

Morphology and evolution of larval outgrowths of Tingidae (Insecta, Heteroptera), with description of new larvae

Éric GUILBERT

Muséum national d'Histoire naturelle, Département Systématique et Évolution,
FRE 2695 CNRS, bâtiment d'Entomologie, case postale 50,
45 rue Buffon, F-75231 Paris cedex 05 (France)
guilbert@mnhn.fr

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ABSTRACT

In the frame of the study of the evolution of Tingidae (Heteroptera), the morphological structure of fifth instars of 13 species is analysed here, through their description, namely *Amblystira peltogyne*, *Aristobyrza uaupenensis*, *Atheas insignis*, *Corythauma ayyari*, *Corythucha mcelfreshi*, *Dictyla rasilis*, *Idiocysta dryadis*, *Kapiriella maynei*, *Leptopharsa gibbicarina*, *Orotingis eueides*, *Urenthius vepris*, *Phatnoma marmorata*, *Eocader vergrandis*. Larvae exhibit outgrowths on the dorsum, which are proper characters. A description and classification of the wide range of outgrowth shapes separated in two main categories is provided. These outgrowths are hypothesized as apomorphic in the framework of the evolution of Tingidae, and an evolutionary scenario of outgrowth morphology is attempted. Species with larvae without outgrowth are more plesiomorphic, and those with outgrowths evolved from the former. Their outgrowths, first simple, became complex during the evolution.

KEY WORDS

Insecta,
Heteroptera,
Tingidae,
evolution,
larvae,
morphology,
tubercles.

RÉSUMÉ

Morphologie et évolution des excroissances larvaires de Tingidae (Insecta, Heteroptera), avec description de nouvelles larves.

Dans le cadre de l'étude de l'évolution des Tingidae (Insecta, Heteroptera), la morphologie des larves de cinquième stade de 13 espèces est analysée, au travers de leur description, à savoir *Amblystira peltogyne*, *Aristobyrza uaupenensis*, *Atheas insignis*, *Corythauma ayyari*, *Corythucha mcelfreshi*, *Dictyla rasilis*, *Idiocysta dryadis*, *Kapiriella maynei*, *Leptopharsa gibbicarina*, *Orotingis eueides*, *Urenthius vepris*, *Phatnoma marmorata*, *Eocader vergrandis*. Les larves portent

MOTS CLÉS

Insecta,
Heteroptera,
Tingidae,
évolution,
larves,
morphologie,
tubercules.

des excroissances sur la face dorsale, caractères qui leur sont propres. Une description et une classification de la disparité de ces excroissances, séparées en deux principales catégories, sont proposées. Ces excroissances sont supposées nouvelles dans le cadre de l'évolution des Tingidae et un scénario évolutif de la morphologie des excroissances est proposé. Les espèces avec des larves sans excroissances sont plus plésiomorphiques et celles avec excroissances ont évolué à partir de ces dernières. Ces excroissances, d'abord simples, sont devenues complexes à travers l'évolution.

INTRODUCTION

Lace-bugs (Heteroptera, Cimicomorpha, Tingidae) are tiny sap-sucker insects characterized in part by their lace-like body structures. They exhibit on the pronotum and the hemelytra morphological traits of very diverse shapes, from small and simple to exaggerated and complex (Guilbert 2001). These characters are restricted to the adults. The larvae exhibit also proper traits, lost by the adults. These traits are outgrowths distributed on the dorsum, also of very diverse shapes (Lee 1969; Livingstone 1978; Péricart 1983; Scholze 1992). There are larvae without any outgrowths to larvae with many developed outgrowths.

Livingstone (1978), followed by Péricart (1983) proposed three categories of outgrowths based on histological studies of four species. He distinguishes three categories of outgrowths: 1) spines of different shapes as processes of the epicuticle; 2) tubular processes as development of the entire cuticle; and 3) tubercles (scoli) as evaginations of the entire integument. Scholze (1992), on the basis of a study on 17 palearctic species, proposed two categories of outgrowths: 1) "first order excrescences", that are evaginations of the entire integument corresponding to the third category defined by Livingstone; and 2) "second order structures", that are cuticular processes corres-

ponding to the first and second categories defined by Livingstone. The first and second categories of Livingstone are based on the shape and size of the processes, while Scholze (1992) considered their morphology. The evagination of the integument have a tracheal cavity, while the cuticular processes have a tubulus inside connected to the surface by a pore. According to Scholze, these cuticular processes are not connected to the subcuticular space, as stated by Livingstone. He also considered that some structures were wrongly included in the second category by Livingstone. These are small evaginations of the integument, having the same size than cuticular processes, but that have a tracheal cavity instead of a tubulus. Thus, they are part of Scholze's first category.

Larvae were never considered in Tingidae relationships, except by Lee (1969) and Guilbert (2004a). Lee described the larvae morphology in 24 species and proposed the first phylogenetic hypothesis of East Asian Tingidae relationships, based on larval characters of fifth instar. In Lee's opinion, the larvae acquired tubercles during evolution. Lee (1969) did not take into account the different shapes of tubercles among species, but the lack of tubercles was hypothesized as plesiomorphic. In recent phylogenetic studies of Tingidae (Guilbert 2001, 2004a), the lack of pronotal and hemelytral expansions in adults, as well as the lack of outgrowths in larvae, were also

hypothesized as plesiomorphic. Through these studies, the aim of this paper is to extend Lee's study to a broader sample of species and to a wider range of characters including the diversity of shapes of larval outgrowths of fifth instar. Larval traits and their evolution will be considered through 13 fifth stage larvae described for the first time.

ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris;
NMNH	National Museum of Natural History, Washington D.C.;
Bishop Museum	Bernice Bishop Museum, Honolulu.

MATERIAL AND METHOD

Fifth instars of 13 species, representing the main different shapes encountered in Tingidae, are described and all were analysed by Scan Electronic Microscope. The specimens stored in alcohol, were washed with potash, 10% sonicated, dried, mounted on aluminium stubs, gold-coated (during 60") and examined under a JEOL SEM.

Despite the histological/ultrastructural studies of Livingstone (1978) and Scholze (1992), no precise terminology among the wide range employed (see Livingstone 1978: table 1) was defined to describe these outgrowths. Following Scholze's study (1992), two categories are considered in this study: 1) evagination of the entire integument corresponding to the first category of Livingstone, and the third category of Livingstone, was called tubercles or scoli by Livingstone, and first order excrescences by Scholtze. Cephalic tubercles of adults, usually called spines in descriptions, are morphologically similar to tubercles; and 2) cuticular processes corresponding to the second categories of Scholze, and the first and second one of Livingstone, were called spines or processes by Livingstone, and second order structures by Scholze.

Thus, for a sake of clarity, the outgrowths of the first category will be called tubercles below, and the one of the second category will be called pro-

jections. The term "process" used by Livingstone is imprecise, while "spine" refers rather to a particular shape than to the structure itself. "Projection" refers to the architecture of the cuticular process, as the function of this outgrowth remains unknown.

All measurements are in mm.

DESCRIPTIONS OF LARVAE

Family TINGIDAE Laporte, 1833
Subfamily TINGINAE Laporte, 1833
Tribe TINGINI Laporte, 1833

Amblystira peltogyne Drake & Hambleton, 1935
(Figs 1; 2)

MATERIAL EXAMINED. — **Brazil.** Espirito Santo state, Res. de Linhares, CVRD (Companhia Vale do Rio Doce), 40 km NNE Linhares, xerophytic semi-deciduous forest, 19°09'47.1"S, 40°01'16.6"W (Sta1), 15.X.1999, É. Guilbert rec., 5 fifth instars (MNHN); 36 km NNE Linhares, semi-deciduous forest (selective extraction), fragment "Mun. de Sooretama", 19°11'20.2"S, 40°06'54.3"W, 17.X.1999, É. Guilbert rec., 5 fifth instars (MNHN).

DESCRIPTION

Body brown fuscous to black, exuvial suture yellowish; legs and antennae whitish except the half apical part of the last antennal segment. No cuticular projection on the body surface, except at base of tubercles; no pilosity on the body surface. Body length, 1.80; width, 0.83.

