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Notes on the biology of *Hypolycaena othona* (Lepidoptera: Lycaenidae) in West Malaysia

by

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Abstract: *Hypolycaena othona* HEWITSON [1865] lays its eggs singly on the inflorescences of orchids. *Spathoglottis plicata* is the first non-epiphytic hostplant recorded thus far. The partially endophytic larvae gnaw holes into the flower buds or unripe seed pods, preferably feeding on the internal tissues. Pupation occurs on the stem of the hostplant. Third and fourth instar larvae possess a dorsal nectary organ and are occasionally visited by ants (e.g., *Crematogaster, Camponotus, Polyrhachis*). Tentacle organs are absent. Ants of various genera constantly visit the hostplant inflorescences due to the presence of nectaries, but the caterpillars are protected from ant-attacks by their myrmecophilous adaptations. During the last two instars the caterpillars produce substrate-borne vibrations when molested. These vibrations consist of groups of low-frequent croaking pulses ("calls"). The pupae stridulate when disturbed, producing chirping or clicking pulses. The morphology of all larval instars and of the pupa is described in detail, including SEM illustrations of the epidermal organs and colour illustrations of the larvae.

Beobachtungen zur Biologie von *Hypolycaena othona* in West-Malaysia

Zusammenfassung: *Hypolycaena othona* HEWITSON [1865] ist eine in der orientalischen Faunenregion weit verbreitete Bläulingsart, deren Larven auf Infloreszenzen von Orchideen spezialisiert sind. Mit *Spathoglottis plicata* wird aus West-Malaysia erstmalig eine nichtepiphytische Wirtspflanze nachgewiesen. *H. othona* legt die Eier einzeln ab, besonders auf die unreifen Samenkapseln. Die Raupen schlüpfen nach 4–5 Tagen. Sie sind teilweise endophytisch und bohren sich, zumindest mit dem Vorderkörper, in die

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Samenkapseln oder in die fleischigen Blütenknospen ein. Die 4 Larvenstadien dauern 13–15 Tage, die Verpuppung erfolgt als Gürtelpuppe am Stengel der Wirtspflanze, und nach einer Puppenruhe von 10–11 Tagen schlüpfen die Imagines.

In den letzten beiden Stadien besitzen die Raupen ein dorsales Nektarorgan, aber keine Tentakelorgane. Sie sind nur schwach myrmekophil und werden im Freiland gelegentlich von Ameisen der Gattungen *Crematogaster*, *Camponotus* oder *Polyrhachis* besucht. In Gefangenschaft ergaben sich auch Assoziationen mit den Ameisengattungen *Meranoplus* und *Myrmicaria*. Wie viele andere Bläulingsraupen produzieren auch die Raupen von *H. othona* bei Störung im 3. und 4. Stadium Vibrationssignale, die ausschließlich auf das Substrat übertragen werden. Die „brummenden“ oder „krächzenden“ Signale sind niederfrequent (< 1000 Hz) und werden vermutlich durch rhythmische vibrierende Muskelkontraktionen erzeugt. Die Puppen stridulieren bei Störung und geben dann höherfrequente, zirpende Laute mit deutlicher Luftschallkomponente von sich.

Morphologie und Biologie der Präimaginalstadien von *H. othona* zeigen sehr große Ähnlichkeit mit der austromelanesischen Art *H. danis*, dagegen deutliche Unterschiede zu anderen Vertretern der Hypolycaeniti, etwa den afrikanischen Vertretern der Gattungen *Leptomyrina* und *Hypolycaena*. Insbesondere die Anpassungen an die innerhalb der Bläulinge wie auch der gesamten Tagfalter fast einzigartige Nutzung von Orchideen als Wirtspflanzen können als Synapomorphie einer Artengruppe innerhalb der Gattung *Hypolycaena* gedeutet werden. Vor einer endgültigen taxonomischen Entscheidung, ob die Artengruppe um *H. othona* als monophyletische Untergattung *Chliaria* aufgefaßt werden kann, bedarf es jedoch weiterer Untersuchungen zur Morphologie und Biologie der Präimaginalstadien orientalischer *Hypolycaena*-Arten.

INTRODUCTION

The lycaenid subtribe Hypolycaeniti is a rather small and morphologically homogeneous group of Palaeotropical hairstreak butterflies. Although currently assigned to the Eumaeini sensu SCOTT & WRIGHT (1990), the phylogenetic relationships of the Hypolycaeniti to other Palaeotropical subtribes remain poorly understood (ELIOT 1973 & pers. comm.). Characters of male genitalia and larval morphology suggest a closer affinity to the Remelaniti and, perhaps, the Iolaiti. Traditionally the Hypolycaeniti comprise the two genera *Leptomyrina* BUTLER 1898 (9 African species, including *Gonatomyrina* AURIVILLIUS [1924]), and *Hypolycaena* FELDER & FELDER 1862 (approximately 48 recognized species including the "genera" *Chliaria* MOORE 1884 and *Zeltus* DE

NICÉVILLE 1890: STEMPFFER 1967, BRIDGES 1988). Recently, LARSEN (1991) has transferred the African genus *Hemiolaus* AURIVILLIUS [1922] (6 species) from the Iolaiti to the Hypolycaeniti on the grounds of genitalic characters, and his action seems very appropriate also in the light of similarities regarding wing pattern and larval morphology. *Hypolycaena* divides nearly equally into African and Indo-Australian species (23 and 25 species, respectively). However, the specific status of several taxa requires further investigation. Life-history information is available for 15 of the total 63 species of the subtribe (summarized in FIEDLER 1991 a). *Leptomyrina* larvae feed inside the succulent leaves of plants of the families Crassulaceae and Aizoaceae. *Hemiolaus caeculus* (HÖPFFER 1855) has been recorded from Olacaceae (cf. MIGDOLL 1988). *Hypolycaena* larvae, in contrast, feed on a wide variety of plant families, preferably on young foliage or inflorescences.

The larvae of a couple of Oriental and Australian *Hypolycaena* species (*othona* HEWITSON, [1865], *kina* HEWITSON [1869], *danis* (FELDER & FELDER 1865), the former two often assigned to the "genus" *Chliaria*) have specialized on orchid inflorescences as food. Although the Orchidaceae are among the largest of all plant families with roughly 20,000 species, they are extremely rarely used as hostplants by lycaenid larvae. Outside the genus *Hypolycaena* only two Neotropical species of *Strymon* HÜBNER [1818] have so far been reported to utilize orchid flowers as occasional hosts, and true orchid-specialists are yet unknown from any other lycaenid taxon (FIEDLER 1991 a). Even among the Nymphalidae as the most diverse butterfly family, though including several monocot-feeding subfamilies, there is yet only a single record of a specialist orchid feeder (ACKERY 1988).

During a research visit to West Malaysia from October to December 1991, I had the opportunity to study the early stages of *Hypolycaena othona* in some detail. *H. othona* is widely distributed in several subspecies from most of India (e.g. Nilgiri mountains: LARSEN 1987, the Bombay region: BELL 1915, Upper Assam: NORMAN 1976) across Myanmar (formerly Burma) and Thailand throughout Sundaland [West Malaysia, Sumatra: ssp. *semanga* (CORBET 1940); Mentawai islands: ssp. *jiwabaruana* (ELIOT 1980); Borneo: ssp. *mimima* (DRUCE 1895); and Java: ssp. *dendrobii* (ROEPKE 1919)] eastwards to Sumbawa (ssp. *maruyamai* TAKANAMI 1989).

The life-histories of an Indian (Bombay) and a Javanese population have been outlined by BELL (1915) and by ROEPKE (1919), respectively. BELL's report was later used in HINTON's review paper (1951). Apparently no further authentic observations have been published since, and subsequent authors (e.g. PINRATANA 1981) just repeat general remarks on the hostplants of *H. othona* at most.

According to BELL (1915), the larvae feed on buds and flowers of at least four genera of epiphytic orchids (*Cottonia, Aerides, Rhynchostylis, Dendrobium*), whereas NORMAN (1976) recorded the larvae as feeding inside the seed pods. BELL observed that the caterpillars are occasionally attended by ants, but did not detail the ants involved. Subsequently, HINTON (1951) listed the caterpillars as having both a dorsal nectary organ (DNO) and a pair of tentacle organs (TOs), whereas all other Hypolycaeniti species studied so far do not possess TOs (reviewed in FIEDLER 1991 a).

