Zootaxa 1845: 47–59 (2008)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Life history and larval chaetotaxy of *Ahmetia achaja* (Lepidoptera, Lycaenidae, Lycaeninae, Theclini, Cheritrina)

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Abstract

Aspects of the life history of *Ahmetia achaja* (Fruhstorfer) and a description of the immature stages are presented. Larval chaetotaxy and morphological features of the eggs and pupae suggest a close phylogenetic relationship with some other members of the subtribe Cheritrina.

Key words: *Acacia megaladena* var. *indo-chinensis*, *Cheritra*, *Cowania*, *Drupadia*, *Horaga*, larval chaetotaxy, setal nomenclature, Siamese onyx

Introduction

The species originally described as *Horaga achaja* by Fruhstorfer (1912) was reassigned to the monotypic genus *Cowania* by Eliot in 1973. At the same time, the man in whose honor Eliot named the new genus was in the process of transferring the same insect to *Drupadia* Moore, 1884 (Cowan, 1974), while noting that it "will probably merit a separate genus". Eliot was unaware that the name *Cowania* was preoccupied by *Cowania* Reinhard, 1952 (Diptera: Tachinidae). The genus name *Ahmetia* was introduced by Özdikmen (2008) as a replacement for *Cowania* Eliot.

Eliot (1973) placed *Ahmetia achaja* (as *Cowania achaja*) in the tribe Cheritrini [later reduced to subtribe Cheritrina due to his inclusion of Riodininae within the Lycaenidae (Eliot, 1992)], largely on the basis of similarities in wing venation and male genitalia to *Drupadia* Moore, 1884. Eliot (1973) also described features of the larval and pupal stages of the Cheritrini, based on descriptions known to him only for *Cheritra* Moore, 1881, and *Drupadia*. These notably include: "larva shaped as in Horagini, but bearing only six dorsal triangular protuberances; pupa without girdle, head uppermost in *Cheritra*". Eliot was not familiar with the immature stages of *A. achaja*, nor apparently of *Drupadia theda* (C. & R. Felder, 1862), both of which similarly depart from the features he deemed characteristic of the tribe (or subtribe) into which he placed them.

Here, we describe the immature stages of *A. achaja* in order to facilitate comparison with other lycaenids and particularly with other members of the Cheritrina. We also re-examine some aspects of lycaenid first instar setal nomenclature and discuss setal homologies, particularly as the condition in *A. achaja* relates to other lycaenids and to the Lepidoptera in general.

Methods

Eggs and larvae of *A. achaja* were collected in the field and reared in captivity. Immature stages were preserved by injection with (3rd and 4th instars) or immersion for 48 hours in (1st and 2nd instars) 10 % acetic acid

Accepted by M. Toliver: 15 Jul. 2008; published: 8 Aug. 2008

to distend the body and prevent oxidative darkening, followed by subsequent long-term storage in 80% ethanol and/or glycerin. First instar larvae were prepared for critical examination by clearing in 5 % KOH, followed by rinsing in distilled water and transfer to glycerin. All specimens were examined using a binocular dissecting microscope and/or a compound microscope with ocular micrometer to facilitate measurement. Dimensions of most major tactile setae are reported to three decimal places, while those of generally much smaller features, such as microscopic proprioceptor setae and chalazae, which were measured at higher magnification, are reported to four decimal places. Because actual dimensions of setae and other features may vary somewhat, reported values should not be considered absolute, but rather indicative of relative size differences. Where slight differences were observed among measured features, an intermediate value (preceded by *ca*) is given; approximations are also given for features whose boundaries are not clearly indicated (*e.g.* micropylar region of the egg and poorly pigmented anal plate in 2nd and 3rd instars). In general, the nomenclature employed here follows Hinton (1946), Stehr (1987), and Hasenfuss & Kristensen (2003). Voucher specimens of *A. achaja* and other taxa observed for comparison are retained in the private collections of the authors.

Life history of *Ahmetia achaja*

Eggs and larvae of *A. achaja* (the Siamese onyx) were found on *Acacia megaladena* Desv. var. *indo-chinensis* I. Niels. (Fabaceae: Mimosoideae) near Vientiane, Laos, in April 2004. The larvae were found as solitary individuals attended by ants of the genus *Crematogaster* and most were found at rest on leaf petioles with their heads in proximity to petiolar nectaries. In captivity the larvae were kept with associated ants and reared on foliage of *A. megaladena* var. *indo-chinensis*. One larva was reared to adult, while others were preserved in various stages of development. Ova and 1st instar larvae of identical structure were found on the same host plant species in association with a smaller species of *Crematogaster* in central Kanchanaburi Province, Thailand, in June 2006. No *A. achaja* adults were observed in association with the larval host plants.

