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STUDY ON THE PHYLOGENETIC RELATIONSHIPS OF THE HOPLIIDS (COLEOPTERA: SCARABAEOIDEA)

HORTENSIA CARRILLO-RUIZ AND MIGUEL ÁNGEL MORÓN

(HCR) Posgrado en Sistemática, Instituto de Ecología, A. C. Apartado Postal 63. Xalapa, Veracruz 91000, México. (e-mail: carrillo@posgrado.ecologia.edu.mx); (MAM) Departamento de Entomología, Instituto de Ecología, A. C. Apartado Postal 63. Xalapa, Veracruz 91000, México (e-mail: moron_ma@ecología.edu.mx)

Abstract.—Hopliids constitute a diverse group with almost cosmopolitan distribution that, according to some authors, has been placed as a tribe of the Melolonthinae or Rutelinae, as a subfamily of Scarabaeidae, or as an independent family. Results of a phylogenetic analysis based on 52 morphological characters of 36 representative species of four subfamilies and 12 tribes of Scarabaeidae (*sensu lato*), show that the hopliids are an independent, natural group, closely related to some Macrodactylini, and are considered a subfamily of Scarabaeidae.

Resumen.—Los hoplinos constituyen un grupo diverso con distribución casi mundial, que según distintos autores se ha situado en los niveles de tribu en los Melolonthinae o Rutelinae o como una subfamilia de Scarabaeidae o como una familia independiente, que requiere de un estudio sistemático integral. Con ayuda de un análisis filogenético basado en 52 caracteres morfológicos de 36 especies representativas de cuatro subfamilias y 12 tribus de Scarabaeidae (*sensu lato*), se propone una hipótesis que demuestra que los hoplinos son una agrupación natural, independiente, cercanamente relacionada con algunos macrodactilinos y que puede ser considerada como una subfamilia dentro de Scarabaeidae.

Key Words: classification, *Hoplia*, Hopliinae, Hopliini, phylogenetic hypothesis, Scarabaeidae

The superfamily Scarabaeoidea is one of the better studied groups of beetles in the world but also with a long history of changes and proposals about their suprageneric classification. Kohlmann and Morón (2003) compared 59 proposals and amendments of classification developed between 1735 and 2001. At present, three classifications are in general use. The most utilized one in Europe is supported in the proposal of Balthasar (1963) who considered the existence of 18 families. In Mexico and part of Latin America, the scheme of Endrödi (1966) has been applied for the last 30 years that included five families: Trogidae, Passalidae, Lucanidae, Scarabaeidae, and Melolonthidae. In the past in North America, the classification in use followed Janssens (1949) that was based on three families: Lucanidae, Passalidae, and Scarabaeidae, but recently Jameson and Ratcliffe (2002) promoted the use of the proposal of Lawrence and Newton (1995) that included 12 valid families of Scarabaeoidea in North America.

Various authors have maintained the "Hoplines" as an independent assembly of "Ruteline" and "Melolontines" based on the presence of one metatarsal claw in the "Hopliini" as the distinctive character (Mulsant 1842, Reitter 1902, Peringuey 1902, Janssens 1949, Medvedev 1976, Iablokoff-Khnzorian 1977).

Other authors placed the hopliids inside the "Melolonthides" (Lacordaire 1856), "Melolonthini" (Gemminger and Harold 1869) , "Melolonthinae" (Dalla-Torre 1913, Arnett 1973, Morón et al. 1997, Evans 2003), and "Melolonthidae" (Bates 1888, Balthasar 1963, Micó 2001) as a tribe or subfamily, and some authors have placed it as a subfamily of Rutelidae (Burmeister 1844, Mulsant and Rey 1871, Paulian 1959, Paulian and Baraud 1982). The most recent proposal was presented by Lacroix (1998) who considered this assembly an independent group with at the family level, but he did not comment on its relationships with other groups of Scarabaeoidea.

Currently this controversy over placement of the hopliids continues, there is no consensus upon the systematic position of the hopliids. Some authors consider them as a subfamily of Scarabaeidae (*sensu* Janssens 1949), other authors as a subfamily of Melolonthidae (*sensu* Balthasar 1963), some others as the family Hopliidae (*sensu* Lacroix 1998), and finally there are those who consider them as a tribe of Melolonthinae inside Melolonthidae (*sensu* Endrödi 1966). It is important to mention that there has been no phylogenetic work on the intergeneric relationships of this group or with in relationships with other groups of Scarabaeoidea. This is the first study to address the systematics of this group using a phylogenetic analysis based on sets of American, European, and South African species of the genera *Hoplia* Illiger, *Gymnoloma* Burmeister, *Pachycnema* Serville, and *Hoplocnemis* Harold, all representatives of the "in-group," and 24 representative species of 12 tribes of the subfamilies Melolonthinae, Dynastinae, Rutelinae, Cetoniinae, Trichiinae, and Orphninae that constitute the "out-group." The objectives are to confirm if the hopliids are monophyletic; if they are an independent group of the traditional higher taxonomic groups of the Scarabaeoidea; and to determine the possible phylogenetic relationships of the hopliids with other groups of Scarabaeoidea.

Diagnosis.—According to Arnett (1973) the "Hopliini" form a group of small to medium size species (3.5–10 mm), with the body covered with scales and setae in variable density, the metatibiae normally lacking the apical spurs, the metatarsomere without onychia and with one or two claws, and, if two claws, they are unequal in size. The adults of hopliids have been observed feeding on foliage and flowers (Boyer 1940, Morón et al. 1997). Micó (2001) reported that the adults of the Iberian species of *Hoplia* feed mainly of pollen of Gramineae, Rosaceae, Plantaginaceae, Asteraceae, Malvaceae, Umbeliferae, and numerous fruit trees.

Geographic distribution.—In his world catalogue, Dalla-Torre (1912-1913) included 62 genera of hopliids, 46 of these distributed in southern Africa and the remainder in America (1), Eurasia (7), Ceylon (1), India (2), and Madagascar (5). In the revision of the "Hopliidae" of Madagascar, Lacroix (1998) indicated that the world fauna comprised 103 genera and 1199 species, when considering that the subfamily Pachycneminae, endemic to southern Africa and Madagascar, represents around 15% of the genera and species of Hopliidae, while the remaining genera and species (85%) are in to the subfamily Hopliinae. Most species of the tribe "Hopliini" (397 species) belongs to the genus *Hoplia* (297 species). Recently, Evans (2003) listed 38 valid species of *Hoplia* from the New World.

Material and Methods

Taxa selection.—In this study, we selected taxa based on the classification proposed by Endrödi (1966) where Melolonthidae is considered as a family of Scarabaeoidea. The Hopliini is considered as one tribe of the subfamily Melolonthinae in the classification proposed by Morón (2004). The out-group was formed with one species representative of the tribe Orphniini (Orphninae: Scarabaeidae), representative species of two tribes of Melolonthinae, representative species of two tribes of Rutelinae, representative species of three tribes of Dynastinae, representative species of one tribe of Trichiinae and representative species of four tribes of Cetoniinae. The in-group was formed with 12 representative species of Hopliids (Table 1).

We studied 198 males deposited in the collections of Instituto de Ecología A. C., Xalapa (IEXA), Canadian National Collection, Ottawa (CNC), University of Nebraska State Museum, Lincoln (UNSM), The Natural History Museum, London (NHML), and the private collections of M. A. Morón, Xalapa, Mexico (MXAL), H. F. Howden (HAHC), and Bruce Gill (BDGC) Ottawa, Canada.