Head armed with five tubercles; a frontal pair of short, straight tubercles, rounded at the apex and ended by several setae; a median tubercle and an occipital pair of tubercles, curved forwards, long and slender, ended also by several setae at the apex. Antennae long and slender, with some scarce long hairs; antennal segment measurements: I, 0.07; II, 0.07; III, 0.67; IV, 0.5.

Pronotum glabrous, without any tubercle.

Mesonotum with a pair of long, wide, globular tubercles at the middle, the tubercles not ramificate, but ended by a bunch of setae at the apex; the hemelytral surface and margins without tubercle.

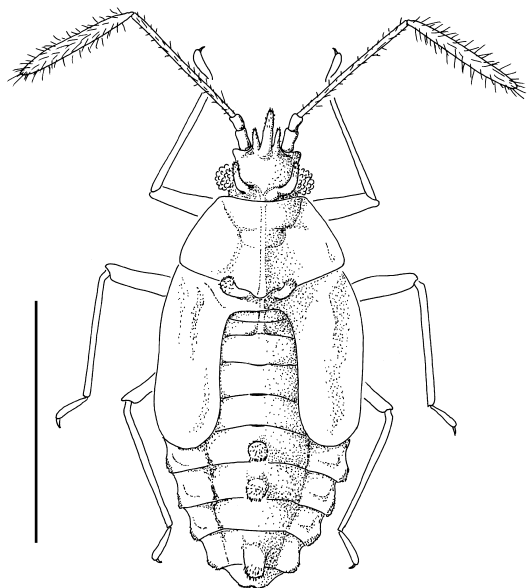


FIG. 1. — *Amblystira peltogyne* Drake & Hambleton, 1935, fifth larvae habitus. Scale bar: 1 mm.

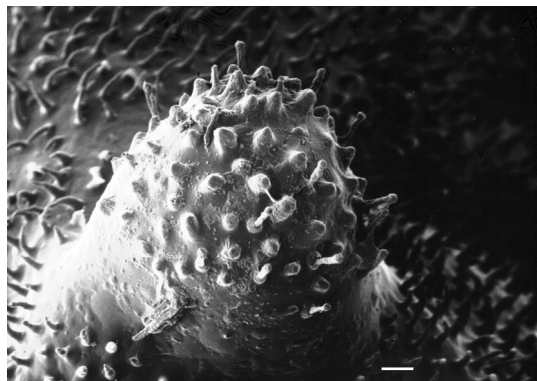


FIG. 2. — *Amblystira peltogyne* Drake & Hambleton, 1935, median abdominal tubercle. Scale bar: 10 μ m.

Abdominal terga without tubercle on the margins, but the posterior part of the margins slightly swollen and with setae. First abdominal tergum with the middle part slightly swollen; second, fifth, sixth and eighth terga with a median short, wide, globular tubercle ended by a bunch of setae at the apex.

Tubercles short, wide, bulbous or globular. They are covered at the apex by numerous small

“bulbes” ended by a pestle-like seta, and at the base by tubular projections. Maximal tubercle length: 0.1 mm.

REMARKS

This is the only known larva of the genus *Amblystira* Stål, 1873. The larva resembles that of *Kapiriella maynei* (Schouteden, 1919) by the globular median tubercles on abdominal segments.

Aristobyrza uaupenensis Carvalho & Costa, 1922 (Fig. 3)

MATERIAL EXAMINED. — **Brazil.** Amazonas Hwy ZF 2, km 19.5, c. 60 km N Manaus, 02°30'S, 60°15'W, 18.IV.1979, Terra firme, canopy fogging, trs#10 tray#707, Adis, Erwin & Montgomery rec., 1 fifth instar (NMNH).

DESCRIPTION

Body yellowish with pale brown spots on hemelytra, pronotum and hind tarsi; body wide, round, covered with long hairs, hairs longer on the margins than on the rest of the dorsum. Body length, 2.5; width, 1.77.

Head wide and short, armed with five tubercles, tubercles long, slender, spiny, erected, covered with small hairs, antenniferous process very short, antennae long and slender, covered with long erected hairs; antennal segments measurements: I, 0.37; II, 0.17; III, 1.00; IV, 0.57.

Pronotum wide, flat, with margins extending laterally on each side of the head, without tubercles nor projections.

Mesonotum wide, flat, abruptly enlarged at base, without tubercles nor projections.

Metanotum with two very short swollen median spots just below the mesotum margin.

Abdominal segments wide, the margins smooth, without tubercles; first segment with two short swollen median spots, but not tubercles. Abdominal scent gland orifices almost invisible.

REMARKS

The larva of *A. uaupenensis* is the only known of the genus. It is similar in appearance to *Nobarnus* spp. and *Orotingis euiedes* Drake, 1960 larvae by

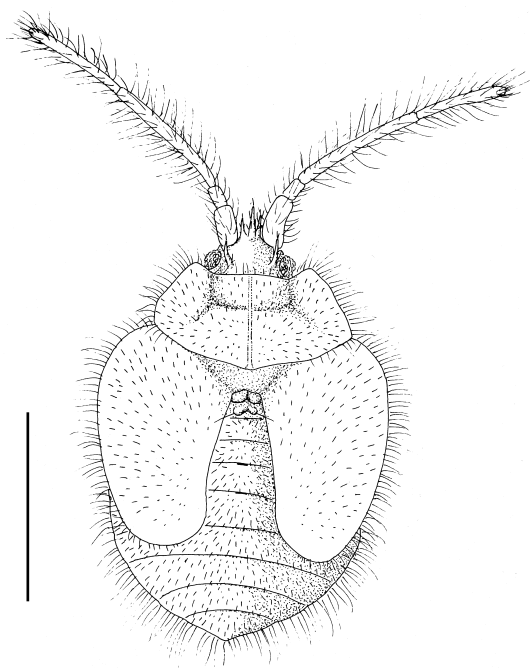


FIG. 3. — *Aristobyrsa uaupensis* Carvalho & Costa, 1922, fifth larvae habitus. Scale bar: 1 mm.

the wide body shape and the absence of tubercles. However, it is easily distinguishable by the hairy margins and dorsum.

Atheas insignis Heidmann, 1909
(Fig. 4)

MATERIAL EXAMINED. — USA. Florida, Volusia Co., De Leon springs, 14.VII.1989, J. Beckwith rec., breeding on *Aeschynomene viscidula* Michaux, 1803, 1 fifth instar (NMNH).

DESCRIPTION

Body uniformly yellowish; tips of last antennal segment and hind tarsi brown; body narrow, glabrous and rugose. Body length, 1.67; width, 0.73. Head wide and flattened, clypeus prominent, without tubercles; antenniferous processes large and spiny; antennae stout and moderately long; antennal segment measurements: I, 0.17; II, 0.07; III, 0.30; IV, 0.23.

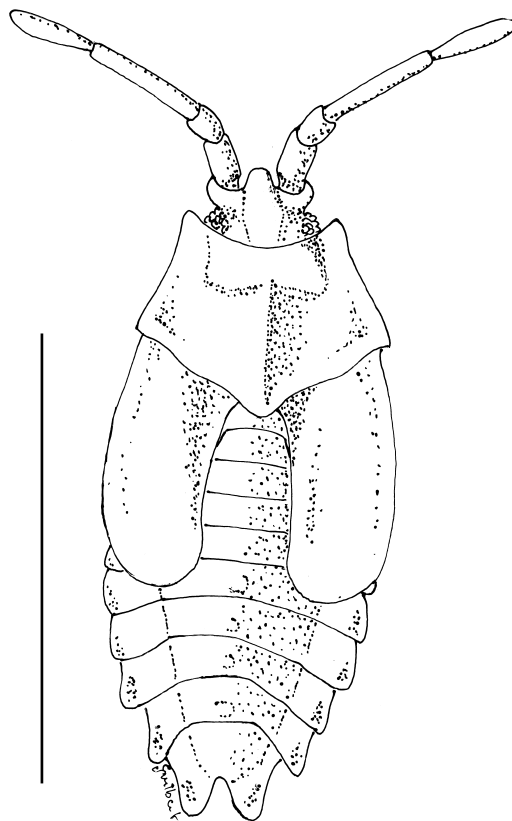


FIG. 4. — *Atheas insignis* Heidmann, 1909, fifth larvae habitus. Scale bar: 1 mm.

Pronotum flat, trapezoidal, without tubercles nor projections; lateral margins slightly extending forwards on each side of the head; posterior margin with a small process emerging. Mesonotum flat and narrow, without tubercles nor projections.

