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# NOTES ON LIFE HISTORIES OF SATYRINAE IN THE SOLOMON ISLANDS (LEPIDOPTERA: NYMPHALIDAE)

ANDREI SOURAKOV[1] AND THOMAS C. EMMEL

Dept. of Entomology & Nematology, Univ. of Florida, Gainesville, Florida 32611
Dept. of Zoology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.– Immature stages of *Mycalesis splendens*, *M. interrupta*, *M. perseus*, *Orsotriaena medus*, and *Argyronympha pulchra* from the Solomon Islands are described, and the taxonomic implications of these data are discussed. *Mycalesis* and *Orsotriaena* exhibit similarities to other Mycalesini, such as the African genus *Bicyclus*, but also show strong intrageneric differences and affinity of *Orsotriaena* to other primitive satyrine tribes. *Argyronympha* shares some characters with other advanced Satyrinae (e.g., Erebiini of the Holarctic region). Divergence of immature stages found in different members of *M. splendens* group supports splitting taxonomic decisions made by the previous authors based on adult morphology.

KEY WORDS: *Argyronympha*, biogeography, eggs, Erebiini, Hypocystini, immatures, larvae, life histories, Mycalesini, *Mycalesis*, *Orsotriaena*, pupae, Solomon Islands, taxonomy.

Accumulating data on the morphology of Satyrinae immature stage has been a principal ongoing project of the first author. During this work, divergence of eggs, larvae, and pupae at different taxonomic levels has been assessed for various satyrine genera (e.g., Sourakov, 1995, 1996; Sourakov and Emmel, 1997a,b). The ultimate goal of the project is to reconstruct the phylogeny of the Satyrinae using the morphology of immatures, characters of which were largely unavailable for earlier studies (e.g., Miller, 1968). However, reaching this goal requires collecting of a wealth of new data through rearing and morphological analysis. Meanwhile, the published fragmented descriptions will, we believe, provide students of a particular genus or tribe with valuable information for smaller-scale evolutionary studies.

During our July-August 1998 expedition to the Solomon Islands, we had the opportunity to obtain eggs from five species of Satyrinae, representing three genera and two tribes: *Mycalesis splendens* Mathew (Fig. 1I), *M. interrupta* Grose-Smith (Fig. 1I), *M. perseus* (Fabricius) (Fig. 3G), and *Orsotriaena medus* (Fabricius) (Fig. 2G) of the Mycalesini, and *Argyronympha pulchra* Mathew of the Hypocystini. Though the last instar larvae and pupae have been previously illustrated for *M. perseus* and for *O. medus* (Parsons, 1998; Igarashi and Haruo, 1998), we are providing more complete descriptions of the biology of these wide-spread taxa and compare them to other *Mycalesis* species of the Solomons and to the con-specific populations from other regions, whose immature stages differ slightly from the presented here.

*M. splendens* and *M. interrupta*, which by some authors (e.g., D'Abrera, 1977) were considered con-specific, were recently shown to be separate species, which also form distinct subspecies on different islands (Tennent, 2001). Only seeing the latter work prior to its publication in this supplement allowed us to identify our material correctly. Our data on immature stages support nicely Tennent's taxonomic conclusions of *M. interrupta* being a distinct species, those conclusions based entirely on adult morphology.

## MATERIALS AND METHODS

Adult females were kept in inflated zip-lock bags, and were exposed to ambient light at the room temperature. In the case of *M. interrupta*, oviposition on unidentified palm sprouts was observed in the wild of Rononggo island. The egg was glued on the underside of the leaf of a 3-inch-tall plant. Therefore, palm leaves were provided for females of this species and to the similar species from Guadalcanal (*M. splendens*) and from Malaita (unidentified). Palm leaves were also given to females of *Argyronympha pulchra* species group: all females of *Argyronympha* were kept together on the assumption that they represent a single species, and it was found only later that some authors (e. g., D'Abrera, 1977) consider every major island to have a separate subspecies or even species of the *A. pulchra* group). We also obtained several eggs from a single *Mycalesis* female from Malaita, where, according to Tennent, two species occur: *M. splendens malaitensis* Uémura and *M. biliki* Tennent. These are cryptic species, differing in male genitalic structures, while a female for the latter of them is unknown. Therefore, correct identification of the female specimen, from which we acquired the eggs, is impossible at the moment.

