

BICYCLUS AND HALLELESIS: THEIR IMMATURE STAGES AND TAXONOMIC RELATIONSHIPS (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.— Immature stages of the satyrine butterflies *Bicyclus safitza* (Westwood), *B. madetes* (Hewitson), *B. vulgaris* (Butler), *B. sanaos* (Hewitson), *B. sandace* (Hewitson), and *Hallelesis halyma* (Fabricius), from Ghana, West Africa, are illustrated and compared. The divergence of the genus *Hallelesis* from members of *Bicyclus*, to which it is closely related, is supported by the appearance of its immatures. Comparison of the morphology of the above species with another member of the tribe Mycalesini (the genus *Henotesia*), as well as with African members of tribes Ypthimini and Maelanitini, shows an increase in size of the third stemmata from primitive to advanced Satyrinae. Contrary to what is widely stated in the literature, some satyrine larvae do not have enlarged third stemmata.

KEY WORDS: Africa, Apaturinae, *Calisto*, *Cercyonis*, eggs, Ethiopian, *Euptychia*, Ghana, hostplants, *Henotesia*, larvae, Maniolini, Melanitini, *Melanitis*, morphology, Mycalesini, Neotropical, New World, pupae, South Africa, *Strabena*, taxonomy, *Ypthima*, Zingiberaceae.

The genus *Bicyclus* consists of a great number of African species and occupies an ecological position there similar to that of *Euptychia* in the New World. There are species of open areas and deep forest; species that are extremely abundant and ones that are so rare that they are known only from a few specimens; species whose larvae are general grass feeders and others that are supposedly so closely associated with a particular grass, bamboo, or even other plant groups so that they do not accept substitute hostplants (e.g., *B. medontias*, whose larva was found feeding on Zingiberaceae (Sjostedt in Condamin, 1973)).

A related genus, *Hallelesis*, was separated from *Bicyclus* Kirby by Condamin (1960) based on the presence in the first genus of the scent-producing hairpencils located in the male genitalia. The immature stages of most of the species of *Bicyclus* and of *Hallelesis* remained largely unknown, although Van Son (1955) illustrates immatures of *B. safitza* (Westwood) from South Africa.

In August 1996, we obtained eggs from a number of African *Bicyclus* species and from *Hallelesis halyma* (Fabricius) during an expedition to Ghana. Larvae of several of the species, such as *Bicyclus sanaos* (Hewitson) (Fig. 1L), *B. vulgaris* (Butler) (Fig. 1F), *B. safitza* (Westwood) (Fig. 1C), *B. sandace* (Hewitson) (Fig. 1J), and *B. madetes* (Hewitson) (Fig. 1A), as well as the larvae of *H. halyma* (Fig. 1B), accepted a substitute diet of several perennial domesticated grasses, and were raised to pupa, or last instar larva. Such rarely-encountered, deep-forest species as *B. nobilis* (Aurivillius) (Fig. 1H), *B. dekeyseri* (Condamin) (Fig. 1E),

B. procora (Karsch) (Fig. 1K), and *B. xeneas* (Hewitson), as well as some of the more common species, such as *B. dorothea* (Cramer) (Fig. 1G) and *B. taenias* (Hewitson) (Fig. 1D), did not lay eggs in captivity: their larvae, obtained from the few eggs which were squeezed out of the dead females, did not accept the substitute host plants. Eggs of *H. halyma* and *B. madetes* were squeezed out of the dead females as well.