Dried specimens were softened with water vapor or in a humidifier in order to dissect the genitalia and mouthparts. These structures were extracted using microforceps and insect pins, card-mounted, and then pinned beneath each specimen. For better definition and to compare the morphology of the structures, they were drawn with the aid of a stereomicroscope and camera lucida (Leica MZ8, 50× to 100×). The lamellae of the antennal club were separated to treat them with KOH (5%) and then dry-mounted for scanning with an electron microscope (Jeol JSM-5600LV, 1,000× to 2,000×). The antennal sensilla on the outer surface of the penultimate antennal segment were classified according to Meinecke (1975). We then proceeded to score each of the 53 morphological characters (Appendix 1).

Phylogenetic methods.—Phylogenetic analyses were performed using 52 morphological characters. The matrix of characters employed for the analysis (Table 2) was built and analyzed using Winclada ver. 1.00.08 (Nixon 2002) and NONA ver. 2.0 (Goloboff 1999). The data were analyzed with a heuristics search routine (1,000 replications). Characters states for the cladistic analysis were polarized by out-group comparison (Maddison et al. 1984, Nixon and Carpenter 1993). Characters are scored only for males, and all the characters were discrete rather than continuous values. Characters were coded as either binary or multistate (0–4). Multistate characters were treated as unordered and with equal weight. The tree was rooted with the Orphninae, *Aegidium cribratum* Bates.

Results and Discussion

The phylogenetic analysis resulted in 30 equally parsimonius trees with a total length (TL) of 178, consistency index (CI) of 0.410, and retention index (RI) of 0.730. The strict consensus tree is shown in the Fig. 1. In this phylogenetic hypothesis, two main clades were obtained. The first clade, including Cetoniinae-Trichiinae (Fig. 1), is supported by a bootstrap value of 91% and five synapomorphies: depressed body shape, protibia with two teeth on external border, antennal sensilla of type A present, head downward, and laterobasal clypeal notch present. The second main clade maintains the relationships among Melolonthinae, Rutelinae, and Dynastinae by three synapomorphies: galea with teeth, labrum with apical edge thickened, and labrum with apical edge sclerotized.

In the second clade (Fig. 1), *Clavipalpus basalis* Moser, a species currently

Table 1. Selected taxa for this study based on the classifications proposed by Endrödi (1966) and Morón (2004). O.G. = out-group; I.G. = in-group.

Taxonomic Level Studied	Species	No. Specimens	
Scarabaeidae			
Orphninae			
Orphniini	*Aegidium cribratum* Bates, 1887	O. G.	5
Melolonthinae			
Melolonthini	*Melolontha melolontha* (Linné, 1758)	O. G.	6
	Phyllophaga obsoleta (Blanchard, 1850)	O. G.	7
	Diplotaxis hirsuta Vaurie, 1958	O. G.	6
Macrodactylini	*Macrodactylus mexicanus* Burmeister, 1845	O. G.	6
	Isonychus ocellatus Burmeister, 1855	O. G.	6
	Ceraspis pilatei Harold, 1863	O. G.	5
	Barybas aurita Bates, 1887	O. G.	5
	Liogenys fusca Blanchard, 1850	O. G.	4
	Clavipalpus basalis Moser, 1918	O. G.	4
Hopliini	*Hoplia festiva* Bates, 1888	I. G.	5
	Hoplia asperula Bates, 1888	I. G.	5
	Hoplia trivialis Harold, 1869	I. G.	5
	Hoplia dispar LeConte, 1880	I. G.	5
	Hoplia surata Bates, 1888	I. G.	5
	Hoplia pollinosa Kryn, 1832	I. G.	5
	Hoplia clorophana Erichson, 1848	I. G.	5
	Hoplia coerulea (Drury, 1773)	I. G.	5
	Gymnoloma femorata Burmeister, 1844	I. G.	5
	Hoplocnemis mutica Burmeister, 1844	I. G.	5
	Pachycnema calcarata Burmeister, 1844	I. G.	5
	Pachycnema squamosa Burmeister, 1844	I. G.	5
Rutelinae			
Rutelini	*Pelidnota virescens* Burmeister, 1844	O. G.	7
Anomalini	*Anomala cincta* Say, 1835	O. G.	7
	Strigoderma sulcipennis Burmeister, 1844	O. G.	7
	Epectinaspis mexicana (Burmeister, 1844)	O. G.	7
	Callirhinus metallescens Blanchard, 1850	O. G.	7
Dynastinae			
Dynastini	*Golofa imperialis* Thomson, 1858	O. G.	6
Pentodontini	*Tomarus sallei* (Bates, 1888)	O. G.	6
	Orizabus clunalis (Leconte, 1856)	O. G.	6
Cyclocephalini	*Cyclocephala lunulata* Burmeister, 1847	O. G.	6
Trichiinae			
Trichiini	*Trigonopeltastes geometrica* Schaum, 1841	O. G.	5
Cetoniinae			
Gymnetini	*Cotinis mutabilis* (Gory & Percheron, 1833)	O. G.	5
Goliathini	*Neoscelis dohrni* (Westwood, 1855)	O. G.	5
Cetoniini	*Euphoria basalis* (Gory & Percheron, 1833)	O. G.	5
Cremastocheilini	*Cremastocheilus knochi* LeConte, 1853	O. G.	5

placed inside Macrodactylini, is found independent and is more basal inside the clade that maintains the relationships of Melolonthinae, Dynastinae, and Rutelinae. They all share one synapomorphy: anterior edge of prementum sinuate.

Table 2. Characters states of taxa used in the phylogenetic analysis.

Species	11111111112222222222333333333344444444445555 12345678901234567890123456789012345678901234567890123
Aegidium cribratum	01110101010113101110111010111020111010011000011111100
Melolontha melolontha	01110001010113121000011010101020110010110010111110011
Phyllophaga obsoleta	01110001010113101100011010101020100011110010111110001
Diplotaxis hirsuta	01110001000113101100011010101020100011110010011111001
Macrodactylus mexicanus	21110001001113121000011000110000110111000110011111001
Liogenys fuscus	01110101000113101100011000111020110011110010011111001
Ceraspis pilatei	21110101302113120000111000001020110111010010011100101
Isonychus ocellatus	01110001001113101000011000110000110111010110011110101
Barybas aurita	01110001012113100001111010010020110111110110000111101
Clavipalpus basalis	01110000001113101100111000110021110010110010010111101
Pelidnota virescens	00110100000113011100111011111120110011110010011011111
Strigoderma sulcipennis	00110000000113001000111011111120110011110110011101101
Epectinaspis mexicana	00110000000113001000111010111120110011110110011111001
Anomala cincta	00110000000113001100111010111120110011110110011011101
Callirhinus metallescens	00110000000113001000111010111120110111110210011101101
Cyclocephala lunulata	01110000000113101100111010111121110111110210010110001
Orizabus isodonoides	01111101000113111100111010111101110110111210011111011
Tomarus sallei	01111103000113111100111010111120110111110210010011101
Golofa imperialis	01111103000113111100111010111121110111110210011111011
Neoscelis dorhni	00001114100001101000111001111011011012101300001111101
Cremastocheilus knochi	01000210110000101000111000111021110010111200001111111
Euphoria basalis	01000211101001101100111001111011011012101300010111101
Cotinis mutabilis	00001214200001101000111001111011011012101302001111101
Trigonopeltastes geometrica	01000012000113121000111000111011011011101100001111101
Hoplia festiva	01110100012113100102100100011020110111110111011111001
Hoplia asperula	01110100012113100102100100011020110111110111011111001
Hoplia clorophana	01110200012113100102100100011020110110110111011111001
Hoplia coerulea	01110200012113100102100100011020110110110111011111001
Hoplia trivialis	01110100003113100002100100011020110111110111011111001
Hoplia dispar	01110000012113100002100100011020110111110111011111001
Hoplia surata	01110000012113100102100100011020110111110111011111001
Gymnoloma femorata	01010200003102120101100100011010110111111211011111001
Pachycnema calcarata	11010103003013100111100100011021121101111311011111001
Pachycnema squamosa	11010103003013100111100100011021121101111311011111001
Hoplocnemis mutica	01010103013013000111100100111021121101101201011111111
Hoplia pollinosa	01110200013113100002100100011020110111110111011111001