Abdominal segments with posterior part of margins enlarged posteriorly, progressively larger from first to last segments; middle of segment slightly swollen, however not forming tubercles.

REMARKS

This is the only species of the genus which larva is known. It is easily distinguishable from other species by the produced posterior part of the abdominal margins.

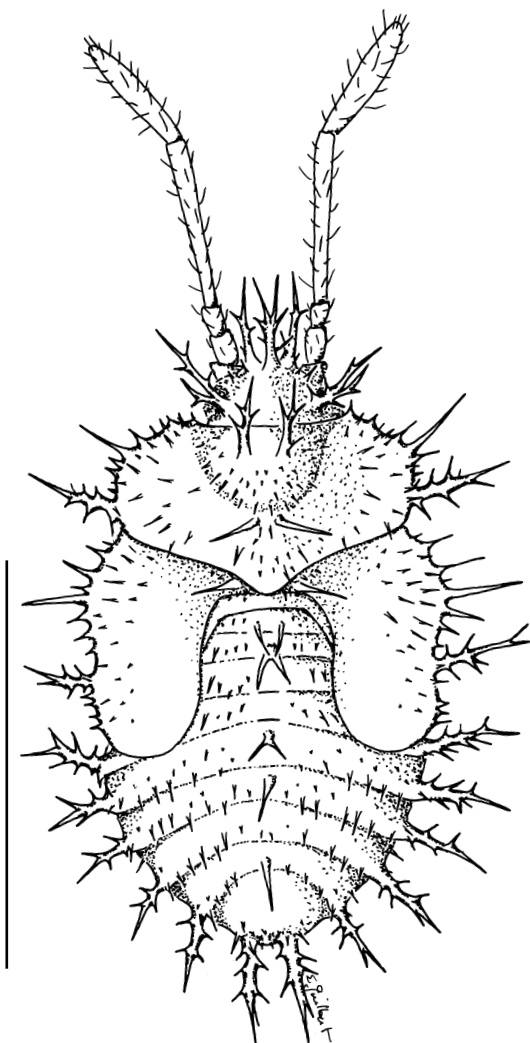


FIG. 5. — *Corythauma ayyari* (Drake, 1933), fifth larvae habitus. Scale bar: 1 mm.

Corythauma ayyari (Drake, 1933)
(Figs 5; 6)

MATERIAL EXAMINED. — **Thailand.** Bangkok, 12 m, infesting *Jasminum* spp., 25.IV.1958, T. C. Maa rec., 12 fifth instars (Bishop Museum).

DESCRIPTION

Body yellowish to clear brown. Body length, 1.60; width, 1.13.



FIG. 6. — *Corythauma ayyari* (Drake, 1933), marginal abdominal tubercles. Scale bar: 100 μ m.

Head covered with small, tubular projections scarcely distributed; also armed with five cephalic tubercles; tubercles long, slender; frontal tubercles ramificate with a seta at the apex of each ramification and at the top; median and occipital tubercles long, slender, bifurcate and also ramificate, with a seta at the apex of each ramification. Antennae short, slender, pilose, the hairs long and scarce. Antennal segment measurements: I, 0.10; II, 0.03; III, 0.50; IV, 0.40.

Pronotum wide and rounded; the antero-median part swollen and bulbous; the margins armed with a pair of spiny, ramificate tubercles on the top of it; a pair of spiny, ramified tubercles on the postero-median part; the margins armed with two long, spiny, ramificate tubercles on the posterior part, and with two or three small, spiny, simple (not ramificate) tubercles on the anterior

part; the surface covered with small, tubular projections, mostly on the antero-median swollen part.

Mesonotum with a pair of long, simple, spiny tubercles ended by a seta at the apex; hemelytral margins armed with a long, slender, ramificate, spiny tubercle on the posterior part, and three small, simple processes on the anterior part; some scarce, small tubular projections located along the margins.

Abdominal terga armed with a long, slender, spiny, ramificate tubercle on each margin, on the posterior tip. The first abdominal tergum with a small simple, spiny pair of tubercles at the middle, the second and fifth with a single median, spiny tubercles bifurcate at the base; the sixth and eighth with a single, simple median spiny tubercle with two setae at the apex; all the terga partly covered by small tubular projections.

Most of the tubercles on the body except the head and the one on anterior part of the pronotum and the hemelytra are long, spiny, ramificate, with four short, lateral ramifications, all ended with a short, pestle-like seta. Maximal tubercle length: 0.27.

REMARKS

This is the only known larva of the genus *Corythauma* Drake & Poor, 1939. The tubercles of *C. ayyari* are similar to the ones of *Ammianus* spp., *Australotingis frazeni* Hacker, 1927 and *Tingis buddleiae* Drake, 1930. The differences between these species are in the distribution and number of ramifications. Other species have ramified tubercles, however, with shorter ramifications.

Corythucha mcelfreshi Drake, 1921 (Figs 7; 8)

MATERIAL EXAMINED. — Mexico. Durango, El Saltito, 15.IX.1976, 9 fifth instars (MNHN).

DESCRIPTION

Body shiny, brown, with yellowish spots on the hemelytra, middle of meso- and metanotum, at the margins of seventh and eighth abdominal segments. Body length, 1.73; width, 1.17.

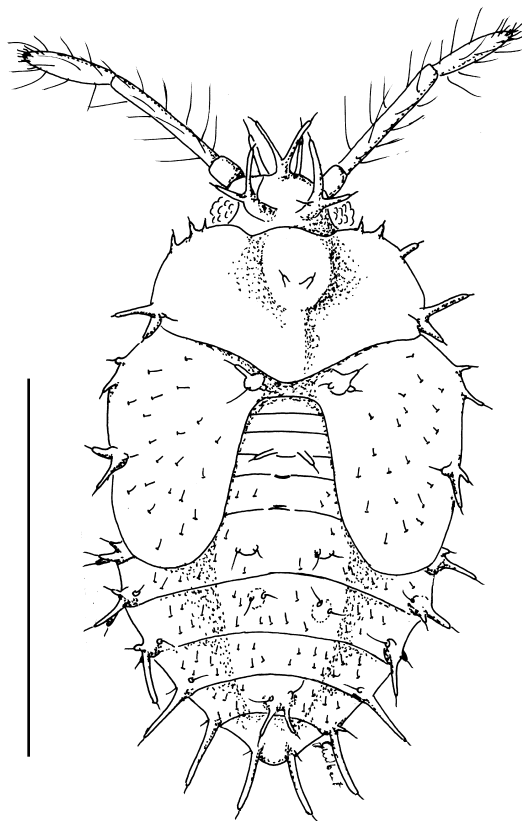


FIG. 7. — *Corythucha mcelfreshi* Drake, 1921, fifth larvae habitus. Scale bar: 1 mm.

Head small, armed with five tubercles, a median one and a frontal and occipital pairs; occipital tubercles ramified at base, made of three long, spiny branches ended by an apical seta, one branch longer than the two other, and a long seta directly inserted at base; frontal tubercles simple, long and spiny; median tubercle trifide at base, made of two long spiny branches laterally directed and a shorter, spiny branch directed forwards; antennae slender and moderately long; antennal segment measurements: I, 0.05; II, 0.03; III, 0.43; IV, 0.23.

Pronotum with margins slightly raised, with three tubercles on the margins; two simple, long and spiny on the anterior part, a longer on the posterior tip, basally ramified, with three unequally long branches and a seta at base; middle



FIG. 8. — *Corythucha mcelfreshi* Drake, 1921, marginal abdominal tubercle. Scale bar: 100 μ m.

of pronotum longitudinally raised as to form a crest, and widely swollen on the third anterior part, bracing the crest; a pair of long simple and spiny tubercles on the swollen part and on the posterior part of the crest.

Mesonotum with a pair of tubercles across the middle; tubercles pedunculate and basally ramified, with four branches, a long one and three short, with two setae inserted at base; margins with three tubercles; two short, simple and spiny one on the anterior part and a ramified one on the posterior part, the tubercle with three branches unequally long and a setae at base; longest tubercle length: 0.30.

Abdominal segment with a tubercle on the margins; tubercles with two branches unequally long and a setae at base, tubercles on the last segment simple and spiny; second, fifth, sixth and eighth abdominal segment with a pair of tubercles across the middle; tubercles simple and spiny on second

segment, with a pedunculate base, one long branch and two setae inserted on fifth and sixth segments, ramified with two long branches and two setae on eighth segment.