COMPARISON OF THE IMMATURE STAGES

EGGS

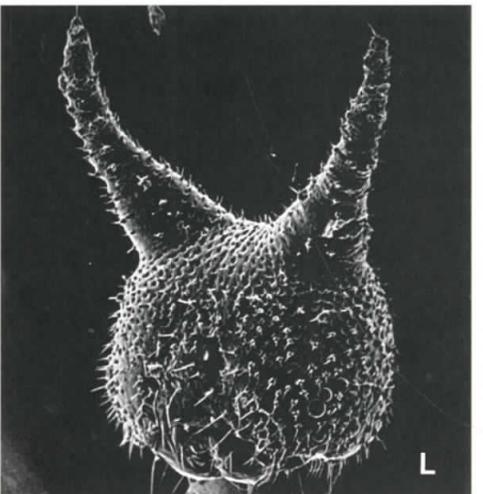
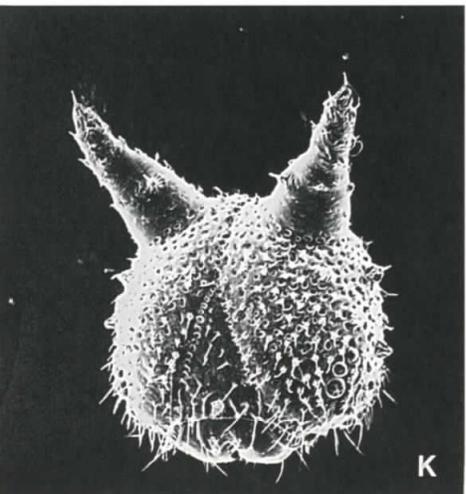
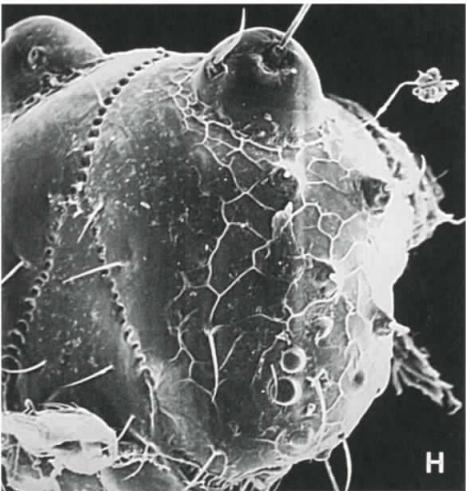
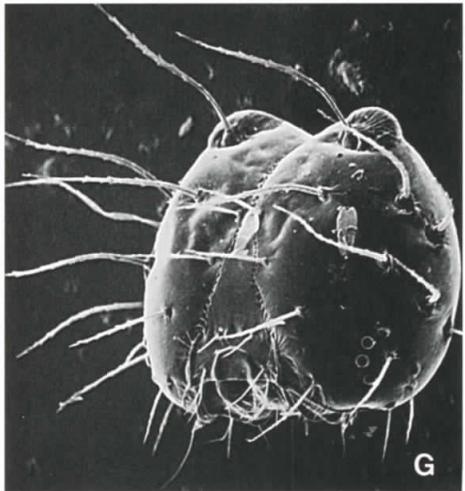
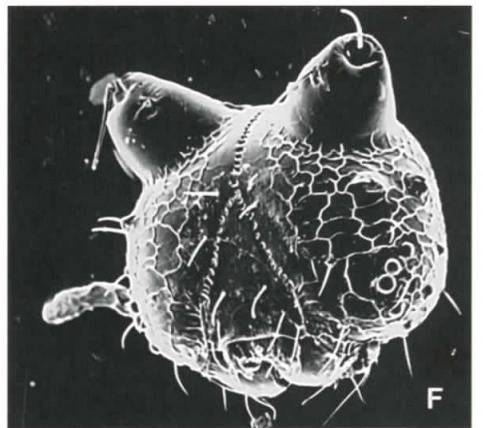
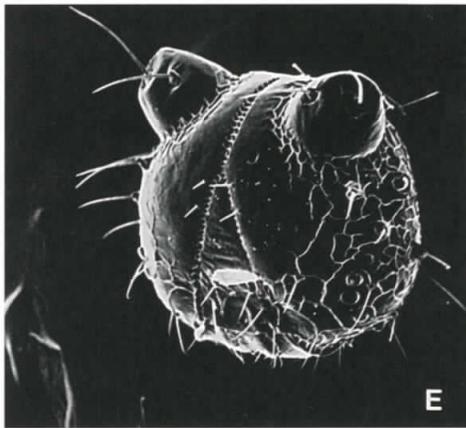
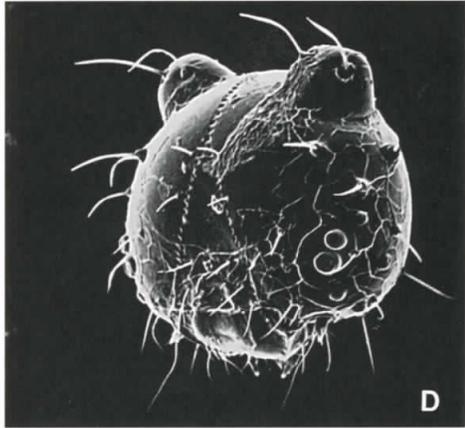
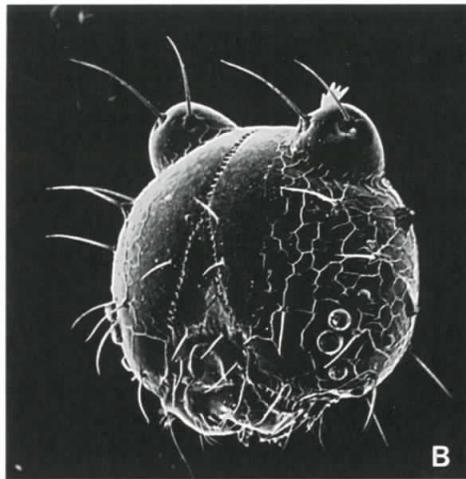
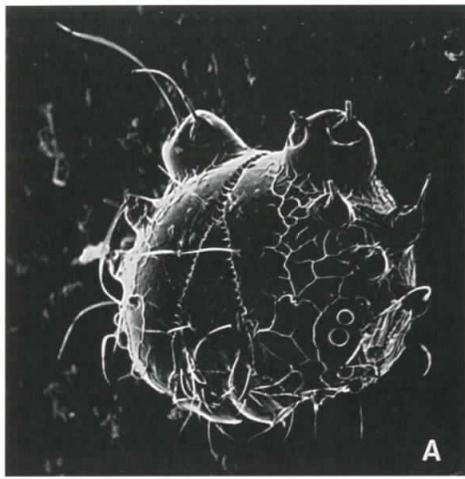
Eggs of *Bicyclus* are white, and range in shape from a hemispheric to a complete sphere, as in *B. nobilis* and *B. xeneas*. The egg of *Hallelesis halyma* is a green sphere. In both genera, the egg surface is comprised of irregularly pentagonal or hexagonal facets, with small variations in their size and structure (e. g., Fig. 6).