The clade Macrodactylini-Melolonthini (Fig. 1) is supported by two synapomorphies: both mesotarsal claws cleft and presence of antennal sensilla of type K. The relationships among *Diplotaxis hirsuta* Vaurie and the clade containing *Phyllophaga obsoleta* (Blanchard) and *Melolontha melolontha* (Linné) (Fig. 1) is supported by a bootstrap value of 55% and two synapomorphies: procoxae transverse and sternites fused along midline. Finally the relationship between *Phyllophaga obsoleta* and *Melolontha melolontha* is supported by a bootstrap value of 68% and three synapomorphies: pronotum with lateral margin crenulate, antennal sensilla of type J present, and the sclerites associated with the *spiculum gastrale* absent.

The clade of Dynastinae and Rutelinae (Fig. 1) is supported by three synapomorphies: clypeal apex entire, procoxae transverse, and the mandibles exposed dorsally. The Dynastinae clade is supported by a bootstrap value of 60% and one synapomorphy: distal

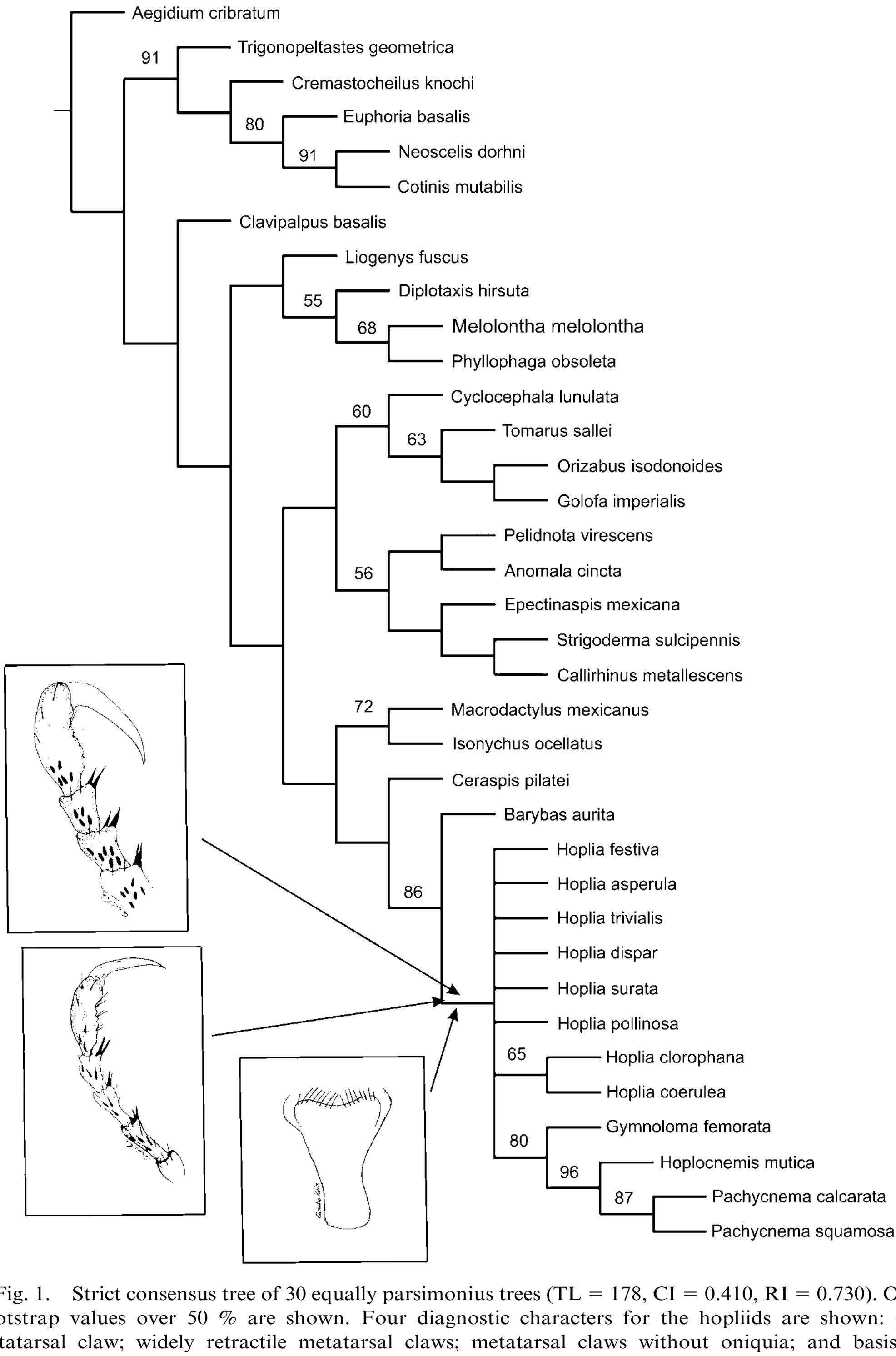

Fig. 1. Strict consensus tree of 30 equally parsimonius trees (TL = 178, CI = 0.410, RI = 0.730). Only bootstrap values over 50 % are shown. Four diagnostic characters for the hopliids are shown: one metatarsal claw; widely retractile metatarsal claws; metatarsal claws without oniquia; and basis of *spiculum gastrale* widened.

edge of labrum curved. The clade of *Tomarus sallei* (Bates), *Orizabus isodonoides* (Leconte) and *Golofa imperialis* Thomson is supported by four synapomorphies: head projections present, frontoclypeal suture present only at sides, clypeal apex dentate; and pygidium semicircular. The clade of *Orizabus isodonoides* and *Golofa imperialis* is supported by one synapomorphy: sensilla of type L absent.

The clade of Rutelinae (Fig. 1) is supported by a bootstrap value of 56% and two synapomorphies: tegumentary diffraction present and base of epipleura thickened. The relationship between *Pelidnota virescens* Burmeister and *Anomala cincta* Say is supported by the presence of antennal sensilla of type G. This last clade is the sister group of *Epectinaspis mexicana* (Burmeister), *Strigoderma sulcipennis* Burmeister, and *Callirhinus metallescens* Blanchard. The relationship of *Strigoderma mexicana* and *Callirhinus metallescens* is supported by the presence of antennal sensilla of type H. The clade Dynastinae-Rutelinae is the sister group of the clade of the assembly of macrodactylids and all the representatives of hopliids. In one clade two species of macrodactylids are found: *Macrodactylus mexicanus* Burmeister and *Isonychus ocellatus* Burmeister. Their relationship is supported by a bootstrap value of 72% and three synapomorphies: both mesotarsal claws cleft, fifth sternite two times longer than fourth sternite, and distal part of the left mandible shortened. The relationships of the clade containing two species of macrodactylids (*Ceraspis pilatei* Harold and *Barybas aurita* Bates) and the clade of the hopliids are supported by two synapomorphies: pygidium covered by scales and abdominal surface covered with scales. *Barybas aurita* appears as the sister taxon of the hopliids, supported by one synapomorphy: lateral margin of the pronotum crenulate.