This report is intended to provide additional information on morphology (including SEM photographs of some epidermal organs), behaviour, and ecology of the immature stages of West Malaysian *H. othona*. Then, the findings are to be compared with results on related species in an evolutionary framework.

RESULTS AND OBSERVATIONS

Study area, habitat, and hostplant

The observations were largely conducted at the Ulu Gombak Field Studies Centre of the University of Malaya, about 20 km north of the Malaysian capital Kuala Lumpur. This area is mainly covered with advanced secondary forest of the lowland dipterocarp type. Two populations of *Hypolycaena othona* were located. One occurred at a swampy clearing (approx. 50 × 50 m) along a former logging path (elevation ca. 200 m), roughly 3 km south of the Gombak Field Station ("Gombak site" hereafter). Between tall grasses and bushes of Malabar rhododendron (*Melastoma malabathricum* [Melastomataceae]) there were numerous specimens of the ground orchid, *Spathoglottis plicata* (Fig. 1). This orchid species commonly grows in open disturbed habitats and along roadsides in South East Asia. Its inflorescences (height 0.5–1.5 m) emerge from a rosette of green leaves and bear 10–25 pink flowers that develop seed pods of 3–5 cm length. On October 30, one specimen of *H. othona* (sex unknown) was observed perching on a *M. malabathricum* bush. No oviposition was observed, and in fact this was the only adult butterfly of the species seen in a 7-weeks period. A close inspection of the surrounding *S. plicata* orchids, however, revealed a number of eggs and egg-shells on unripe seed pods. Three visits on

November 5, 14 and 20, also furnished eggs and larvae of various instars. On December 8, no more eggs, larvae or pupae could be observed, neither were there any adults flying around. Only a few egg-shells indicated the former presence of a colony of *H. othona*.

A second population was found on November 17 in the Genting highlands at an elevation of approx. 1000 m ("Genting site" hereafter). Along the old Genting road numerous *S. plicata* inflorescences bore eggs or egg-shells, and some showed heavy signs of larval feeding activities. On two plants with large inflorescences (more than 20 seed pods each) seven mature larvae and two second instar caterpillars were found, while on another plant a single pupa could be located. The Genting site was not visited a second time.

The egg and oviposition sites

The eggs (diameter 0.8 mm) are white and roughly hemispherical with a distinct chorionic sculpturing as typical for lycaenid ova (e.g. DOWNEY & ALLYN 1981, 1984). They rather closely resemble the eggs of African *Hypolycaena philippus* (FABRICIUS 1793) or, especially, *Leptomyrina* spp. (CLARK & DICKSON 1971). In total, nearly 100 eggs or egg-shells were located. Usually only one egg (or egg-shell) was found per seed pod indicating that oviposition occurs singly. As in other Hypolycaeniti species the egg-shells are not eaten by the larvae after hatching and thus remain visible on the plants for at least two weeks (Fig. 5). In less than 10 cases two eggs were found on the same seed pod, and in all these cases one of the eggs had already hatched. Even on plants with numerous seed pods there were rarely more than 2 eggs per total inflorescence (e.g. Table 1). Apart from the unripe seed capsules which bore roughly 90 % of the eggs observed, some ova were also found on flower buds or even on the stem among the flowers. No unhatched eggs were found on older seed capsules.

Table 1: Distribution of *Hypolycaena othona* eggs/egg-shells and larvae on inflorescences of *Spathoglottis plicata* (census on 14 November 1991, Gombak site).

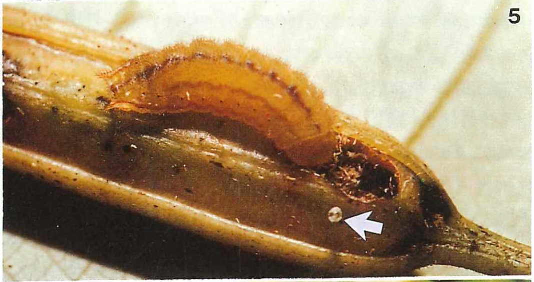
Eggs per inflorescence	1	2	3	6
Number of plants	15	2	3	1
Larvae	1 L_3 + 1 L_4	–	1 L_1 + 1 L_3	–


1


2


3


4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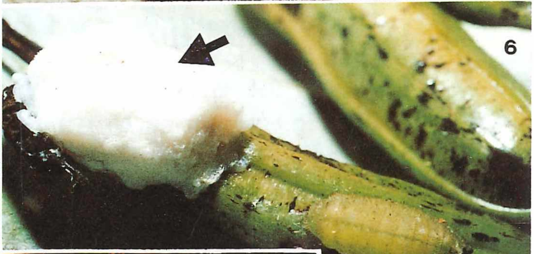
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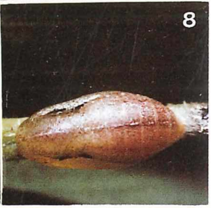
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All *S. plicata* plants bearing eggs of *H. othona* grew in open, sunny conditions. Two groups of 4–5 large plants each, growing at the shaded edge of the Gombak site (less than 10 m from the nearest colonized plant), received no eggs during the observation period. Single plants or isolated small groups (2–5 individuals) scattered along the road likewise never carried eggs or larvae.

The inflorescences of *S. plicata* were almost invariably visited by ants at least as long as any terminal flower buds or open flowers were present. (As in other orchids, flowering and seed maturation in *S. plicata* proceeds from the basal to the distal end of the inflorescence.) The ants harvested secretions from nectaries located at flower buds or the base of floral pedicels. Extra- and circum-floral nectaries are common in tropical orchids, and the ants they attract have been shown to reduce the level of herbivory, thereby increasing the reproductive fitness of the plants (RICO-GRAY 1989, RICO-GRAY & THIEN 1989, FISHER et al. 1990, and references therein). The ant taxa observed at *S. plicata* inflorescences are summarized in Table 2, together with data on the presence of *H. othona* eggs and immatures. The presence of ants obviously has no deterrent effect on ovipositing *H. othona* females, neither is there any apparent preference to lay eggs only at particular ant species.

From the above observations the following can be inferred with regard to oviposition behaviour. Females of *H. othona* search for appropriate orchid inflorescences primarily where hostplants are abundant, and they select unshaded, "apparent" plants bearing young seed pods or closed flower buds. Putatively the appropriate status of the hostplant is ascertained via chemical cues after having settled down on an inflorescence. Then she lays a single egg and leaves for another potential

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Colour plate: Fig. 1: Inflorescence of the ground orchid *Spathoglottis plicata*, a new hostplant of *Hypolycaena othona* in West Malaysia. **Fig. 2:** Newly eclosed adult of *H. othona*. **Fig. 3:** Second instar larva, boring into flower bud. **Fig. 4:** Third instar larva. **Fig. 5:** Fourth instar larva with feeding marks on orchid seed capsule. Arrow: Remnants of egg-shell. **Fig. 6:** Green colour variant of mature larva at prepupal stage. Arrow: Protective foamy secretion covering chrysomelid larva. **Fig. 7:** Ochreous pupa in natural position head-down on hostplant stem. **Fig. 8:** Fresh pupa showing persistence of purplish colour. **Fig. 9:** Mature larva with extensive purplish colouration in natural feeding position on flower buds. **Fig. 10:** Arctiid caterpillar (Spilosomini) feeding on *S. plicata* flowers. Note presence of *Crematogaster* ants that do not interfere with the herbivorous caterpillar.

hostplant. Whether or not ants serve as (additional) oviposition cues is unknown. It also remains to be investigated if and how the egg-laying females interact behaviourally with the ants visiting the orchid flowers. Clearly, direct observations of oviposition behaviour would be rewarding.

Table 2: Synopsis of the ant taxa observed attending inflorescences of *S. plicata*, and the presence of *H. othona* immatures. *Crematogaster* sp. 1 is the small brown species observed at the Gombak site, sp. 2 the larger black one from the Genting site.

