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YPTHIMA AND *YPTHIMOMORPHA*: THEIR IMMATURE STAGES AND TAXONOMIC RELATIONSHIPS (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.– Immature stages of the satyrine butterflies *Ypthima doleta* Kirby, *Ypthima condamini nigeriae* Kielland, and *Ypthimomorpha itonia* Hewitson from Ghana, West Africa, are illustrated and compared. The divergence of *Ypthimomorpha itonia* from these members of *Ypthima* Hübner, is supported by the appearance of its immatures. The relatedness of these African species to Oriental members of *Ypthima* is then discussed. *Ypthimomorpha* is found to be closer morphologically to the Oriental cluster. It is proposed that *Ypthimomorpha* or its immediate ancestor represent an evolutionary bridge between Oriental and African groups of *Ypthima*. The immature stages of these latter two groups are different when preserved material from Africa is compared with illustrations of immatures of the four *Ypthima* species from Taiwan and Japan, as well as two species from Nepal (*Ypthima avanta* and *Y. sakra*). Therefore, the recognition of the monotypic genus *Ypthimomorpha* without simultaneous creation of a new generic name for the African *Ypthima* group is not defensible taxonomically.

KEY WORDS: Africa, Antarctica, Asia, Australia, Colorado, eggs, Ethiopian, evolution, Ghana, hostplants, Japan, larvae, Madagascar, Nepal, Oriental, pupae, South Africa, Taiwan, Ypthimiini.

The genus *Ypthimomorpha* Van Son was separated from *Ypthima* Hübner on the basis of adult characteristics, such as wing venation (vein R1 arising from the radial stalk beyond the upper angle of the cell) and genitalic structures (absence of an accessory plate in the valve of the male and of the posterial plate of the ostium of the female) (Van Son, 1955). In his magnificent work on the Nymphalidae of South Africa, Van Son illustrates life histories of almost all of the South African Satyrinae with meticulous paintings by Dickson. However, for both the genus *Ypthima* (a large genus of about 180 species found mostly in the Oriental Region, with only about 21 species found in Africa), and the genus *Ypthimomorpha* (a monobasic African genus considered by its author a sister genus of African *Ypthima*), the immature stages remained undescribed.

We obtained eggs of *Ypthima doleta* Kirby and *Ypthima condamini* Kielland during an expedition to Ghana in August 1996. *Y. doleta* appeared to be a species commonly found in disturbed habitats throughout the country. *Y. condamini* was found in the savanna habitat of Shai Hills Resource Reserve west of Accra. Eggs of *Ypthimomorpha itonia* Hewitson were collected from females taken in the Cape Coast area on the forest edges of a dry tropical deciduous forest remnant patch near Kissi and Komenga (40 km south of Takoradi). All three species were raised on a variety of grasses, and their immatures were photographed and preserved.

IMMATURE STAGES

EGGS

Eggs of all three species are laid singly and are white hemispheres. Under high magnification, the surface appear to be composed of irregularly shaped facets.

