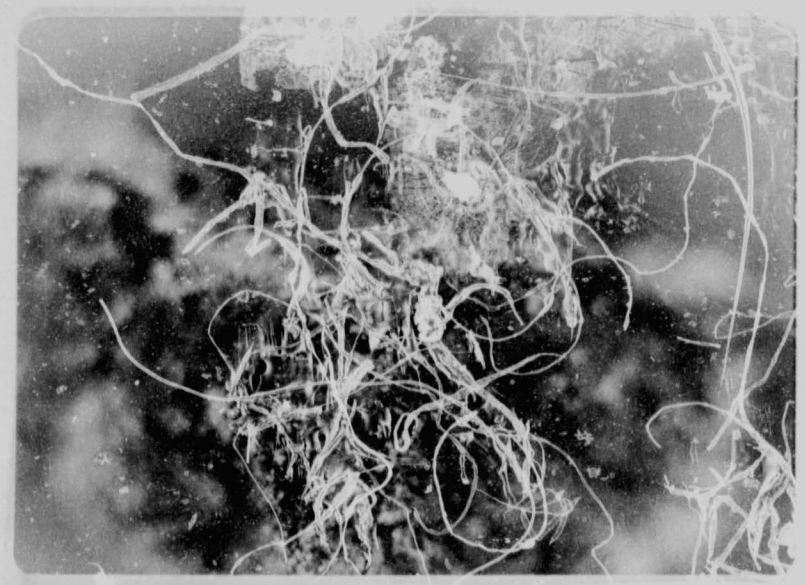


Fig. 11. Final instar larvae of *Durbania amakosa natalensis* van Son.

Iolaus (Argiolaus) trimeni Wallengren

This species was bred from specimens collected at Florida in the Transvaal. The eggs are laid singly on the leaves of the parasitic plant *Loranthus rubromarginata* (Loranthaceae). The larvae at first feeds on the surface of a leaf, in troughs, filling the part eaten with its body, but as it grows bigger it feeds on the edge, wrapping the fleshy first segment round the edge of the leaf and completely covering its head. The final instar larva is black and greyish-white and mimics a bird dropping. Both honey-gland and tubercles are present

in the second and subsequent instars. The larvae do not appear to be ant associated in any way.

The pupa is secured to a twig or to the bark of the host-tree by the cremastral hooks only.

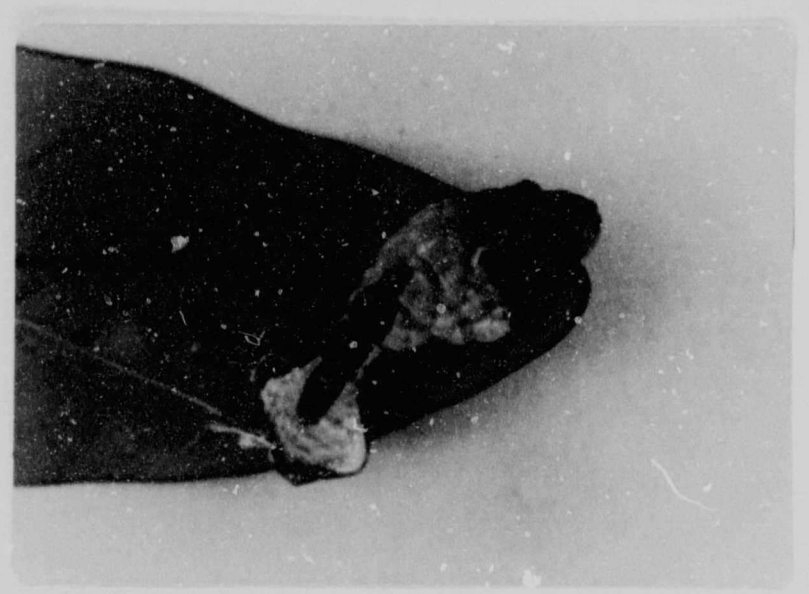


Fig. 12. Final instar larva of *Iolaus (Argiolaus) trimeni* Wallengren.