The clade of the hopliids (Fig. 1) is supported by a bootstrap value of 86% and seven synapomorphies: clypeal apex entire, protibiae with three well-defined teeth, antennal sensilla of type K present, one metatarsal claw, widely retractile metatarsal claws, metatarsal claws without onychia, and base of *spiculum gastrale* widened. The clade of *Hoplia clorophana* Erichson and *Hoplia coerulea* (Drury) is supported by a bootstrap value of 65% sharing two synapomorphies: loss of frontoclypeal suture and prementum with anterior edge entire. South African taxa are placed in another clade, supported by a bootstrap value of 80% and five synapomorphies: body depressed, elytra covered with setae and scales, metatibiae with one apical spur, labrum with anterior edge thin, and labrum with anterior edge entire. The node of *Hoplocnemis* and *Pachycnema* is supported by a bootstrap value of 96% and six synapomorphies: clypeus with apex dentate, mesepimeron exposed dorsally, metatibiae thickened, galea without teeth, molar surface of left mandible without teeth or ridges, and prementum with anterior edge membranous. The clade formed by the two species of *Pachycnema* is supported by a bootstrap value of 87% sharing two synapomorphies: anterior edge of labrum notched and body shape quadrate.

Our analysis demonstrated that some traditional groups of the subfamily Melolonthinae are not monophyletic. Representatives of such groups (*Liogenys, Clavipalpus, Macrodactylus, Ceraspis*) are distributed in different lineages inside the tree (Fig. 2). But the species of *Macrodactylus* and *Isonychus*, as representatives of Macrodactylini (*sensu stricto*), are located near the species of *Ceraspis* and *Barybas* (Macrodactylini *sensu lato*), and are the closest relatives of the hopliids.

This phylogenetic hypothesis supports hopliines as a subfamily of Scarabaeidae

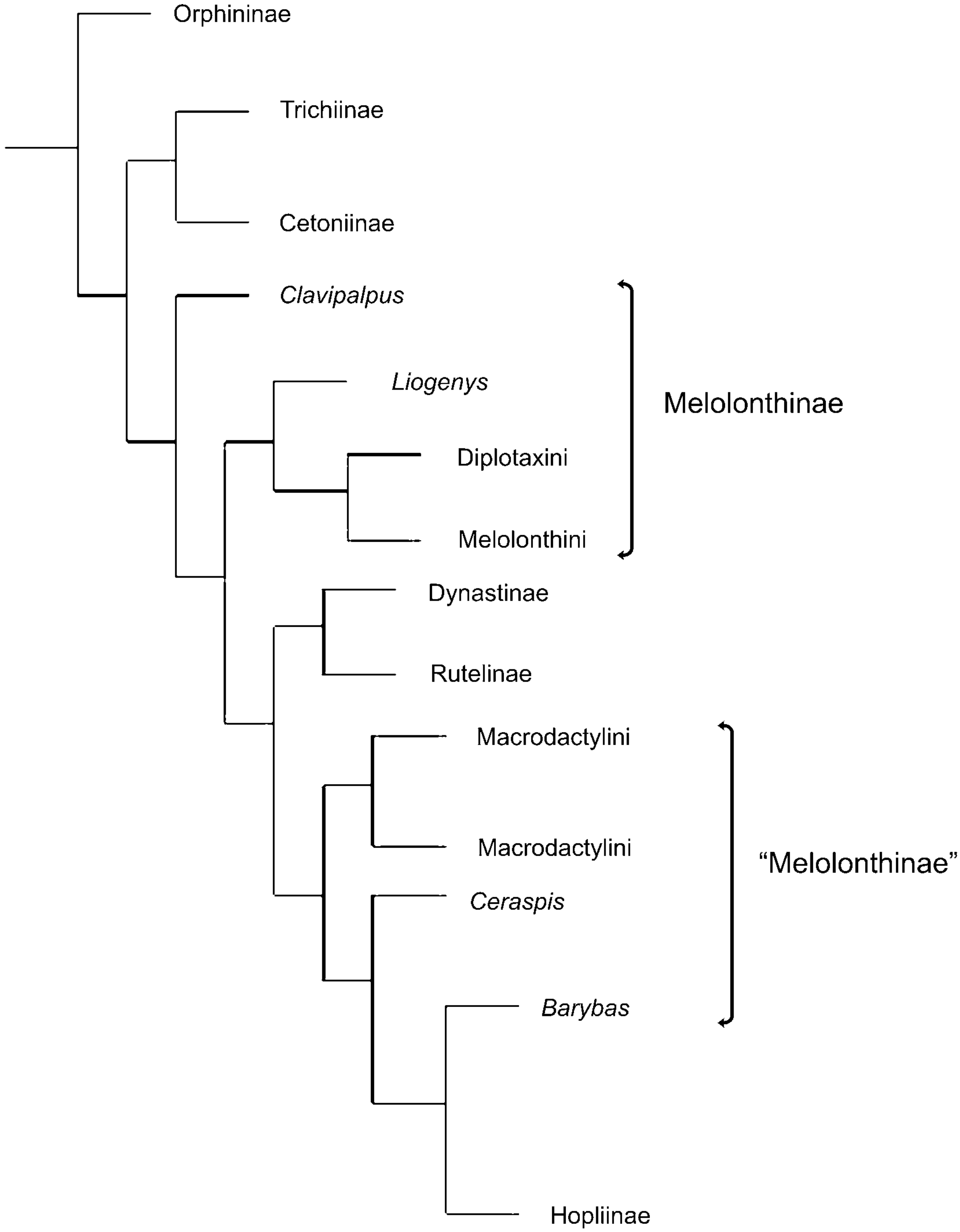

Fig. 2. Cladogram of the relations of the hopliids with the subfamilies of Melolonthidae.

(*sensu* Lawrence and Newton 1995) with the same rank of Melolonthinae, Rutelinae, and Dynastinae. Future detailed analysis based on more taxa of hopliines and macrodactylines is necessary to corroborate the existence of two or three tribes inside Hopliinae. Based on the present analysis we confirm that:

a) hopliines constitute a monophyletic group; and b) it is a group independent from Melolonthinae and Rutelinae and closely related to some macrodactylines.