LARVAE

First instar larvae

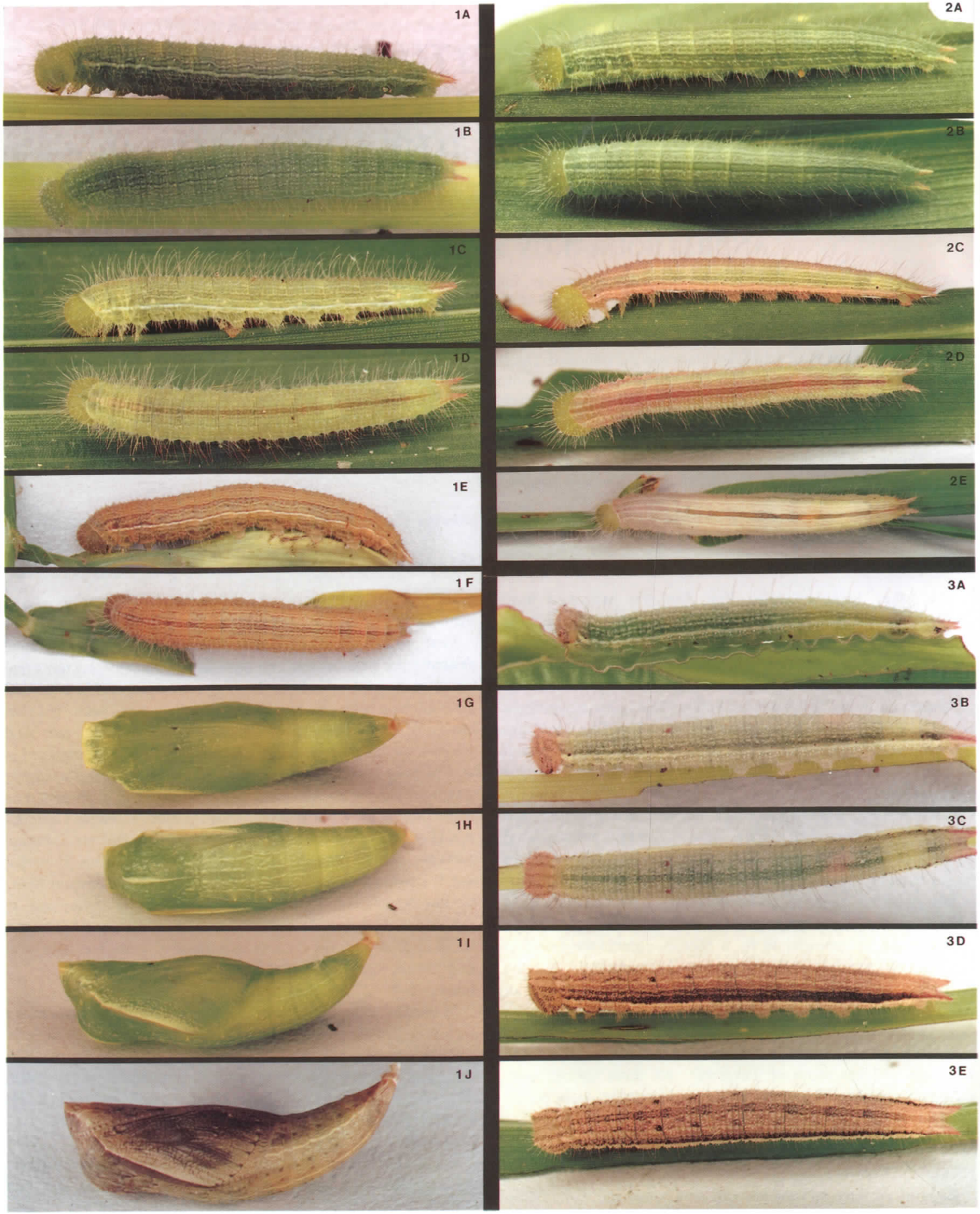
First instar larvae are white when hatched, with the head ground color pale brown. The head of *Ypthimomorpha* has some brown spots. After feeding, the body turns green. The head and the body bear long serrate setae that end in a small bulb. The first instars of these three species have similar structural and setal patterns on their heads (Fig. 4A-C and Fig. 5). Stemmata 3 is significantly larger than the rest, which is typical for higher satyrines. Stemmata 1, 2 and 3 are arranged in a straight line rather than in the circular mode which is more usual for Lepidoptera (Fig. 4A-C and Fig. 5). The sizes of the head are 0.49mm, 0.44mm, and 0.58mm in 1st instar larvae of *Y. doleta*, *Y. itonia*, and *Y. condamini*, respectively. Each species has two short horns on the dorsolateral portion of the head. In *Y. itonia* and *Y. condamini*, both the P1 and P2 setae come off the head horns, while in *Y. doleta*, the P1 seta is positioned more medially with its pinacula (base) separated from the horn (Fig. 4A-C).

Instars 2-4

In the 2nd through 4th instars, *Y. doleta* and *Y. condamini* are similar in general pattern, maintaining a light-green ground color with dark-green longitudinal stripes (Fig. 1A, B and 2A, B). The spiracular stripe is substantially more pronounced in *Y. doleta* (Fig. 1A), however, being bordered both dorsally and ventrally by broader dark-green stripes.

Last instar

In the final instar, *Y. doleta* has three distinct forms: entirely green, green with brown middorsal stripe (Fig. 1C, D), and entirely brown (Fig. 1E, F). All of these forms are notably distinct from *Y. condamini*, which acquires reddish coloration in