In contrast to the *M. splendens* group, *M. perseus* and *O. medus* are common and widespread species of open habitats and, without doubt, feed on a wide variety of native and exotic grasses. Females of these two species collected on Guadalcanal were provided only with dry grass stems, on which they readily laid eggs. All females were fed daily with 25% sugar solution.

Larvae of all instars were photographed, using extension tubes and ring flash. Scanning Electron Microscopy was performed on a Hitachi S-520 instrument, after eggs and larvae had been prepared by a critical point drying procedure.

Larvae of *Mycalesis* Hubner and *Orsotriaena* Wallengren were reared to the pupal stage on a variety of lawn grasses. Larvae of *Argyronympha* Mathew refused substitute hosts and, therefore, only eggs and first instar larvae are available for description.

## MORPHOLOGY OF IMMATURE STAGES

**Eggs:** In Mycalesini (*Mycalesis* and *Orsotriaena*), the eggs are round and white, with thin shell; at closer magnification, they are covered with shallow concave hexagonal cells. This structure is similar to that observed in African Mycalesini previously illustrated for genus *Bicyclus* Kirby and the genus *Hallelesis* Condamin (Sourakov and Emmel, 1997a, p. 20).

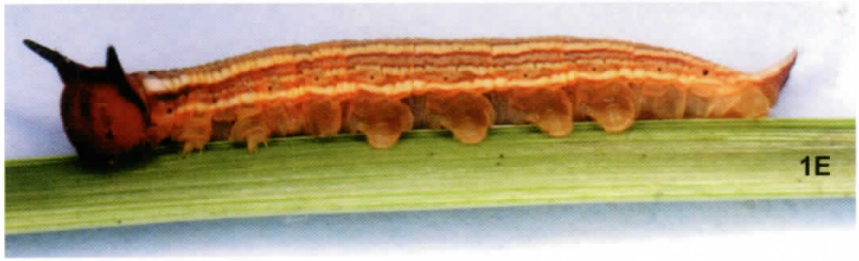
1. This study was completed during the first author's employment at the California Academy of Sciences, San Francisco, CA 94118.


1A


1B


1C


1D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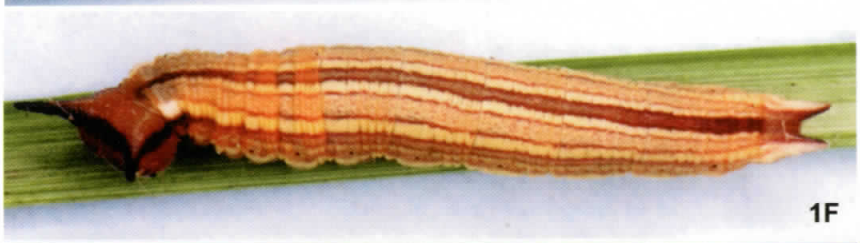
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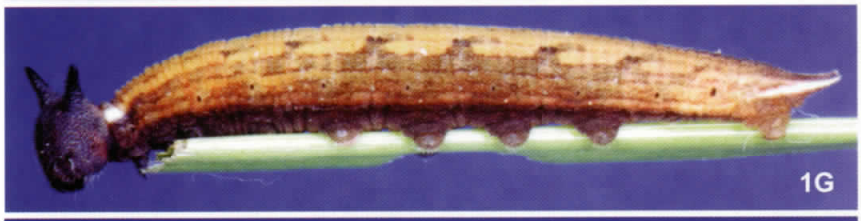
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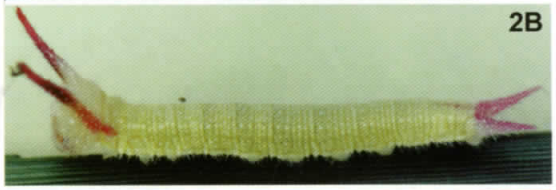
1I


4


2A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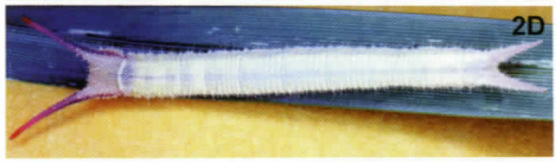
2D


2F


2F


2G


3F


3A


3B


3C


3D


3E


3G

In *Argyronympha*, the egg is much more nymphaloid, with vertical ribs and hemispherical shape (Fig. 5A), supporting the notion (Miller, 1968) of the Hypocystini being a primitive tribe (Miller's conclusion was based on the adult character of long front legs, atypical of other Satyrinae). The differences in egg size shown in Fig. 5A could be an individual variation, but might also be traced to populations from different islands, populations that are considered by some to be separate species.