Ant species or genus	eggs present	larvae present
Crematogaster sp. 1	+	+
Crematogaster sp. 2	+	+
Myrmicaria sp.	+	–
Meranoplus mucronatus	–	–
Polyrhachis sp.	+	+
Anoplolepis longipes	+	–
Hypoclinea sp.	+	+
Camponotus sp.	+	+

Larval stages: Morphology and behaviour

FIRST INSTAR: After 4–5 days (n = 6) the yellowish or reddish larva bit a large hole in the upper side of the egg-shell through which it hatches. The remaining chorion was not eaten, and the caterpillars soon started to crawl about on the seed pods. Then they gnawed a hole into the green pericarp and bored into the densely packed unripe seeds on which they preferably fed. Some larvae entirely tunneled into their hostplant, while in others the rear end remained visible, projecting from the entrance of the feeding hole. Alternatively, first instar larvae may only feed externally on the outer green tissue, leaving a small pit in which they exactly fit. Boring took place anywhere on the seed pods except at the thick fusion sutures of the three carpels. A few larvae also bored into fleshy flower buds in a similar manner. The first instar lasted 3–4 days (n = 10) at ambient light conditions and temperatures (L:D = 12:12 h; maximum temperature 26–28 °C, minimum 20–22 °C), and the larvae grew to approx. 3 mm in length. To the end of the first instar, the purplish pattern of the following stage became visible. Most larvae under observation left their feeding holes and moulted externally on the seed pods, resting on a silk pad. Typically the casted exuviae were eaten soon after moulting.

SECOND INSTAR: After the first moult the yellowish larvae develop a distinct dull purple mid-dorsal band. Most larvae additionally bear a supraspiracular and a subspiracular lateral band on either side (e.g. Fig. 3). The extent of purple colouration is markedly variable. Feeding behaviour is similar to that of the previous instar. The caterpillars bore into the seed pods or flower buds (Fig. 3), with their head and thorax, or sometimes entirely, disappearing in their feeding tunnels. To get rid of their frass, the larvae usually protrude their rear ends and drop out the faecal pellets. The second instar lasts only 2—3 days (n = 8).

Second instars have well developed secondary setae and are roughly cylindrical in shape, as typical for many endophytic lycaenid larvae. Under a stereo microscope a dorsal nectary organ (DNO) is discernible on the dorsum of the seventh abdominal segment, but no secretion acts have been actually observed with young larvae (see below). Tentacle organs are absent in this and all subsequent stages.

THIRD INSTAR: The overall shape of third instars approaches the more flattened, "onisciform" *gestalt* of typical Lycaeninae caterpillars (Fig. 4). Like in most endophytic lycaenid larvae, however, their cross-section remains somewhat rounded. In addition, there appear two distinct caudal projections on the last abdominal segment ("tail-points" of BELL 1915; cf. "suranal scoli" of BROCK 1990). The colouration is largely similar to the previous instar. The dull-purple mid-dorsal, supra- and subspiracular bands are usually well developed, but variable. Often they are confluent around the DNO, while in some individuals the lateral markings are weak or absent on the thorax. The DNO is well developed and functional.

The feeding behaviour was similar to second instars. The caterpillars now caused significant damage to the seed pods and more often fed entirely hidden within the capsules. At least in captivity feeding occurred day and night. The third instar lasted 3—4 days (n = 11), and the caterpillars grew to 9 mm in length.

FOURTH (FINAL) INSTAR: Morphologically these are very similar to third instars, but exhibit a more pronounced colour polymorphism. Most larvae remain yellowish with more or less extended purple markings (Fig. 5), and one mature larva found in the field on 20 November was almost totally purplish (Fig. 9). A few caterpillars, however, turned into a uniformly green colour without distinct reddish markings (Fig. 6).

During the final instar the larvae fed nearly constantly and produced large amounts of frass. They often hollowed out the seed pods completely. At least in captivity all caterpillars fed on more than one seed pod, and the feeding signs observed in nature as well indicated that one seed pod is not always sufficient to support larval development. Most larvae were largely hidden in the capsules with only the anal end visible from outside. If the caterpillars fed entirely hidden in their hostplants, they regularly crawled backwards to the entrance of their feeding tunnels to defaecate. Although in captivity sometimes substantial amounts of frass accumulated in the hollowed seed pods, such contamination of the food resources is unlikely to occur in nature. In the field, several mature caterpillars were also seen feeding externally (Fig. 9). Even large larvae refused to feed on expanded flowers, but readily accepted buds and sometimes gnawed at fleshy stalks. Cannibalism (e.g. towards moulting individuals) did never occur, although up to 6 mature caterpillars were kept in plastic vials of only 120 ml volume.

After 3—6 days (n = 8) the caterpillars stopped feeding at a length of 16 mm, left their seed capsules, and settled down for pupation spinning a silk pad and a girdle. In captivity, pupation occurred externally on the seed pods or among the filter paper that covered the bottom of the rearing vials. One pupa was found in the field, attached head-down to the stem of the hostplant inflorescence (Fig. 7). The prepupal stage during which the larvae remained immobile lasted about 1—2 days, the entire fourth instar took 4—7 days (n = 8).

Epidermal organs

The integument of final instars of *Hypolycaena othona* shows the typical honeycomb structure of many lycaenid larvae (e.g. Fig. 12 & 13). Only the prothoracic shield, although not as highly sclerotized as, for example, in many Deudorigiti, has an uncreased cuticle (Fig. 11). From the second to fourth instar the caterpillars bear an increasingly dense coat of secondary setae. Predominantly these are straight, slightly dentate (probably mechanosensory) setae inserted into characteristic prominent sockets (Fig. 12). The straight setae are rather long and slender (150—300 μm), but distinctly shorter (60—100 μm) and somewhat cone-like hairs (Fig. 13) occur amidst the longer ones. Also transitional types can be found.

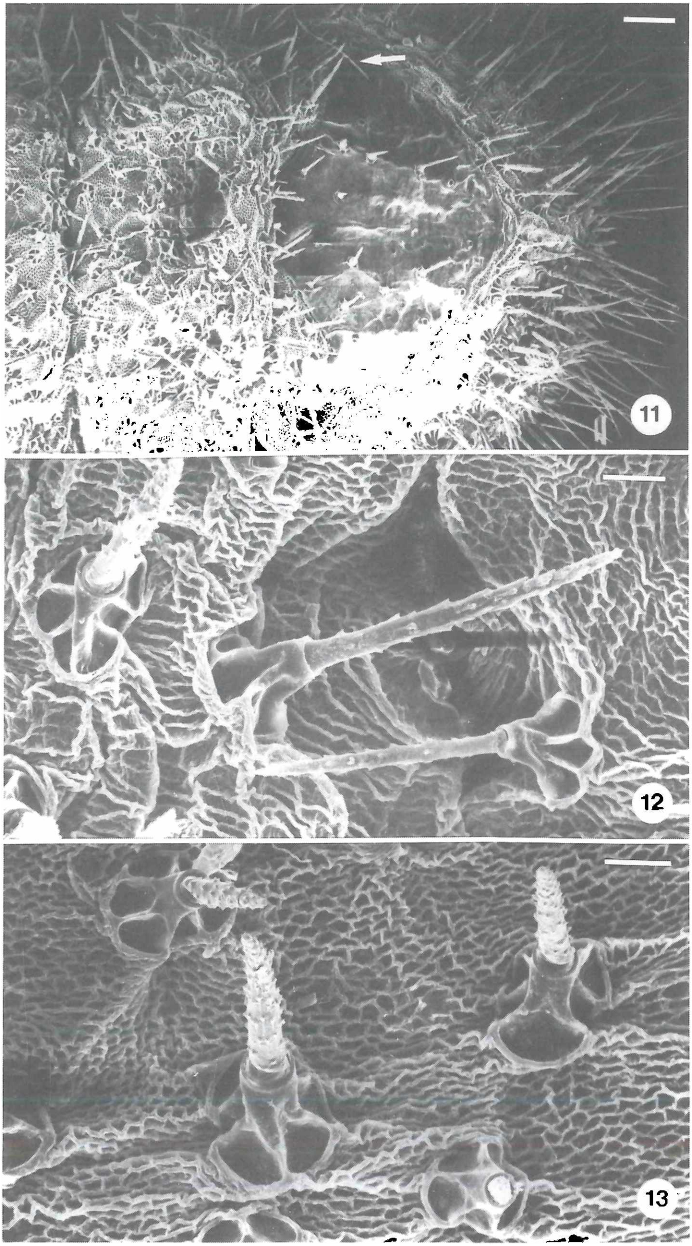


Fig. 11–13: *Hypolycaena othona*, mature larva. **Fig. 11:** Prothoracic shield with uncreased cuticle. Arrow: filiform seta. Scale = 150 µm. **Fig. 12:** Long straight (mechanosensory?) setae with dentate hair shaft. Scale = 30 µm. **Fig. 13:** Short straight setae. Note typical honeycomb structure of the cuticle. Scale = 30 µm.