1A
1B
1C
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1F
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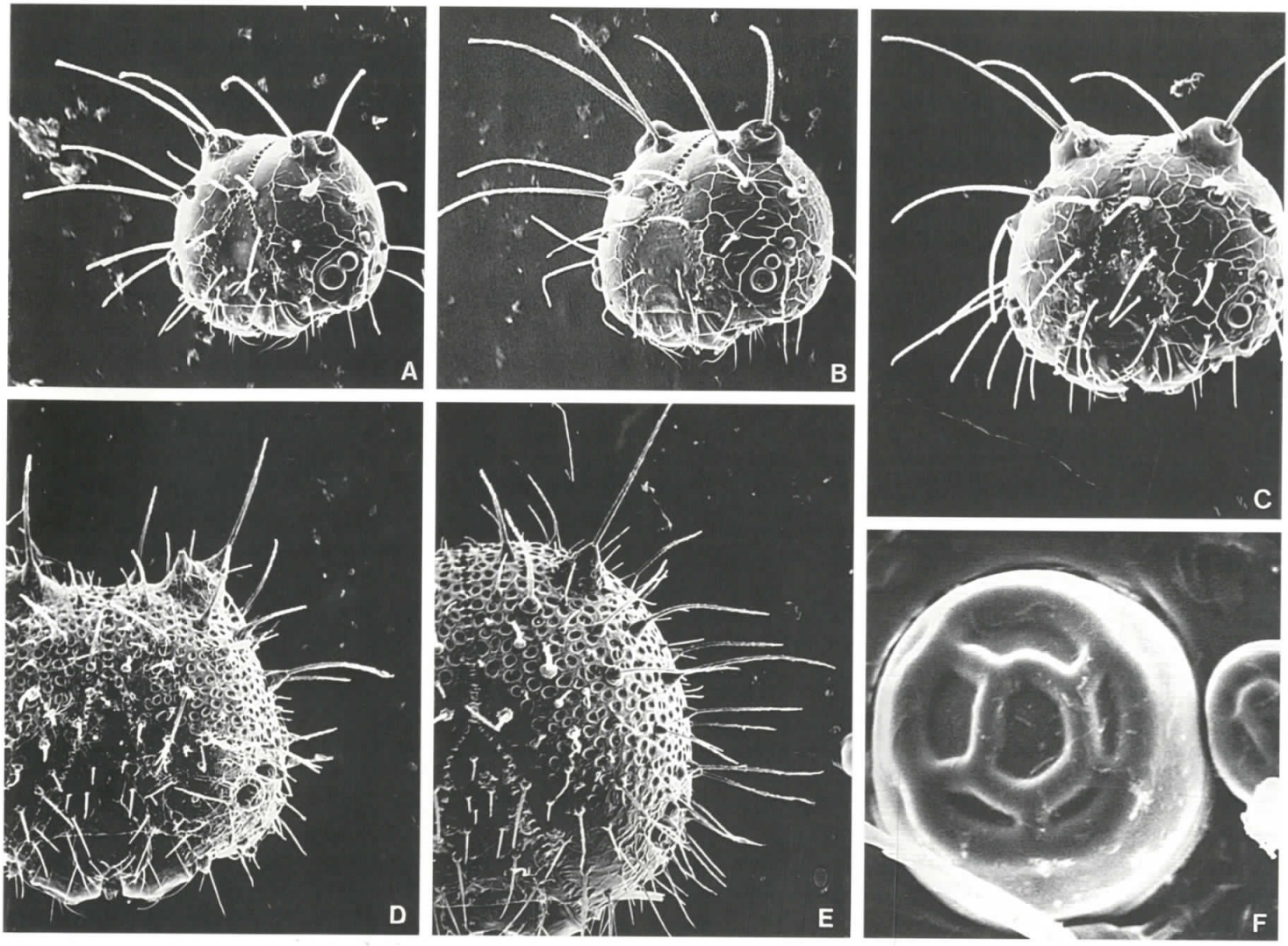

Fig. 4. (A-C) 1st instar larval head capsule of (A) *Ypthimomorpha itonia* (X100); (B) *Ypthima doleta* (X100); (C) *Y. condamini* (X100). (D-E) 2nd instar head capsules of head capsules of (D) *Ypthimomorpha itonia* (X75); (E) *Ypthima doleta* (X75) (F) Facet type structure in third stemmata of *Ypthima doleta* larva (second instar (X750).

subdorsal, spiracular, and the subspiracular stripes. Its middorsal stripe turns dark-red (Fig. 2C, D), which persists into the lighter-ground-colored prepupa (Fig. 2E).

Ypthimomorpha itonia is pale green in the 3rd instar, with dark-green middorsal and spiracular stripes and with pink anal forks (Fig. 3A). In the 4th instar, there is a pair of red subdorsal spots appearing on the first abdominal segment (Fig. 3B, C). The 5th instar, however, is brown, with the middorsal and especially the spiracular stripes now colored dark-brown instead of dark-green (Fig. 3D, E). The first four abdominal segments of the 5th instar now each bear a pair of large dark brown spots subdorsally.

The head is round and green, with long white setae in both *Ypthima* species. In *Ypthimomorpha*, the head is tapered dorsally and bears two small but distinct horns. It is pale brown with dark brown longitudinal stripes that somewhat intensify in the 5th instar. Most of the secondary setae are very short, and even the longer setae are still only half the length of these of the two *Ypthima* species. The same concerns the body setae.

