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JUVENILE STAGES OF *CYBDELIS*, A KEY GENUS UNITING THE DIVERSE BRANCHES OF THE EURYTELINAE (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT.– The early stages of *Cybdelis* (Nymphalidae) combine characters from all lineages of the Eurytelinae. Eggs are laid singly on the underside of mature leaves of *Tragia volubilis* (Euphorbiaceae), a common foodplant in Biblidini, Eurytelini, *Dynamine* and some Epicaliini. Unlike most genera of Eurytelinae (except *Dynamine*, *Sea* and some *Eunica*), larvae do not construct frass chains. Some morphological features of the first and last instar larvae and pupa are like those of the Catagrammini, but the egg is very similar to those of the Epicaliini.

KEY WORDS: *Antigonis*, *Archimestra*, *Batesia*, behavior, Biblidini, *Biblis*, *Bolboneura*, Brazil, Burseraceae, *Byblia*, Catagrammini, Caryocaraceae, *Catonephele*, *Cyclogramma*, *Diaethria*, *Dynamine*, eggs, Epicaliini, *Eunica*, Euphorbiaceae, *Eurytela*, Guttiferae, *Hamadryas*, larvae, *Lucinia*, *Mestra*, *Myscelia*, *Panacea*, *Paulogramma*, *Peria*, *Perisama*, pupae, *Pyrrhogyra*, Rutaceae, *Sallya*, *Sea*, Venezuela, *Vila*.

Numerous life cycle studies of Neotropical butterflies have been published (see compendia in DeVries, 1987, and Lamas *et al.*, 1995). Some important groups, however, have still not been reared or are poorly documented. In the nymphalid subfamily Eurytelinae, important Neotropical genera whose juveniles are still undescribed include *Vila*, *Archimestra*, *Batesia*, *Bolboneura*, *Peria*, *Lucinia*, *Antigonis*, *Cyclogramma*, *Paulogramma*, several groups of *Eunica*, and *Cybdelis* (*Sea* excluded). Since knowledge of immatures is important in biological, evolutionary, and systematic studies in Lepidoptera (Brown and Freitas, 1994), a full report on any of these genera ought to be useful to guide future work on the Eurytelinae and the whole Nymphalidae.

The genus *Cybdelis* includes 3 species (or 4 if *Sea sophronia* (Godart) is included, as suggested by some authors) distributed throughout the montane regions of South America (D. W. Jenkins, pers. comm.); all three are sympatric in Peru and Bolivia. The genus is in the subfamily Eurytelinae, tribe Epicaliini and subtribe Eunicina, together with the genera *Sallya* and *Eunica* (Jenkins, 1990; Otero, 1990; Harvey, 1991). *Cybdelis phaesyla* (Hübner, 1831), the type-species of the genus, occurs at mid to high elevations in southern Brazil (Brown, 1992) with a subspecies in the Andes; *C. mnasylus* (Doubleday, 1848) occurs from Bolivia north to Venezuela. This paper records the foodplant and early stages of these two species of *Cybdelis*, comparing them with other Eurytelinae.

STUDY SITES AND METHODS

Immatures of *C. phaesyla* were found in the Serra do Japi, Jundiaí, São Paulo, southeastern Brazil (23°11'S, 46°52'W), a mountain range (700-1300m altitude) covered by semideciduous mesophytic forest (Leitão, 1992). A single first instar larva was collected in March 1994 near the Research Station, and 11 additional immatures (3 eggs, 3 second instar and 5 third instar larvae) were collected in April 1995 near the DAE dam. Larvae were reared following Freitas and Oliveira (1992). Immatures of *C. mnasylus* were collected in the Sierra de Mérida, near Mérida, western Venezuela (near the Chorrera de las González, on the road to the Mesa de Ejido, 1560m, and near the town of Tabay, in Mucuy baja, 1750m), in patches of secondary forest bordering farmland. Egg size is given as height and diameter; the head capsule size is the distance between the two groups of ocelli; size of cephalic horns was also measured.