Morphology of immature stages

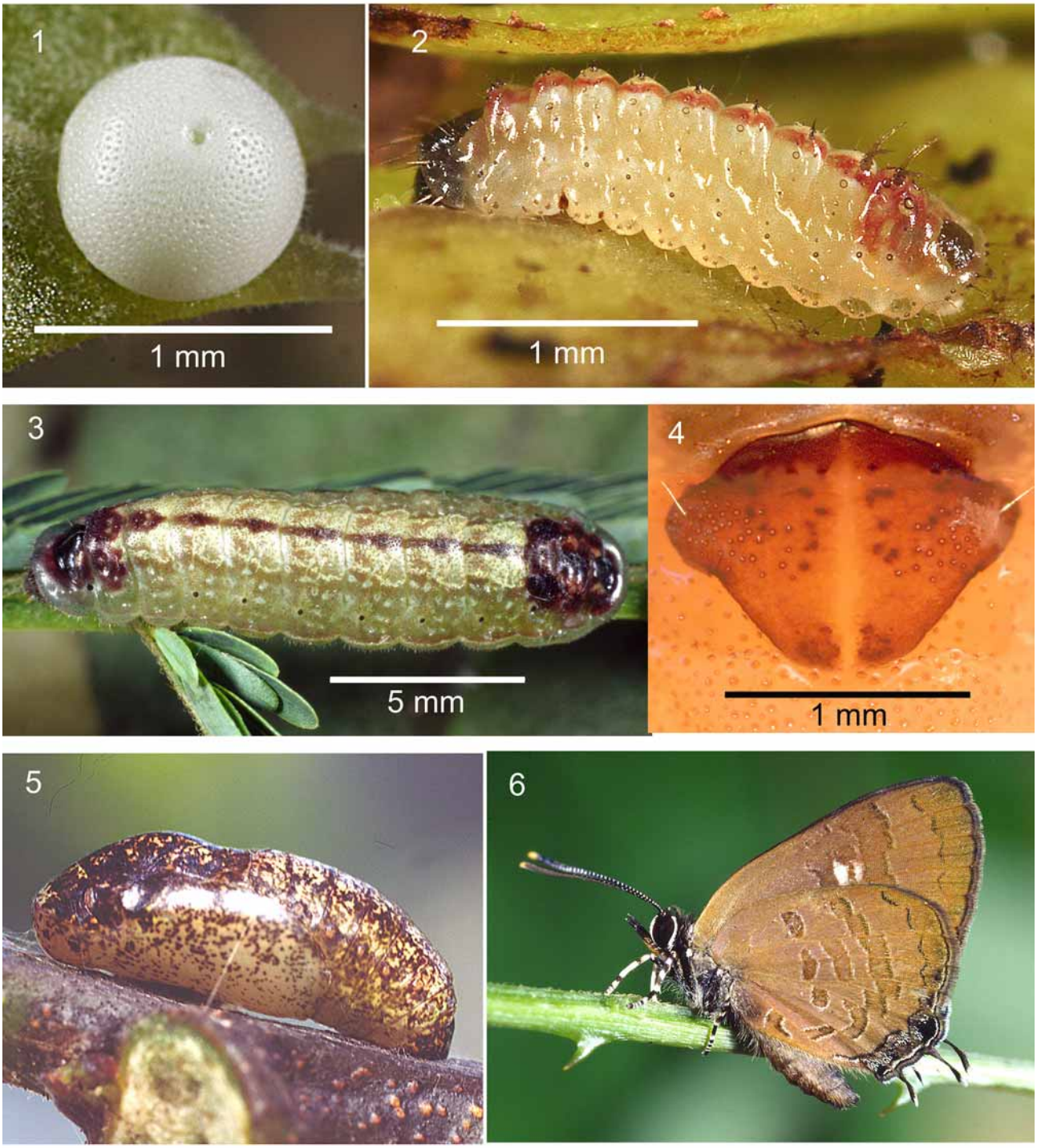
Egg (Fig. 1). White, echinoid (nearly hemispherical), surface smooth with minute punctures (aeropyles). Mean width of ova 0.85 mm (0.79–0.86 mm) (n=8); height uniformly 0.52 mm (n=3) [This measurement is based on fewer observations than that for width due to the loss of the apical portion in hatched ova.] Micropylar area circular, slightly indented, not sharply delineated (*ca* 0.1 mm diameter).

Larva. The most striking feature of first instar *A. achaja* larvae is the presence of greatly enlarged erect dorsal setae on abdominal segments A6 and A7 (Figs. 2, 9). These setae are about ten times longer than dorsal setae on T2–A5, which, in turn, are generally much shorter than other tactile setae (especially L group) on the same segments.

In describing details of *A. achaja* first instar chaetotaxy, novel terminology is employed for certain setae whose homologies have been either incorrectly or ambiguously applied by various workers with respect to other lycaenid taxa. The terminology employed here represents an attempt to standardize the specialized 1st instar lycaenid chaetotaxy and is based on patterns observed among lycaenid taxa representing several lycaenid subfamilies and tribes (Curetinae, Miletinae, Lycaeninae: Aphnaeini, Lycaenini, Theclini, Polyommatini). For further details see Discussion section below.

1st instar (n=4). Neonate (Figs. 2, 9): Pale greenish with middorsal reddish stripe from T2–A8, expanding laterally nearly to spiracles on A7 and A8. Head, prothoracic shield, and supranal shield dark brown. Dorsal setae brown, mostly short, stout, with few minute spicules, arising from relatively large brown chalazae, but

D1 greatly enlarged on A6 and A7 and more conspicuously spiculate. The following measurements are based on a composite of four individuals for which minor differences in some setal sizes were observed. Setal patterns were the same for all four individuals, except that D2 setae on A7 were absent in two individuals (one from each collection site).



FIGURES 1–6. Life stages of *A. achaja*. 1) egg; 2) 1st instar larva; 3) last instar larva; 4) prothoracic shield of mature larva; 5) pupa; 6) adult male. Orientation is cephalad to the left (Figs. 2, 3, 5, 6) or at top (Fig, 4).

Head (Figs. 7, 8) width in dorsal view, 0.30 mm; 17 pairs of cranial setae and their respective lengths as follows: **A1** (0.030 mm), **A2** (0.070 mm), **A3** (0.023 mm), **AF1** (0.027 mm), **S1** (0.024 mm), **S2** (0.030 mm), **S3** (0.030 mm), **SS1** (0.038 mm), **SS2** (0.038 mm), **SS3** (0.048 mm), **L1** (0.020 mm), **P1** (0.050 mm), **P2**

(0.040 mm), **MD1** (0.0067 mm). **MD2** (0.0067 mm), **MD3** (0.0067 mm), **MG1** (0.0050 mm); 10 punctures: **AFa**, **Fa**, **Ga**, **La**, **MDa**, **Pa**, **Pb**, **Sa**, **Sb**, **SSa** (additional SS punctures on ventral cranium not shown). Frons with a pair of mesal lenticles (**F1** setae absent) and mesal to them a pair of punctures (**Fa**); clypeal setae **C1** (0.045 mm), **C2** (0.086 mm). Labrum with six setae and one puncture, as depicted in Fig.7. Mandibles with distal six teeth and two setae.

Body (Figs. 9, 10, 11)

T1. Prothoracic shield (Fig. 10) brown, 0.31 mm wide and 0.27 mm long, with five pairs of setae and one pair of lenticles: **XD1** mesal-most at anterior margin (0.154 mm long and 0.008 mm wide basally), spiculate, tapered; **XD2** at anterolateral margin (0.154 mm long and 0.007 mm wide basally), with few short spicules; dorsal lenticle **DL** at anterior margin midway between **XD1** and **XD2**; **D1** posterior to **DL** (0.163 mm long and 0.01 mm wide), with few spicules; **SD1** ("sensory seta") near mid-lateral margin (0.064 mm long and *ca* 0.004 mm wide), slender, tapered, with relatively prominent slender spicules; **D2** (0.055 mm long and 0.005 mm wide), with few minute spicules, posteromesal to **SD1**. Three punctures present posterior to **D1** and anteromesal to **SD1**. Three anterior fringe setae (**F1**, **F2**, **F3**) in echelon anterolateral to the shield (Fig. 9), respectively from anterior to posterior 0.50, 0.11, and 0.02 mm long. Two setae (**L1**, **L2**) anteroventral to spiracle, about same length (*ca* 0.09 mm). Three setae (**SV3**, **SV2**, **SV1**) in horizontal line above base of coxa, respectively 0.050, 0.080, and 0.040 mm long. Three microscopic proprioceptor setae: **MXD1** behind the shield, **MV2** and **MV3** anterior to the **SV** group.