REMARKS

The only known *Corythucha* Stål, 1873 larvae described since then is the one of *C. ciliata* (Say, 1832). The two larvae are very similar and difficult to distinguish. The tubercles of both species are characteristic to the genus, and have not been observed on other larvae.

Dictyla rasilis (Drake & Maa, 1955)

(Figs 9; 10)

MATERIAL EXAMINED. — Taiwan. Tzepeng Taitung Hsien, on *Solanum* sp., I-II.1964, T. C. Maa rec., 10 fifth instars (Bishop Museum).

DESCRIPTION

All the body except the tubercles uniformly brown; tubercles white. Body smooth and glabrous. Body length, 1.40; width, 0.87.

Head armed with five tubercles, a median one, a frontal and an occipital pairs; the tubercles simple, straight, long and slender; antennae long and slender; antennal segment measurements: I, 0.07; II, 0.07; III, 0.47; IV missing.

Pronotum with a median pair of tubercles near the anterior margin, with three tubercles at each side on the lateral margins, the most posterior tubercle directed upwards, the other laterally directed.

Mesonotum with a median pair of tubercle; hemelytral margins with three tubercles on each side, the most posterior one directed upwards, the other laterally directed.

Abdominal terga with a tubercle on each margin; second, fifth and eighth terga with a median tubercle.

All the tubercles are long, not spiny but ended by a corolla-like apex, the apical margins reflexed downwards onto the tubercles like petals, with a single short setae in the middle, the sides covered by transversal lines or collarettes of denticles; maximal process length: 0.17.

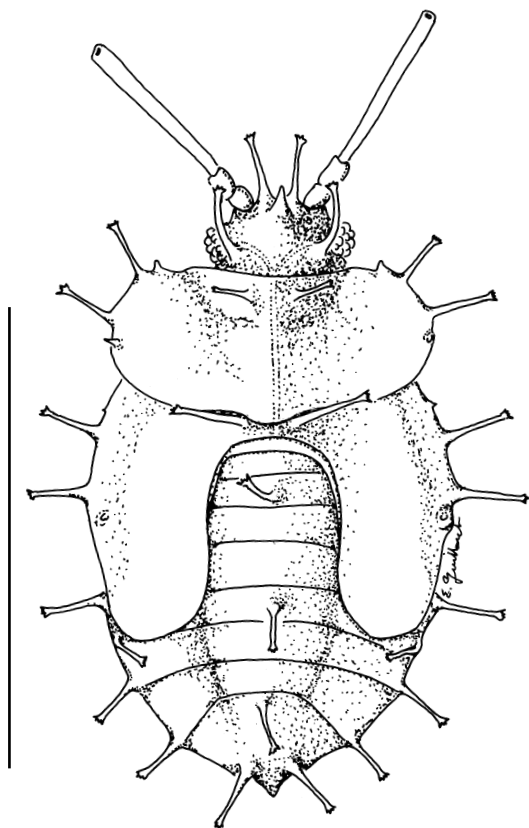


FIG. 9. — *Dictyla rasilis* (Drake & Maa, 1955), fifth larvae habitus. Scale bar: 1 mm.

REMARKS

Larvae of 13 other *Dictyla* Stål, 1874 species are known through the 89 species of the genus. They can be separated into two groups: 1) species without any tubercles on the body, except the head; and 2) species with tubercles. In the latter group, the distribution of the tubercles is always the same. Their length varies among species, but they exhibit the same shape, i.e. straight and ended by a corolla-like apex, however with some differences. The coloration of the larvae and the slight differences of the tubercles allow to distinguish the species. Other genera such as *Cochlochila* Stål, 1873 and *Naochila* Drake, 1957 have larvae that exhibit the same corolla-like apex than *Dictyla*. The larvae are very similar, however, the adults have different characters that are easily distinguishable.

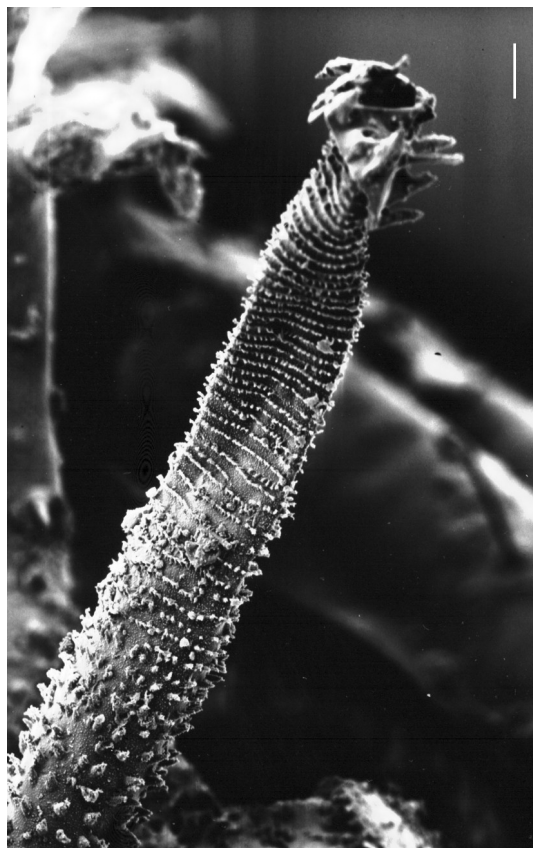


FIG. 10. — *Dictyla rasilis* (Drake & Maa, 1955), marginal abdominal tubercle. Scale bar: 10 μ m.

Idiocysta dryadis Drake & Poor, 1943 (Figs 11; 12)

MATERIAL EXAMINED. — Fiji. Viti Levu I, Foster's peak, 10 km N of Suva, 110 m, 4.IX.1981, W. C. Gagne rec., 3 fifth instars (Bishop Museum).

DESCRIPTION

All the body yellowish, covered with tiny projections star-like all over the dorsum. Body length, 1.5; width, 0.77.

Head armed with a frontal pair and a median short tubercles, an occipital pair of slender tubercles longer than the latter. Antennae long and slender, covered with short hairs; antennal segment measurements: I, 0.05; II, 0.05; III, 0.37; IV, 0.30.

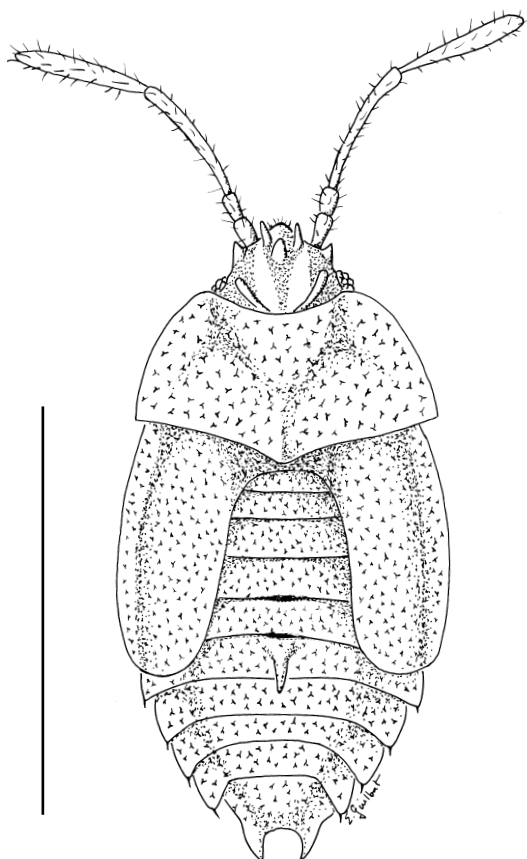


FIG. 11. — *Idiocysta dryadis* Drake & Poor, 1943, fifth larvae habitus. Scale bar: 1 mm.

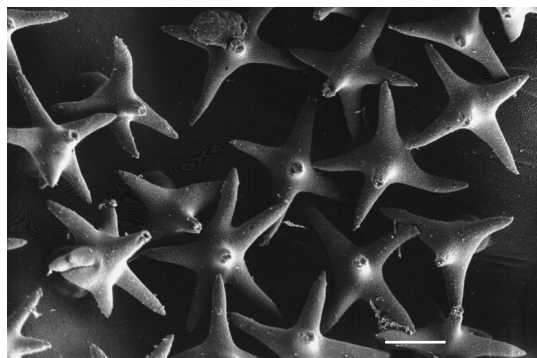


FIG. 12. — *Idiocysta dryadis* Drake & Poor, 1943, projections on the abdomen. Scale bar: 10 μ m.