**First instar larvae**: This stage in the past proved to be most conservative among closely related Satyrinae. Such seems to be the case with the Mycalesini considered here. There are practically no structural differences between larvae (Fig. 5B, E, F), and in fact, they are similar to the previously studied African members of the tribe (Sourakov and Emmel, 1997a).

Coloration of the head, however, is a different matter: white with some brown markings on the front in *O. medus* (Fig. 2A), it is glossy black in *M. perseus* (Fig. 3A), light brown in *M. interrupta* and in Malaita unidentified population (Fig. 1A), and glossy black in *M. splendens* (Fig. 1B).

In *Argyronympha* (Fig. 5C-D), the head is covered with loose reticulation and the stemmata are strongly enlarged, especially the stemma 3, which is the feature of the most advanced members of Satyrinae (Sourakov, 1997). The head lacks horns and the setae of both head and body are short and bulbous terminally, with long setae only on the anal segment. With these features, the larvae resemble those of the northern temperate genus *Erebia* Dalman (Sourakov, unpublished).

**Later instars:** Divergence of larvae increases with instars. In *O. medus*, the head horns become very long, the ground coloration of the head and body remains green, and only head horns and anal projections are pink (Fig. 2C-D). In *M. perseus*, the head horns are short throughout the larval stage, while body coloration changes. The larva is green in the second instar (Fig. 3B-C), but wide reddish-brown mid-dorsal and spiracular stripes appear in the later instars (Fig. 3D-E). In the second instar of *M. splendens*, the head horns are equal in length to those of the second instar of *O. medus* (Fig. 6), but do not increase in length in further instars as much as the length increases in larvae of the latter species (Fig. 1E-H).

*M. splendens* and *M. interrupta* still have noticeable differences in the second and third instars. The second instar larvae of *M. splendens* have a green body with head and anal projections colored dark brown (Fig. 1C), while *M. interrupta* has light brown mid-dorsal and spiracular stripes and light brown head (Fig. 1D). In the last instar (Fig. 1G-H), these two species become similar.

Head setae, which are long in *O. medus* and *M. perseus* (Fig. 6A, C), are short in *M. splendens/interrupta* (Fig. 6B). The head surface of the latter two species is practically smooth, and only slightly reticulate. It is coated with rougher reticulation in *M. perseus*, and is covered with the numerous tubercle-like projections in *O. medus* (Fig. 6).

**Pupae:** In *Mycalesis*, pupae are similar, with slight differences in shape and coloration (Fig. 1J and 3F), resembling those of African Mycalesini, as illustrated in Sourakov and Emmel (1997a), for example. However, the *Orsotriaena* pupa is strikingly different (Fig. 2E, F), with narrow and long body shape and with very long pilifers, resembling *Zethera* Felder of Zetherini and *Lethe* and *Neorina* Westwood of Lethini (Wolfe, 1996; Igarashi and Haruo, 1998).

## DISCUSSION

As is the case with many groups of organisms, the biogeography of Satyrinae is a puzzle. Due to the lack of fossils, we can only guess the age of the modern genera and tribes. It is clear, though, that the dispersal of the Satyrinae (if the present distribution could be explained by it) has happened after the evolution of the major modern lineages. This conclusion is supported by similarities between butterfly populations of lands as far apart as Africa and the Solomon Islands: for instance, the immature stages of *Mycalesis* described here are similar in many respects to those of *Bicyclus* in Africa.

*Argyronympha*, a member of the Hypocystini, the tribe endemic to the Australian region, shows similarities to, for example, *Erebia* of Erebiini or *Cercyonis* of Maniolini in the Holarctic Region. Miller (1968) states that Mycalesini or Hypocystini are the most likely links between Elyminiinae and Satyrinae, which are the primitive and the advanced subfamilies, respectively, of the old family Satyridae in Miller's classification (Fig. 7). Data presented in this paper suggest that Mycalesini show similarities to Ypthimini and Pronophilini (e. g., round shape and faceted structure of round thin-shelled eggs, larval head horns), while *Argyronympha* of Hypocystini is closer in its egg and first instar larval morphology to Maniolini, Satyrini, and Erebiini. Proper cladistic analysis of the subfamily is needed to determine inter-tribal relationships in satyrines.