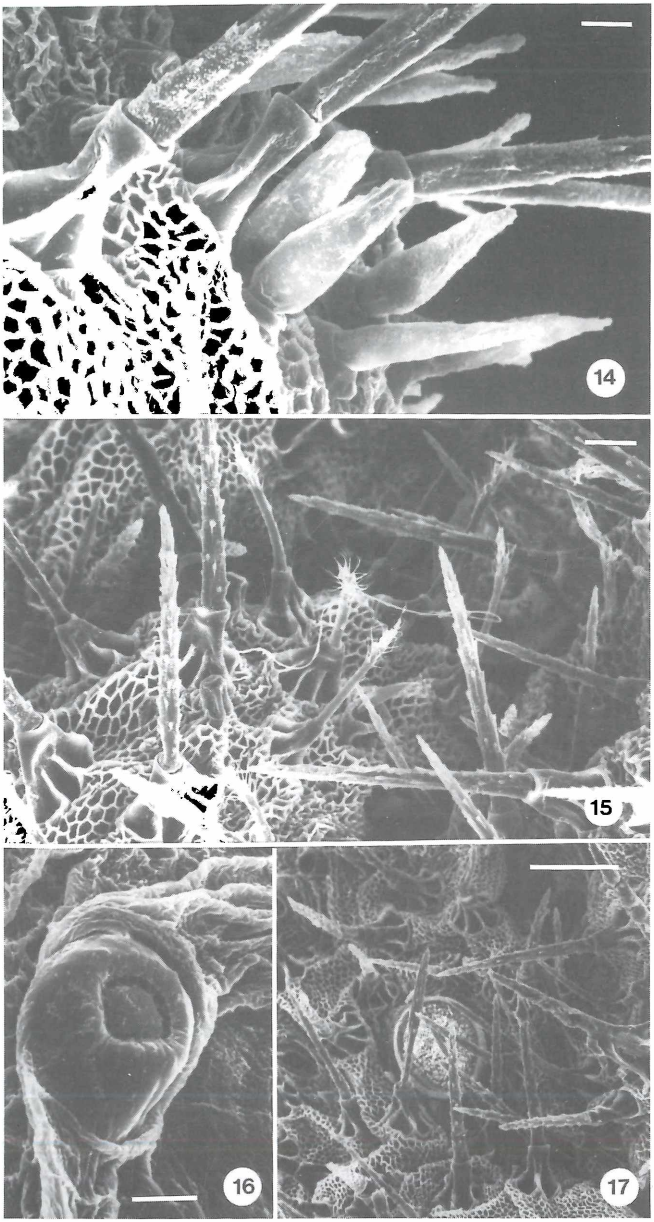


Fig. 14–17: *Hypolycaena othona*, mature larva. **Fig. 14:** Setae on anterior margin of the prothorax. Scale = 15 µm. **Fig. 15:** Group of dendritic hairs (6 such hairs visible) located above the spiracle of first abdominal segment. Scale = 30 µm. **Fig. 16:** Pore cupola organ. Scale = 10 µm. **Fig. 17:** Spiracle of seventh abdominal segment. Scale = 100 µm.

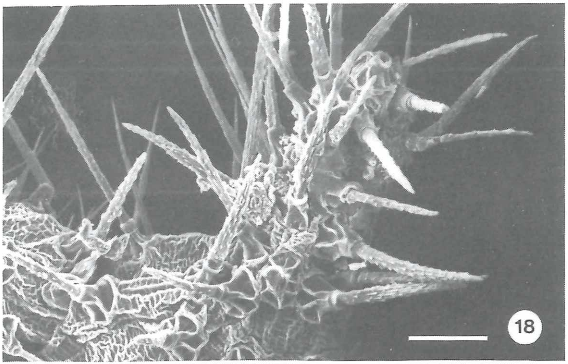
At the anterior margin of the prothorax there are a few modified stout setae (60 μm long) with a smooth surface (Fig. 14). One filiform seta each is located at the latero-posterior edge of the prothoracic shield (Fig. 11). The only other prominent hair type found is a small field of 5—10 dendritic setae above the spiracle of the first abdominal segment (Fig. 15).

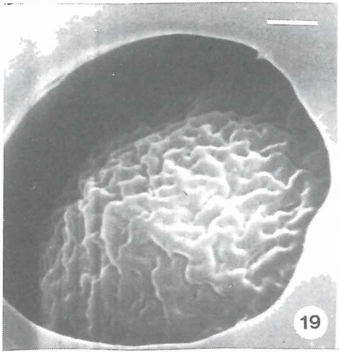
The DNO is well developed, but is only surrounded by straight setae. Specialized hairs (e.g. dendritic setae), as they are often to be found around the DNO of lycaenid larvae, are absent. Tentacle organs are lacking, but a pair of epidermal pits at the expected locations (without any specialized setae) may represent rudiments of these myrmecophilous organs. Pore cupola organs (PCOs; Fig. 16) occur sparsely scattered all over the integument. A distinct abdominal plate is not developed. The tail-points only bear a number of straight secondary setae with no further specialized hair types or glands discernible (Fig. 18).

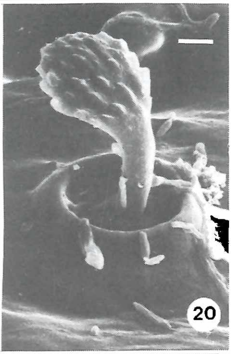
Myrmecophily and substrate-borne vibrations

Hypolycaena othona caterpillars possess PCOs, and a DNO from the second to fourth instar, but they lack a pair of TOs. It is not clear whether the DNO in the second instar is truly functional. In the field, all first and second instars were ignored by the numerous ants tending the nectaries, and in captivity second instars were ignored by ants (*Meranoplus mucronatus* and *Crematogaster* sp. [both Myrmicinae] tested). Third and fourth instars, however, were sometimes attended by ants, and secretions from the DNO were cleary visible on a number of occasions.

On November 14, a fourth instar larva at the Gombak site was observed with 2 *Crematogaster* workers antennating its DNO and harvesting the secretions. These ants belong to a small, highly trophobiotic *Crematogaster* species that commonly attended the orchid nectaries and which was also observed in association with various lycaenid caterpillars (*Surendra florimel* DOHERTY 1889, *Jamides* spp.) on different hostplants (FIEDLER, unpubl.). On the same day, one third and one mature fourth instar were located on a flower stalk occupied by *Polyrhachis (Myrma)* sp. (Formicinae), but only one worker ant briefly visited the younger caterpillar and antennated its DNO. A third instar on an inflorescence colonized by another ant species (*Hypoclinea* sp. [Dolichoderinae]) was ignored.







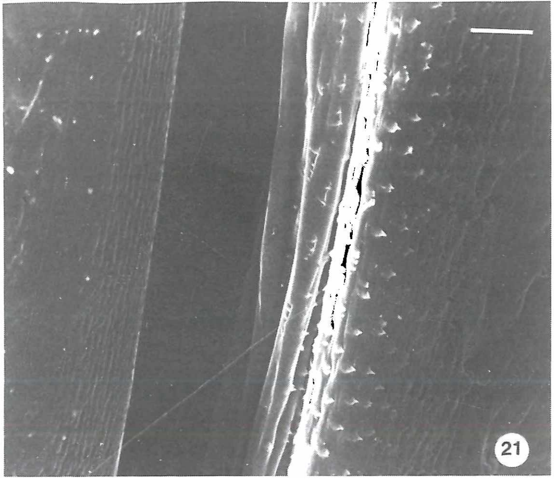


Fig. 18: Tail-point of mature larva of *Hypolycaena othona*. Scale = 100 µm. **Fig. 19–21:** Pupa of *H. othona*. **Fig. 19:** Pore cupola organ with folded surface of sieve plate. Scale = 1 µm. **Fig. 20:** Sensory(?) hair, located near the 6th abdominal spiracle. Scale = 5 µm. **Fig. 21:** Stridulatory organ of pupal exuvia. Stridulatory plate of A5 on the left, file with teeth (on A6) on the right. The large gap between the tergites results from adult eclosion. Scale = 20 µm.