Pronotum and hemelytra without any tubercle. Abdomen without any median tubercle except on the fifth tergum; tubercle simple, short and slender, ended by a small seta. Abdominal margins with a tiny posterior tubercle ended with small setae; short, stout tubercle on ninth tergum margins longer than the other, and with some setae all along.

Projections star-like, with four to five spiny lateral tips, and a central one directed upwards.

REMARKS

This is the only known larva of the genus. The presence of a single median tubercle on the fifth abdominal tergum is characteristic to the species. All other larvae have different tubercle distribution.

Kapiriella maynei (Schouteden, 1919) (Figs 13-15)

MATERIAL EXAMINED. — **Cameroon.** Dschang, III.1954, 18 fifth instars (MNHN).

DESCRIPTION

Body entirely brown, covered by some short hairs scarcely distributed, without projections. Body length, 1.73; width, 0.87.

Head glabrous, armed with a frontal pair of short and slender tubercles, an occipital pair and a median long, slender and erected tubercle. Antennae long, slender, covered with long erected hairs; antennal segment measurements: I, 0.17; II, 0.10; III, 0.67; IV, 0.40.

Pronotum with a short and small median keel on the posterior part, ended posteriorly by a sharp tip; a pair of median, stout, short, bulbous tubercles with several setae at the apex; a short, stout, spiny tubercle on the posterior part of margins.

Mesonotum with a median pair of stout, bulbous tubercles bearing several setae at the apex; hemelytral margins with a short, stout, spiny tubercle at each side at the middle length.

Abdominal terga margins with a stout, short tubercle at each side; second, fifth, sixth and eighth terga with a stout, bulbous tubercle on the middle.

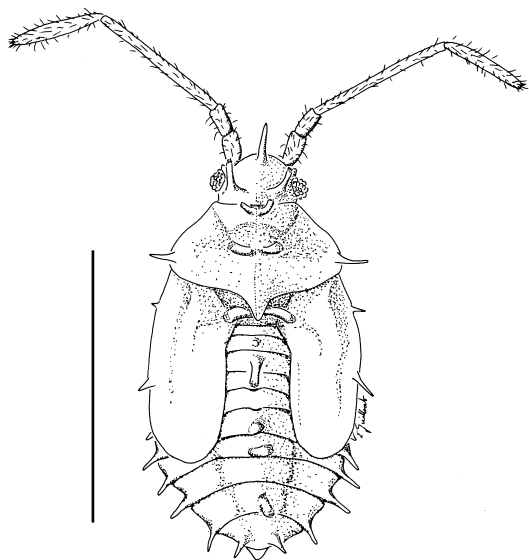


FIG. 13. — *Kapirella maynei* (Schouteden, 1919), fifth larvae habitus. Scale bar: 1 mm.



FIG. 14. — *Kapirella maynei* (Schouteden, 1919), marginal abdominal tubercles on. Scale bar: 10 μ m.

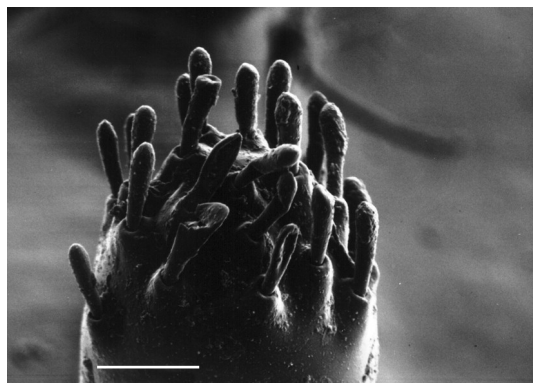


FIG. 15. — *Kapirella maynei* (Schouteden, 1919), detail of median abdominal tubercles on. Scale bar: 10 μ m.

The marginal tubercles are short and stout. They bear some long and fine setae on the side and two to three setae at the apex. The median tubercles of the abdominal terga are longer, stouter, bulbous, with many short, pestle-like setae and some one or two tubular setae at the apex. The median pronotal tubercles are shorter than the median abdominal; maximal tubercle length: 0.13.

REMARKS

This is the only known larva of the genus. It is similar to *Amblystira peltogyne* in the shape of the median tubercles on abdominal terga.

Leptopharsa gibbicarina Froeschner, 1976 (Figs 16; 17)

MATERIAL EXAMINED. — **Colombia.** San Onofre, 2.V.1962, Mariau rec., 5 fifth instars (MNHN).

DESCRIPTION

Body entirely brown, glabrous, smooth. Body length, 1.27; width, 0.70.

Head armed with a pair of occipital tubercles and a median one, all long, slender and erected. Antennae long and slender; antennal segment measurements: I, 0.17; II, 0.13; III, 0.73; IV missing.

Pronotum with a median, longitudinal, small keel, with a pair of tubercles in the middle across

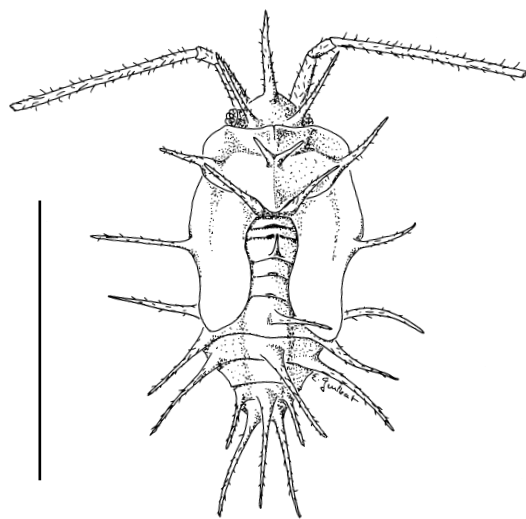


FIG. 16. — *Leptopharsa gibbicarina* Froeschner, 1976, fifth larvae habitus. Scale bar: 1 mm.

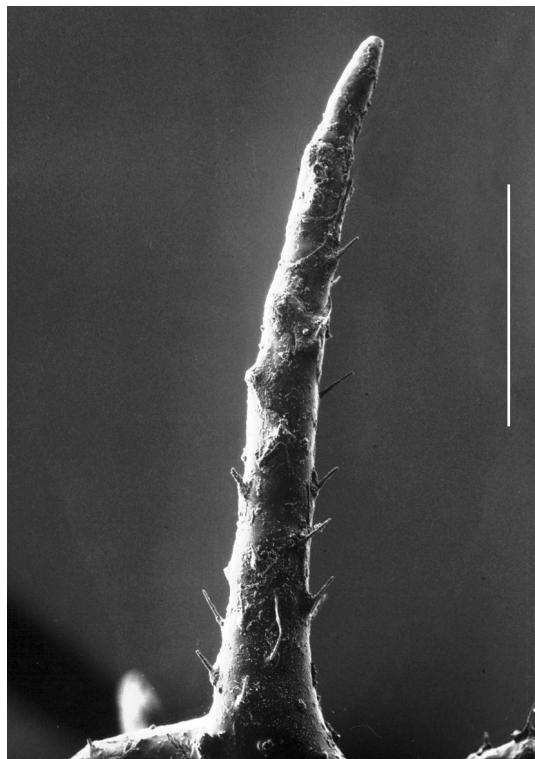


FIG. 17. — *Leptopharsa gibbicarina* Froeschner, 1976, marginal abdominal tubercles. Scale bar: 100 mm.

the keel, and a tubercle on each posterior part of the margins.

Mesonotum with a pair of tubercles in the middle; hemelytral margins with two tubercles on each side.

Abdominal terga swollen on the middle part, with a marginal tubercle on each side; second, fifth, sixth and eighth terga with a median tubercle.

Tubercles long, simple, spiny and erected, with short setae all along; maximal tubercle length: 0.43.

REMARKS

This is the only known larva of the genus. The tubercles are similar to the one of *Stephanitis* spp. and *Hyalochiton* spp., they differ in the number and the length of the setae along the tubercles.