In both *Ypthima* and *Ypthimomorpha*, each stemma is divided into several (usually 5-6) facets by elevated ridges of transparent exocuticular matter, homogeneous with the rest of the stemma's exocuticular lens. This feature is especially well expressed in the large third stemma (Fig. 4F). In the later instars, this structure remains the same, though, the central facet becomes larger than the marginal ones. This structure might serve to increase sensitivity of these visual organs to the stimulus of movement, analogous to the way the division into ommatidia works in the compound eyes of adult insects (e.g., Chapman, 1971).

PUPAE

Pupae of *Ypthima doleta* are of two distinct color forms: green with minor white markings (Fig. 3-2G, I), and gray with extensive black and white markings (Fig. 3-2J). Such polymorphism in pupal color occurres frequently in butterflies in general and particularly in satyrines (e.g., Sourakov, 1995, 1996). The pupa of *Ypthimomorpha itonia* has brown-black wings and thorax, and a dark-red abdomen. Its structural differences from the pupa of *Ypthima doleta* are shown in Fig. 3-7. The *Y. doleta* pupa is

Fig. 1-3. (1) *Ypthima doleta*: (1A-1B) 4th instar larva; (1C-1D) 5th instar larva: green form;(1E-1F) 5th instar larva, brown form; (1G-1I) Pupa, green form; (1J) Pupa, brown form. (2) *Ypthima condamini*: (2A-2B) 4th instar larva; (2C-2D) 5th instar larva; (2E) Prepupa. (3) *Ypthimomorpha itonia*: (3A) 3rd instar larva; (3B-3C) 4th instar larva; (3D-3E) 5th instar larva.

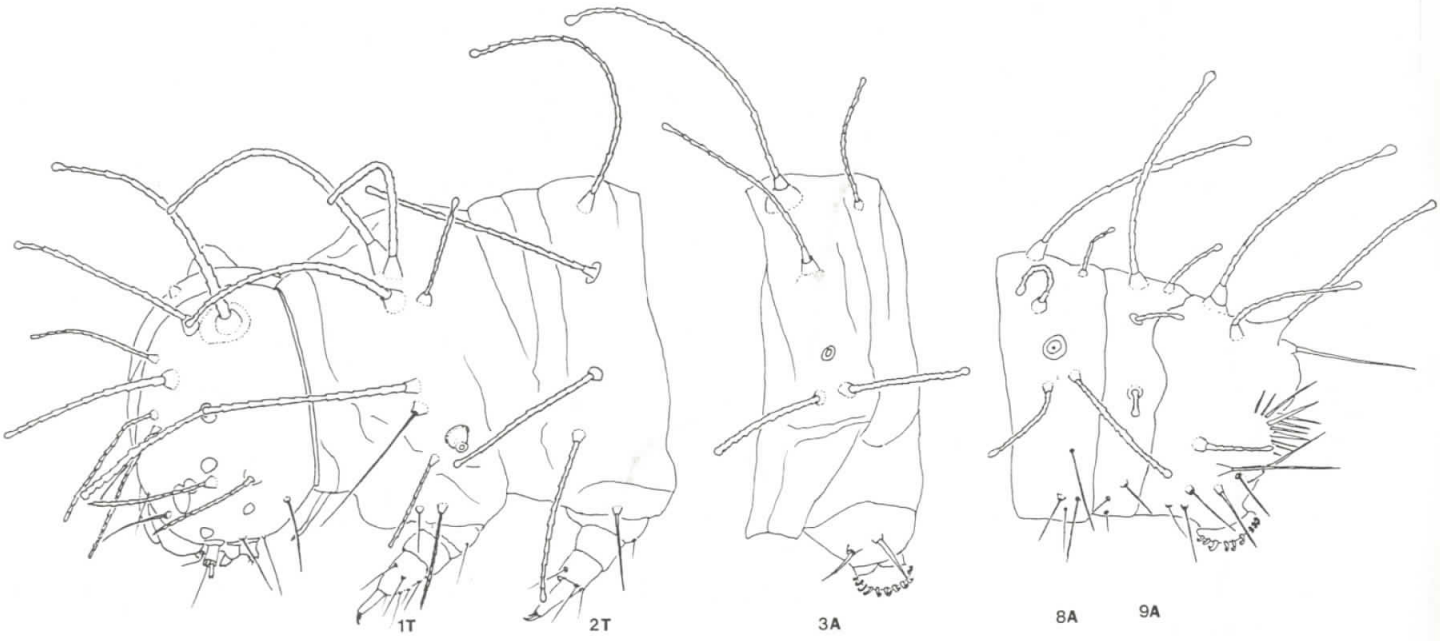

Fig. 5. Chaetotaxy of the 1st instar larva of *Ypthima doleta*: 1T, 2T = thoracic segments 1-2; 3A, 8A, 9A = abdominal segments 3, 8-9.

somewhat longer, with the last abdominal segment being furrowed and the cremaster area being considerably larger with many more hooks than in the pupa of *Ypthimomorpha*. The abdomen of the latter is angled to the body axis much more than in the pupa of *Y. doleta* (Fig. 3-7A). Additionally, the anal plate and anal opening are quite different in structure, being positioned on the convex surface of the pupa in the case of *Y. doleta*, and being tucked into a pit on the ventral surface of *Ypthimamorpha*'s cremaster (Fig. 3-7B).