On November 17, several fourth instars were located at the Genting site on two orchids with large numbers of ants (a black *Crematogaster* species and a small member of *Camponotus* subgenus *Orthonotomyrmex*). Workers of both ant species were repeatedly, but never simultaneously, observed antennating the caterpillars, especially at the DNO. These two ant species co-occurred on the same plants without direct interference (possibly a case of parabiosis; see HÖLLDOBLER & WILSON 1990 for a discussion of such interactions between *Crematogaster* and *Camponotus*). When transferred to the laboratory, the ant-caterpillar associations with both ant species remained rather stable for 2 days, when the caterpillars pupated and the ants were fixed.

Further caterpillars were caged with ants to observe the interactions in more detail. The small *Crematogaster* (the same species observed in association with a caterpillar at the Gombak site) readily accepted fourth instar caterpillars and often elicited DNO secretions during the first hours of the experiment. The association, however, tended to be highly unstable, and inspections at irregular intervals during the following 4 days revealed that ants were only from time to time directly attending the larvae. Nevertheless, the caterpillars were by no means disturbed by the presence of ants and continued feeding and defaecating.

Workers of a second ant species, *Meranoplus mucronatus*, were introduced to another group of larvae. This slowly moving, highly trophobiotic ant species has been observed tending the nectaries of the hostplant orchid and has also been found associated with lycaenid caterpillars (*Jamides* sp., *Eooxylides tharis* (GEYER [1837]); FIEDLER, unpubl.). The ants at first completely ignored the mature caterpillars, but on the third day of the experiment one worker ant was observed feeding on a DNO secretion droplet. During the subsequent days the same *Meranoplus* ants never paid attention to prepupae or pupae.

In a third trial, 4 workers of a highly trophobiotic earth-nesting *Myrmicaria* sp. (also observed tending the orchid inflorescences) were enclosed with one fourth instar caterpillar. On several occasions during the following two days the caterpillar was antennated at the DNO by an ant, and DNO secretions were observed repeatedly. Again the caterpillar-ant association was unstable, and at no time more than one ant tended the larva. After three days only one ant was still alive, indicating that the secretions provided by a single mature caterpillar were not sufficient to nourish 4 workers for a longer period. Judging from these observations in captivity, *Meranoplus mucronatus* and *Myr-*

micaria sp. can be assumed to be at least occasional visitors of *H. othona* caterpillars. Vouchers of all ant species mentioned are in the author's collection.

Repeated tests using a BAUER & HÄSELBARTH light-weight stethoscope revealed that third and fourth instars are capable of producing substrate-borne vibrations (cf. SCHURIAN & FIEDLER 1991). Second instars appeared to be mute, whereas in fourth instars vibrations occurred up to the prepupal stage. No signals audible to the human ear could be detected (larvae tested on filter paper, in the plastic rearing vials, on the stethoscope membrane, and in the hollow of the observer's hand), suggesting that air-borne components are absent (except possible secondary resonance effects at most). Observations on several European lycaenids indicate that the larval vibrational signals are produced via rhythmic muscle contractions of high frequency and are strictly substrate-borne (FIEDLER & KIRCHNER, unpublished; also DEVRIES 1991).

The vibrational signals of *H. othona* larvae consist of distinct rumbling or croaking "calls" with an estimated dominant sound frequency far below 1 kHz (estimated from comparisons with records of *Polyommatus* LATREILLE 1804 and *Lycaena* FABRICIUS 1807 caterpillar calls; FIEDLER, unpubl.). Usually, 1—3 calls were produced per second, after a larva had been transferred to the stethoscope membrane. When molested more heavily (e.g. after pinching with forceps) the calls tended to occur more frequently and with a greater amplitude. Generally, calls of third and fourth instar larvae were very similar to each other, but no recording equipment was available allowing a more detailed analysis.

The pupa

The pupae are 10—12 mm in length. Fresh pupae retain the colour polymorphism of mature larvae and are either entirely light green or, mostly, with a more or less extensive hint of purple on thorax and abdomen. The wing cases are always light greenish. Immediately above the wing cases there is a distinctly blackish suture, and rows of small blackish dots occur also on the abdominal tergites (Fig. 7 & 8).

The pupal integument bears rather few secondary setae. PCOs occur in clusters around the prothoracic and abdominal spiracles. The PCOs are inserted in minute pits, and their sieve plates do not elevate above the remaining integument (Fig. 19). Mainly around the spiracles there occurs another type of short (20–30 μm), presumably sensory setae (Fig. 20). There is no visible cuticular scar of the DNO.

After 8–9 days the pupae become ochreous (Fig. 7), and after 9–10 days the pigmentation of the eyes is clearly visible. Then the colouration of the wings and body develops rapidly, and 10–11 days after pupation (n = 12) the adults eclose (Fig. 2). Thus, the entire developmental cycle lasts 27–31 days (egg: 4–5, larva: 13–15, pupa: 10–11 d). Adult eclosion occurred between 8.30 and 12.00 local time (n = 11), and since all animals were kept under ambient conditions, these data indicate that eclosion in nature takes place in the late morning as well. Spreading of the wings was achieved within 10 min, but the butterflies usually did not commence flying earlier than 1 h after eclosion.

The pupae stridulate when disturbed (e.g. after manipulation with forceps). Pupal sounds consist of distinct chirping calls that are displayed with a frequency of roughly 1–3 calls per second. Stridulation mainly occurs immediately upon disturbance, but can continue for up to a minute if the pupa is sufficiently stimulated through permanent molestation. The sounds are easily detectable using a stethoscope (SCHURIAN & FIEDLER 1991), but they are also audible to the human ear through the air at a distance of at least 5–10 cm. For these tests the pupae were placed on the stethoscope membrane (without using the ear-connection tube), or on a sheet of filter paper. Hence, the pupae are truly capable of producing air-borne stridulatory signals as has been demonstrated for numerous lycaenid species (DOWNEY & ALLYN 1978).

The pupae showed a variable readiness to stridulate. There was, however, no clear pattern. Five pupae stridulated whenever tested, although sometimes persistent molestation was necessary to elicit this behaviour. Three pupae did not respond at all on two subsequent days, whereas another refused stridulating on one day, but readily did on the following morning. The ability to stridulate was present from the first day of the pupal stage until at least two days prior to eclosion (older pupae not tested).

In *Hypolycaena othona* the pupal stridulation organ is situated at the modified intersegmental region between the fifth and sixth abdominal segment. This organ consists of a "file" with minute cuticular teeth on A6 that can rub against a field of parallel cuticular furrows on A5 ("stridulation plate"; Fig. 21). In *H. othona*, as in most other lycaenid pupae, the abdominal segments not involved in composing the stridulatory organ are largely immoveable against each other. Hence, contractions of the dorsal longitudinal musculature of the pupae result in flection movements of this particular intersegmental region and thereby produce the stridulatory signals (see DOWNEY & ALLYN 1973, 1978).

Other herbivores on *Spathoglottis plicata*

The inflorescences of *S. plicata* suffer heavily from herbivory. At both observation sites, the commonest seed predator was a chrysomelid beetle which was apparently unaffected by the permanent presence of ants. The chrysomelid larvae always fed under a thick layer of a white, foamy secretion (Fig. 7). These larvae entirely destroyed large numbers of seed pods. The adult beetles were also regularly present on the plants.

On two orchid inflorescences, one arctiid caterpillar (tribe Spilosomini) each was found feeding (Fig. 10). Both these plants showed significant feeding damage and were occupied by a black *Crematogaster* species. When the same plants were checked two days later, one inflorescence had been taken over by a large *Camponotus* species. Both arctiid caterpillars had disappeared from unknown reasons (predation by the large ants?).

DISCUSSION

Comparison to other life-history records of *Hypolycaena othona*

The above observations from West Malaysia largely confirm previous records. *H. othona* caterpillars are thus variable in colour from green to entirely purplish, with possible differences according to geographic origin or hostplant colour. They have a partly endophytic way of feeding, tunneling into fleshy tissues of their hostplants' inflorescences (e.g. flower buds, seed pods, flower stalks). Clearly they are not restricted to one of these plant parts and readily switch between buds and seed pods depending on availability. This well explains the somewhat contrasting records of BELL (1915: flower buds) and NORMAN (1976: seed pods). Open flowers and green leaves, however, are avoided.