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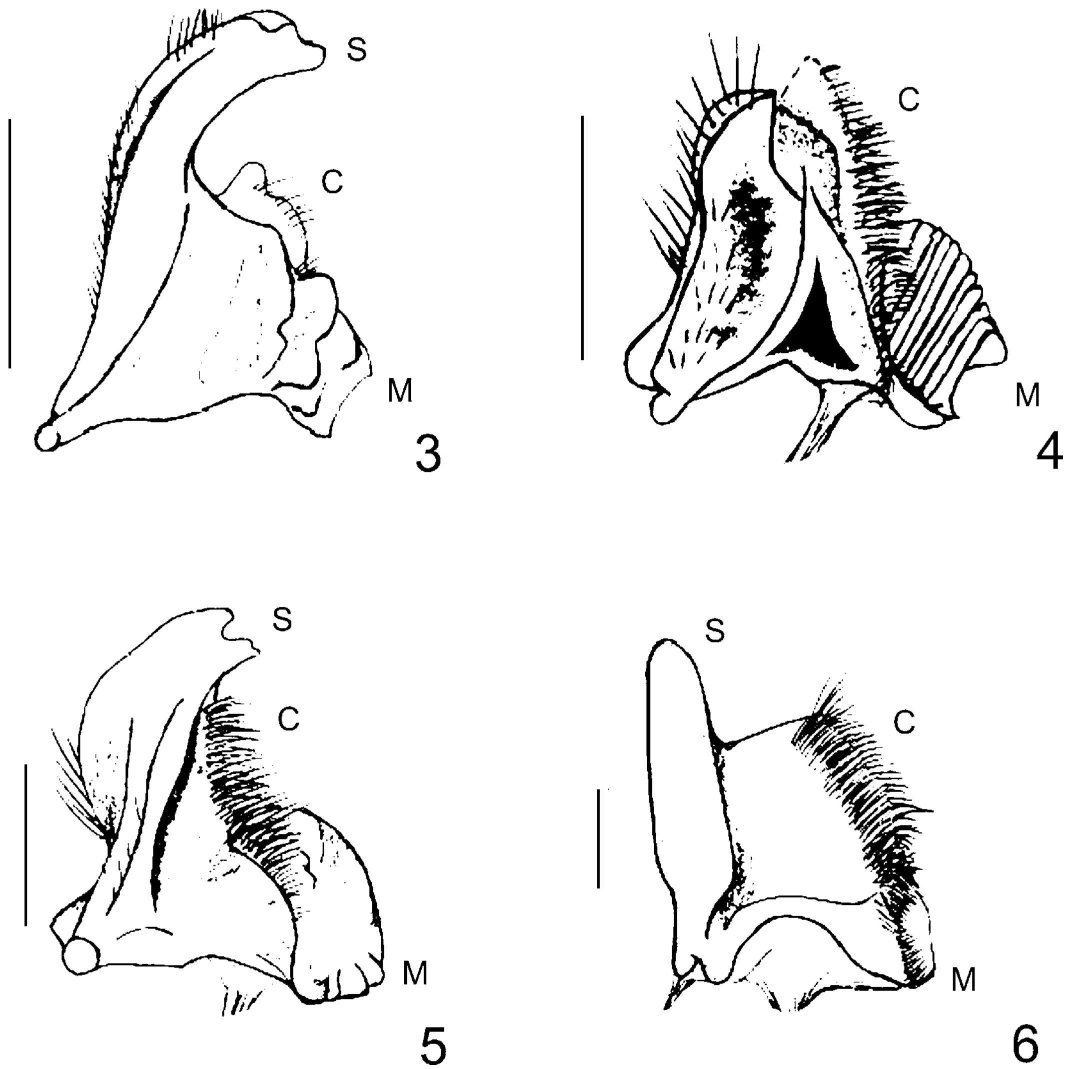
Appendix I

List of the characters used for the phylogenetic analysis. Numbers in parentheses indicate the state assigned for each character.

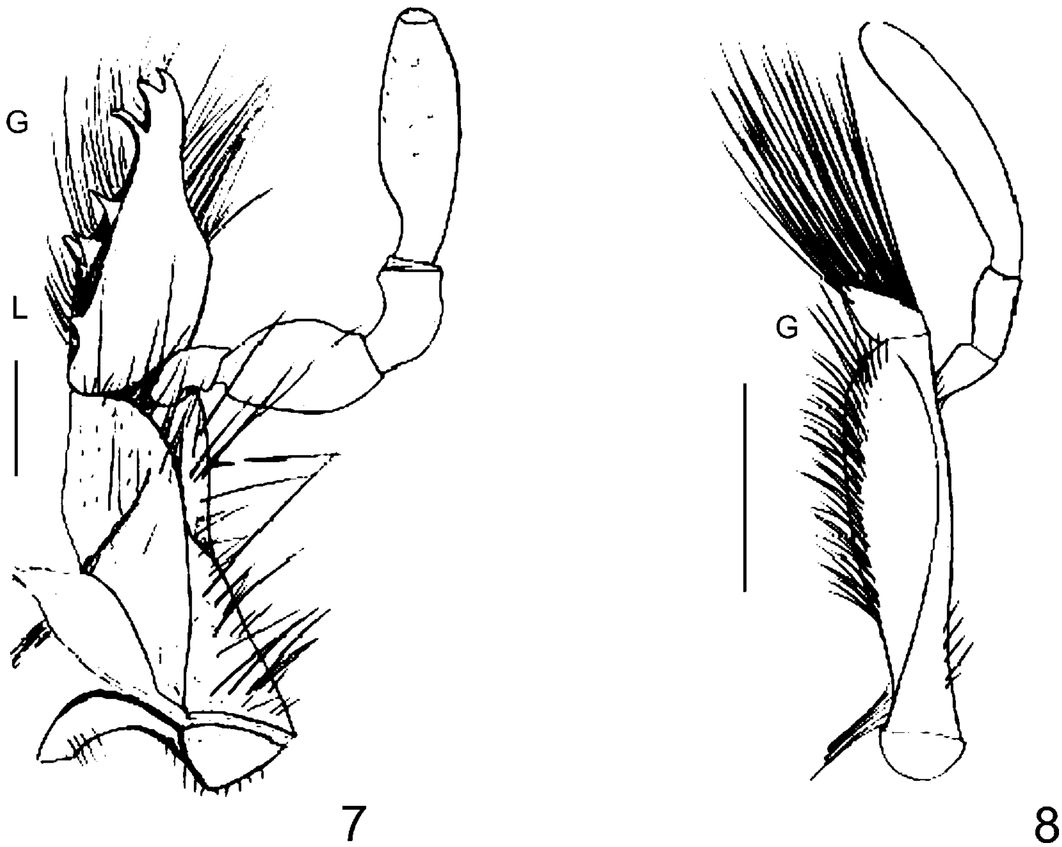
1. Body proportions, determined as the total length measured from the apex of clypeus to the apex of elytra divided among the maximum elytral width. Two times longer than wide (0), 1.5 times longer than wide (1), 3 times longer than wide (2).
2. Tegumentary diffraction, considered as iridescent, vitreous or metallic shine of cuticular surface. Present (0), absent (1).
3. Dorso-ventral body shape. Depressed (0), not depressed (1).
4. Position of head with regard to longitudinal axis of body. Downward (0), raised (1).
5. Head projections, as horns, tubercles or keels. Absent (0), present (1).
6. Frontoclypeal suture. Complete (0), printed only at sides (1), absent (2).
7. Laterobasal clypeal notch. Absent (0), present (1).
8. Clypeal apex. Entire(0), sinuate (1), bilobate (2), dentate (3), ornate (4).
9. Base of pronotum. Rounded (0), straight (1), lobate (2), dentate (3).
10. Lateral margin of pronotum. Entire (0), crenate (1).
11. Elytral vestiture. Without setae or scales (0), with setae (1), with scales (2), with setae and scales (3).
12. Mesoepimera. Dorsally exposed (0), not dorsally exposed (1).
13. Posthumeral notch of elytra. Present (0), absent (1).
14. Setae on posthumeral notch of elytra. Scarce, less than 20 setae (0), abundant, more than 20 setae (1), not apply (2).
15. Base of epipleural fold. Thick (0), thin (1).
16. Pygidium proportions, determined by dividing maximum pygidial width upon total length of pygidium. Semitriangular, from 0.60–0.95 times wider than long (0),

semicircular, from 1.00–1.91 times wider than long (1), ovate, from 2.20–2.92 times wider than long (2)