COMPARISON WITH ORIENTAL *YPTHIMA*

Wing venation and genitalia are often used in designating genera in Lepidoptera. These characters, like all others, are subject to variation, convergent evolution, reversals and parallelisms. Therefore, it is useful to support them with the evidence from other characters, including those derived from the immature stages. In *Ypthimomorpha*, the immature stages have a number of characters that separate it from the African *Ypthima* species examined. On the other hand, by looking at the illustrations of immature stages of *Ypthima* from the Oriental region (Lee and Chang, 1988; Shirozu and Hara, 1969; Kawada, 1996), one can notice similarities of these species to *Ypthimomorpha*. For example, the coloration of *Y. formosana* Fruhstorfer and *Y. multistriata* Butler larvae from Taiwan is superficially similar to those of *Ypthima* species from Africa. However, in both species, setae are shorter than not only those of our two African *Ypthima* species, but also those of *Ypthimomorpha itonia* (Lee and Chang, 1988). In *Ypthima* species whose life histories are illustrated from Japanese material, the last instar larvae of *Y. argus* Butler exactly match those of *Ypthimomorpha itonia* in coloration and shape of head and body (Fig. 7A) (Shirôzu and Hara, 1969; Kawada, 1996). The coloration of *Y. motschulskyi* larva is similar to the green-form coloration of *Y. doleta*, though the close-up photo-

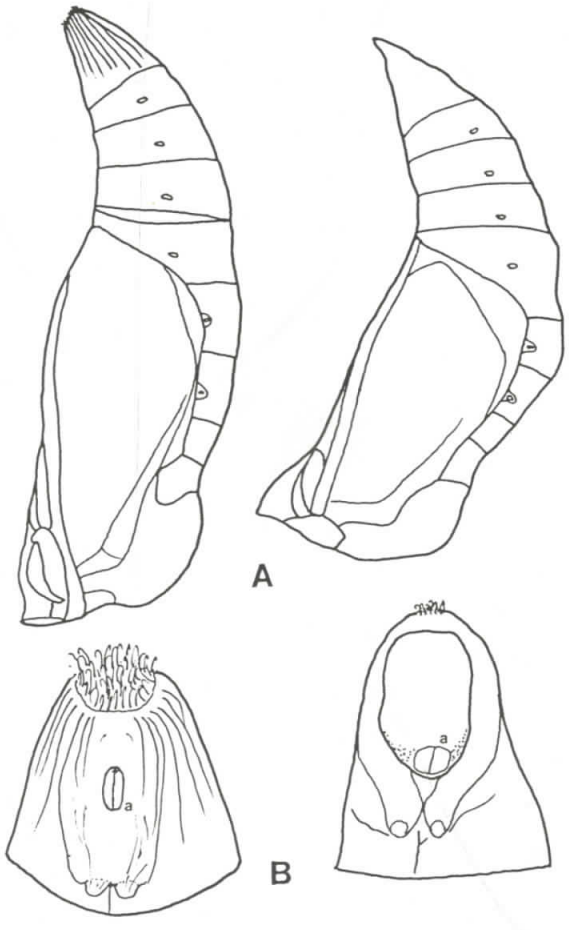

Fig. 6. The structural differences between pupae of *Ypthima doleta* (Left) and *Ypthimomorpha itonia* (Right): (A) Pupa, lateral view; (B) Last abdominal segment, a = anal opening.