Genus *Orsotriaena* exhibits plesiomorphic characters found in other tribes (Zetherini and Lethini), and therefore, might be the more ancestral of the two Mycalesini genera examined here.

Of interest is the observation of larval divergence in the *M. splendens* group. The adults of this species and *M. interrupta* are extremely similar, with slight differences in wing pattern and male genitalia (see Tennent, 2001 for complete account). We, for example, did not notice these differences until the difference in head color was noted in the larvae. The divergence in immature stages, caused by different selective pressures on different islands, might be the cause of the ongoing adaptive radiation.

The above case where larvae are more divergent than adults is not unique on the intrageneric level: the first author's study of the West Indian genus *Calisto* (Satyrinae) showed often higher morphological divergence among immatures of this genus than was found in its adults (e.g., Sourakov, 1996, 2000).

Finally, when comparing the immatures illustrated here with the illustrations found in Igarashi and Haruo (1998), we can see that the last instar larva and the pupa of *M. perseus* from the Philippines are different from the population described here. Larvae lack the pink stripes, while pupae have a row of white paradorsal spots, respectively. We also can note that the immatures of *M. splendens* group are the closest in appearance to the ones of *M. ita* C. & R. Felder, the species to which it is also the closest in wing pattern characters (other species illustrated in the above work are *M. ingoleta* C. & R. Felder; *M. sangaica* Butler; *M. tagala* C. & R. Felder; *M. anaxoides* Marshal; and *M. maianeas* Hewitson).

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Fig. **1**. *Mycalesis splendens* group: (1A) 1st instar larva, Malaita population; phenotype of this larva is also characteristic of *M. interrupta*; (1B) 1st instar larva, *M. splendens guadalcanalensis*; (1C) the same, 2d instar larva; (1D) 2d instar larva of *M. i. Interrupta*, Ronongga island; (1E-1F) the same, 4th instar larva; (1G-1H) the same, 5th instar larva; (1I) adult females, *M. i. interrupta* Ronongga island (top) and *M. splendens guadalcanalensis*, Guadalcanal island (bottom); (1J) pupa, *M. splendens guadalcanalensis*. Fig. **2**. *Orsotriaena medus*: (2A) 1st instar larva; (2B) 3d instar larva; (2C-2D) 4th instar larva; (2E-2F) Pupa; (2G) Adult male. Fig. **3**. *Mycalesis perseus*: (3A) 1st instar larvae; (3B-3C) 2d instar larva; (3D-3E) 5th instar larva; (3F) Pupa; (3G) Adult male. Fig. **4**. *Argyronympha pulchra*.