Orotingis eueides Drake, 1960

(Fig. 18)

MATERIAL EXAMINED. — NE New Guinea. Morobe district, Lake Trist 1600 m, on *Streblis urophyllus* (Moraceae), 21-26.XI.1966, G. A. Samuelson rec., 4 fifth instars (Bishop Museum).

DESCRIPTION

Body shiny, glabrous, wide, uniformly brown; legs and antennae except the third apical part of the last segment clear brown to yellowish. Body length, 1.83; width, 1.73.

Head wide, without tubercles; antenniferous processes spiny; antennae short, pilose; antennal segment measurements: I, 0.07; II, 0.07; III, 0.33; IV, 0.40.

Pronotum very wide, extending forwards beyond the head, without tubercle, the margins finely dentate.

Hemelytra wide, without tubercle, the margins finely dentate and bearing some scarce fine hairs. Abdominal terga wide, greatly swollen in the middle part, without tubercle, margins rounded and slightly dentate.

REMARKS

This is the only known larva of the genus. It resembles *Nobarnus* spp. larvae by the broad

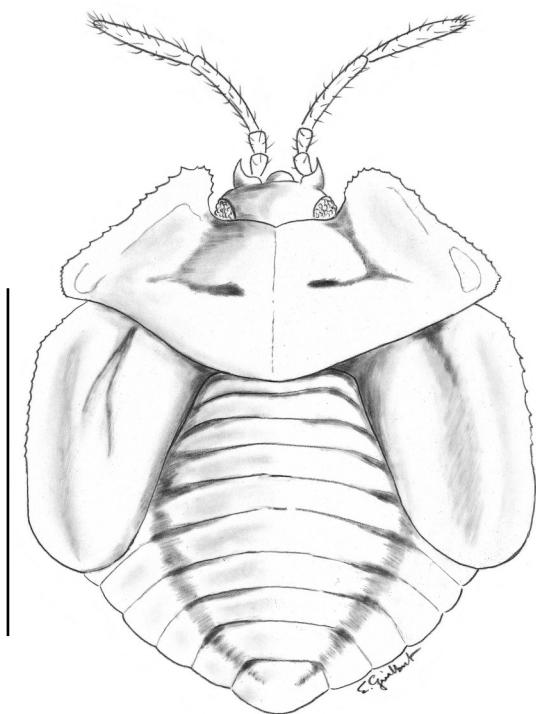


FIG. 18. — *Orotinus eueides* Drake, 1960, fifth larvae habitus. Scale bar: 1 mm.

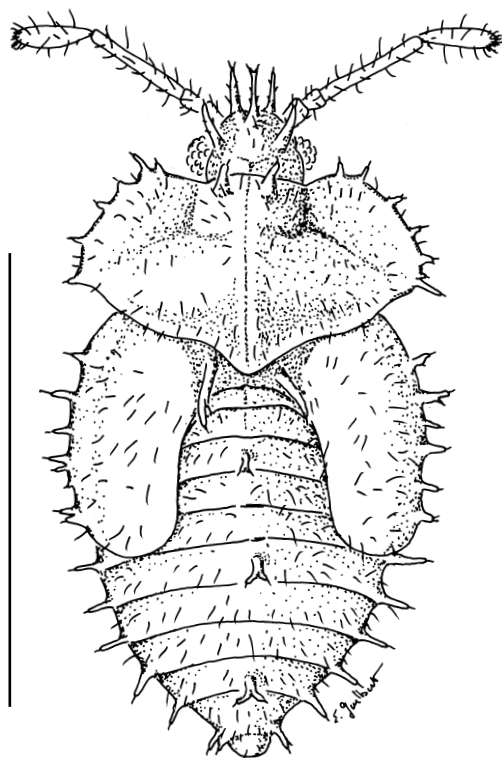


FIG. 19. — *Urenthius vepris* Drake, 1945, fifth larvae habitus. Scale bar: 1 mm.

body. However, it is easily distinguishable by the margins or the paranota which are finely dentate and extending forwards beyond the head.

Urenthius vepris Drake, 1945
(Figs 19-21)

MATERIAL EXAMINED. — Mali. Kigoni, on *Abutilon* sp. (Malvaceae), 6.II.1973, G. Pierrard rec., 27 fifth instars (MNHN).

DESCRIPTION

Body yellowish to brown, with some small spots darker on the pronotum, the hemelytra, and around the tubercles; body covered by small tubular projections. Body length, 1.53; width, 0.93.

Head armed with five tubercles (a pair of occipital, a pair of frontal and a median); the tubercles being almost bifide, with small tubular projec-

tions along, and two setae at the apex. Antennae short, with some scarce, long hairs; antennal segment measurements: I, 0.07; II, 0.07; III, 0.43; IV, 0.17.

Pronotum with the antero-median margin slightly elevated, bearing a pair of bifide tubercles with a seta at the apex; the lateral margins with four small, stout, bifide tubercles, and some other smaller tubercles, not bifide and bearing a seta at the apex.

Mesonotum with a median pair of long tubercles; hemelytral margins with four to five small, bifide tubercles and some other smaller, not bifide tubercles.

Abdominal terga margins with a small, bifide tubercle on each side; second, fifth and eighth tergum with a median, long, bifide tubercle.

The median tubercles are stout, short, bifide, both "branches" are ended by a bulbous seta.



FIG. 20. — *Urenthius vepris* Drake, 1945, marginal abdominal tubercle. Scale bar: 10 μ m.

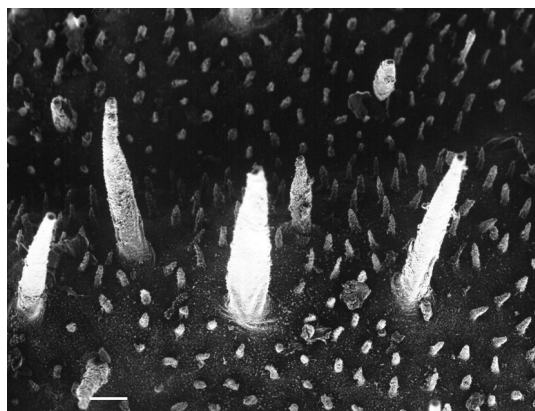


FIG. 21. — *Urenthius vepris* Drake, 1945, projections on the abdomen. Scale bar: 10 μ m.

Lateral tubercles are smaller than the median one, also bifide but somewhat with a single ramification shorter than the principal; both bifurcation

bearing a short bulbous setae; maximal tubercle length: 0.10.

REMARKS

Three other larvae of *Urenthius* species are known: *U. Chobauti* Horváth, 1907, *U. euonymus* Distant, 1909 and *U. Hystricellus* (Richter, 1869). They differ in the shape of the tubercles. *Urenthius chobauti* and *U. vepris* have simple short tubercles; *U. hystricellus* has longer tubercles, with two to three short ramifications; and *U. euonymus* has short bifid tubercles.

Subfamily CANTACADERINAE Stål, 1873
Tribe PHATNOMINI Drake & Davis, 1960

Phatnoma marmorata Champion, 1897
(Fig. 22)

MATERIAL EXAMINED. — **Ecuador.** Napo Res. Ethnica Waorani, 1 km S Onkone gare camp, Trans. Ent., 220 m, 00°39'10"S, 76°26'W, 21.VI.1994, T. L. Erwin *et al.* rec., 4 fifth instars (NMNH).

DESCRIPTION

Body entirely yellowish to brown, dorsum entirely covered with star-like projections. Body length, 2.83; width, 1.57.

Head elongate, armed with seven long, stout tubercles directed forwards, an occipital, a frontal and a jugal pairs and a single clypeal tubercle; antenniferous processes short and spiny. Antennae long and slender, antennal segment measurements: I, 0.07; II, 0.05; III, 0.67; IV, 0.23.

Pronotum with margins slightly raised and extended laterally; with three marginal tubercles on each side, and a single median tubercles at the anterior and posterior margins. Tubercles short and curved, the anterior one directed forwards, the posterior one directed backwards and the middle one raised. The median tubercles shorter than the marginal one.

Mesonotum with a very short tubercle on each margin, curved and directed backwards, and with a very short median tubercle.