T2–3. Three pairs of erect, short, stout, spiculate setae in dorsal group, each arising from a relatively large, stout chalaza; **D1** nearest dorsal midline (*ca* 0.05 mm long) directed dorsally and slightly anteriorly; **D2** posterolateral to **D1** (*ca* 0.04 mm long), directed slightly posteriorly; **SD3** anterolateral to **D1** (*ca* 0.04 mm long) and slightly mesal to **D2**, directed more anteriorly than **D1**; **D1** chalaza 0.018 mm high; **D2** and **SD3** chalazae 0.015 mm high. A prominent lenticle (**SDL**) lateral to **D2**, about midway between **D2** and **SD2**. **SD1** near anterior segmental line and slightly posterodorsal to T1 spiracle; **SD2** more dorsal, posterolateral to **SDL**; both **SD** setae simple, similar in length (0.04 mm), and more slender than **D1**, **D2**, and **SD3**. Three simple lateral setae (**L1, L2, L3**, respectively *ca* 0.05, 0.05, and 0.06 mm long) below the level of the T1 spiracle. Two simple subventral setae **(SV1, SV2**), both *ca* 0.05 mm long, above the base of the coxa; **V1** seta mesal to the coxa (not visible in Fig. 9). Six microscopic proprioceptor setae near the anterior segmental boundary: **MD1** anterior to **SDL**, **MSD1** and **MSD2** slightly dorsal to **SD1**, **MV1** below the **L** group, **MV2** and **MV3** more ventral.

A1–A2. Similar to T2 and T3 with the following differences: **SDL** shifted dorsally and slightly more anterior (lateral to **SD3**); smaller lenticle (**SDL.2**) posterolateral to **SDL**; **SD2** shifted slightly dorsally; lateral group (**L1, L2, L3, L4, L5**) mid-way between spiracle and single subventral seta (**SV1**); ventral seta (**V1)** in line with mesal side of T3 coxa. Three microscopic proprioceptor setae: **MD1** slightly more dorsal than its position on T3; **MSD1** near anterior edge of spiracle; **MV3** near segmental margin anterior to **SV1**.

A3–A5. Similar to A1 & A2 with following differences: **SV1** slightly longer, with **SV2** much shorter and directly anterior to it; **P1** and **P2** present on prolegs. Prolegs on A3–6 with 9–12 lateral crochets in single series (*ca* 0.009 mm long) and a mesoseries of four longer crochets, two on each side of fleshy lobe: 0.027 mm long nearest lobe, 0.036 mm long further from lobe.

A6 Similar to preceding segment, but **D1** greatly enlarged (*ca* 0.4 mm long) with prominent lateral spicules; **D2** shifted slightly more lateral, posterior to **SDL**.

A7 (Figs. 9, 11). Similar to A6, but **DL** present and adjacent to **D1**; **SDL** and **SDL.2** absent; **SD3** lateral to **DL**; **D2** close to **D1** and posterior to **DL** (sometimes absent); **SD1** dorsal to spiracle; **SD2** shifted laterally, postero-dorsal to **SD1**; spiracle shifted slightly dorsally and somewhat enlarged, similar in size to T1 spiracle; **MSD1** slightly dorsal to spiracle; four setae in lateral group (**L1–4**); single **SV1** and **V1** setae.

A8 (Figs. 9, 11). Reduced and partially fused with A9**.** Dorsal lenticle (**DL)** placed near the anterior dorsal segmental margin; MD1 anterolateral to DL (only depicted on right side in Fig. 9); a small seta (possibly **D1**,

but interpreted here as **SD1** of A8) posterolateral to **DL**; another small seta (possibly **SD2**, but interpreted here as **SD1** of A9) directly posterodorsal to the spiracle; **MSD1** slightly dorsal to spiracle; lateral group apparently with six setae (the posterior two presumed to be **L1** & **L2** of a partially fused A9); **SV1** and **V1** as in A7.

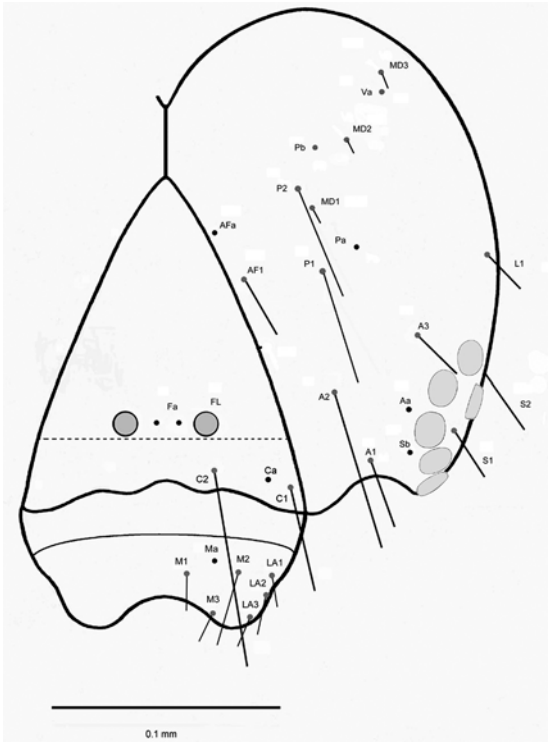


FIGURE 7. Cranial diagram, 1st instar *A. achaja*, frontal view. See text for explanation of labels.

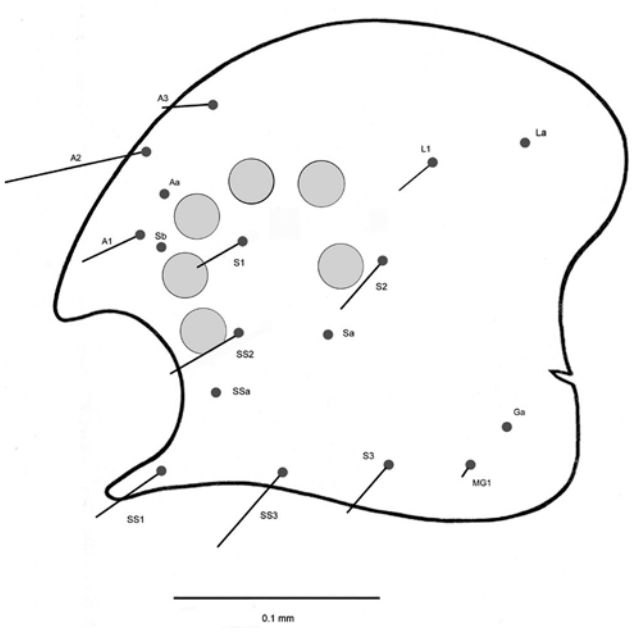


FIGURE 8. Cranial diagram, 1st instar *A. achaja*, ventrolateral view. See text for explanation of labels.