B. Myrmecophilous

(I) Not dependent on ants

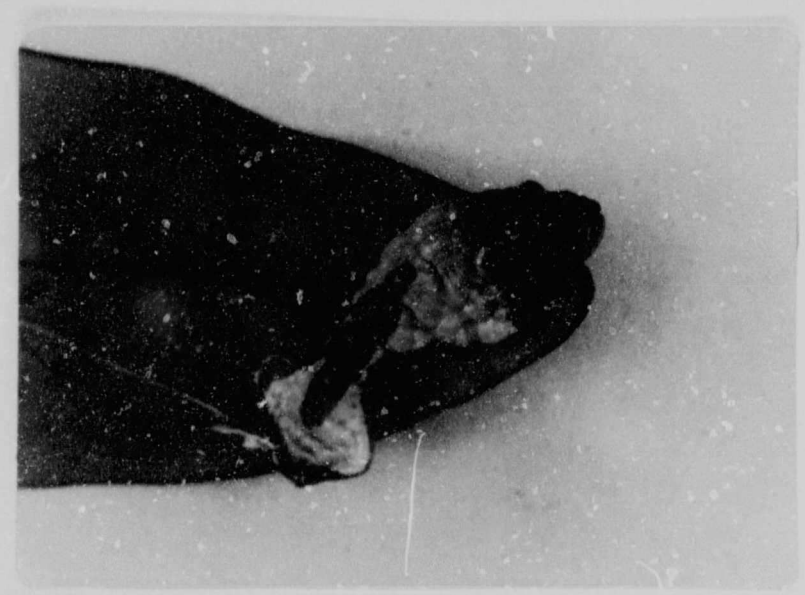
These are species which are usually found associated with ants on their foodplants, but can be bred successfully in the laboratory in their absence.

Myrina silenus ficedula Trimen

This species was bred from eggs and larvae collected at Florida, Naboomspruit and several other localities in the Transvaal. It feeds on several species of *Ficus*, including *F. cordata* Thunb., *F. capensis* Thunb., *F. natalensis* (Mig.) Hochst., *F. stipulata* L. (Moraceae). The eggs are laid singly on a leaf or twig of the foodplant

in the second and subsequent instars. The larvae do not appear to be ant associated in any way.

The pupa is secured to a twig or to the bark of the host-tree by the cremastral hooks only.



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The young larvae feed on the surface of a leaf, protected under a silken mat. The older larvae feed on the edge of the leaf, appearing to rely on their shape and coloration for protection. Young fruit are also occasionally burrowed into. The honey-gland and tubercles are present in the second and subsequent instars. The larvae are attended by various species of ant belonging to the genus *Camponotus*.

The pupa is secured to a twig or to the bark of the tree, often among the tangled roots, by the cremastral hooks only.

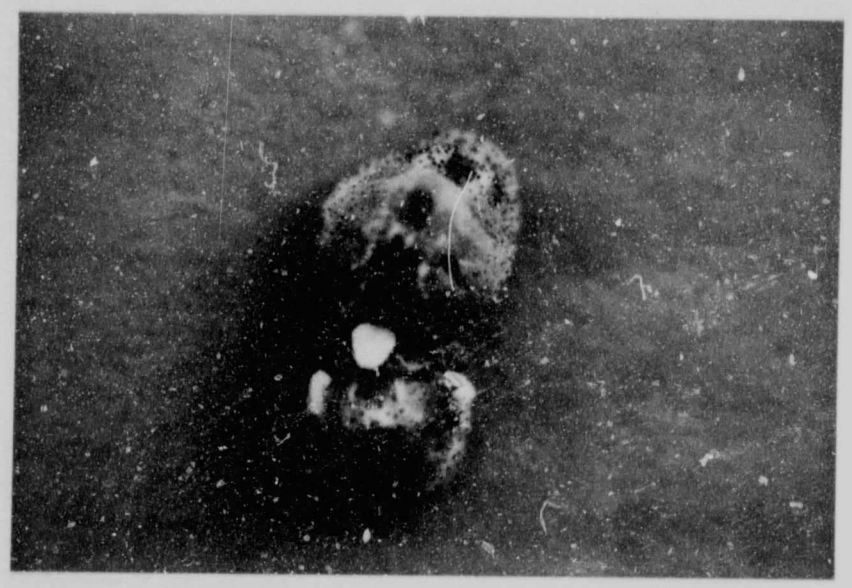


Fig. 13. Final instar larva of *Myrina silenus ficedula* Trimen attended by ants, *Camponotus* sp.