The observations on Malayan *H. othona* revealed differences to previous records concerning two major characters. Firstly, HINTON (1951) was not correct in listing *H. othona* larvae as possessing tentacle organs (TOs). These organs are clearly entirely absent, as in all other known Hypolycaeniti larvae. The pair of epidermal pits on the expected locations of the TOs on the eighth abdominal segment may, however, represent a vestige. Since TOs have been reported from most Theclini and Eumaeini subtribes (e.g. Iolaiti, Deudorigiti), the absence of these organs in the larvae of Hypolycaeniti (as well as in the Remelaniti and Eumaeiti) must be a secondary loss. The scar of the DNO on the pupal epidermis stated to be present in Indian *H. othona* (BELL 1915, HINTON 1951) could not be found in Malaysian pupae, but the expression of such scars tends to be variable and has no biological significance (functional pupal DNOs are extremely rare).

The second deviating observation is concerned with hostplant choice. All *H. othona* hostplants hitherto recorded are epiphytic orchids of the genera *Aerides, Cottonia, Dendrobium, Rhynchostylis* and others. *Spathoglottis plicata* is the first ground orchid ever observed to be utilized as host, and the finding that at least two populations in Peninsular Malaysia made use of this plant species demonstrates that *H. othona* is not a true canopy specialist restricted to epiphytic hosts, but can at least occasionally colonize hostplant populations of lower strata if available.[1] This plasticity may have been important in colonizing the huge and climatically diverse distribution area ranging from India across Sundaland to Sumbawa.

Comparison with related species

Among the Hypolycaeniti species with known immature stages, the Austro-Melanesian *Hypolycaena danis* most closely parallels to *H. othona*. The caterpillars and pupae of *H. danis* are nearly indistinguishable, and its larvae also feed on orchid inflorescences, sometimes even reaching pest status in gardens (COMMON & WATERHOUSE 1981). Undoubtedly *H. danis* larvae will exhibit a similarly low level of myrmecophily as does *H. othona*. For a third Oriental species, *H. kina*, only the orchid hostplant has been recorded, but given the close affinity of the adults of *H. othona* and *H. kina* it is feasible to assume that the caterpillars and pupae of both species are very similar, too. Two other Oriental species, *H. balua* (MOULTON [1912]) and *H. pahanga* (CORBET 1938), also have extremely similar adults and appear to be very closely related to *H. othona*, suggesting that their larvae may feed on orchid inflorescences as well.

Unfortunately there is no life-history information available on the majority of Indo-Australian *Hypolycaena* species. Neither the larvae

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[1]: Recently, PARSONS (1991) has recorded the ground orchis *Spathoglottis papuana* as hostplant of *Hypolycaena danis.*

of the widespread *H. amasa* HEWITSON [1865] (often treated as a distinct genus *Zeltus*), nor, for example, the immatures of *H. sipylus* (FELDER 1860), *H. thecloides* (FELDER & FELDER 1860) or the *H. merguia* species group [e.g., *merguia* (DOHERTY 1889), *umbrata* SEKI & TAKANAMI 1988, *toshikoae* HAYASHI 1984, *amabilis* (DE NICÉVILLE 1895)] have been described. Judging from external adult morphology, species like *sipylus* or *thecloides* bear some affinities to the *othona* group, and it would be interesting to investigate as to whether their larvae are specialized flower- or even orchid-feeders. The lack of life-history information for all these species, although they are in part widespread in the Oriental region, could indicate that their immature stages live in the rainforest canopy with its diverse epiphyte flora.

Hypolycaena erylus and its probable Austro-Melanesian sister-species *H. phorbas* have a very different larval biology and morphology. Both species are polyphagous external feeders on young growth of at least 12 tree or epiphyte families. Their caterpillars are typical flat and onisciform lycaenid larvae, with only short secondary setae and a well-developed DNO from the second instar on. They lack the tail-points of *H. othona* and *H. danis*. Colour markings of the highly variable larvae consist of light and brown dorsal stripes on a green or brownish background (JACOBSON 1912, COMMON & WATERHOUSE 1981). The pupae are similar to those of *H. othona* in shape. All larval instars and the pupae of both species are closely associated with a specific host ant (*Oecophylla smaragdina* F.), this symbiosis apparently being obligatory as far as the lycaenids are concerned (JACOBSON 1912, VALENTINE & JOHNSON 1988, MOSS 1989).

Life-history data are available for 3 African *Hypolycaena* species, namely *H. pachalica* BUTLER 1888, *lochmophila* TITE 1967 and *philippus*. These species are polyphagous on young foliage as well as flowers and fruits of trees and shrubs, the recorded hostplants covering at least 9 plant families (FIEDLER 1991 a). The larva of *H. philippus* is green, of general lycaenid shape, and it has no tail-points (CLARK & DICKSON 1971).

The early stages of 3 species of the related African genus *Leptomyrina* were also figured by CLARK & DICKSON (1971)[2]. Their illustrations

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[2]: The photographs given by MIGDOLL (1988: pp. 88–89) do not illustrate *Leptomyrina hirundo* (WALLENGREN 1857) and *gorgias* (STOLL [1790]) as indicated, but *Anthene butleri livida* (TRIMEN 1881), a species sharing habitat and hostplant with *Leptomyrina*, but belonging to an entirely different systematic group, namely Polyommatini-Lycaenesthiti; cf. CLARK & DICKSON (1971).

show that the caterpillars are again of the onisciform lycaenid type, but with some resemblance to *H. othona* in the morphology and distribution of secondary setae. In *Leptomyrina* spp. as well as in *H. othona* the dominant hair type are straight sensory setae on elevated sockets, and modified setae are absent from the DNO. The larvae of *Leptomyrina* feed inside the succulent leaves of herbaceous Crassulaceae and Aizoaceae (CLARK & DICKSON 1971, FIEDLER 1991 a).

The only illustration of the mature caterpillar of *Hemiolaus caeculus* HOPFER 1855, which has recently been transferred to the Hypolycaeniti (LARSEN 1991), shows a flat onisciform lycaenid larva with a dense cover of short hairs, lacking tail-points (MIGDOLL 1988). Apparently, this species feeds on the foliage, and not inflorescences, of its hostplants (Olacaceae). The overall shape of the larva of *H. caeculus* closely parallels that of other Hypolycaeniti caterpillars, whereas the larvae (and pupae) of true Iolaiti tend to have highly aberrant morphologies yielding camouflage on their mistletoe hostplants (e.g., CLARK & DICKSON 1971). Thus, although structural characters need to be investigated in more detail, larval morphology supports the novel placement of *Hemiolaus*.

The information here compiled suggests the following character combination of ancestral Hypolycaeniti larvae: onisciform caterpillars with DNO, but lacking TOs; straight sensory setae on sockets as main type of secondary setae; low numbers of dendritic setae and PCOs; four larval instars (an optional additional instar has been reported from *H. philippus* and *Leptomyrina* spp., possibly an adaptation to overcome dry periods?); DNO present from the second instar onward; external feeders on young foliage and inflorescences of woody plants, with a tendency to bore into their food where possible; facultative myrmecophily.

Models for this stage are provided by some of the African *Hypolycaena* species. Starting from this groundplan, the genera *Leptomyrina* and *Hemiolaus* have evolved specializations towards their particular hostplants and feeding habits. When the Oriental region was colonized by descendants of African Hypolycaeniti stock[3], at least two evolutionary routes were followed. One species group (*erylus* and *phorbas*) developed

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[3]: According to ELIOT (1973) it is likely that, akin to other African lycaenid taxa with Afro-Oriental distribution (e.g. Aphnaeini, Iolaiti, Deudorigiti, Lycaenesthiti), Hypolycaeniti travelled from west to east via the Arabian peninsula rather than vice versa.

an obligatory symbiosis with the abundant and highly dominant weaver ant *Oecophylla smaragdina,* with all the characters selected for in highly myrmecophilous species: polyphagy on young, nutrient-rich hostplant tissues, ant-induced oviposition, reduction of larval hairiness, and a high DNO secretion rate.

Another pathway led to the specialization on orchid inflorescences as larval food, in combination with partly endophytic life-habits, a reduction of the extent of myrmecophily, an elaborate camouflage of the larvae, and the development of tail-points that may play a role in camouflage. Such tails are, however, not unique among the Lycaenidae and recur in several African Iolaiti hairstreaks (*Stugeta* DRUCE 1891; *Argiolaus* DRUCE 1891; *Epamera* DRUCE 1891: CLARK & DICKSON 1971).