A9 (Figs. 9, 11). Greatly reduced and partially fused with both A8 and A10; its two L setae (L1 and L2) closely associated with the L group of A8. Interpretation of the posterior-most two setae of the L group of fused A8+9 as L1 and L2 of A9 is based on apparent homology with the condition in *Drupadia*. Both *D. ravindra* and *D. theda* have identical patterns of L setae placement in which the anterodorsal-most L seta on

A7 and A8+9, as well as the posterodorsal-most L seta on A8+9, are clavate, while other L setae on those segments are unmodified (Ballmer, pers. obs.). A short seta just posterodorsal to the A8 spiracle is interpreted here as SD1 of A9; SV1 and V1 as in A7–A8.

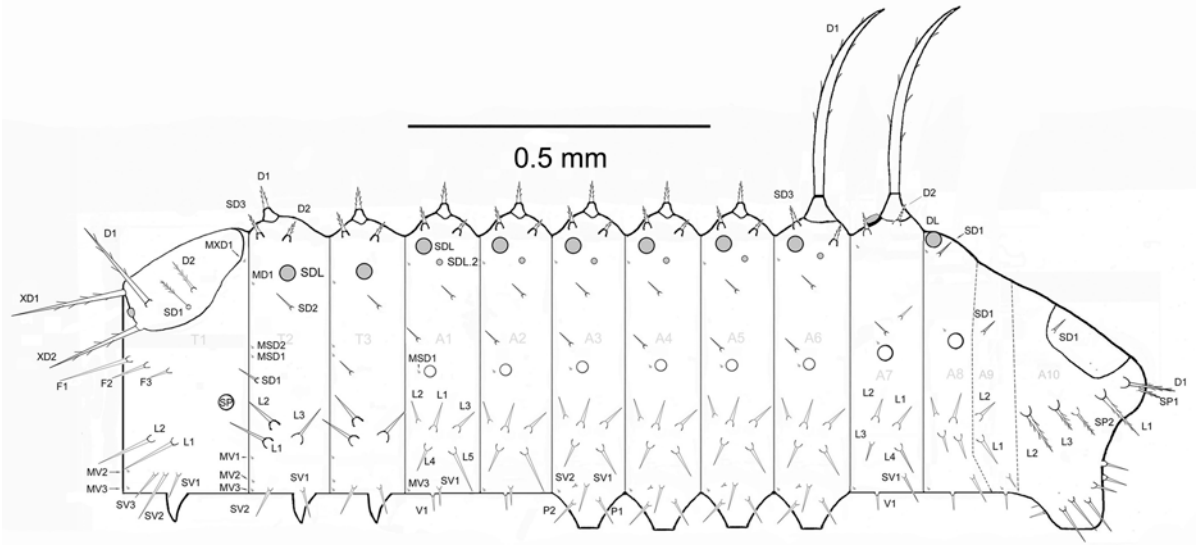


FIGURE 9. 1st instar *A. achaja* diagram, lateral view of body. See text for explanation of labels.

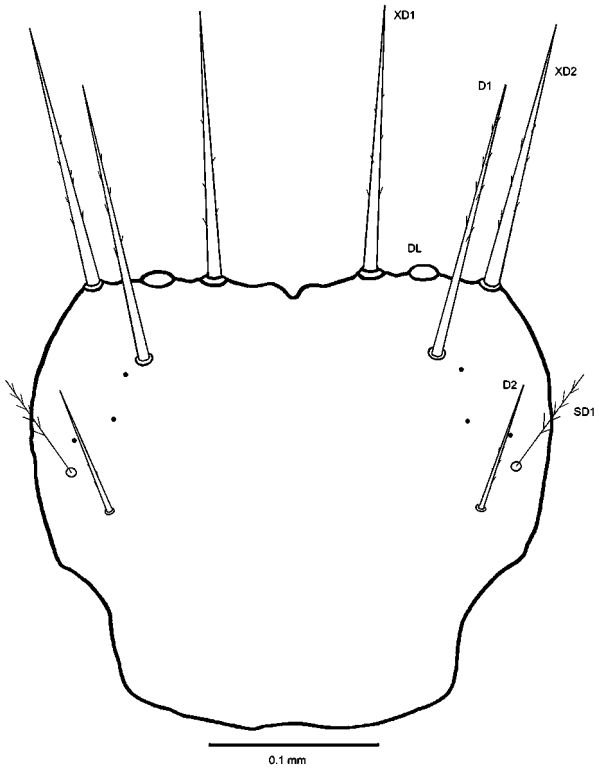


FIGURE 10. 1st instar *A. achaja* prothoracic shield, cephalad at top. See text for explanation of labels.

A10 (Figs. 9, 11). Not distinctly separate from A9, except at the lateral fold where a prominent indentation marks the boundary with the partially fused A8+9. Homologies for the setae present on A10 in Lepidoptera are not obvious and various workers have interpreted them differently. Hinton declined to homologize the setae of the anal segment(s), while Stehr (1987) and Hasenfuss & Kristensen (2003) placed the D and SD

group setae on the sclerotized anal plate (on the A10 dorsum) and all lateral setae below the lateral line (= lateral fold in lycaenids). In our interpretation, based on a comparative survey of lycaenids, the lateral setae (L group) are on or above the lateral line.

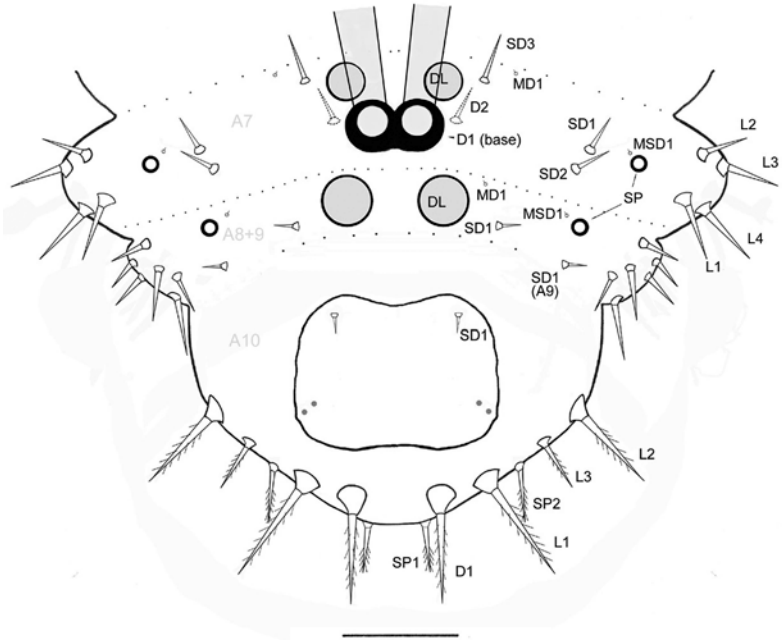


FIGURE 11. 1st instar *A. achaja* terminal segments (A7–10), dorsal view, cephalad at top. See text for explanation of labels.