(I1) Dependent on ants

These are species which, although they are entirely herbivorous, need the presence of ants to complete their life cycle.

Poecilmitis lycegenes (Trimen)

This species was bred from eggs, larvae and pupae collected near Karkloof in Natal. It feeds on several plant species in the study area

including the following:- *Royena hirsuta* L., *Diospyros lycioides* Desf. (Ebenaceae), *Myrsine africana* L. (Myrsinaceae), and *Rhus* sp. (Anacardiaceae). The larvae were attended on the plants by the ant *Crematogaster liengmei* For. which were also tending coccids on the same plants.

The female *P. lycegenes* appears to lay only where the *C. liengmei* ants occur, since the females have been observed to oviposit directly on the foodplant only when the ants were present. The females have also been observed to oviposit on stones and pieces of grass along the well established pheromone trails of the ants leading from their nests to the plants. One female was watched for two hours during which time she laid a number of eggs along the ants' pheromone trail. She laid on the ground, pieces of dead and living grass and stones all within 10mm of the trail. The ants generally followed the same path every day to and from the plants where they tended the coccids and the lycaenids. A colony of *C. liengmei* was kept in a formicarium with a permanent food source and a plant with a number of coccids feeding on it. The ants laid a permanent trail some 30cm long to the food source and from there another trail about 100cm long to the plant. The trail to the plant was perfectly straight and direct. Over a period of weeks the trail pheromone deposited by the ants discoloured the paper on the floor of the formicarium. The width of the discoloured area varied between 1-2mm. The ants when moving on this trail did not deviate more than 7mm on either side of the trail pheromone. Over the weeks the paper in the formicarium had become covered in a fine layer of greyish dust, except for the area on either side of the discoloured trail where it had become dislodged by the movement of the ants along the trail. When looking at the formicarium the path followed by the ants was quite obvious, consisting of a straight white band some 15mm wide with a dark centre nearly 2mm broad running nearly the length of the arena. It appears that the female *P. lycegenes* can detect the trail pheromone laid by the ants and oviposits near it, probably within the area of deviation by the ants.

The ants pick up the newly emerged *P. lycegenes* larvae and carry them to the plants, as other ant species have been recorded doing with homopterans. The young *P. lycegenes* larvae feed on either the upper or under surfaces of the leaves but, as they grow, they feed on the edge and later, starting from the tip, they eat the whole leaf. The young

larvae shelter on the centre of a well concealed leaf. As the larvae get older they leave the plants during the day and shelter, usually several together and always attended by ants, under nearby rocks. If the ants' nest is near enough they will shelter in it. The larvae find their way back to the plants by following the pheromone trails of the ants.

The honey-gland is present in the second and subsequent instars. The tubercles are present in all instars (see Table 2), developing from a simple elongated mole which can only be unfolded 'in and out', to a fleshy eversile projection bearing 8 spiculate setae. The larvae produce large quantities of liquid from the honey-gland upon which the ants feed. The ants are apparently necessary to keep the honey-gland clean because larvae kept in captivity without ants soon develop a fungal infection in the gland and die. An attempt was made to remove the excess fluid produced by the gland with a piece of blotting paper, but this procedure was usually unsuccessful.

Clark and Dickson (1971) record that the larvae pupate within leaf-shelters, but in the colony studied at Karkloof twelve pupae were found within the brood chamber of the ants nest, while only one was found on the host plant. The pupae are attached by their cremastral hooks and are dark brown to black in colour.

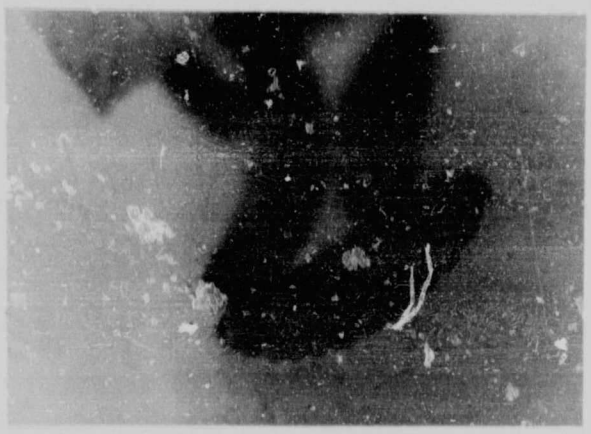


Fig. 14. Final instar larvae of *Poecilmitis lycegenes* (Trimen).