LARVAE

First instar larvae

First instar larvae are all superficially similar in appearance: white when hatched; body turns green and shiny after feeding; head is black and shiny, with two horns (e.g., Fig. 5(2A)). When viewed under the SEM, some structural differences become noticeable between *Bicyclus* species and *H. halyma*. The differences within *Bicyclus* are restricted to the size of setal pinacula and of the head horns and length of the head setae. Thus, *B. safitza* has the pinacula of the lateral setae strongly enlarged (Fig. 2A). In *B. xeneas* (Fig. 2E) and *B. nobilis*, the head horns are larger in proportion to the head size than in the rest of *Bicyclus*. In some species, such as *B. safitza* (Fig. 2A), head setae are

Fig. 1. Satyrinae of Ghana: (A) *Bicyclus sangmelinae*; (B) *Hallelesis halyma*; (C) *Bicyclus safitza*; (D) *B. taenias*; (E) *B. dekeyseri*; (F) *B. vulgaris*; (G) *B. dorothea*; (H) *B. nobilis*; (I) *Ypthima doleta*; (J) *Bicyclus sandace*; (K) *B. procora*; (L) *B. sanaos*. © 1997 Andrei Sourakov



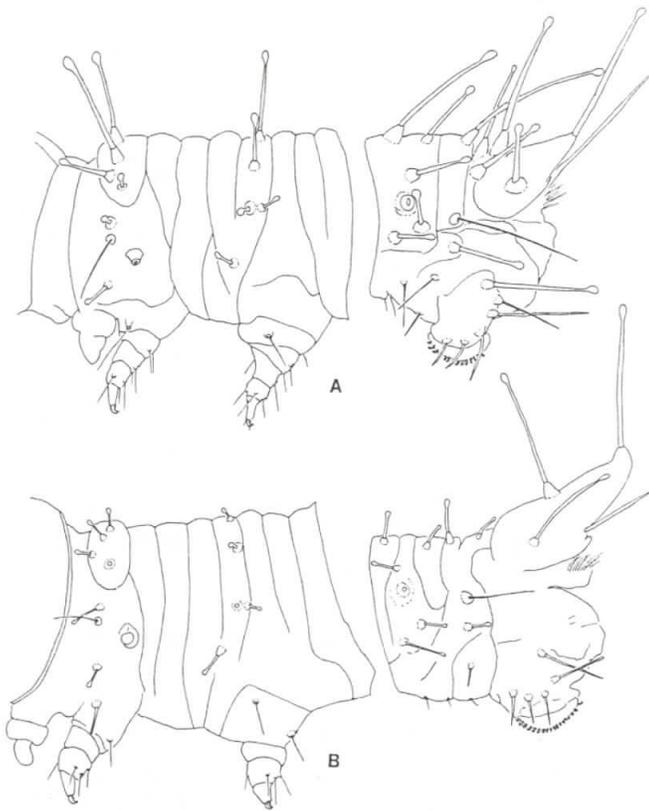


Fig. 3. Chaetotaxy of the first two thoracic and last two abdominal segment of the first instar larvae of (A) *Bicyclus safitza*; (B) *Hallelesis halyma*.

longer than in others (e. g., *B. procora*, Fig. 2B). The head of *H. halyma* (Fig. 2F) has much more extensive reticulation than those of *Bicyclus*, and this reticulation extends much further into the frontal and occipital parts of the head than it does in *Bicyclus*. The horns are larger, stemmata are smaller, and setae are shorter, relative to the head size. The schematic drawings of the first two thoracic and last two abdominal segments of *B. safitza* and *H. halyma* (Fig. 3) show differences in chaetotaxy and shape of the body. These differences are restricted to the setal length (which is greater in *B. safitza*) and size of the anal projections (which are larger in *H. halyma*). *B. safitza* (Fig. 3A) has at least three more setae on the last abdominal segment (two of which are positioned on the anal projections) than *H. halyma* (Fig. 3B).