A quadrate, brown, sclerotized anal plate (0.17 mm wide and 0.15 mm long) dominates the dorsum of A10 and is somewhat remote from a fringe of 6 pairs of prominent spiculate setae along the lateral fold. An additional nine simple setae occur on each anal proleg. The anal plate bears a pair of short setae (0.018 mm long), here interpreted as SD1, near the anterolateral angles and two pairs of punctures near the posterolateral angles. We interpret the 4 pairs of prominent fringe setae along and just dorsal to the distal margin of the posterolateral fold (extension of the lateral fold) as D1 and L1–3 (0.075, 0.090, 0.075, and 0.020 mm long, respectively). Two additional setae supraproct SP1 and SP2 (0.040 and 0.045 mm long, respectively), each prominently spiculate only in the distal half, are placed just below the posterolateral fold but above the anus. Nine setae occur on the anal proleg: 3 laterally, 3 posteriorly, and 3 mesally with a small lenticle. [Lenticle and one mesal seta not visible in Fig.9] Anal prolegs with 6–7 lateral crochets arrayed in an arc and increasing in length (0.009 – 0.036 mm) from posterolateral to anteromesal; two mesal crochets (posterior to lobe), the more anterior 0.036 mm long and the posterior-most 0.044 mm long.

2nd instar (n=2): Head width 0.46 mm (n=2), dark brown. Mandible with 7 teeth on distal margin and a molar ridge extending from clypeal condyle and ending in a small tooth just mesal to 2nd tooth; 2 mandibular setae. Body light green with middorsal reddish stripe extending to dark brown supranal shield. Prothoracic shield dark brown, 0.54 mm wide and 0.36 mm long, with few scattered setae and lenticles. **SD1** ("sensory setae") on prothoracic shield 0.10 mm long, slender, tapered. Other secondary setae on shield, sparse, to 0.03 mm long. Two lenticles on shield, 0.02 mm wide, anterior to **SD1** setae. Prominent setae at anterior margin T1 (0.04–0.13 mm long). Longest dorsal setae on T2–A6 (0.02 mm long), arising from chalazae 0.020 mm high and 0.035 mm wide. Lateral setae visibly similar in dimensions on T1– A9+10 (*e.g*. 0.06 mm long on A1). A7 with 15–16 lenticles and 10 setae near margin honey gland (=DNO). No apparent eversible tubercles (=ETOs). Anal plate pale brown (at least in preserved specimens), subtriangular, widest at posterior margin (*ca* 0.20 mm long and 0.25 mm wide). Setae along anal fringe, 0.04–0.07 mm long.

3rd instar (n=1): Head width 0.875 mm, black (dark brown). Mandibles as in 2nd instar. Body colored as in 2nd instar. Prothoracic shield 0.94 mm wide and 0.79 mm long; with scattered short setae and lenticles; **SD1** ("sensory setae") 0.135 mm long, slender, tapered. Dorsal setae on T2 *ca* 0.02 mm long, from relatively broad buttressed chalazae, to *ca* 0.04 mm wide. Honey gland (DNO) on A7 well-developed, with numerous lenticles (to 0.04 mm wide) and short, stout, tapered setae (*ca* 0.015 mm long). Eversible tubercles (ETOs) present near spiracles on A8. Anal plate pale brownish (at least in preserved specimens), widest at posterior margin (*ca* 0.3 mm long and 0.5 mm wide). Most lateral fringe setae short; at anal margin mostly *ca* 0.035 mm long, but longer at posterolateral angle of anal margin (0.115 mm long).

4th instar (Fig. 3) (n=2): Head width 1.38–1.40 mm, black; frontal sutures not pigmented. Mandibles as in 3rd instar. Body colored as in 2nd and 3rd instars. Longest setae at anterior margin of T1 0.21 mm long. Prothoracic shield (Fig. 4) 1.61 mm wide and 1.07 mm long; dark brown with ragged nonpigmented midline; few short setae and numerous small lenticles at lateral angles (mostly around relatively prominent **SD1**). **SD1** slender, tapered, 0.270 mm long. Longest dorsal setae on all segments posterior to T1 brown, stout and tapered, 0.024 mm long, arising from buttressed chalazae, 0.048 mm wide. Lateral fringe setae simple, tapered, not pigmented, to 0.29 mm long. Longest setae at anal margin 0.25 mm long. Honey gland (DNO) with numerous lenticles and short setae around margin. The latter may be somewhat clavate or capitate and lack pigment. Bases of eversible tubercles (ETOs) with numerous lightly pigmented lenticles and/or short nonpigmented setae. Supranal shield brown centrally and narrowly along irregular perimeter (otherwise virtually nonpigmented), subtriangular, broadest at posterior margin (*ca* 0.6 mm long and. 1 mm wide). Prolegs (A1–6) with 18–26 crochets (biordinal mesoseries) on each side of spatulate lobe; lateral series with 12 crochets (uniordinal).

Pupa (Fig. 5). Mottled brown, more-or-less cylindric, somewhat elongate (sausage-shaped); closely appressed (parallel) to the pupation substrate; in addition to the usual cremastral attachment, a silken filament girdles the thorax. Although macroscopically glabrous, few scattered short setae (*ca* 0.04 mm long) are present, primarily anterodorsally on the thorax, while numerous small lenticles (PCOs) are more generally distributed over the dorsal and lateral body surfaces (but not the wings). The single larva reared to maturity produced a pupa 9 mm in length (Fig. 5).

Adult (Fig. 6). Well-described and/or illustrated elsewhere, most recently by Eliot, (1973), Cowan (1974), Pinratana (1981), and D'Abrera (1986). Ground color of wings predominantly brown ventrally, with thecline markings similar to *Drupadia*, but dorsally reminiscent of *Horaga*.

Developmental notes

At the Vientiane collection site, ova and all larval instars were present concurrently, indicating that oviposition (by one or more females) had occurred over a period of at least several days. At the Kanchanaburi site, one neonatal larva was found along with several ova in clusters of 2–3, mostly near the bases of leaf axils on a single host plant. All ova hatched within three days of collection. In both instances the host plants were in semi-shady situations within secondary forest and in a stage of rapid vegetative growth. Eggs and larvae were found in association with young foliage.

The duration of the complete larval growth period was not observed. It is likely that under field conditions larvae would require at least four weeks to reach maturity. A last instar larva collected on April 15 pupated on April 22 and eclosed on May 1st.