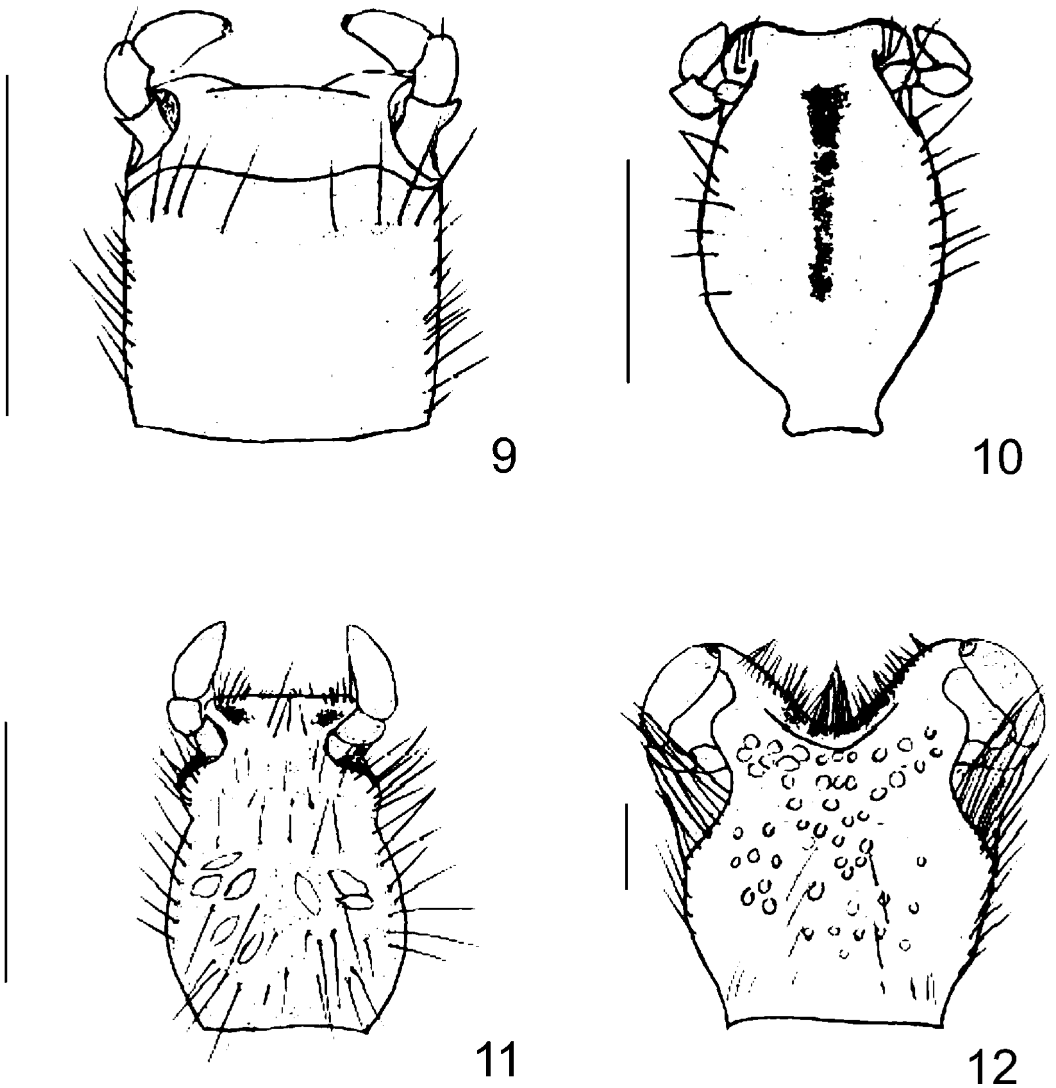
17. Pygidial vestiture. With scales (0), without scales (1).
18. Number of well defined teeth on protibial external border. 1–2 (0), 3–4 (1).
19. Metatibia proportions, determined by dividing total length of metatibia upon it maximum width. Narrowed, 4–9 times longer than wide (0), thickened, 1–3 times longer than wide (1).
20. Apical spurs of metatibiae. 2 spurs (0), 1 spur (1), without spurs (2).
21. Apices of mesotarsal claws. Cleft in both claws (0), entire in one or both claws (1).
22. Number of metatarsal claws. One (0), two (1).
23. Movement of metatarsal claws. Widely retractile (0), scarcely retractile or moveless (1).
24. Metatarsal onychia. Present (0), absent (1).
25. Shape and position of procoxae. Conical (0), transverse (1).
26. Mesosternal process. Absent (0), present (1).
27. Abdominal vestiture. With scales (0), without scales (1).
28. Abdominal sternites. Fused along midline (0), not fused (1).
29. Length of fifth abdominal sternite. Two times longer than preceeding (0), with same length of preceeding or shorter than this (1).
30. Mandibles. Not exposed dorsally (0), exposed dorsally (1).
31. Form of distal part of left mandible. Shortened (Fig. 4) (0), elongated (Fig. 6) (1), curved (Figs. 3, 5, 25) (2).
32. Apex of left mandible. With teeth (Figs. 3, 5, 25) (0), without teeth (Fig. 6) (1).
33. Conjunctivus of left mandible. Large (Figs. 4, 6) (0), reduced (Figs. 3, 5, 25) (1).
34. Molar surface of left mandible. With teeth or blades (Fig. 3) (0), with ridges (Figs. 4, 25) (1), without teeth, blades or ridges (Figs. 5–6) (2).
35. Apex of galea. With teeth (Figs. 7, 26) (0), without teeth (Fig. 8) (1).
36. Lacinia. Reduced (Fig. 8) (0), fused with galea (Figs. 7, 26) (1).
37. Consistency of anterior edge of prementum. Membranous (0), sclerotized (1).
38. Form of anterior edge of prementum. Entire (Fig. 11) (0), sinuate (Figs. 9–10, 27) (1), notched (Fig. 12) (2).
39. Disc of mentum. Longitudinally furrowed (Fig. 10) (0), without furrow (Figs. 9, 27) (1).
40. Lateral edge of labrum. Elongated (Fig. 16) (0), shortened (Figs. 13, 28) (1).
41. Thickeness of anterior edge of labrum. Thick (0), thin (1).
42. Form of anterior edge of labrum. Lobate (Fig. 13) (0), sinuate (Figs. 16, 28) (1), curved (Fig. 14) (2), notched (Fig. 15) (3).
43. Consistency of distal edge of labrum. Membranous (0), sclerotized (1).
44. Basis of *spiculum gastrale*. Narrowed (0), widened (1), absent (2).
45. Sclerites associated with *spiculum gastrale*. Present (0), absent (1).
46. Sensilla type A. Present (Fig. 17) (0), absent (1).
47. Sensilla Type F. Present (Figs. 18, 23) (0), absent (1).
48. Sensilla Type G. Present (Figs. 19, 23) (0), absent (1).
49. Sensilla Type H. Present (Fig. 20) (0), absent (1).
50. Sensilla Type J. Present (Fig. 21) (0), absent (1).
51. Sensilla Type K. Present (Fig. 22) (0), absent (1).
52. Sensilla Type L. Present (Figs. 17–18, 20–24) (0), absent (1).