Later Instars

In the later instars, the species's differences in the general appearance of larvae increase. Head capsules of the second instar larvae of *H. halyma*, *B. sandace*, and *B. sanaos* are shown in (Fig. 2J-L). In *H. halyma* (Fig. 2L and Fig. 4(1E)), the horns stay long throughout the larval development, and the head and body setae remain short and stout. In *Bicyclus*, some variation in setal and horn length occur: in the second instar of species such as *B. safitza* and *B. vulgaris*, the horns remain relatively short, while

the setae, especially primary ones, are long (Fig. 2J). Other species such as *B. sandace* or *B. madetes* share common appearance with *H. halyma*: the head horns become longer, while all the head setae are short (Fig. 2K). However, unlike *H. halyma*, in all of the *Bicyclus* the horns are long only in the second through 4th instars, while in the final instar they become relatively short. In the final instar, the horns either remain thin and pointed, as in *B. safitza* (Fig. 5(2F)), *B. sandace* (Fig. 4(3D)) and *B. madetes* (Fig. 4(3C)), or become thick and bulky as in *B. sanaos* (Fig. 4(4D)) and *B. vulgaris* (Fig. 5(1E)). Bodies of all *Bicyclus* larvae are much shorter and wider than the body of *H. halyma*. The larva of the latter maintains a slender and long outline, amplified by elongated anal forks and head horns, and by the well-defined longitudinal stripes (Fig. 4(1A-1D)). The color patterns of *Bicyclus* larvae are somewhat uniform, and are formed by the darker middorsal stripe widened in the abdominal segments 1-7, by the zig-zagged subdorsal stripe with subdorsal spots, and by the thin and straight subspiracular stripe. In the second and third instars, this color pattern is vague. It becomes better expressed in the 4th instar. In all of the above instars, the ground color remains green, while in the final instar it is brown (of different tones in different species). In case of *B. madetes*, the pattern described above remains very vague through the 4th instar, and we did not observe the 5th instar and are unable to make a complete description of biology of this species.

Normally, the outside layer of stemmata is formed by lens-shaped transparent exocuticle covered with a thin layer of epicuticle. In *Hallelesis* and *Bicyclus*, the stemmata are relatively large, and their transparent cuticular lens is divided into uneven parts by the ridges of material homogenous with the rest of the lens (Fig. 7). These facets are of different shapes and arrangements in different species, though not always consistent among different individuals and instars of the same species.

PUPAE

The pupae of *Bicyclus* to a great extent share a common shape and the larvae pupate in a similar way. They differ specifically mostly in their color pattern and in the extent of their abdomens being bent ventrally (Fig. 5(3A-6C)). Unfortunately, we were unable to raise *H. halyma* to the pupal stage, and therefore are unable to compare it to pupae of *Bicyclus*.

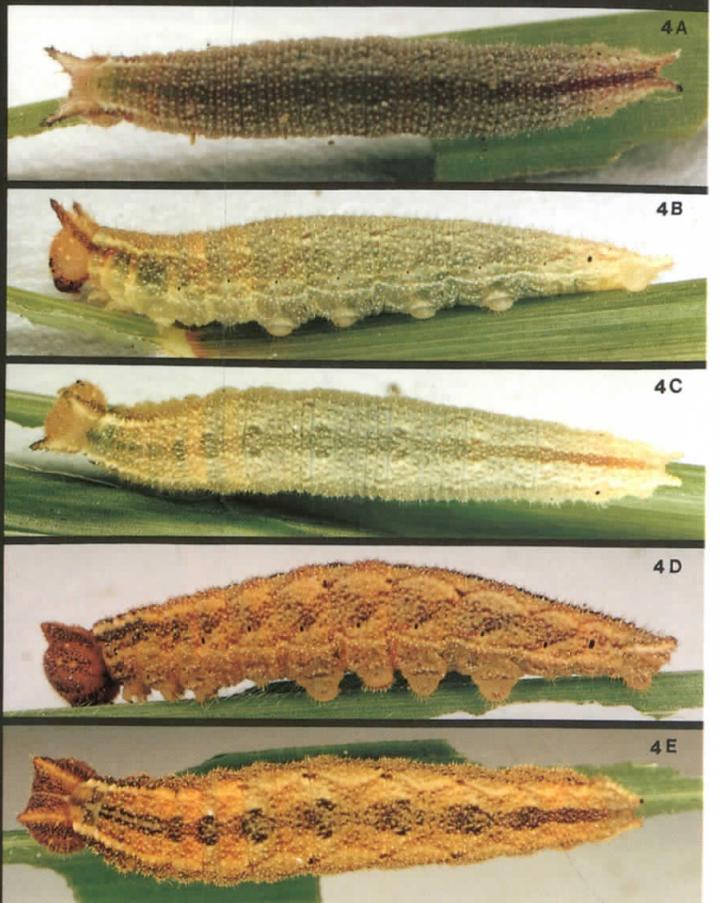
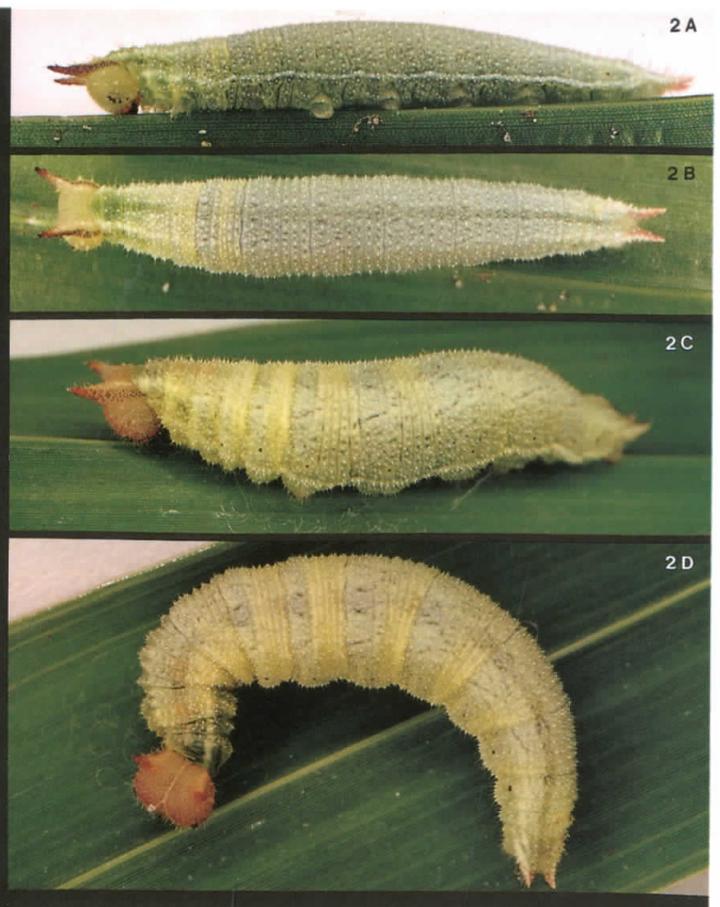
DISCUSSION