Discussion

First Instar Setal Terminology

Hinton's (1946) classic work on the homology and nomenclature of the setae of lepidopterous larvae set a standard now followed by most workers with minor adjustments. Nevertheless, the specialized larval morphology and chaetotaxy of Lycaenidae depart from the basic lepidopteran plan in many instances, thereby creating uncertain setal homologies and necessitating a modified setal nomenclature. Novel nomenclature is employed for some setae, which may have been misidentified or poorly named in previous works regarding lycaenid first instar chaetotaxy. Although this nomenclature may be broadly applicable within the family, ongoing studies may disclose new information concerning setal homologies and a justification for future additional changes in setal nomenclature.

The specialized lycaenid prothorax is generally larger than other segments in order to receive the retractable head. The prothoracic shield is reduced to a relatively small sclerotized dorsal cap usually containing (in 1st instar larvae) five pairs of primary setae, although fewer or more setae occur in various taxa (Ballmer & Pratt, 1992; Ballmer & Wright, per. obs.). In *Ahmetia* two pairs of long setae at the anterior margin of the shield are presumed to be XD1 and XD2; between them is a lenticle (PCO or sieve plate). Posterior to each lenticle is another long seta (D1) and posterolateral to D1 is a somewhat less prominent seta (D2). The lateralmost pair of setae, anterolateral to D2, is SD1 ("sensory seta"); this seta has also been termed XD2 (Downey & Allyn, 1979, 1984; Wright, 1983) and D2 (Sidhu & Rose, 2004). The homology of this seta with SD1 is based on its peculiar structure, which is usually very slender and emanating from a flat pinacular disc (sometimes recessed below the surrounding cuticle). It has been observed as somewhat "vibratory" in nature, an apparent tonosensillar adaptation for detecting the approach of flying predators (Tautz, 1977 & 1978; Tautz & Markl, 1978). The peculiar structure of this seta allows it to be identified on the prothoracic shield in subsequent instars (Lawrence & Downey, 1966; Wright, 1983; Ballmer & Pratt, 1988; Duarte *et al.*, 2005).

In many Lepidoptera other than Lycaenidae there are two tonosensillar setae on T1. In Hepialidae the more ventral of the two setae generally has been homologized with SD1, while the more dorsal seta has been homologized with D2 by some workers (Hinton, 1946; Hasenfuss & Kristensen, 2003) and as SD2 by others (Wagner, 1987; Grehan & Rawlins 2003). In other families having two tonosensillar setae on T1, the more ventral seta has been identified as L1 and the more dorsal seta as SD1 (Hasenfuss & Kristensen). Thus, while we use SD1 for the tonosensillar setae on the *A. achaja* T1 shield, further studies may indicate a different homology.

New terminology is employed here for a group of setae anterior and lateral (subdorsal) to the dorsal shield on T1 in many, if not all, lycaenid first instars. Although varying in number and length among various taxa, these setae generally provide sensory function near the anterior margin of T1 between the widely separate shield and lateral setal group. These setae may consist in part of SD, XD, and/or L setae, and perhaps of some "new" or "extra" setae beyond the basic complement of primary setae. Various workers have termed these setae respectively, from anterior to posterior: MD1, MSD1, MSD2, and L1 (Downey & Allyn, 1979, 1984; Wright, 1983), MSD1, MSD2, and L1 (Duarte *et al*., 2005; Ballmer, 2008); or simply "fringe setae" plus SD2 and/or SD1 (Ballmer & Pratt, 1992; Sidhu & Rose, 2004). The use of MD1, MSD1 and MSD2 for these tactile setae, based on the presumption that they are derived from corresponding microscopic proprioceptor setae, such as occur on T2 and T3, is contrary to opinion that such proprioceptor setae do not occur on T1 in any Lepidoptera (Hinton, 1946; Stehr, 1987). Because MD1, MSD1, and MSD2 are not reported to occur on T1 in even the most primitive Lepidoptera, one may presume that they must have been lost very early in the evolution of the order, if indeed they were ever present. Even if such setae were present in an extinct ancestor, their recurrence in a single highly specialized family, such as the Lycaenidae, seems unlikely. Because homologies for this group of setae are ambiguous, we refer to them provisionally as "fringe setae" (F) and assign to them sequential numbers beginning with the anterior-most seta (F1).

We use the term SD3 for the pair of "extra" subprimary dorsal setae found in association with D1 and D2 setae on T2–A7; this terminology follows established usage for other lycaenids (Scott, 1986; Ballmer & Pratt, 1992; Pratt *et al.*, 1993; Sidhu & Rose, 2004). Use of MD1 for the same setae (Downey & Allyn, 1979, 1984; Duarte *et al.*, 2005), based on presumption that they are enlarged derivatives of microscopic dorsal proprioceptor setae, is inappropriate inasmuch as true microdorsal setae (MD1) are also present on the same segments. True MD1 setae are easily overlooked due to their minute size; however the presence of microscopic MD1, together with macroscopic SD3, has been confirmed in several lycaenid taxa representing Curetinae, Lycaeninae, and Miletinae (Wright, pers obs.). Whether it is more appropriate to refer to these setae as dorsal (*e.g*. D3) or subdorsal (SD3) is ambiguous, because their position may vary somewhat (from dorsal to subdorsal) among taxa and among segments on individual larvae. The term SD3 was originally suggested (by DW), because the specialized morphology of these setae in polyommatines is often more similar to that of SD1 and SD2 than to D1 and D2 setae (Ballmer & Wright, pers. obs.). Nevertheless, that rationale needs to be tested through study of the differential structure of these setae in all lycaenid taxonomic groups.

We follow Hasenfuss & Kristensen (2003) in using the term MSD1 for the small seta anterior or anterodorsal to the spiracle on abdominal segments A1–8. The "M" indicates it is a microscopic proprioceptor. Hasenfuss & Kristensen (*op. cit.*) apply the designation "MSD1(=SD2)", which unfortunately permits continuing confusion that this tiny seta might be homologous with tactile seta SD2. Hinton (1946) referred to this seta as SD2, although noting that "in the majority of groups, including the Eriocraniidae, Monotrysia, and many of the more primitive Ditrysia, SD2 is a minute seta which, as regards size, would appear to belong to the system of proprioceptors". Its function is most likely related to recognition of body spatial orientation near the spiracular ostium. MSD1 is found routinely on abdominal segments of lycaenid larvae, including first instars, often together with longer tactile SD1 and SD2 (Figs. 9 & 11), and mature larvae covered with a forest of secondary setae (Wright, 1983, Fig. 40). The subdorsal macrosetae (SD1 and SD2) on T2, T3, and A1–8 appear homologous, evidenced by their similar serial positions and structure in *Ahmetia* and many other lycaenids (Downey & Allyn, 1979, 1984; Sidhu & Rose, 2003; Ballmer, 2008; Ballmer & Wright, pers. obs.).