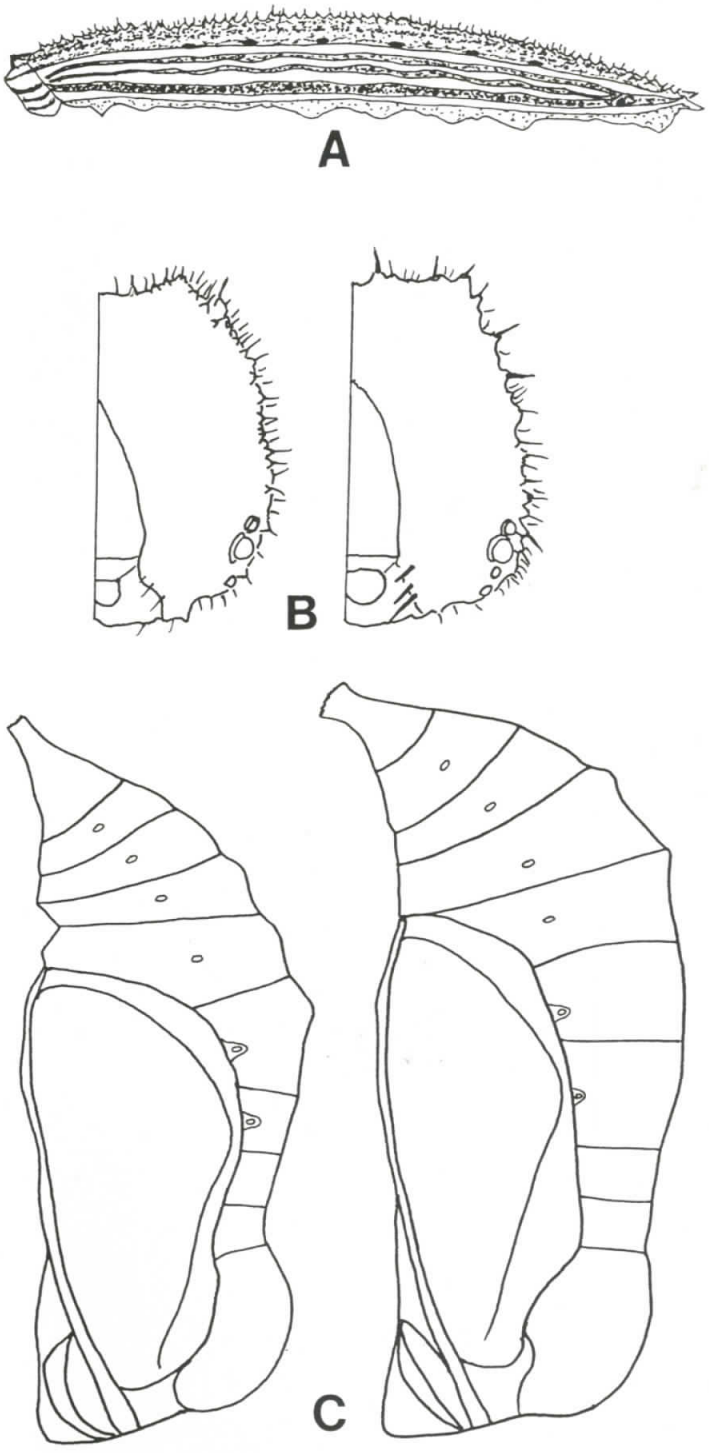

Fig. 7. (A) Last instar larva of *Ypthima argus*; (B) Heads of the last instar larvae of *Ypthima argus* (left) and *Y. motschulskyi* (right); (C) Pupae of *Ypthima argus* (left) and *Ypthima motschulskyi* (right) (after photographs from Shirozu & Hara, 1969).

graph of the head capsule of the last intar larva in Shirozu and Hara (1969), leaves no doubt of the closeness of this species to *Ypthimomorpha itonia*, rather than to described African *Ypthima*. Their heads have a triangular, rather than round shape and they bear short and stout, rather than long and thin setae (Fig. 7B). The pupal structure of all four illustrated Oriental species appear more similar to the ones of *Ypthimomorpha* (e.g., Fig. 7C). In the case of *Ypthima argus*, the similarity to *Ypthimomorpha itonia* extends into the adult wing pattern as well: both *Ypthimomorpha itonia* and *Ypthima argus* consistently have seven well-developed eyespots on the underside of the hindwing, while "typical" *Ypthima* has two or three.

Two *Ypthima* species from Nepal were recently raised by the senior author, following his 1997 expedition to this country. The new data on Nepalese *Ypthima* support the conclusions noted above. Larvae of both *Ypthima sakra* Moore (Fig. 9A-B) and *Ypthima avanta* Moore (Fig. 10A-B) have the coloration and shape of the head capsules more similar to those of *Ypthimomorpha itonia*, than to members of African *Ypthima*. The pupal structure of *Y. sakra* (Fig. 9C-E) also supports the affinity of this species to *Ypthimomorpha* (pupae of *Y. avanta* were not available for comparison).

TAXONOMIC IMPLICATIONS

According to Miller (1968), the tribe Ypthimiini originated in Asia, and later moved through continental land bridges to the other continents, evolving into Euptychiini in South America and greatly diverging in tropical Africa. If we assume that this hypothesis is correct, the evolutionary history of the genus could be pictured as shown in Fig. 8. It is obvious that since the time when Oriental and African subgroups began separation, both have undergone a significant evolution. The observed similarity between *Ypthimomorpha itonia* and Oriental *Ypthima* species, combined with the theory of the Asian origin of *Ypthima*, suggests that *Ypthimomorpha* is the most primitive taxon among African *Ypthima*.