RESULTS

Natural History

Eggs of *Cybdelis phaesyla* are laid singly on the under surface of mature leaves of *Tragia volubilis* (Euphorbiaceae), a common second-growth urticant vine also used in the Serra do Japi by *Biblis hyperia* and two species of *Dynamine*. Although this vine grows as high as six meters when climbing on trees, immatures appear to be commonest on leaves from 20cm to 2m above ground level, in wet shady environments. Eggs of *C. mnasylus* are also laid singly on the under surface of mature leaves of *Tragia volubilis* and a probably new species of *Tragia* (Euphorbiaceae) (L. Gillespie, pers. comm.).

Larvae of *Cybdelis* species did not build frass chains in the field nor in the laboratory, and did not tend to jump off the leaf when disturbed. Regurgitating digestive fluids, known in *Eunica* (Freitas and Oliveira, 1992), and in some other Eurytelinae like

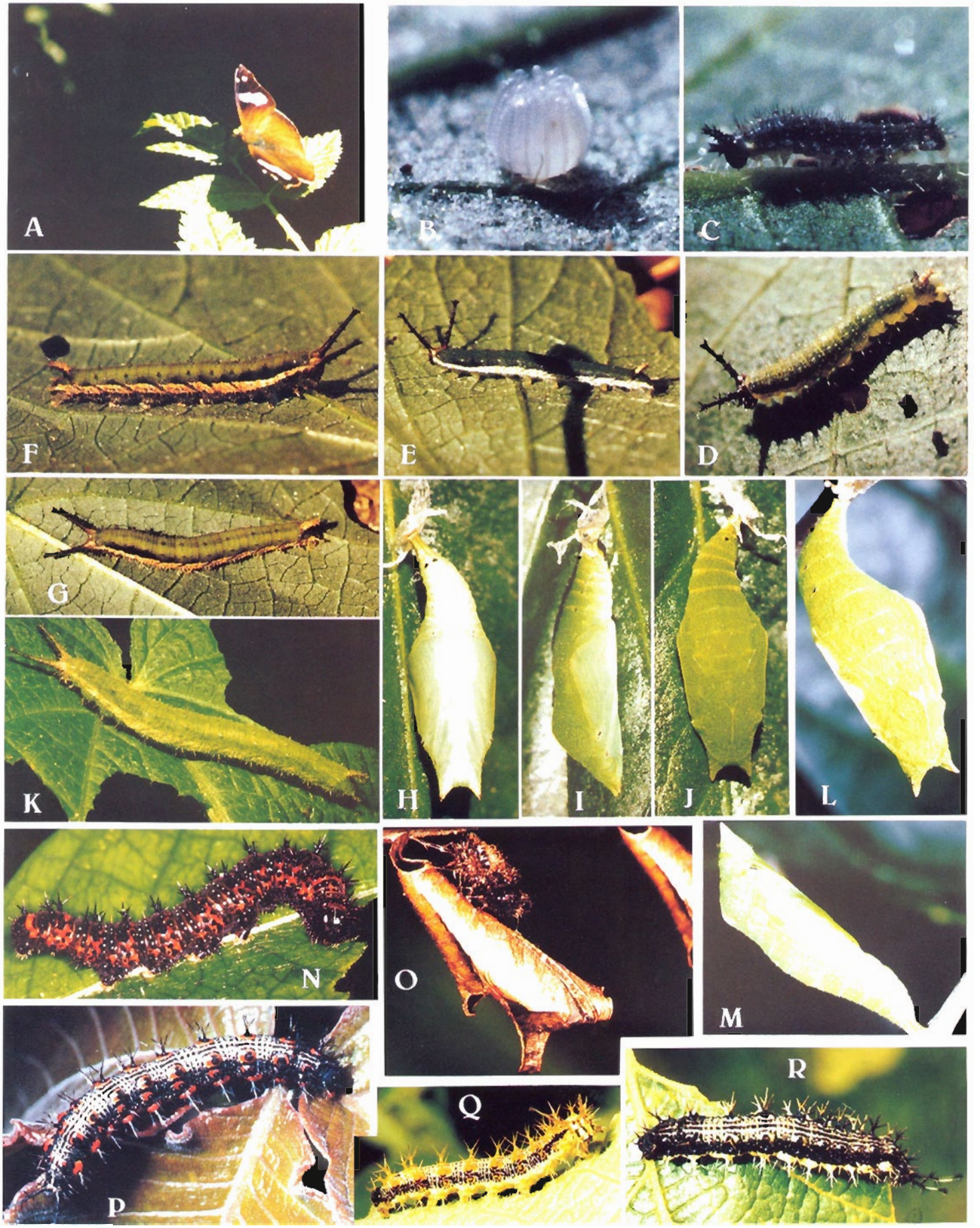

Fig. 1 Eurytelinae adults and larvae – ***Cybdelis phaesyla***: A) adult male of perching. B) egg. C) second instar larva. D) third instar larva E) fourth instar larva F-G) fifth instar larvae H-J) pupa (ventral, lateral, dorsal). ***Cybdelis mnasylus***: K) fifth instar larva. L-M) pupa (dorsal, lateral). ***Sea sophronia***: N) fifth instar larva. O) pupa (rotated 90° from normal position [likewise in Otero, 1994]: down is to the right). ***Eunica bechina***: P-R) three different forms of fifth instar larva (photos A-J by Keith S. Brown Jr., photos K-O by L. Daniel Otero; photos P-R by Paulo S. Oliveira).

Hamadryas amphinome (L. D. Otero, pers. obs.) was also not seen in *Cybdelis* larvae.

Of the eight larvae of *C. phaesyla* collected in 1995, all five third instar larvae and one second instar larva were parasitized by a tachinid fly.