Taxonomy

The generic limitations of *Hypolycaena* are still subject to taxonomic inconsistencies. BRIDGES (1988) keeps *Tatura, Zeltus* and *Chliaria* as distinct genera. No acceptable phylogenetic reasoning has ever been advanced to legitimate *Tatura* and *Zeltus,* and following STEMPFFER (1967) these taxa should clearly be treated as synonyms. Likewise there is little doubt that separating *Chliaria* from *Hypolycaena* as a distinct genus renders the latter paraphyletic. However, the name *Chliaria* might be suitable to characterize the probably monophyletic orchid-feeding species group on subgeneric level.

Type species of *Chliaria* is *othona.* BRIDGES (1988) lists the following further species under *Chliaria: balua; kina; pahanga; tora* KHEIL 1884 from India to Sundaland; *schroederi* HAYASHI 1984; and *irawana* HAYASHI, SCHRÖDER & TREADAWAY 1984 from the Philippines. Since the morphology and biology of the immature stages of *H. danis* are nearly identical to those of *othona,* this Australian species must necessarily be included into this group, though *H. danis* has hitherto never been referred to as *Chliaria.* In contrast, other species were originally described as belonging to *Chliaria* (*shirozui* HAYASHI 1984 from the Philippines, also *merguia* and *amabilis*), but later transferred to *Hypolycaena* s. str., usually without a phylogenetic reasoning.

Although the shift towards orchids as hostplants doubtless provides an exceptional synapomorphy of the *othona* species group, and larval morphology may yield further synapomorphies (e.g. the tail-points), it is yet unclear whether *Chliaria* truly deserves subgeneric rank. The reason is that the prevalence of these characters among the remaining

Oriental *Hypolycaena* species is still unknown. In particular, one cannot rule out that species like *H. sipylus* or *H. thecloides*, which rather closely resemble the *othona* group in some adult external characters, also have orchid-feeding larvae with tail-points. As *H. sipylus* is the type species of *Hypolycaena*, a possible relationship of this latter species to orchids would invalidate this character as synapomorphy of *Chliaria*. Hence, a final decision about the delimitations and taxonomic status of *Chliaria* should be deferred until data on morphology and hostplant use of more Indo-Australian species become available.

Myrmecophily

The degree of myrmecophily is rather low in most Hypolycaeniti except the two specialists *H. erylus* and *H. phorbas*. Nevertheless, ant-associations have been observed in the African *Leptomyrina* spp., *H. philippus*, *nigra* BETHUNE-BAKER 1914, and *lebona* HEWITSON [1865], as well as in the Oriental *H. othona* (FIEDLER 1991 a). According to the categorization of FIEDLER (1991 b), the larvae of most of these latter species can be scored as moderately myrmecophilous. In *H. othona*, the ant-associations are non-specific and facultative, involving ants of at least 2 subfamilies and 5 genera. Given the nearly constant presence of a variety of nectar-harvesting ants on the hostplant inflorescences, further ant-associates of *H. othona* will undoubtedly exist.

Due to the low permanence of ant-associations in the field as well as in captivity, the protective benefits which the caterpillars may derive from the presence of ants (e.g. PIERCE & EASTEAL 1986) are supposedly limited. Some potential predators might be deterred by the presence of ants. Since only very few older instars and a single pupa were found in the field, mortality can be assumed to be high despite of the prevalence of ants on the hostplants. No assessment of the rate of parasitism is yet possible, since almost all reared individuals originated from eggs or larvae collected at a very young stage. Anyway, no parasitoids were recorded. The ants presumably derive almost no nutritive benefits from tending *H. othona* ants. The few secretion acts observed suggest that only minor amounts of DNO (and presumably also PCO) secretions are delivered. The pupae appear to be largely unattractive, and casual and momentary ant-associations are to be expected at most (see FIEDLER 1988 for a discussion of pupal myrmecophily).

It has not yet been established whether substrate-borne vibrations of lycaenid caterpillars are really correlated with myrmecophily. DEVRIES

(1990, 1991 a) has found experimental evidence that vibratory signals of certain riodinid larvae help to attract ants, and on the grounds of a comparative survey he has suspected a similar correlation to occur among the Lycaenidae as well. Own observations on 27 lycaenid species from 13 genera in 2 subfamilies, as well as the data of DeVries (1991 a) on 20 additional species covering 12 further genera, suggest that the ability to produce vibratory signals is almost universal among the Lycaenidae. Only 6 Neotropical myrmecoxenous Eumaeiti species appear to be mute.

Of the 47 lycaenid species known to vibrate so far, 3 *Lycaena* species and *Callophrys rubi* (Linnaeus 1758) are not known to be tended by ants, and three species of *Allotinus* Felder & Felder 1865 rarely interact with ants while feeding on trophobiotic Homoptera (Fiedler, unpublished). Others like *Prosotas dubiosa* (Semper [1879]) or *Hypolycaena othona* are only occasionally visited by ants. This indicates that within the Lycaenidae, vibratory abilities are more widespread and less closely connected with myrmecophily than in the Riodinidae.

Hypolycaena othona larvae only vibrated when disturbed, and although tactile molestation has turned out to generally stimulate vibratory signals, it appears that myrmecoxenous or weakly myrmecophilous larvae do not or rarely vibrate spontaneously. Thus, larval vibrations in such species, including *H. othona*, might rather serve as a defensive device, whereas in more closely ant-associated species the spontaneous vibrations may enhance larval attractiveness to ants. If this interpretation comes true, the correlation within the Lycaenidae would be that myrmecophilous species produce spontaneous and more complex vibratory signals, whereas myrmecoxenous or weakly myrmecophilous species only utter simple "calls" as a reaction to disturbance. Qualitative observations tentatively support this view (Fiedler, unpubl.). In this respect it is noteworthy that the obligate myrmecophile *H. erylus* has been reported to produce vibrations constantly (DeVries 1991 a), whereas the low-level myrmecophile *H. othona* only makes short series of calls when disturbed. DeVries (1991 a) also notes call-production by a *Hemiolaus* species from Madagascar without giving further details.

Herbivory on orchid inflorescences

Despite their huge species diversity, orchids are fed upon only by extremely few butterfly species. This infers that orchids must be chemically well defended against this large guild of herbivores. Two interrelated characters of the Hypolycaeniti can be seen as important prerequisites for the acquisition of orchid-feeding. Firstly, the caterpillars of some *Hypolycaena* species are polyphagous, and it is conceivable that polyphagous herbivores, although far from being optimized feeders, possess the ability to digest even "aberrant" hostplants like orchids to some degree. Secondly, hostplant specificity is often lower among lycaenids that feed on young foliage or inflorescences (like *Hypolycaena*), and this might account for a rather high rate of "oviposition mistakes" in such species as well as rather high survival rates of "misplaced" larvae (cf. CHEW & ROBBINS 1984). In fact, polyphagy as well as the acquisition of unusual and aberrant hostplant niches among the Lycaenidae are highly correlated with a predilection of young foliage or inflorescences as larval food (FIEDLER 1991 a). Thus, the Hypolycaeniti had the phyletic predisposition that allowed the switch towards orchids. Interestingly, the only parallel case is provided by the two Neotropical *Strymon* species *yojoa* (REAKIRT [1867]) and *mulucha* (HEWITSON [1867]) that use orchids as minor hosts. *Strymon*, like *Hypolycaena*, is essentially a polyphagous flower-feeding hairstreak genus (FIEDLER 1991 a).

One important barrier, besides plant chemistry, for many Lepidoptera to utilize orchids is certainly the widespread association between tropical orchids and ants with the help of nectaries or even domatia (RICO-GRAY 1989, FISHER et al. 1990). Ants have been shown to reduce the herbivory pressure in orchids (RICO-GRAY & THIEN 1989) as well as in many more plant taxa with nectaries (e.g. WHALEN & MACKAY 1988). Any herbivore on such plants is in need of protective mechanisms to avoid ant-attacks. The myrmecophilous organs and related adaptations of lycaenid caterpillars provide an exceptionally effective example of such mechanisms. The other herbivores observed on the orchids were either protected by foamy secretions (chrysomelid beetle larvae; these were the most effective herbivores throughout the observation period), or by long hairs (arctiid caterpillars) that allowed coexistence with small *Crematogaster* ants.