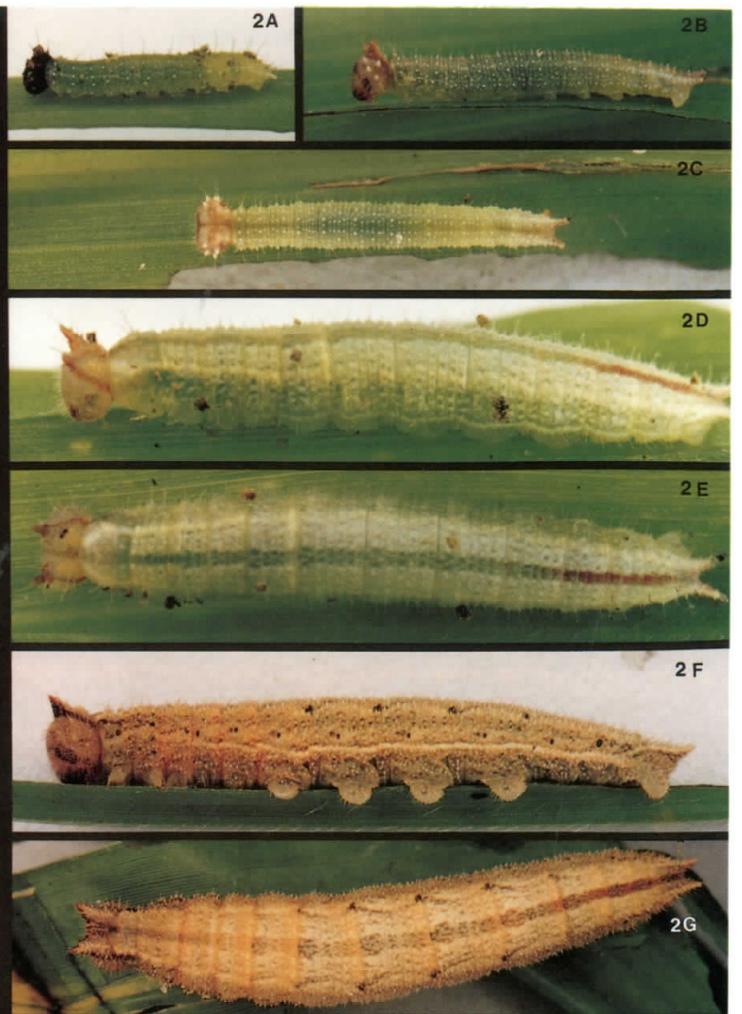
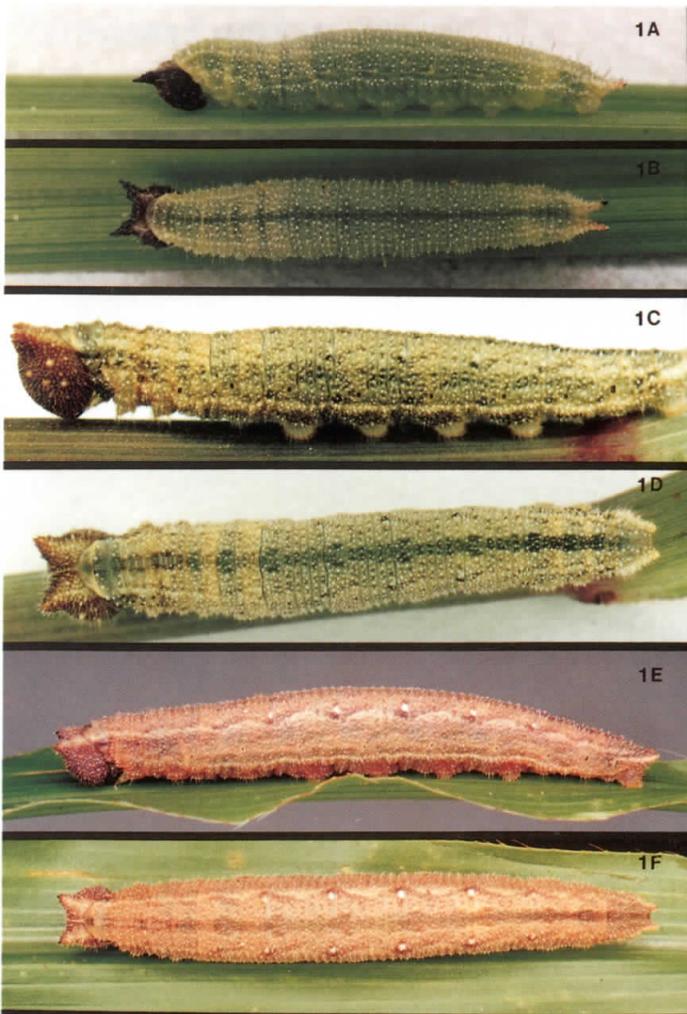
Information on life histories provides us not so much with tools for identification of hard-to-find immature stages, but with the understanding of ecological strategies that are employed by closely related butterflies to survive environmental pressures and reduce the competition among themselves.