Adults of both sexes of *Cybdelis* are often seen on the ground in sunny patches. Males puddle beside streams where *Dynamine* and *Eunica* are common; when startled, they may fly rapidly to a nearby low leaf (*C. phaesyla* in São Paulo; Fig. 1A) or leave the area entirely (*C. mnasylus* in SW Acre, Brazil); both show an exaggerated wariness similar to *Eunica*. Male *Cybdelis phaesyla* have been seen defending territories from high hillside perches, chasing and expelling other males from the area, very much like *Sea* on hilltops. Both sexes of *C. mnasylus* congregate in the neighborhood of the *Tragia* host plant, which may play a role in mate location and mating. Males of *C. mnasylus* make rapid inspection flights over the host plant foliage and that of neighboring plants, alighting on leaves with wings open and flying out after other males that pass by, without expelling them. When a passing or approaching female is persecuted, she tries to evade and lands in nearby vegetation, where she is gradually approached and even touched by the male, while she rapidly vibrates her partly closed wings. This courtship behavior resembles that of *Dynamine* and *Catonephele*.

Descriptions of Early Stages

Cybdelis phaesyla

EGG (Fig. 1B): white, rounded, somewhat flattened at the top, with 10 prominent vertical ridges (keels) and 12 horizontal (transverse) ridges observed only on the keels. Height and greatest diameter about 0.95mm.

LARVA: *First Instar*: Head dark brown, body white, changing to dark green after feeding (due to visible intestinal contents), body with long black setae (about 0.23mm) arising from sclerotized conical insertions (prothoracic setae longer than the others), legs and prolegs translucent; prolegs with 12 to 14 crochets; maximum length 3mm; average width of head capsule 0.52mm (n = 3), duration 3 days (n = 2). The chaetototaxy of the first instar larva is given in Fig. 2A.

Second Instar (Fig. 1C): head black with two short, thick, and spiny horns; body dark green, with numerous dark-setose tubercles; legs and prolegs unpigmented; maximum length 5.5mm; average width of head capsule 0.8mm (SD = 0.024mm, n = 8); average length of horns 0.45 mm (SD = 0.032mm, n = 8), duration 3 to 4 days (n = 4).