Larvae of *H. othona* are fully tolerated by the ant genera observed on their hostplant *Spathoglottis plicata*, and they may even gain some additional protection against enemies through attendant ants. Other lycaenid caterpillars, as well, are immune to ant-attacks on plants with nectaries (e.g. New Guinean *Philiris:* WHALEN & MACKAY 1988) or on myrmecophytes (Malayan *Arhopala:* MASCHWITZ et al. 1984).

Myrmecophilous Riodinidae species feed significantly more often on plants with nectaries as hosts (DEVRIES 1991 b), and there is accumulating evidence that such plant taxa are well represented in the host range of Lycaenidae caterpillars (e.g. PIERCE 1985). Perhaps, the occupation of ant-associated plants as hosts (as "enemy-free space": ATSATT 1981) was one of the prime selective factors that enhanced the independent evolution of myrmecophily in the butterfly families Riodinidae and Lycaenidae.

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References

ACKERY, P. R. (1988): Hostplants and classification: a review of nymphalid butterflies. – Biol. J. Linn. Soc. **33:** 95–203.

ATSATT, P. R. (1981): Lycaenid butterflies and ants: selection for enemy-free space. – Amer. Nat. **118:** 638–654.

BELL, T. R. (1915): The common butterflies of the plains of India. Part 17. – J. Bombay Nat. Hist. Soc. **23:** 481–497.

BRIDGES, C. A. (1988): Catalogue of Riodinidae and Lycaenidae (Lepidoptera: Rhopalocera). – Urbana (Illinois), 816 pp.

BROCK, J. P. (1990): Early stages. Pp. 78–107 *in:* O. KUDRNA (ed.): Butterflies of Europe, vol. 2, Introduction to Lepidopterology. – Aula-Verlag, Wiesbaden, 557 pp.

CHEW, F. S., & ROBBINS, R. K. (1984): Egg-laying in butterflies. – Symp. R. Entomol. Soc. London **11:** 65–79.

CLARK, G. C., & DICKSON, C. G. C. (1971): Life histories of the South African lycaenid butterflies. – Purnell Publ., Cape Town, 271 pp., 108 pls.

COMMON, I. F. B., & WATERHOUSE, D. F. (1981): Butterflies of Australia. 2nd ed. – Angus & Robertson Publ., London/Sydney/Melbourne/Singapore/Manila, 682 pp.

DEVRIES, P. J. (1990): Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. – Science **248:** 1104–1106.

——— (1991 a): Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera): Morphological, acoustical, functional, and evolutionary patterns. – Amer. Mus. Novit. **3025:** 1–23.

——— (1991 b): Evolutionary and ecological patterns in myrmecophilous riodinid butterflies. Pp. 143–156 *in:* HUXLEY, C. R., & CUTLER, D. F. (eds.): Ant-plant interactions. – Oxford Univ. Press, xviii + 601 pp.

DOWNEY, J. C., & ALLYN, A. C. (1973): Butterfly ultrastructure. 1. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. – Bull. Allyn Mus. **14:** 1–47.

——— (1978): Sounds produced in pupae of Lycaenidae. – Bull. Allyn Mus. **48:** 1–14.

——— (1981): Chorionic sculpturing in eggs of Lycaenidae. Part I. – Bull. Allyn Mus. **61:** 1–29.

——— (1984): Chorionic sculpturing in eggs of Lycaenidae. Part II. – Bull. Allyn Mus. **84:** 1–44.

ELIOT, J. N. (1973): The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. – Bull. Brit. Mus. Nat. Hist. (Entomol.) **28:** 371–505, 6 pls.

FIEDLER, K. (1988): Die Beziehungen von Bläulingspuppen (Lepidoptera: Lycaenidae) zu Ameisen (Hymenoptera: Formicidae). – Nachr. entomol. Ver. Apollo, Frankfurt, N.F. **9:** 33–58.

——— (1991 a): Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). – Bonner zool. Monogr. **31:** 1–210.

——— (1991 b): European and North West African Lycaenidae and their associations with ants. – J. Res. Lepid. **28:** 239–257.

FISHER, B. L., DA SILVEIRA LOBO STERNBERG, L., & PRICE, D. (1990): Variation in the use of orchid extrafloral nectar by ants. – Oecologia **83:** 263–266.

HINTON, H. E. (1951): Myrmecophilous Lycaenidae and other Lepidoptera – a summary. – Proc. Trans. Sth. London Entomol. Nat. Hist. Soc. **1949–1950:** 111–175.

HÖLLDOBLER, B., & WILSON, E. O. (1990): The ants. – Springer, Berlin/Heidelberg, xii + 732 pp.

JACOBSON, E. (1912): Symbiose zwischen der Raupe von *Hypolycaena erylus* GODART und *Oecophylla smaragdina* FAB. – Tijdschr. Entomol. **55:** 9–14.

LARSEN, T. B. (1987): The butterflies of the Nilgiri Mountains of Southern India (Lepidoptera: Rhopalocera). – J. Bombay Nat. Hist. Soc. **84:** 291–316.

——— (1991): The butterflies of Kenya and their natural history. – Oxford Univ. Press, xxii + 490 pp., 64 pls.

MASCHWITZ, U., SCHROTH, M., HÄNEL, H., & THO, Y. P. (1984): Lycaenids parasitizing symbiotic plant-ant partnerships. – Oecologia **64:** 78–80.

MIGDOLL, I. (1988): Field guide to the butterflies of South Africa. – New Holland Press, London. 256 pp.

MOSS, J. T. S. L. (1989): Observations on *Hypolycaena phorbas phorbas* (FABRICIUS) (Lepidoptera: Lycaenidae) on Carlisle Island, Queensland. – Austr. Entomol. Mag. **16:** 85–86.

NORMAN, T. (1976): Additions to the food plants of Indian Rhopalocera. – J. Bombay Nat. Hist. Soc. **73:** 228–229.

PARSONS, M. (1991): Butterflies of the Bulolo-Wau valley. Handbook no. 12 of the Wau Ecology Institute. – Bishop Mus. Pr., Honolulu, 280 pp., 22 col., 3 b/w pls.

PIERCE, N. E. (1985): Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. – Amer. Nat. **125:** 888–895.

——, & EASTEAL, S. (1986): The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. – J. Anim. Ecol. **55:** 451–462.

PINRATANA, A. (1981): Butterflies in Thailand. Vol. **4.** – Viratham Press, Bangkok, viii + 216 pp., 36 pls.

RICO-GRAY, V. (1989): The importance of floral and circum-floral nectar to ants inhabiting dry tropical lowlands. – Biol. J. Linn. Soc. **38:** 173–181.

——, & THIEN, L. B. (1989): Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). – Oecologia **81:** 487–489.

ROEPKE, W. K. J. (1919): Het Orchideen-blauwtje (*Chliaria dendrobii*). – Teysmannia **30:** 115–121 [not seen by the author].

SCHURIAN, K. G., & FIEDLER, K. (1991): Einfache Methoden zur Schallwahrnehmung bei Bläulings-Larven (Lepidoptera: Lycaenidae). – Entomol. Z. **101:** 393–398.

SCOTT, J. A., & WRIGHT, D. M. (1990): Butterfly phylogeny and fossils. Pp. 152–208 *in:* KUDRNA, O. (ed.): Butterflies of Europe, vol. 2: Introduction to lepidopterology. – Aula-Verlag, Wiesbaden, 557 pp.

STEMPFFER, H. (1967): The genera of the African Lycaenidae (Lepidoptera: Rhopalocera). – Bull. Brit. Mus. Nat. Hist. (Entomol.), Suppl. **10:** 1–322.

TAKANAMI, Y. (1989): A list of Lycaenidae from Sumbawa in the Lesser Sunda Islands, captured by Mr. K. MARUYAMA [in Japanese, with English title and original description]. – Kontyû to Shizen **24:** 36–40.

VALENTINE, P. S., & JOHNSON, S. J. (1988): Some new larval food plants for North Queensland Lycaenidae (Lepidoptera). – Austr. Entomol. Mag. **14:** 89–91.

WHALEN, M. A., & MACKAY, D. A. (1988): Patterns of ant and herbivore activity on five understory euphorbiaceous saplings in submontane Papua New Guinea. – Biotropica **20:** 294–300.

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