An alternative hypothesis is that *Ypthima* evolved prior to separation of Madagascar from Africa, and prior to the separation of the Africa and Australia continents from Antarctica. This hypothesis would explain better the present distribution of *Ypthima*, but would contradict the generally accepted time frame for evolution of the modern genera of butterflies. Among butterflies found in the 35 million year old fossil shales of Florissant, Colorado, only several species belong to presently existing genera (Emmel *et al.*, 1992), while the disconnection of Australia from Antarctica supposedly happened 50 million years ago. Also, the general endemism pattern of world Lepidoptera suggests that only primitive moth families have gained their present distribution through the continental drift process, rather than land-bridge and sea-rafting dispersal, to which the present distribution of the higher Lepidoptera is attributed (Heppner, 1991).

If the phylogenetic assumptions illustrated in Fig. 8 are correct, placing *Y. itonia* into a separate genus, without recognizing a number of other genera within the *Ypthima* group, is not defensible from the point of view of evolutionary systematics. This action would damage the monophyly of *Ypthima*, making this genus a paraphyletic group, and would create a second paraphyletic genus, *Ypthimomorpha*. In the absence of a worldwide revision of *Ypthima* which could determine taxonomic status of its African and Oriental subgroups, it would be safer for now to consider *Ypthimomorpha* to be a subgenus of *Ypthima*.

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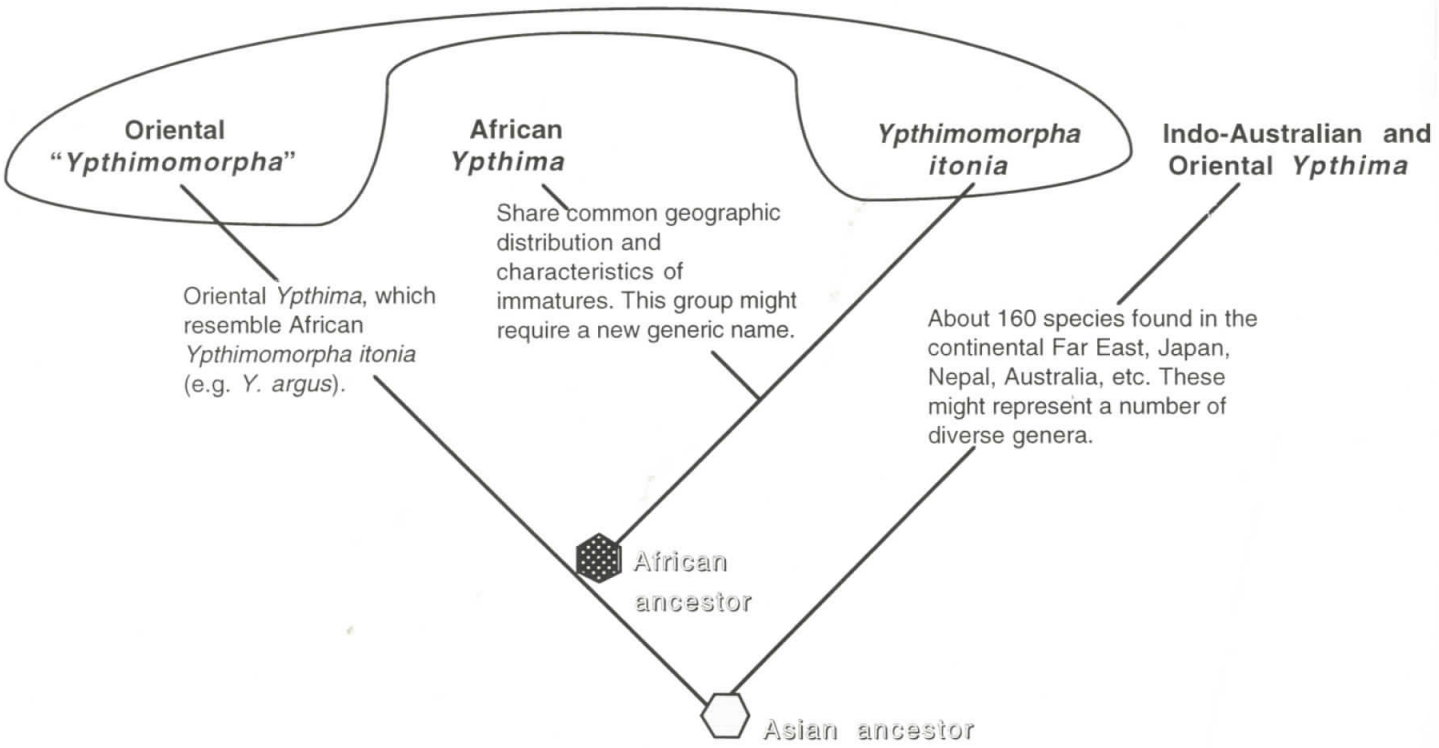

Fig. 8. Cladogram of *Ypthima*, based on the available information on life histories in the group and on the assumption of the Asian origin of the genus. This cladogram suggests that either none or all of the clades should be assigned separate generic names, in order to preserve the monophyly of the genus *Ypthima*.