Third Instar (Fig. 1D): head with numerous warts, black frontally, buff dorsally at base of two long diverging black horns that are armed with accessory spines in the middle and end distally in a knob crowned with short spines; body green with a broad lateral white stripe and short scoli (sclerotized spinose tubercles); three longer scoli, one mid-dorsal on the suture 8A/9A and two lateral on the anal segment (10A); legs and prolegs unpigmented; maximum length 9.7 mm; average width of head capsule 1.21mm (SD = 0.084mm, n = 9); average length of the horn 1.85mm (SD = 0.15mm, n = 9), duration 3 to 5 days (n=5).

Fourth Instar (Fig. 1E): head as in third instar; body green with a lateral white stripe and very short scoli, except three long posterior scoli (8A/9A and 10A) as in third instar; legs and prolegs unpigmented; maximum length 15mm; average width of head capsule 1.91mm (SD = 0.14mm, n = 8); average length of the horn 3.58mm (SD = 0.46mm, n = 8), duration 3 to 5 days (n = 4).

Fifth Instar (Fig. 1F-G): head more buffy dorsally than in previous instars and with a white front; body greenish with a brown-speckled lateral white stripe and very short scoli (except for a long thick posterio-

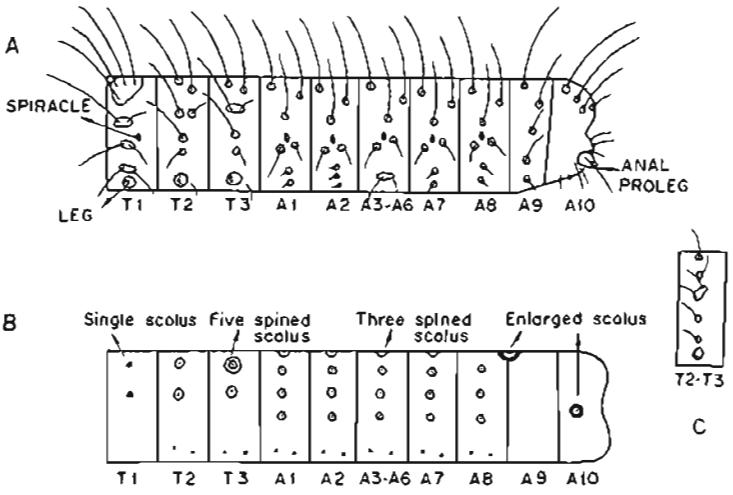

Fig. 2. A) Chaetotaxy of first instar larva of *Cybdelis phaesyla*. B) Distribution of scoli in a fifth instar larva. C) Chaetotaxy of T2 or T3 of first instar larva of *C. mnasylus*.

dorsal scolus on 8A and two lateral scoli on the anal segment 10A); legs translucent yellow and prolegs with a small grayish lateral plate. The placement of the scoli on the body is shown in Fig. 2B. Maximum length 30mm; average width of head capsule 2.5mm (n = 4); average length of the horn 5.05mm (n = 4), duration 6 to 7 days (n = 3). Prepupa assumes a "J" position, fixed on the substrate by the anal prolegs and abundant silk.

PUPA (Fig. 1H-J): Entirely green, with small black spots at the base of the wing pads, EHTs (base of the cremaster), and abdominal segments 4-7; smooth, with a dorsal indentation between the abdomen and thorax, and two pronounced head cones. Abdominal segments mobile; average length 2.10cm (n = 4), maximum width at wing pads 0.68cm, separation of points of head cones 0.30cm, duration 10 to 12 days (n = 3).

Cybdelis mnasylus

EGG: very similar to that of *C. phaesyla*, but with 14-15 prominent vertical ridges (keels) and no visible transverse ridges except at apex. Diameter 0.68-0.78mm (n = 7).