Poecilmitis aureus van Son

This species was bred from specimens collected at Heidelberg in the Transvaal. The foodplant is *Clutia pulchella* L. (Euphorbiaceae). It is constantly attended by ants belonging to the genus *Crematogaster*.

This species is closely related to *P. lycegenes* and its habits appear to be rather similar. The females have been observed to oviposit directly on the foodplant and on rocks near the pheromone trails of their host ants. The eggs are laid singly and are white when first laid, developing a pinkish colour within a few hours. The young larvae feed on the surface of the leaves and the older larvae feed on the edges. During the day the older larvae leave the foodplants and shelter under nearby rocks, constantly attended by ants.

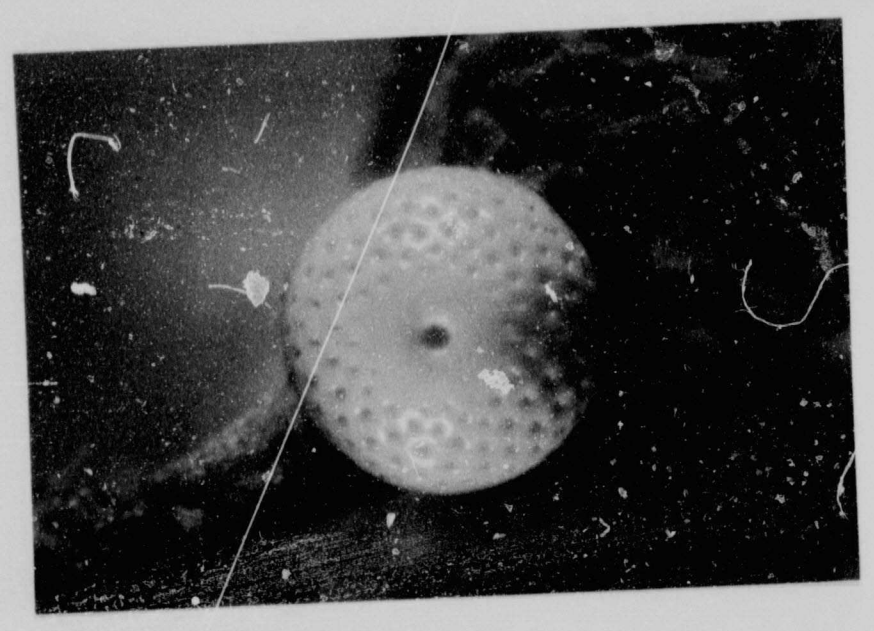
No pupae were found in the wild so where [illegible]uld not be ascertained. The pupae are attached by their [illegible]ooks and are dark brown to black in colour

Fig. 15. Final instar larva of *Poecilmitis aureus* van Son with an ant, *Crematogaster* sp., investigating the honey-gland.

Spindasis namaqua (Trimen)

This species was bred from eggs, larvae and pupae collected near

A.



B.