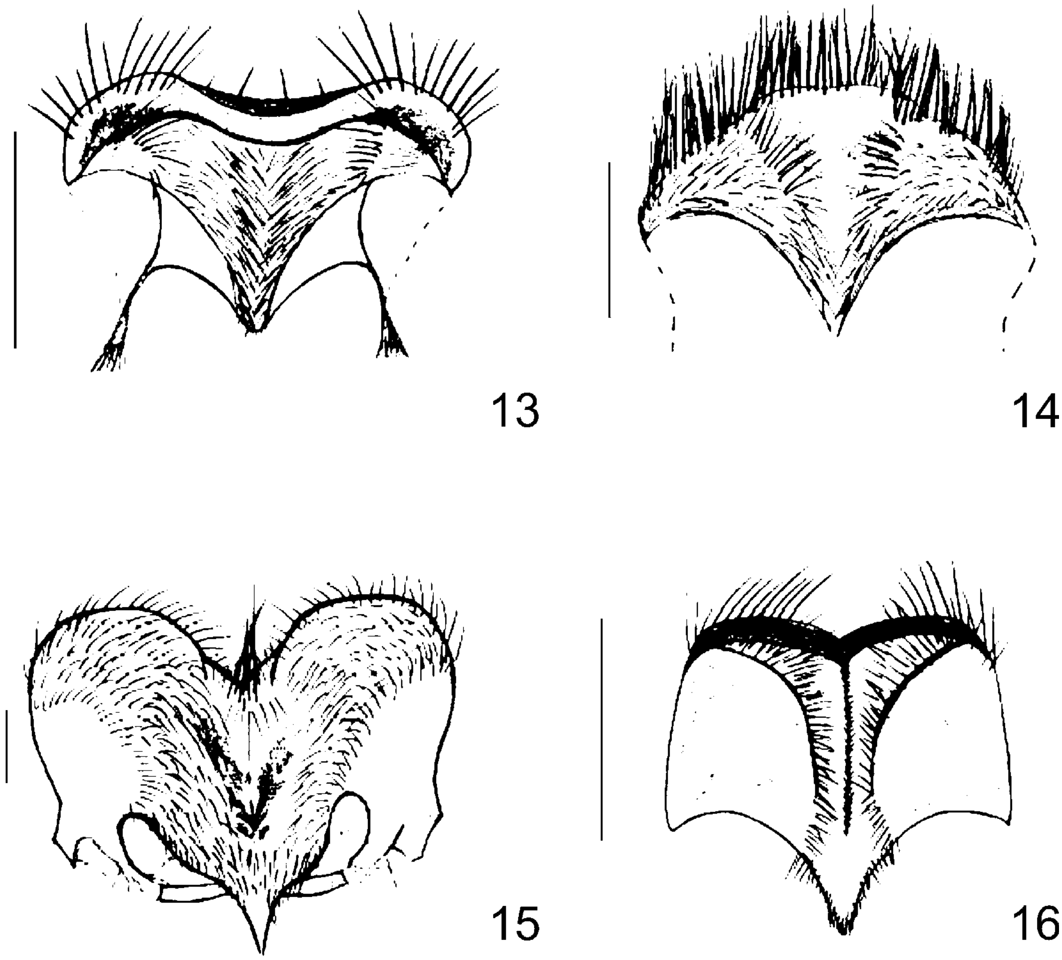
Figs. 3–6. Left mandible, adult, dorsal view. 3, *Diplotaxis hirsuta*. 4, *Macrodactylus mexicanus*. 5, *Anomala cincta*. 6, *Cotinis mutabilis*. C, conjunctivus; M, molar area; S, scissorial area. Scale bar =1 mm.



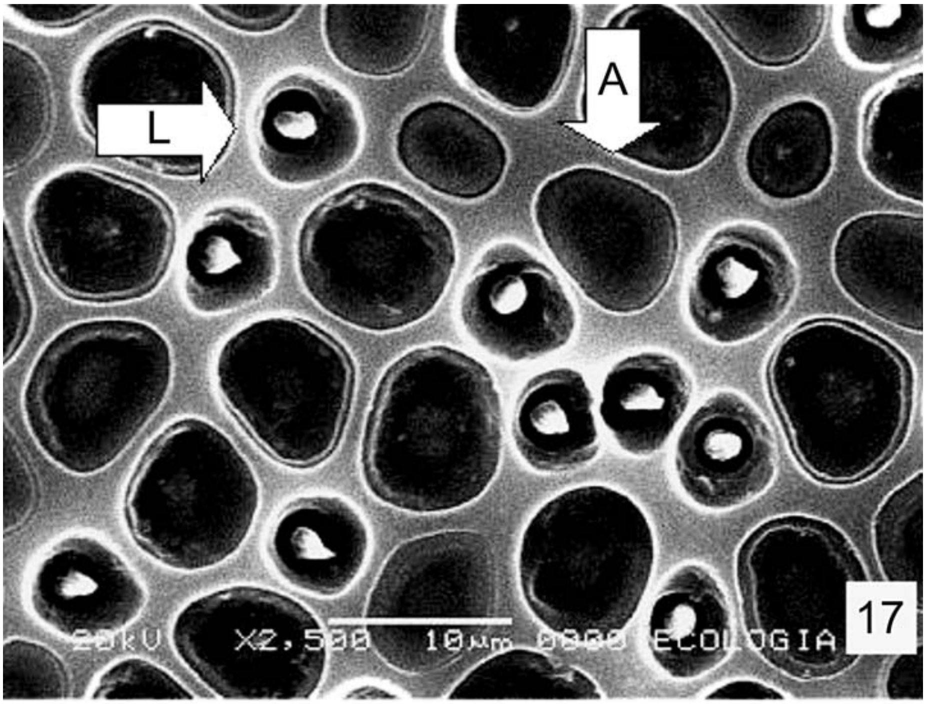
Figs. 7–8. Left maxilla, adult, ventral view. 7, *Golofa imperialis*. 8, *Trigonopeltastes geometrica* Schaum, 1841. G, galea; L, lacinia. Scale bar =1 mm.

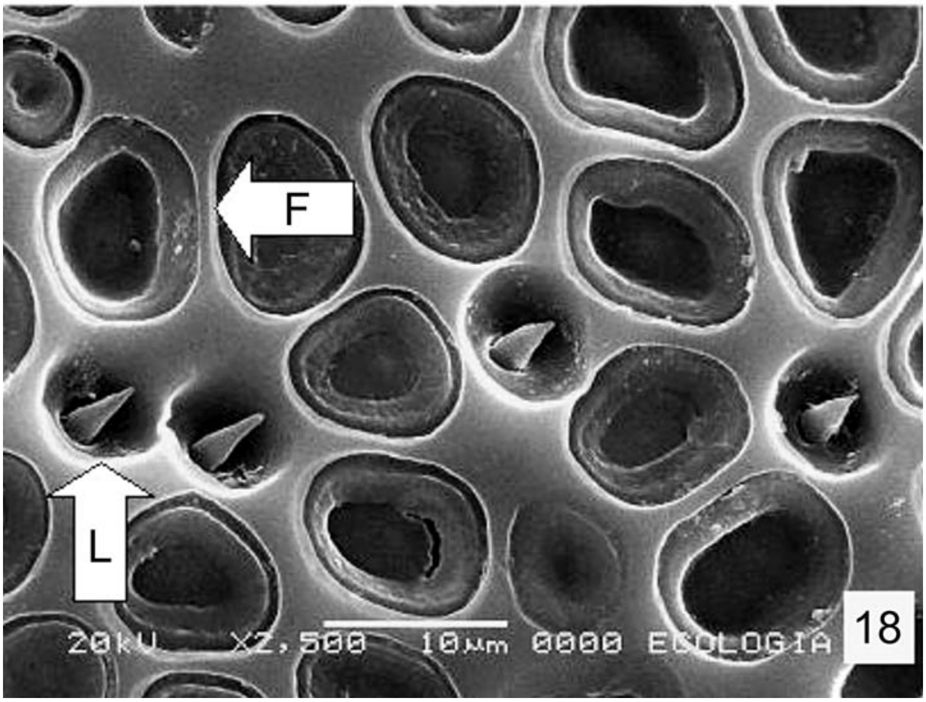


Figs. 9–12. Labium, adult, ventral view. 9, *Diplotaxis hirsuta*. 10, *Macrodactylus mexicanus*. 11, *Hoplia clorophana*. 12, *Cotinis mutabilis* (Gory & Percheron, 1833). Scale bar =1 mm.