LARVA: First to fifth instar larvae and pupae very similar to those of *C. phaesyla*. The first instar larvae have long setae (about 0.24mm) in sclerotized insertions, with distribution on the body nearly identical to that of *C. phaesyla*, except on the meso- and metathorax (Fig. 2C). Fifth instar (Fig. 1K, 3) lighter green than in *C. phaesyla* with depigmented scoli and lateral stripe. Pupa (Fig. 1L-M) with white blotches laterally.

DISCUSSION

Species of *Tragia* (Euphorbiaceae) have been recorded as the primary host plant of primitive Eurytelinae, including all Eurytelini (*Byblia*, *Eurytela*: Van Son, 1979) and Biblidini (*Biblis*, *Mestra*, *Vila*: pers. obs.), the West Indian *Archimestra* (D. Wetherbee, reported in Smith *et al.*, 1994); and some *Dynamine* (see also DeVries, 1987), and also as secondary hosts of some Epicaliini (*Myscelia* and *Hamadryas*). The genus is not known to be used in the subtribe Eunicina, whose members mostly use other Euphorbiaceae. *Sea sophronia*, possibly congeneric with *Cybdelis*, has been reported on *Plukenetia penninervia* (Euphorbiaceae) (Otero, 1994), while *Eunica* species are known from *Gymnanthes*, *Mabea*, and *Sebastiana*, as well as the plant fami-

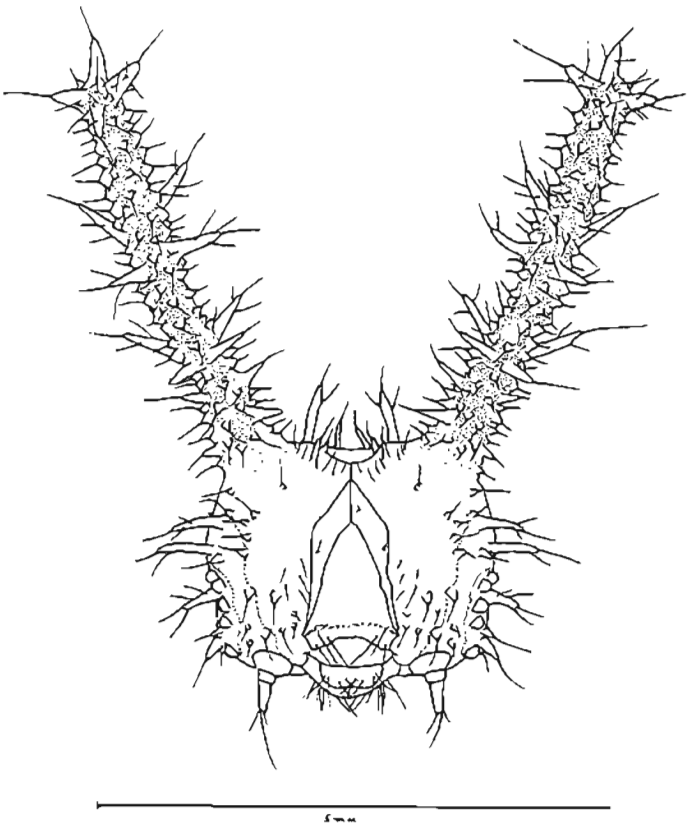

Fig. 3. Head capsule of a fifth instar larva of *Cybdelis mnasylus*.

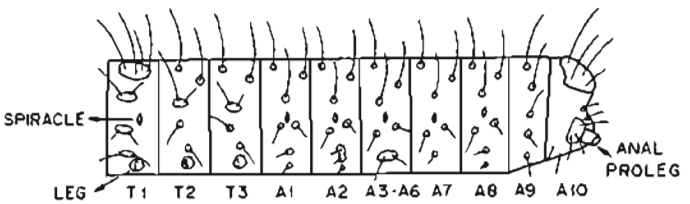

Fig. 4. Chaetotaxy of first instar larva of *Sea sophronia*.

lies (Burseraceae, Guttiferae, and Caryocaraceae) (Jenkins, 1990; Freitas and Oliveira, 1992; personal observations).