Thus, observations on the female and larval behavior suggest that there are three different degrees of host specificity that have evolved in *Bicyclus*: (1) Host choice generality in oviposition by the female, combined with host plant generality in the larvae; (2) Host choice specificity in oviposition by the female, combined

Fig. 2. (A-I) Head capsules of the first instar larvae: (A) *Bicyclus safitza*; (B) *B. procora*; (C) *B. vulgaris*; (D) *B. taenias*; (E) *B. xeneas*; (F) *Hallelesis halyma*; (G) *Melanitis leda*; (H) *Henotesia ankaratra* (Ward); (I) *Strabena vinsoni*; (J-L) Head capsules of the second instar larvae: (J) *Bicyclus vulgaris*; (K) *B. sandace*; (L) *Hallelesis halyma*.

Fig. 4. Larvae: (1) *Hallelesis halyma*: (A-B) Fourth instar; (C-F) Fifth instar larva (2) *Bicyclus madetes*: (A-B) Fourth instar; (C-D) Fifth instar larva (3) *Bicyclus sandace*: (A) Third instar; (B-C) Fourth instar; (D-E) Fifth instar (4) *Bicyclus sanaos*: (A) Third instar; (B-C) Fourth instar; (D-E) Fifth instar © 1997 Andrei Sourakov





with host plant generality in the larvae; (3) Host choice specificity in oviposition by the female, combined with host plant specificity in the larvae.¹

We would like to note a remarkable similarity of the described color patterns of the mature larvae and pupae of the African genus *Bicyclus* to the ones of the genus *Calisto*, found only in the Caribbean and illustrated by Sourakov (1996). The distribution of these genera as well as their distant evolutionary relationships (Miller, 1968) make us suppose that the above similarities are a consequence of convergent evolution.

In comparing *Bicyclus* to Neotropical genera of satyrines, such as *Calisto* or *Euptychia*, we find more similarities in the ecological strategies that different members of these groups employ. Some species (e.g., *B. safitza*, *B. sanaos*) have successfully become polyphagous, and have relatively high rate of reproduction. The density of other species (e.g., *B. nobilis*, *B. xeneas*) is low, and their distributions are most likely to be determined by the limited distribution of their host plant species, as it is often the case in butterflies (e.g., Sourakov, 1996; Dantchenko *et al.*, 1996).

Information on morphology of immatures also provides us with characters that help to understand evolutionary relationships within the studied group, as well as relationships of this group with other higher taxa. Thus, based on the morphology of the first instar larvae, we can conclude that *H. halyma* is closer to *B. xeneas* and *B. nobilis* than to any other of the examined *Bicyclus*. Their closeness is supported by the spherical shape of the eggs; large size and cut-off shape of the head horns in the first instar larvae; shorter setae of the latter; general wing pattern; low population densities and forest habitat preferences; and a supposed host-plant specificity, indicated by refusal to lay eggs in captivity. The genus *Hallelesis* was split off *Bicyclus* based on a single character of the presence of hairpencils in male genitalia (Condamin, 1960, 1963). This character is now supported by a number of other features found in larvae, which separate *Hallelesis* from *Bicyclus*. However, in view of the modern concepts of evolutionary taxonomy, we can neither approve or reject Condamin's taxonomic decision, as we do not know whether *Hallelesis* is a highly divergent species of the *Bicyclus* evolutionary line, or a sister group that evolved before the genus *Bicyclus* diverged. To