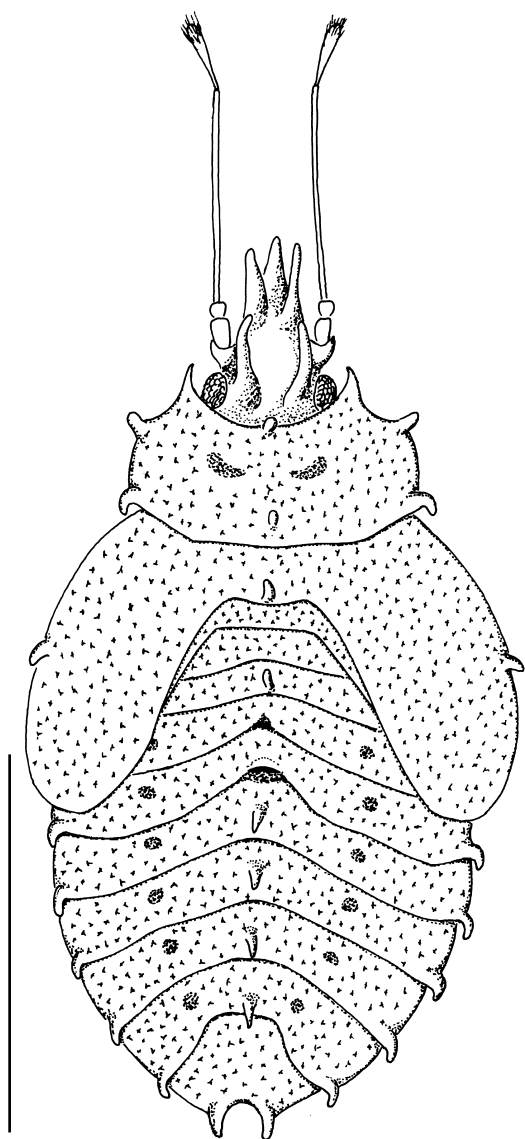


FIG. 22. — *Phatnoma marmorata* Champion, 1897, fifth larvae habitus. Scale bar: 1 mm.

Abdomen with margins slightly raised, each segment with a tubercles on the posterior tip of the margins, tubercles short, curved and directed backwards; second, fifth, sixth, seventh and eighth segments with a tubercle on the median line, the tubercles short and spiny. Scent glands opening on fourth segment with the margins raised as to form almost a very short tubercle.

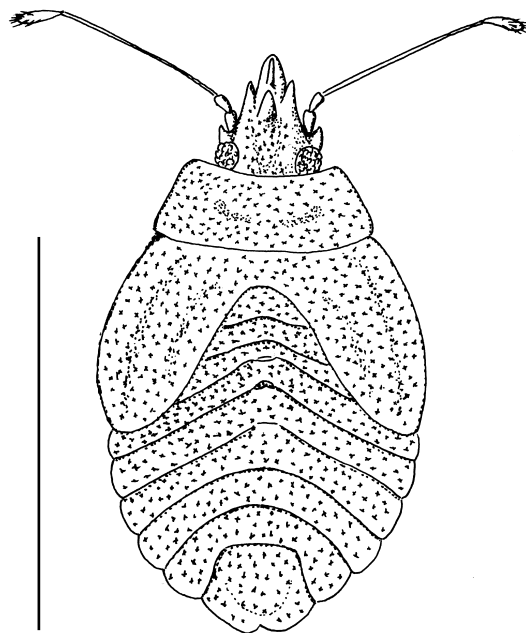


FIG. 23. — *Eocader vergrandis* Drake & Hambleton, 1934, fifth larvae habitus. Scale bar: 1 mm.

REMARKS

Fifth instars of only two species of *Phatnoma* Fieber, 1844 are known, *P. maynei* Schouteden, 1916 and *P. marmorata*. The tubercles of the fifth instar of *P. maynei* are short bulbous protuberances, much shorter than the one of *P. marmorata*. The larva of *P. marmorata* is the only one, among the species in this study, having a median tubercle on the seventh abdominal tergum. This is also the case of some of the other known Cantacaderinae nymphs.

Eocader vergrandis Drake & Hambleton, 1934 (Fig. 23)

MATERIAL EXAMINED. — **Brazil.** Rio de Janeiro, Niteroy, 1.IV.1921, Clima rec., 1 fifth instar (NMNH).

DESCRIPTION

Body yellowish to brown, oval; dorsum covered with star-like projections. Body length, 1.67; width, 1.00.

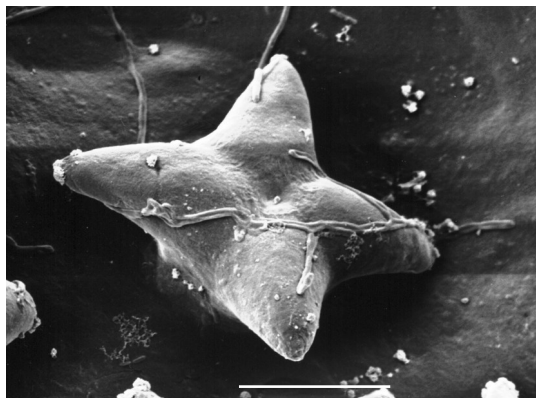


FIG. 24. — *Acalypta musci* (Schrank, 1781), projections on the abdomen. Scale bar: 10 μ m.

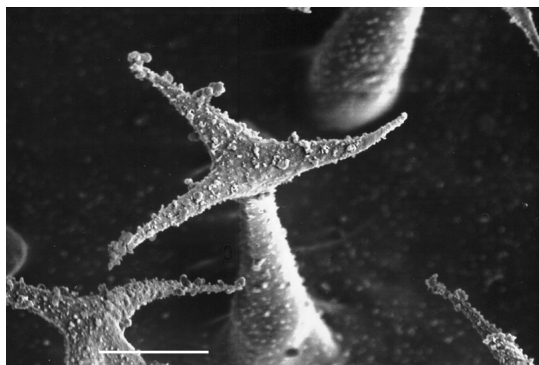


FIG. 25. — *Tingis buddleiae* Drake, 1930, projections on the abdomen. Scale bar: 10 μ m.

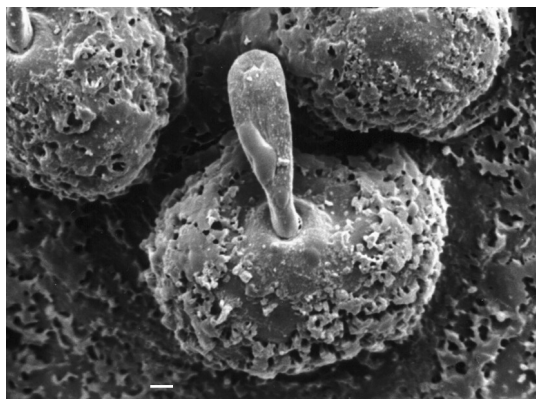


FIG. 26. — *Physatocheila dissimilis* Guilbert, 1997, projections on the abdomen. Scale bar: 10 μ m.

Head elongate, armed with six short and stout tubercles, a clypeal and a supraclypeal one, and a frontal and a jugal pairs; antenniferous processes short and spiny; antennae slender and moderately long; antennal segments measurements: I, 0.05; II, 0.03; III, 0.50; IV, 0.17.

Pro-, meso-, metanotum, and abdominal segments without tubercle; the median part of metanotum and abdominal segments swollen.

REMARKS

Two species of *Eocader* Drake & Hambleton, 1934 are known. The larva of *E. vergrandis* differs from the one of *E. bouclei* (Bruner, 1940) by the absence of small bulbous median tubercles on the sixth, seventh and eighth abdominal terga. Otherwise the two larvae are similar.

DISCUSSION

MORPHOLOGY

As pointed out by Lee (1969), tubercles distribution can be divided into two groups: the cephalic tubercles, which are mostly conserved through adults; and the thoracic and abdominal tubercles, which are always absent in adults. The distribution of cephalic tubercles is the same in the larvae and in the adults. However, some species lost tubercles through larva to adult. The adult of *Idiocysta dryadis* lost occipital tubercles, the adult of *Kapiriella maynei* lost occipital and median tubercles, and the adult of *Corythucha mcelfreshi* lost the five cephalic tubercles. The cephalic tubercles are always simpler in adult when complex in larvae. These observations remind heterochrony phenomenon, which will be discussed below in an evolutionary context.