The immatures of *Cybdelis* combine features of other genera in several tribes of the subfamily Eurytelinae. Most interesting is the fact that the larvae, like those of *Sea* (Otero, 1994), do not build frass chains; almost all genera of Eurytelinae including Euphorbiaceae-feeding *Sallya* and solitary larvae of *Eunica* construct and rest on frass chains in early instars (Van Son, 1979; Jenkins, 1990; Freitas and Oliveira, 1992). Frass chains are considered to be a safe refuge against walking predators, and may be especially advantageous on plants with extrafloral nectaries and foraging ants (Freitas and Oliveira, 1996). This behavior is also absent, however, in larvae of *Biblis hyperia* and *Dynamine mylitta* feeding on *Tragia* in the Serra do Japi. This characteristic thus may be related with some trait of this host plant, but frass chains were recorded in larvae of the Paleotropical genera *Byblia* and *Eurytela*, both feeding on African species of *Tragia* (Van

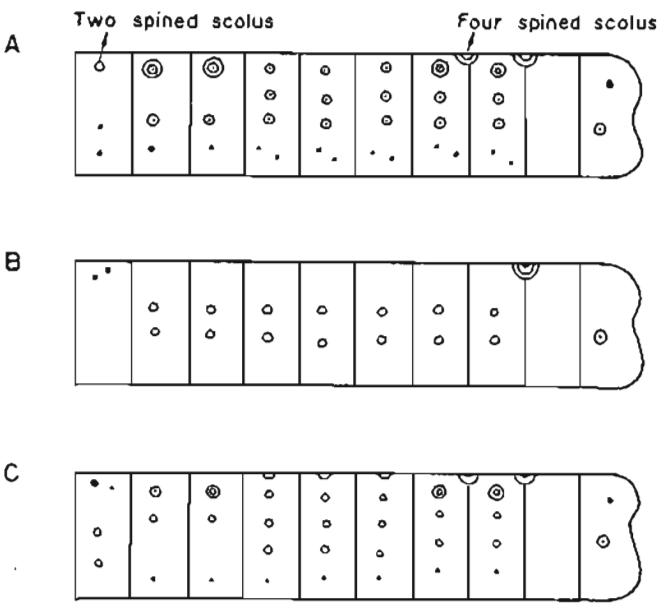

Fig. 5. Distribution of scoli in fifth instar larvae of *Eunica* species (codes same as in Fig. 2): A) *Eunica bechina*. B) *E. monima*. C) *E. tatila*.

Son, 1979). In *Dynamine*, other reasons might exist for the absence of this behavior, including the habit of several species of feeding inside flowers of Euphorbiaceae vines in the genus *Dalechampia*.

The long setae of first instar larvae are atypical in the Epicaliini, being found only in *Biblis*, *Mestra*, *Eurytela*, *Byblia* and *Dynamine*, all using species of *Tragia* as larval host plant (except species of *Dynamine* that feed on *Dalechampia* flowers) (Van Son, 1979, and pers. observ.). All these genera represent primitive lineages of Eurytelinae (Jenkins and Freitas, in prep.); all remaining Eurytelinae have very short setae in first instar larvae, with sclerotized insertions (Freitas and Oliveira, 1992 and unpublished results), except the genus *Sea* (Fig. 4). Larvae of *Cybdelis* and *Sea* have long setae with sclerotized insertions, joining features of two different lineages of Eurytelinae.