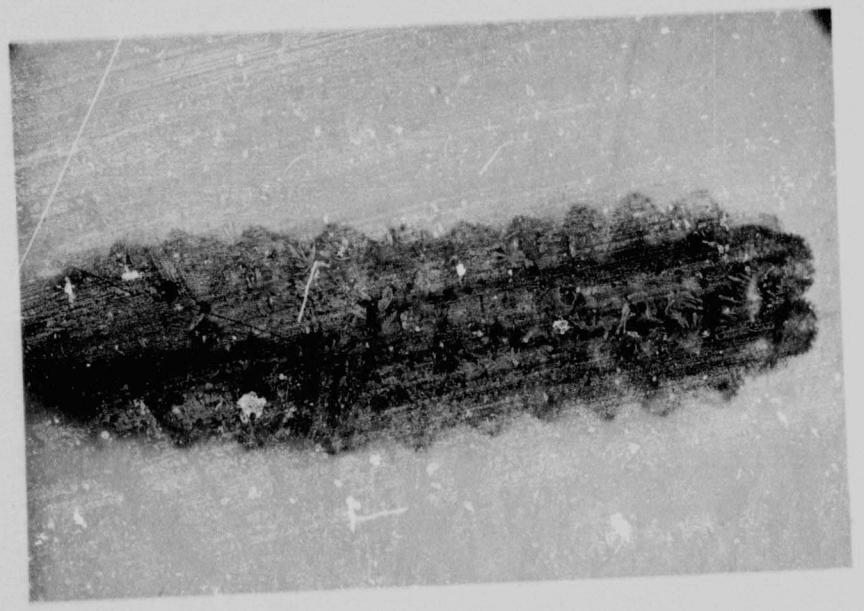


Fig. 16. *Spindasis namaqua* (Trimen). A. Egg. B. Final instar larva.

Garies, Namaqualand in the Cape. The larvae feed on *Zygophyllum refractum* Grünb. (Zygophyllaceae). From observations made it appears that the female *S. namaqua* will only oviposit on the foodplant if the correct ant is present. The ant in this instance is a species of *Crematogaster*. The white eggs are laid singly on the leaves of the foodplant.

The young larvae feed on the surface of the leaves, while the older ones feed on the edges. The larvae shelter during the day in the soil at the base of the plants in a chamber specially constructed by their attendant ants. The tubercles are present in all instars, but the honey-gland only appears in the third and subsequent instars.

The larvae pupate in the chambers at the base of the plant. The pupae are brown and are attached by their cremastral hooks.

Spindasis phanes (Trimen) (fig. 17)

This species was bred from eggs and larvae collected at Hennops River in the Transvaal. The larvae feed on *Ximenia caffra* Sond. From observations made it appears that female *S. phanes* will only oviposit on the foodplant if the correct ant species is present. In this instance the host ant is *Crematogaster castanea* Smith. The eggs are whitish and are laid singly on the leaves of the foodplant.

The young larvae feed on the surface of the leaves and the older ones feed on the edges. The young larvae can generally be found on the leaves constantly attended by the host ants. The older larvae though search out crevices in the bark and shelter there during the day. The tubercles are present in all instars, but the honey-gland only appears in the third and subsequent instars.

The larvae pupate in crevices in the bark of the host trees. The pupae are attached by their cremastral hooks and they are dark brown in colour.

Aloeides dentatis (Swierstra) (see p. 63)

This species was bred from eggs, larvae and pupae collected at Witpoortjie, near Krugersdorp in the Transvaal. The foodplant is *Hermania depressa* N.E.Br. (Sterculiaceae).

A.

B.

Fig. 17. Final instar larva of *Spindasis phanes* (Trimen).
A. Dorsal view. B. Lateral view.

The female oviposits two eggs in quick succession on the under surface of the leaf of the foodplant only after she has detected the presence of the correct ant *Acantholepis capensis* Mayr (see p. 65). The first two instars never leave the foodplant and feed on the surface of the leaves. In the third and subsequent instars the larvae shelter during the day in the nest of the host ant. During the night the larvae, constantly attended by ants, follow the *Acantholepis capensis* pheromone trails out to the foodplant. The older larvae feed on the edges of the leaves. The larvae go into diapause in the ants nest during winter when the foodplant is absent. The honey-gland is absent, but the tubercles are present in all instars.

The larvae pupate on the floor of the tunnels in the ants nest only attached by their cremastral hooks.

Fig. 18. Fifth and sixth instar larvae of *Aloeides dentatis* (Swierstra), with the ant, *Acantholepis capensis* Mayr.

3.2.2 Phyto-predaceous (all myrmecophiles)

In the species of this group the first two instars feed entirely on plant matter. After the second moult the larvae are carried by

ants into their nests where they feed on the ant brood. They are continually attended by the ants and are treated as if they are ant brood. The most important genus in Africa belonging to this group is *Lepidochrysops* Hedicke. All their life histories are rather similar to that of the following examples.

Lepidochrysops trimeni (Bethune-Baker)

The life history of this species was described in great detail by Claassens (1976) from specimens collected at Camps Bay, Cape Province. The foodplants are *Selago spuria* L. and *S. serrata* Berg. (Selaginaceae). The eggs are laid singly on the inflorescences of the foodplant. The first and second instars feed on the buds and flowers and after the second moult are carried by the ant *Camponotus maculatus* (Fabricius) into their nests. The lycaenid larvae are deposited by the ants amongst their own brood. The lycaenid larvae feed at first on the silken material of the cocoons, but as they get larger feed on the ant pupae and larvae. Trophallaxis occasionally occurs between the lycaenid larvae and the ants.