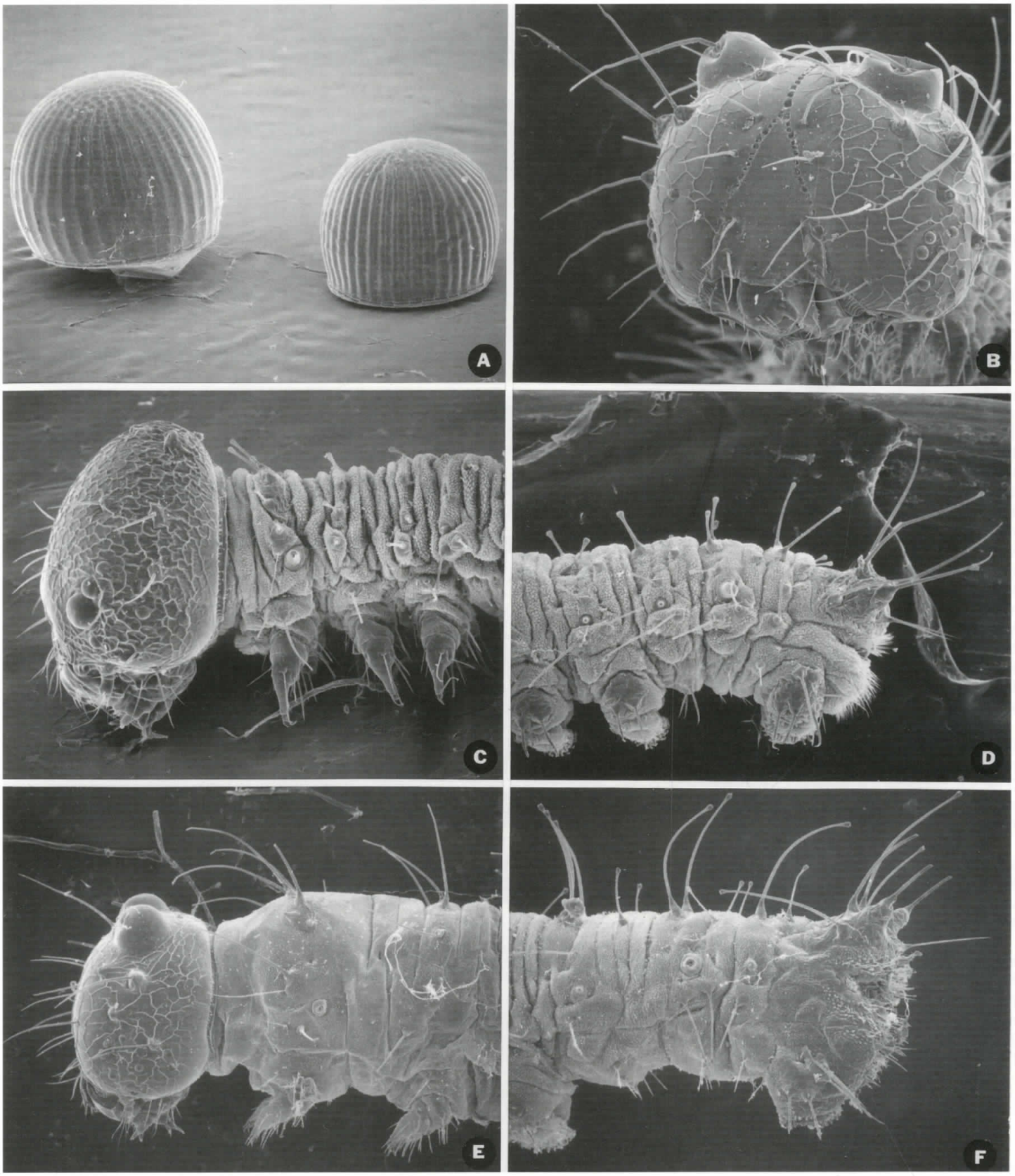


Fig. 5. (A) Eggs of *Argyronympha pulchra* (X50); (B) Head of the 1st instar larva of *Orsotriaena medus*; (C-D) 1st instar larva of *Argyronympha pulchra*, front (C), and back (D); (E) Front end of the 1st instar larva of *O. medus*; (F) Back end of the 1st instar larva of *M. perseus*.