Last instar larvae have very short body scoli, as in the Catagrammini. Although this is rare in the Epicaliini, the length of the body scoli (and head scoli also) appears to be variable in *Eunica* (Fig. 5), with reduction occurring in several species. *E. bechina* (Hewitson, 1852) (Fig. 1P-R, Fig. 5A) and *E. tatila* (Herrich-Schäffer, 1855) (Fig. 5C) have normal long scoli like *E. mygdonia* (Godart, 1824) (see Jenkins, 1990), while *E. monima* (Stoll, 1782) (Fig. 5B) has strongly reduced scoli both on the body and head capsule, with the subdorsal series of body scoli completely lacking. Larvae of *Sea sophronia* are very different from those of *Cybdelis phaesyla* in color and form, bearing well developed body scoli and short horns on the head capsule (Fig. 1N; Otero, 1994). The differences in the last instar larvae of *Cybdelis* and *Sea* might be sufficient to maintain the two genera separate.

The pupa of *Cybdelis* has the general shape of Epicaliini and especially Catagrammini pupae, very similar to those of *Eunica*, *Sallya*, *Myscelia*, and *Diaethria*, but very different from the pupae of the other genera feeding on *Tragia*. The pupa of *Sea sophronia* (Fig. 1O; Otero, 1994) also is very different from that of *Cybdelis*

TABLE 1. Comparison of characters of juvenile Eurytelinae.

Tribe/species	Egg	Body setae of 1st instar larva	Body scoli of 5th instar larva	Head scoli,5th instar larva	Pupa	Host plant
Biblidini	single, pilose corion, small keels	long, with sclerotized insertions	long and branched	long, ca. 3x head height	lateral shields	*Tragia* (Euphorbiaceae)
Eurytelini	single, pilose corion, small keels	long, with sclerotized insertions	long and branched	long, 2 to 2.5x head height	lateral shields	*Tragia* (Euphorbiaceae)
Dynamine	single, smooth	long, without sclerotized insertions	branched with spines globose at the tip	absent	small abdominal keel	*Dalechampia* and *Tragia* (Euphorbiaceae)
Epicaliini	single or grouped, smooth, small, large or no keels	short, with sclerotized insertions	long and branched	variable, 0.5 to 2.5x head height	smooth, some have foliose ocular caps	Euphorbiaceae, Rutaceae(?), Burseraceae, Caryocaraceae
Catagrammini	single, smooth, large keels epecially in egg apex	short, with sclerotized insertions	several species with extreme reduction in size	long, 2.5 to 4x head height	smooth, some projections	Sapindaceae
Sea sophronia	grouped, smooth, large keels	long, with sclerotized insertions	long and branched	short, 0.5x head height	abdominal and thoracic keels	*Plukenetia* (Euphorbiaceae)
Cybdelis mnasylus	single, smooth, large keels	long, with sclerotized insertions	short, one long dorsal on 8A, two lateral on 10A	long, about 2x head height	smooth, small ocular caps	*Tragia* (Euphorbiaceae)
Cybdelis phaesyla	single, smooth, large keels	long, with sclerotized insertions	short, one long dorsal on 8A, two lateral on 10A	long, about 2x head height	smooth, small ocular caps	*Tragia* (Euphorbiaceae)

and other Eunicina, resembling *Pyrrhogyra* (Fig. 1H-J, L-M; DeVries, 1987:147). The egg of *Cybdelis* follows the pattern of other Epicaliini and of *Dynamine*, although more rounded than in *Eunica* and *Sea* and with transverse ridges only visible on the keels as in *Sea*. The eggs of *Biblis*, *Mestra*, *Byblia* and *Eurytela* are rounded with smooth longitudinal ridges and a conspicuous pilosity on the chorion (Van Son, 1979; and pers. observ.).

Even though the superficial resemblance of the first instar larva of *Cybdelis* with other *Tragia*-feeding Eurytelinae could be related with some feature of the host plant, the genus *Cybdelis* seems to represents a link between primitive genera in the tribes Biblidini and Eurytelini, and the advanced Epicaliini and Catagrammini. Additional work on Eurytelinae juveniles could help in the understanding of evolution in this subfamily. Unsolved questions include the position of *Dynamine* and the relationships among the various other lineages within the subfamily. While the mixture of characters from all these groups in *Cybdelis* helps to affirm the unity of these lineages, it does not contribute to their resolution (Table 1).

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