In the Hepialidae, which is often considered ancestral to the Ditrysia, the abdominal segments possess long tactile SD1 and SD2, but lack subdorsal microsetae. In many Ditrysia families long tactile SD2 is absent, while a tiny proprioceptor seta is present near each spiracle. This situation may have misled Hinton (1946) and other workers to homologize the ditrysian spiracular proprioceptor (MSD1) with SD2.

The setation of A10 is unresolved in most (if not all) present chaetotaxic systems. This segment presents a dilemma for the total number of setae, their position, and homology (Grehan & Rawlins, 2003). Hasenfuss (1973) applied sensory innervation to derive provisional homologies. Fittingly, Stehr (1987) and Hasenfuss & Kristensen (2003) divided the segment into two essential parts (anal shield & anal proleg) and designated names for setae originating in those regions. Both schemes maintain that the primary lateral setae (L-group) originate below the lateral fold on the anal proleg. This is visibly not the condition in lycaenids. The terminal lateral setae of first instars of lycaenines (Wright, 1983), theclines (Scott, 1986; Ballmer & Pratt, 1992; Duarte *et al.*, 2005), polyommatines (Lawrence & Downey, 1966; Downey & Allen, 1979, 1984; Sidhu & Rose, 2004), and curetines (Wright, pers. obs.) reside on or above the lateral body fold. This situation indicates that the lycaenid L-group terminates on the last tergite, with the D-group, above the anal slit and anal proleg. Apomorphies occur commonly in first instars of lycaenids; this is especially true regarding setal number and morphology. However, we are unsure whether the spatial orientation of an entire setal group on A10 (i.e. L-group) represents a radical reorganization or a plesiomorphic condition universal to all Lepidoptera. Resolution awaits further research with novel approaches across the order.

Phylogeny

The proposed systematic position of *A. achaja*, as closely allied to *Cheritra* and *Drupadia* in the Cheritrina (Eliot, 1973), is loosely substantiated by comparison of the immature stages. In overall 1st instar setal pattern, *A. achaja* is similar to *D. ravindra* (Horsfield, [1828]) and *D. theda*. A consistent feature is the presence of three SV setae on T1 in all three species. We have not found this condition among other lycaenids thus far examined; however, Lawrence & Downey (1966) report that three SV setae occasionally occur in *Everes comyntas* (Godart, [1824]). The unusual occurrence of six setae in the lateral group on the fused A8+9 segment of *A. achaja* is also shared by *D. ravindra* and *D. theda* (Ballmer, pers. obs.).

A major distinction between 1st instar larvae of *A. achaja* and the *Drupadia* species is the state of dorsal setae D1 and D2. In *D. ravindra* and *D. theda*, D1 is of similar length (rather long, slender, and recurved) on T2–A6, while D2 is nearly as long and curved as D1 on T2, but much shorter and curved on T3–A6, and absent on A7 (Ballmer, pers. obs.). In contrast, D1 in *A. achaja* is short, stout and straight on T2–A5, but much longer, stouter, and recurved on A6 and A7, while D2 remains short and straight on all segments T2–A7. The extraordinary length of D1 setae on A6 and A7 of 1st instar *A. achaja* invites comparison with some distantly related and notably myrmecophilous lycaenids. For instance, an extraordinarily prominent pair of dorsal setae on A7 (and much shorter dorsal setae on T2–A6) occurs in 1st instar *Acrodipsas illidgei* (Waterhouse & Lyell, 1914) (Samson, 1989; Ballmer, pers. obs.) and *Anthene emolus* (Godart, [1824]) (Ballmer, pers. obs.). Coincidentally, *A. illidgei* is obligately associated with ants in the genus *Crematogaster* (Samson, 1989), while *A. emolus* is invariably associated with *Oecophylla smaragdinus* (Fabricius) (Fiedler, 1991; Ballmer, pers. obs.).

Some features of the *A. achaja* immature stages indicate an ambiguous phylogenetic relationship with other Cheritrina and perhaps a greater (or at least more plesiomorphic) affinity with *D. theda* than with *D. ravindra*. The *A. achaja* egg chorion is smoothly hemispheric with minute punctations, while that of *D. theda* is similarly smooth, but with slightly larger punctations (Ballmer, pers. obs.). In contrast, the chorionic surface of the *D. ravindra* egg is prominently cratered, as is that of *Cheritra freja* (Fabricius, 1793) (Igarishi & Fukuda, 1997, 2000; Ballmer, pers. obs.). Furthermore, post 1st instar larvae of *A. achaja* are smoothly rounded dorsally (onisciform) with inconspicuous setae, as in *D. theda* (Igarishi & Fukuda, 2000; Ballmer, pers. obs.), while *Cheritra freja* and *D. ravindra* larvae have prominent fleshy dorsal processes (Igarishi & Fukuda, 1997; Ballmer, pers. obs.), which Eliot (1973) considered diagnostic for the tribe. Likewise, the pupa of *A. achaja* resembles that of *D. theda* in overall morphology (sausage-shaped, smooth cuticle, mottled in shades of brown), attachment (cremaster plus silken girdle), and orientation (appressed to substrate) (Igarishi & Fukuda, 2000; Ballmer, pers. obs.), while the pupae of *D. ravindra* and *C. freja*, are somewhat cristate, angulate at the junction of thorax and abdomen, tuberculate and cryptically marked to resemble rough bark, fastened only by the cremaster, and oriented with the head uppermost, away from the substrate (Igarishi & Fukuda, 1997; Ballmer, pers. obs.).

Acknowledgments

This research was carried out, in part, under permitted authority of the National Research Council of Thailand, within the scope of a research project titled “Life Histories and Systematics of Lycaenidae in Thailand”. Dr. Banpot Napompeth of the Thailand National Biological Control Research Center (retired) and Dr. Chaweewan Hutacharern of the Royal Forest Department (retired) offered advice and encouragement in establishing this project. Mr. J. F. Maxwell, Curator of the Chiang Mai University Herbarium, identified voucher plant specimens. Dr. J. J. S. Burton provided transportation, companionship, and much encouragement for fieldwork undertaken in Lao PDR and Thailand.

References

Ballmer, G.R. (2008) Life history of *Purlisa gigantea* (Lepidoptera: Lycaenidae: Theclini) in South Thailand. *Tropical Lepidoptera Research*, 18(1), 32–39.

Ballmer, G.R. & Pratt, G.F. (1989) A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. *Journal of Research on the Lepidoptera*, 27(1) (1988), 1–81.