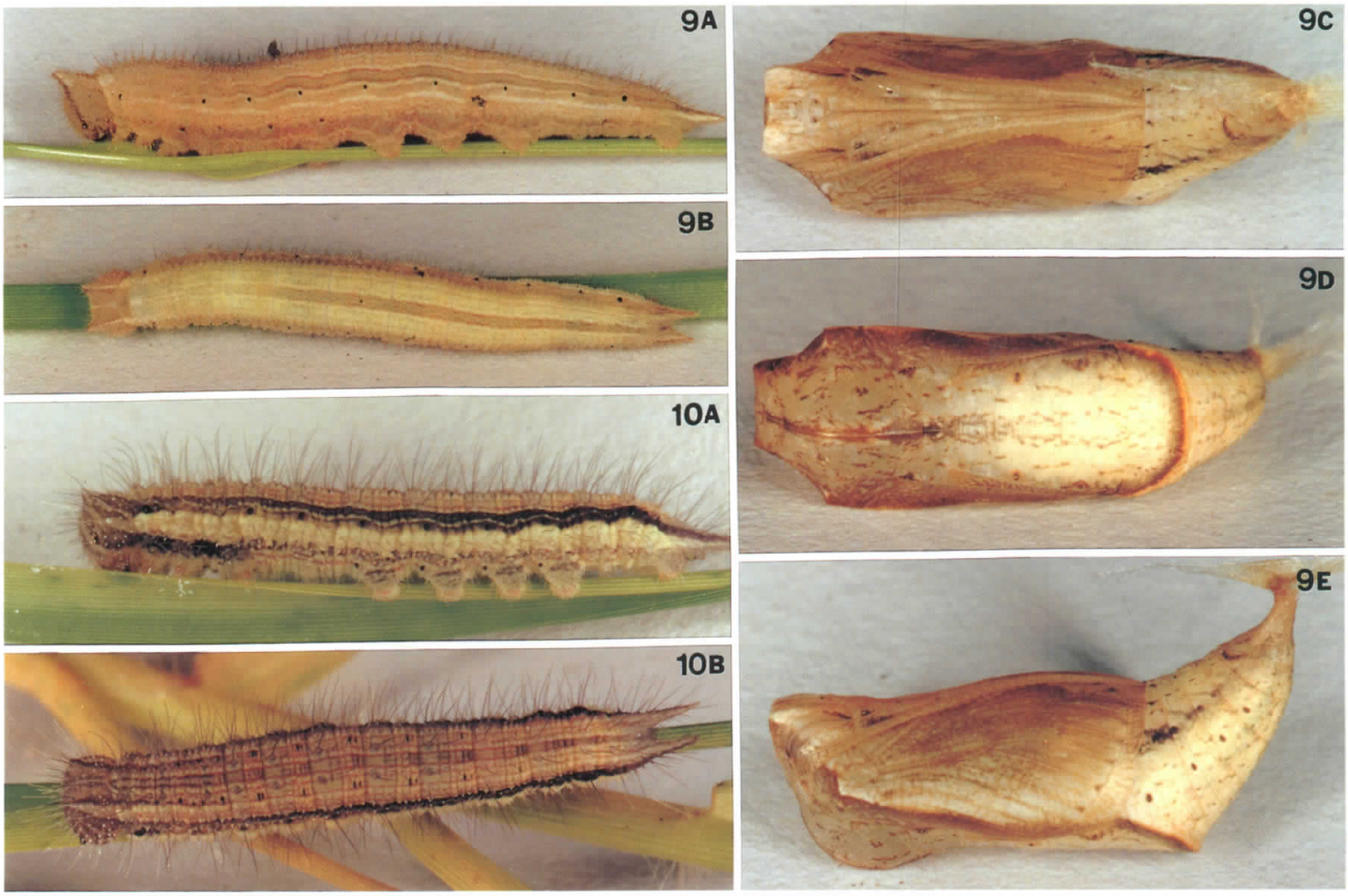

Fig. 9-10. Immature stages of two *Ypthima* species from Nepal: (9) *Ypthima sakra*, 5th instar larva (9A-B) and pupa (9C-E). (10) *Ypthima avanta*, 5th instar larva (10A-B). (© 1997 A. Sourakov).