The larvae pupate in the tunnels of the ants nest. The imagines, their wings still folded, run along the tunnels until they find the exit. The wings are expanded outside the nest.

Lepidochrysops ignota (Trimen) (see p. 81)

This species was bred from larvae collected at Witpoortjie, near Krugersdorp in the Transvaal. The foodplant is *Becium obovatum* (Benth.) N.E.Br. (Labiatae). The eggs are laid singly on the flowers on which the larvae are to feed. The first and second instars feed on the seeds and after the second moult are carried by the ant *Camponotus niveosetosus* Mayr into their nests. The *L. ignota* larvae feed at first on the ant pupae, but as they get larger they feed on the larvae as well. Trophollaxis occasionally occurs between the lycaenid larvae and the ants. The honey-gland is present in the second and subsequent instars, but there are no tubercles.

No pupae were found but it is assumed that they pupate in the tunnels of the ants nest as do other members of the genus.

3.2.3 Predaceous

A. Feeding on Homoptera

(I) Independent

The larvae of the species in this group prey exclusively on Homoptera, but are either totally ignored or are attacked by the ants attending the Homoptera.

Spalgis lemolea Druce

This species was bred from material collected by Mr. I. Bampton at Nova Lisboa, Angola in 1973. The eggs are laid on the lower surfaces of the leaves among colonies of the coccid *Dactylopius* sp. on which the larvae feed. The larvae are very well concealed among the coccids as they are usually densely covered with the white waxy secretions of the hosts. The larvae and coccids are often under a common covering or encrustation of shed cuticles and hardened secretions. The tubercles and honey-gland are absent. It pupates on a leaf or a twig or branch.

(II) Myrmecophilous

The larvae in this group feed on Homoptera but are also nearly always attended by ants.

Thestor basutus (Wallengren)

The life history of this species was first described by Clark and Dickson in 1960 from specimens collected above the Inchanga Valley in Natal. The eggs are laid singly or occasionally in small clusters on plants on which there are ants and psyllids. During the first to third instars the larvae live among the psyllids, upon which they feed, but on moulting into the fourth instar they enter ants nests, in which they have been found in the larval and pupal states. The ants associated with the larvae were *Anoplolepis custodiens* Smith. The tubercles and honey-gland are absent.

They pupate unattached in the ants nest. There are no cremastral hooks.

Lachnocnema bibulus (Fabricius)

This species has been bred a number of times by Lamborn (1914), Clark (1940), Clark and Dickson (1970) and Owen (1971). The eggs are usually laid singly just below colonies of adult and immature jassids. The newly emerged larvae make their way up the stem to where the jassids are aggregated. In the early instars they feed on jassid eggs and small nymphs, but full grown *L. bibulus* larvae feed on both young and adult jassids. Clark and Dickson (1970) record that final instar larvae rear themselves up over a jassid and suddenly pounce on it, or crawl up behind it and seize the wing tips. Ants (*Camponotus* sp.) are in constant attendance upon both jassids and the larvae. Owen (1971) reports that he saw ants take something from the mouth of the *L. bibulus* larvae and noted that it appeared to be regurgitated liquid food.

The full-grown larvae pupate on the leaves of the plant secured by the cremastral hooks and a silken girdle.

B. Feeding on ants

These are species of lycaenid which feed exclusively on ant brood in the nest.

Thestor dicksoni dicksoni Riley

This appears to be the only South African species belonging to this group. Observations on the early stages were first published by Clark and Dickson (1971).

The eggs are usually laid in small clusters on twigs or other dry pieces of vegetation. The newly emerged larvae are carried by the ants *Anoplolepis custodiens* Smith into their nests where they are believed to feed on the ant brood. They pupate in the tunnels of the ant nest.

Liphyra brassolis Westwood

This species from the Indo-Australion region is the best documented of the group. The early stages have been described by Dodd (1902) and Hinton (1951). The *L. brassolis* larvae feed exclusively on the larvae of the ant *Oecophylla smaragdina* F. The mouth-parts of the *L. brassolis* larvae are modified for sucking and the juices of their prey are sucked