1. Interestingly, we did not observe the last of the possible four combinations: (4) Host choice generality in oviposition by female combined with host plant specificity in the larvae. Such a combination of host-related attributes was previously observed in a number of *Calisto* (Satyrinae) species from Hispaniola, where the eggs would often be readily dropped by females into even an empty plastic container, but larvae would refuse any of the substitute species of grass offered to them (Sourakov, 1996). Such "egg-wasteful" behavior, though common in moths, is more rare in butterflies, in which first instar larvae usually lack the ability of the moth's larvae to disperse with the wind or to crawl far from the oviposition site, not to mention that butterflies are usually much more host-specific than moths. We suppose that the above behavior can evolve in species that are so closely associated with large masses of their host plant that dropped eggs do not go to waste, but fall close enough to the plant for the larva to find it. Apparently, this behavior did not evolve in African satyrines discussed in the present paper.

Fig. 5. (1-2) Larvae: (1) *Bicyclus vulgaris*: (A-B) Second instar; (C-D) Fourth instar; (E-F) Fifth instar; (2) *Bicyclus safitza*: (A) First instar; (B-C) Second instar; (D-E) Fourth instar; (F-G) Fifth instar (3-6) Pupae: (3) *Bicyclus vulgaris*; (4) *B. safitza*; (5) *B. sanaos*; (6) *B. sandace* (A) Lateral view; (B) Ventral view; (C) Dorsal view. (© 1997 Andrei Sourakov)

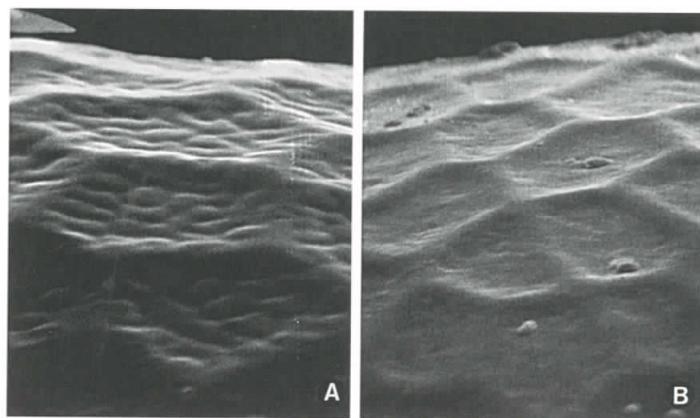


Fig. 6. Egg structure of (A) *Bicyclus dekeyseri* and (B) *Hallelesis halyma* (X1000)

solve this dilemma, one would have to conduct a cladistic analysis of the group.

Little is known on the vision of larvae, though the morphology of stemmata consists roughly of the same components as the eye of an adult: a light-sensitive cell layer on the stemmata's bottom and an outside cuticular lens (sometimes another lens is present inside the stemmata). The outside lens serves to focus the light on light-sensitive cells. The only other satyrine group where we so far have encountered the peculiar morphology of the larval stemmata shown in Fig. 7 is the genus *Ypthima* Hübner, belonging to Ypthimiini, a tribe rather distantly related to the *Bicyclus* tribe. There are three possible explanations to the appearance of this feature: (1) the number of "facets" correspond to a particular set of epidermal cells from which the cuticle of the stemmata has been secreted; (2) the ridges appeared through selection in response to the increase of the stemmata's size to strengthen them mechanically; (3) these ridges break up the cuticular lens into smaller lenses, which focus a mosaic image from different directional lines of sight onto the layer of sensitive cells at the bottom of the stemmata. Only the third explanation, should it prove correct, would indicate that caterpillar's visual organs in these advanced butterflies are much more functional than previously thought. The described structures might work analogously to the compound eye of an adult, which is better adapted for movement perception than for form perception, due to a system of small units (ommatidia) composing it (Chapman, 1971). All three explanations, however, will remain pure speculation until additional evidence is obtained.

Comparison of the stemmata size in *Bicyclus* larvae with those of *Henotesia* Butler (Fig. 2H), *Strabena* Mabille (Fig. 2I), *Ypthima*, *Cercyonis* (in Sourakov, 1995), and *Melanitis leda* (Fig. 2G) leads us to propose a hypothesis on the evolution of stemmata in satyrine larvae. It is well documented that Satyrinae differ from other Lepidoptera by an enlarged third larval stemmata (e.g., Scott, 1986; Scoble, 1994). However, stemmata of *Melanitis leda* L., a species belonging to the relatively primitive tribe Melanitini, are small and equal in size, as in Apaturinae, the subfamily of Nymphalidae closely related to Satyrinae (e.g., in Dantchenko *et al.*, 1996). In *Bicyclus*, as well as in *Hallelesis* and *Henotesia*, all of which belong to a more advanced tribe, the Mycalesini, stemmata 1, 2, and 3 progressively increase in size. This increase becomes even greater in the even more advanced tribe Ypthimiini,