Ballmer, G.R. & Pratt, G.F. (1992) *Loranthomitoura*, a new genus of Eumaeini (Lepidoptera: Lycaenidae: Theclinae). *Tropical Lepidoptera*, 3(1), 37–46.

Cowan, C.F.C. (1974) The Indo-Oriental genus *Drupadia* Moore (Lepidoptera: Lycaenidae). *Bulletin of the British Museum of Natural History (Entomology)*, 29(6), 281–356 + 6 plates

D'Abrera, B. (1986) *Butterflies of the Oriental Region Part III Lycaenidae & Riodinidae*. Hill House, Melbourne. 672 pp.

Downey, J.C. & Allyn, A.C. (1979) Morphology and biology of the immature stages of *Leptotes cassius theonus* (Lucas) (Lepid.: Lycaenidae). *Bulletin of the Allyn Museum*, 55, 1–27.

Downey, J.C. & Allyn, A.C. (1984) Chaetotaxy of the first instar larva of *Hemiargus ceraunus antibubastus* (Hbn.) (Lycaenidae). *Bulletin of the Allyn Museum*, 90, 1–4.

Duarte, M., Robbins, R.K. & Mielke, O.H.H. (2005) Immature stages of *Calycopis caulonia* (Hewitson, 1877) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), with notes on rearing detritivorous hairstreaks on artificial diet. *Zootaxa* 1063, 1–31.

Eliot, J.N. (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum of Natural History (Entomology)*, 28(6), 371–505 + 6 plates.

Eliot, J.N. (1992) *The Butterflies of the Malay Peninsula by A. Steven Corbett and H.M. Pendlebury, revised by J.N. Eliot. 4th Edition.* Malaysian Nature Society, Kuala Lumpur, 595 pp. + 69 plates.

Fiedler, K. (1991) Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zoologische Monographien*, Nr. 31. 210 pp.

Fruhstorfer, Hans (1912) Uebersicht der Lycaeniden des Indo-Australischen Gebiets. Begründet auf die Ausbeute und die Sammlung des Autors. *Berliner entomologische Zeitschrift*, 56(3/4), 197–272, f. 1–4 (early April).

Grehan, J.R. & Rawlins, J.E. (2003) Larval description of a New World ghost moth, *Phassus* sp., and the evolutionary biogeography of wood-boring Hepialidae (Lepidoptera: Exoporia: Hepialoidea). *Proceedings of the Entomological Society of Washington.*, 105(3), 733–755.

Hasenfuss, I. (1973) Vergleichend-morphologische Untersuchung der sensorischen Innervierung der Rumpfwand der Larven von *Rhyacophila nubila* Zett. (Trichoptera) und *Galleria mellonella* L. (Lepidoptera). Ein Beitrag zur Problem der Homologie and Homonomie ihrer larvalen Sensillenmuster. *Zoolische Jahrbucher fur Anatomie und Ontogenie der Tiere* 90, 1–54, 175–253

Hasenfuss, I & Kristensen, N.P. (2003) Skeleton and muscles: immatures. (pp.133–164) *In* Kristensen, N. P. (Ed.) *Lepidoptera, moths and butterflies. Volume 2: Morphology, physiology, and development. In: Fisher, M. (Ed.), Handbook of Zoology, Volume IV Arthropoda: Insecta*, Walter de Gruyter, Berlin.

Hinton, H.E. (1946) On the homology and nomenclature of the setae of Lepidopterous larvae, with some notes on the phylogeny of Lepidoptera. *Transactions of the Royal Entomological Society of London*, 97, 1–37.

Igarishi, S. & Fukuda, H. (1997) *The Life Histories of Asian Butterflies, Volume 1*. Tokai University Press, Tokyo. 551 pp.

Igarishi, S. & Fukuda, H. (2000) *The Life Histories of Asian Butterflies, Volume 2*. Tokai University Press, Tokyo. 713 pp.

Lawrence, D.A. & Downey, J.C. (1966) Morphology of the immature stages of *Everes comyntas* Godart (Lycaenidae). *Journal of Research on the Lepidoptera*, 5, 61–96.

Özdikmen, H. (2008) Replacement names for two preoccupied butterfly genus group names (Lepidoptera: Papilionoidea). *Munis Entomology & Zoology*, 3 (1), 321–322.

Pinratana, A. (1981) *Butterflies in Thailand, Volume Four.* Viratham Press, Bangkok. 216 pp.

Pratt, G.F., Wright, D.M. & Ballmer, G.R. (1993) Multivariate and phylogenetic analyses of larval and adult characters of the Editha Complex of the genus *Lycaena* (Lepidoptera: Lycaenidae). *Journal of Research on the Lepidoptera*, 30(3–4) (1991), 175–195.

Samson, P.R. (1989) Morphology and biology of *Acrodipsas illidgei* (Waterhouse and Lyell), a myrmecophagous lycaenid (Lepidoptera: Lycaenidae: Theclinae). *Journal of the Australian Entomological Society*, 28, 161–168.

Scott, J.A. (1986) *The Butterflies of North America. A Natural history and Field Guide.* Stanford University Press, Stanford, CA. 583 pp.

Sidhu, A.K. & Rose, H.S. (2004) Chaetotaxy of first instar caterpillar of world's smallest butterfly, *Freyeria putli* (Kollar) (Lycaenidae: Papilionoidea: Lepidoptera). *Journal of Entomological Research*, 28(1), 55–61.

Stehr, F.W. (1987) Order Lepidoptera. *In* Stehr, F. W. (Ed), *Immature Insects Volume 1*. Kendall/Hunt, Dubuque, IA. pp.

288–305.
Tautz, J. (1977) Reception of medium vibration by thoracic hairs of caterpillars of *Baratha brassicae* L. (Lepidoptera, Noctuidae). I. Mechanical properties of the receptor hairs. *Journal of Comparative Physiology*, 118, 13–31.
Tautz, J. (1978) Reception of medium vibration by thoracic hairs of caterpillars of *Baratha brassicae* L.(Lepidoptera, Noctuidae). II. Response characteristics of the sensory cell. *Journal of Comparative Physiology*, 125, 67–77.
Tautz, J. & Markl, H. (1978) Caterpillars detect flying wasps by hairs sensitive to airborne vibration. *Behavioral Ecology and Sociobiology*, 4, 101110.
Wagner, D. (1987) Hepialidae (Hepialoidea). *In* Stehr, F. W. (Ed), *Immature Insects Volume 1*. Kendall/Hunt, Dubuque, IA. pp. 347–349.
Wright, D.M. (1983) Life history and morphology of the immature stages of the bog copper butterfly *Lycaena epixanthe* (Bsd. & Le C.). *Journal of Research on the Lepidoptera*, 22(1), 47–100.