Thoracic and abdominal tubercles are distributed as follows: a tubercle on each side of the lateral margins of pronotum and a tubercle on each side of the lateral margins of hemelytral pads; one to three additional tubercles on these lateral margins, in front of the first major tubercle; a median pair on the mesonotum and on the metanotum; a pair on the margins of each abdominal tergum; median tubercles, paired or unpaired on the first,

second, fifth, sixth, seventh and eighth abdominal terga. Abdominal and thoracic marginal tubercles have always the same shape. Median tubercles are sometimes different than the marginal one. They are always lost in the adults.

Tubercles have a wide range of different shapes. They can have ramifications, which are ended by a structure usually ampulla-like or spiny. As stated by Scholze (1992), tubercles can also bear projections (second category of Scholze), observed mainly at the base of the tubercles. These projections have various shapes: pestle, spoon, drop, and also spine, depending on species. Setae also are distributed along the tubercles or at the apex. Through their high diversity of shapes, tubercles exhibit general scheme that can be categorized into six states.

- 1) Tubercles short, simple and curved, with or without ampulla at the apex (*P. marmorata*);
- 2) tubercles long, slender and spiny (*L. gibbicarina*, Fig. 17) or stout (median abdominal tubercles in *K. maynei*, Fig. 15), without ramification or peduncle, with or without long setae along the sides;
- 3) tubercles long, slender, without ramifications or setae along the sides but small rows of tiny denticles, and ended by a sort of corolla with a spiny seta in the middle (*D. rasilis*, Fig. 10);
- 4) tubercles ramified, with spiny or bulbous ampulla at the apex of each ramification, or emerging from small peduncles. They are stout, short, bifid at the apex, with pestle-like ampulla at the apex (*U. vepris*, Fig. 20). They are long, slender, spiny, with ramifications in *C. ayyari* (Fig. 6). Each ramification is ended by an ampulla, corolla-like in *C. ayyari*;
- 5) tubercles short, with ramifications bunch-like (*C. mclfreshi*, Fig. 8), made of a short and stout peduncle from where merge four simple spiny branches with a pestle-like ampulla at the apex, and along setae at the base;
- 6) tubercles short, stout, globular with bulbous ampulla along the sides and at the apex on small peduncles (*K. maynei*, Fig. 14), bulbous with a wide base (*A. peltogyne*, Fig. 2). The base of the tubercles in *A. peltogyne* is covered by projections. The ampullas are pestle-like in both species.

The third state is specific to *Dictyla*, *Cochlochila*, *Naochila* species, and shows some variation in the shape of the apex. The fifth state is specific to *Corythucha* species and the shape is almost the same between species. The fourth state is the most prevalent and shows a great variation between species in number, length and distribution of the ramifications.

Projections, when present, are generally distributed all over the dorsum. They do not present any morphological changes during development, and are always lost by the adults. They exhibit also a great diversity of shapes. However, the main shapes were grouped and categorized this way:

- 1) projections tubular (*U. vepris*, Fig. 21). The projections are somewhat spiny in *U. vepris*. These projections have an orifice at the apex and are spread out on the dorsum;
- 2) projections star-like, with three to five tips (*I. dryadis*, Fig. 12). The “stars” are on a short, stout peduncle, and the tips are short and wide on *Acalypta musci* (Schrank, 1781) (Fig. 24). The peduncle is long and slender and the tips are spiny on *Tingis buddleiae* Drake, 1930 (Fig. 25), slender on *I. dryadis* while stouter than the two species above. There is a central tip directed upwards on *I. dryadis*, and ended by an orifice. The projections on *A. musci* have also an orifice at the middle, while they do not have on *T. buddleiae*;
- 3) projections buttons or granules-like are observed on species that are not considered in this study (*Physatocheila dissimilis* Guilbert, 1997; Fig. 26). They do not have orifice.

EVOLUTION

The six categories of tubercles as well as the three types of projections here defined correspond to the major shapes. These categories characterize genera or groups of genera. Variations of shapes within each state would characterize species or groups of species. However, shape of tubercles and projections, presence and number of ramifications, their organization on the main axis would generate many states in each category. For example, the corolla shape of tubercles varies within *Dictyla* and *Cochlochila* species; the bunch shape of tubercles varies within *Corythucha*

species, and star-like projections differ between *Acalypta* Westwood, 1840 species. The phylogenetic study on East Asian Tingidae made by Lee (1969) provided a tree based only on larval characters and their development. It took into account the presence and the absence of tubercles, but not their morphology. Outgrowth main morphology was included in a recent study of the evolution of Tingidae (Guilbert 2004a). These studies concerned different taxa samples, but they show the same trends of evolution: species acquired outgrowths during the evolution and these outgrowths became more complex. According to Lee (1969), Tingidae first acquired unpaired head tubercles, then marginal tubercles on thorax and abdomen, and median tubercles on abdominal terga in several steps, until species having the whole set of tubercles. The same main scheme is observed by Guilbert (2004a), with some minor variations. Species acquired tubercles which became complex during the evolution in three clades independently, and with some reversals at the apex of two clades. Miridae, the sister-group of Tingidae, as well as Vianaidinae, which is basal to all other Tingidae, have larvae without outgrowths on the body. Thus, the presence of tubercles is new for Tingidae, however homoplastic.

In addition to the acquisition of tubercles, their morphology becomes more complex through evolution. The evolutionary sequences are almost the same in Guilbert (2004a) and Lee (1969) studies. In Guilbert's study, tubercles are short, simple and spiny in "intermediate" species (species between basal species without tubercles and apical species with more complex tubercles). This is the case of *I. dryadis* and *U. vepris*. This step is not observed in Lee study. In the next steps species exhibit the different states of tubercles. *Dictyla* spp. including *D. rasilis*, and *Cochlochila* spp. exhibit tubercles ended with a corolla. *Monostira* spp. and *Leptopypha* spp. exhibit small, stout, globular tubercles like did *A. peltogyne* and *K. maynei*. In Lee's study, the tubercles become longer, have setae all along (*Stephanitis*, *Galeatus* and *Uhlerites* spp.), and acquired ramifications later (*Ammianus*, *Lasiacantha* spp., *T. buddleiae*).

In Guilbert's study, tubercles acquired ramifications (*C. ayyari* and *C. mcelfreshi*) before becoming longer and having setae all along (*L. gibbicarina*). Such sequences of tubercle evolution are based on two different small samples of taxa. The evolutionary sequences suggested are general trends, which have to be explored more precisely. Because of irresolution in two apical clades in Guilbert's study, the question of evolutionary sequences still remains to specify, i.e. to know if evolution of shapes is a linear sequence from simple to ramified tubercles passing through the different other states, or if it is a radiation from simple tubercles to several other states independently.

Seidenstücker (1954) considered the presence of tubercles as "primitive", because thoracic and abdominal tubercles are lost by the adults, and cephalic tubercles are reduced in adults. However, in some species adults present thoracic relictual tubercles, namely *Furcilliger* spp. Others have cephalic tubercles not reduced but bifurcate: *Belenus* spp. and *Placotingis merga* Drake, 1960. Such observations suggest heterochony phenomenon. However, the larvae of these species and their phylogenetic position are unknown. If such species have larvae with tubercles that persist at adult stage, it would suggest pedomorphosis. If they do not have tubercles, their presence at adult stage could be apomorphic. Peramorphosis as heterochronic phenomenon was suggested to explain that adults as well as larvae become complex during the evolution (Guilbert 2004a). Moreover, it was also suggested to explain that larvae become more complex during the development by acquiring more tubercles through immature stages in some species (Guilbert 2004b). If peramorphosis is observed in a general context of the evolution of Tingidae, can pedomorphosis occur in the same time in particular taxa?

CONCLUSION

Larvae were little considered in Tingidae systematics, because more difficult to collect than

adults. They were often described but never included in phylogenetic studies, except the two ones mentioned here. Their remarkable morphology should provide phylogenetical informations for a better understanding of Tingidae evolution. Guilbert (2004a) and Lee (1969) studies are a first step in this direction. They show the same general trends of outgrowth evolution, while dealing with different taxa samples. The next step would be to integrate the great variety of shape as characters. However, much more larvae should be considered to define these characters. Moreover, these studies dealt with the last immature stage. The other stages should also be taken into account, particularly to clarify the question of heterochronic phenomenon among Tingidae.

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