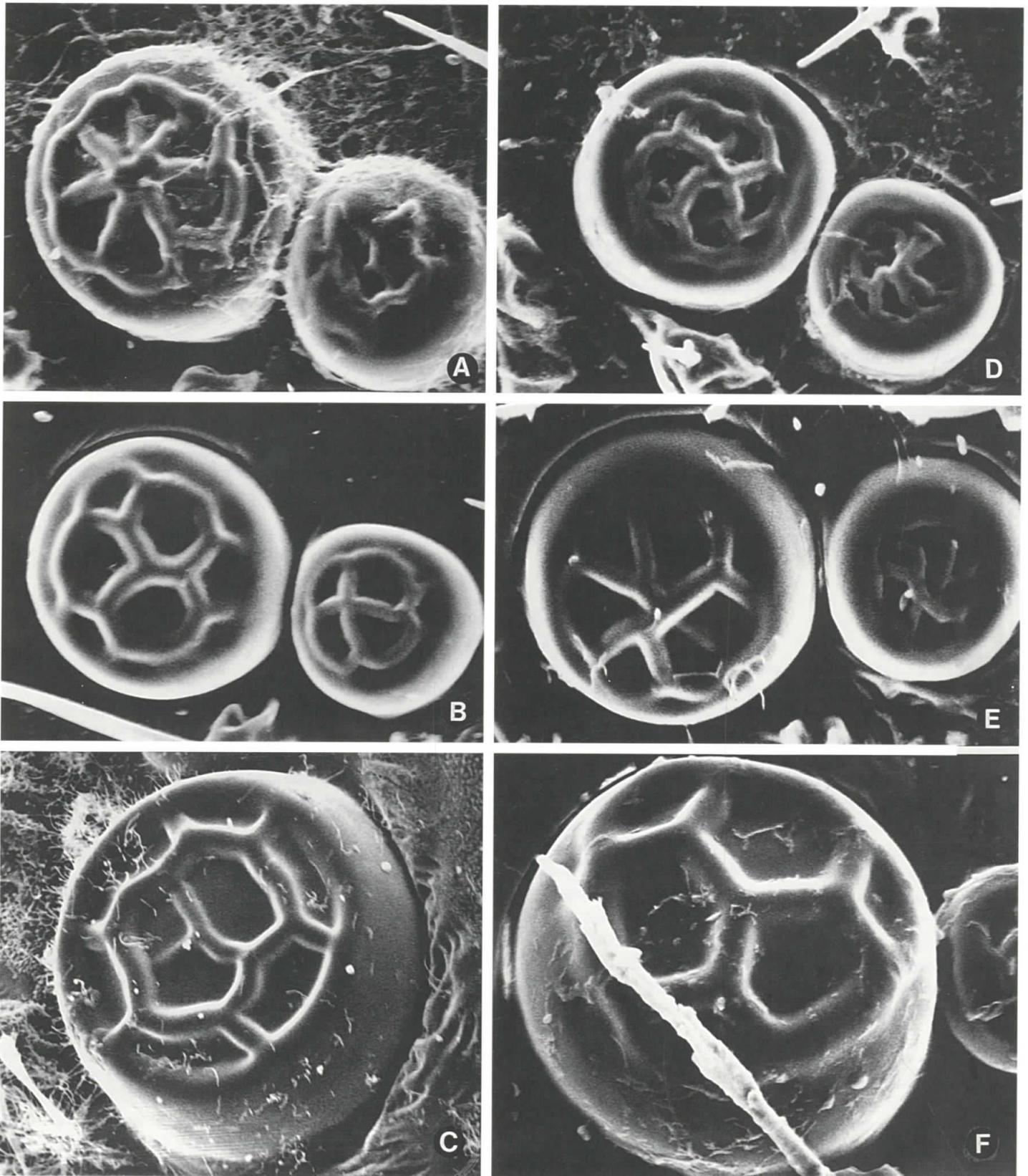


Fig. 7. Faceted structure of stemmata, found in second through fifth instar larvae of *Bicyclus* and *Hallelesis*: (A) *Bicyclus sanaos*; (B) *B. vulgaris*; (C) *B. safitza*; (D) *Hallelesis hallyma*; (E) *B. sandace*, (F) *Ypthima doleta* (A, B, D, E) Second instar, X750; (C) Fifth instar, X380; (F) Fourth instar, X750.

which we have observed in *Ypthima* and *Strabena* species, and in *Cercyonis* of the advanced tribe Maniolini. Therefore, it appears that the enlargement of the stemmata is linked to general evolutionary advancement of the Satyrinae.

So, if future examinations of this character in other Satyrinae does not reject our hypothesis, and if the evolutionary history and assignment of genera to tribes was conducted correctly in the last and only comprehensive revision of the higher satyrine taxa (Miller, 1968), the large size of the satyrine third stemmata might prove to be steadily evolving throughout the satyrines' evolutionary history, and might represent a selectively advantageous feature. Among possible selective reasons for enlarged stemmata could be that they provide better vision in searching for food, for detection of potential predators and parasitoids, and for appropriately safe shelter from weather (as, for example, during overwintering in a larval stage), or for protected pupation site.

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