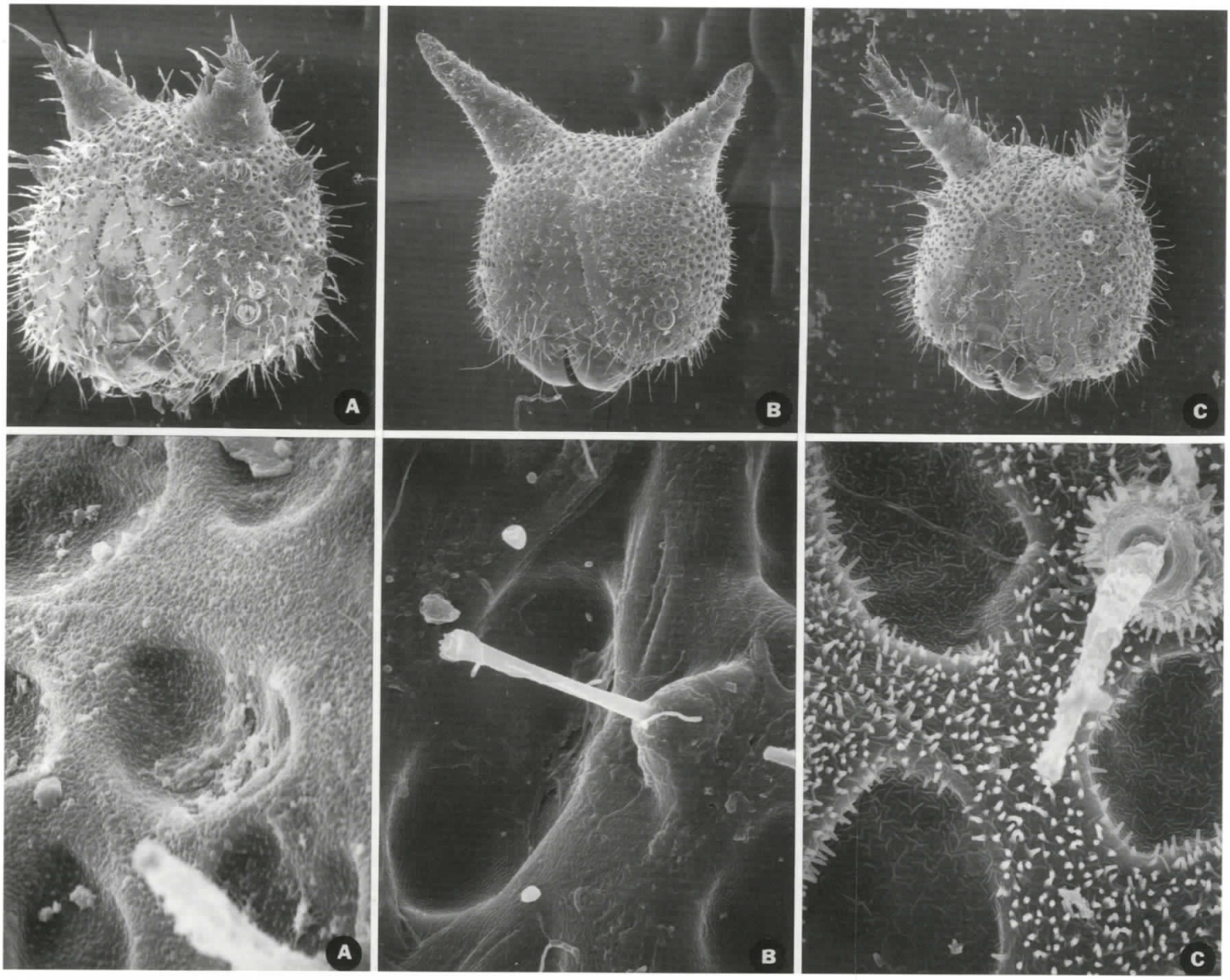


Fig. 6. Entire head (top) and a close-up of the head surface (bottom) of the second instar larvae of (A) *Mycalesis perseus*; (B) *Mycalesis splendens*; (C) *Orsotriaena medus*.

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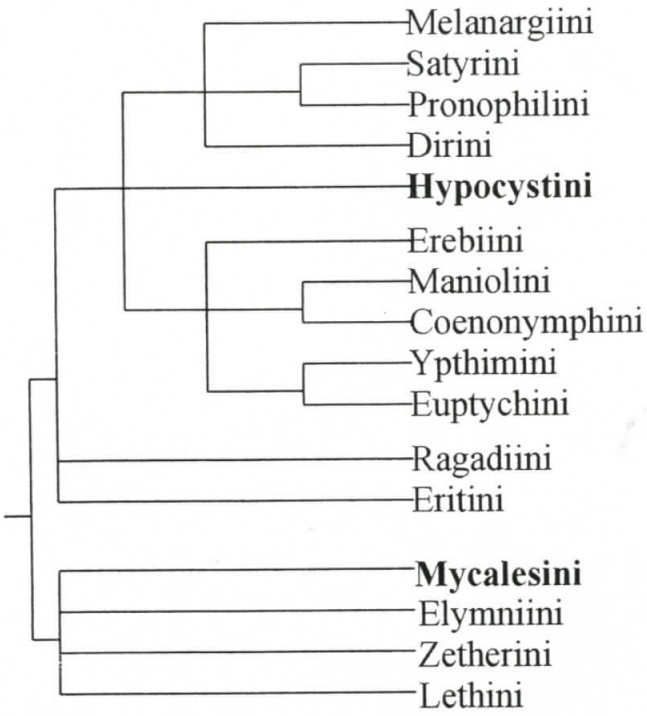


Fig. 7. Position of the tribes mentioned in text on the current phylogenetic tree of Satyrinae (after Miller, 1968).

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