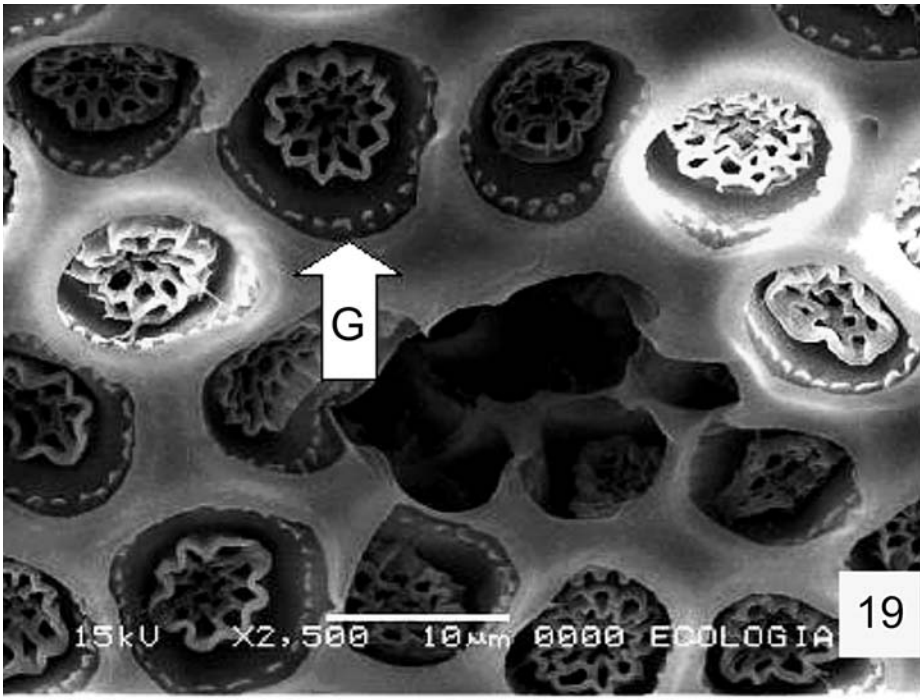


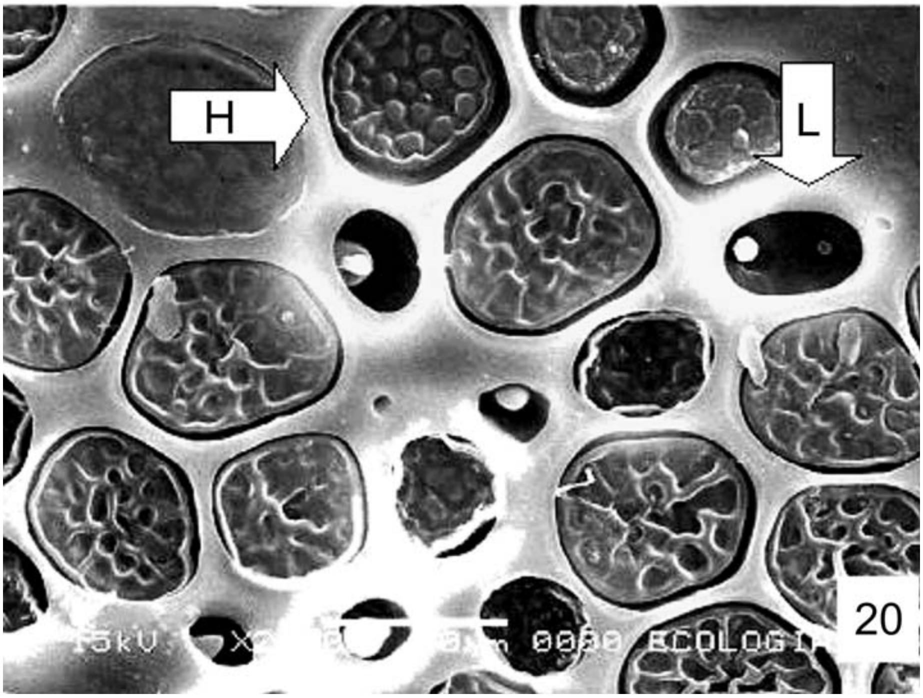
Figs. 13–16. Labrum, adult, ventral view. 13, *Diplotaxis hirsuta*. 14, *Tomarus sallei*. 15, *Cotinis mutabilis*. 16, *Trigonopeltastes geometrica*. Scale bar =1 mm.



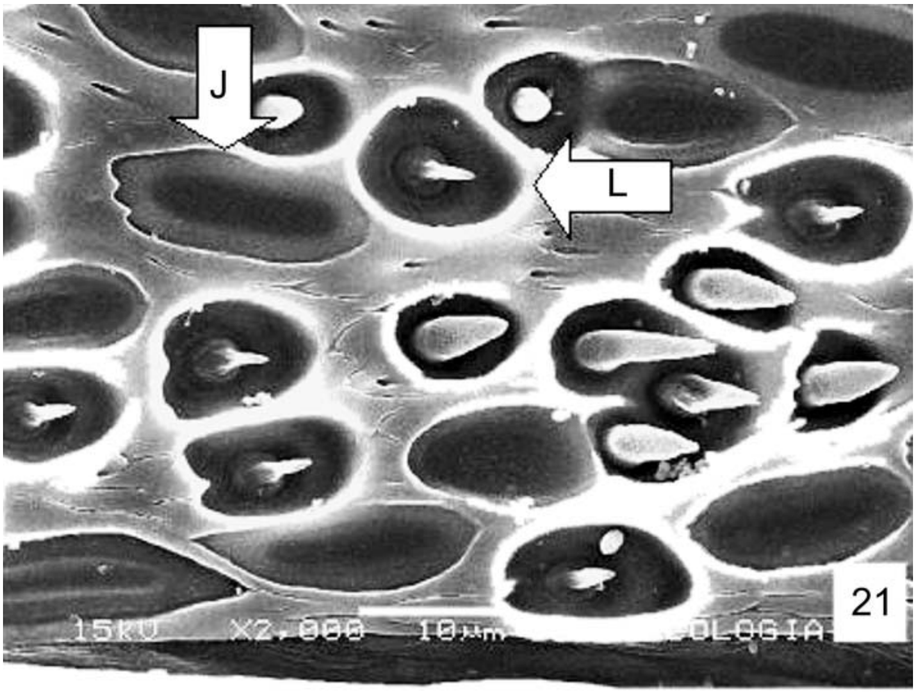


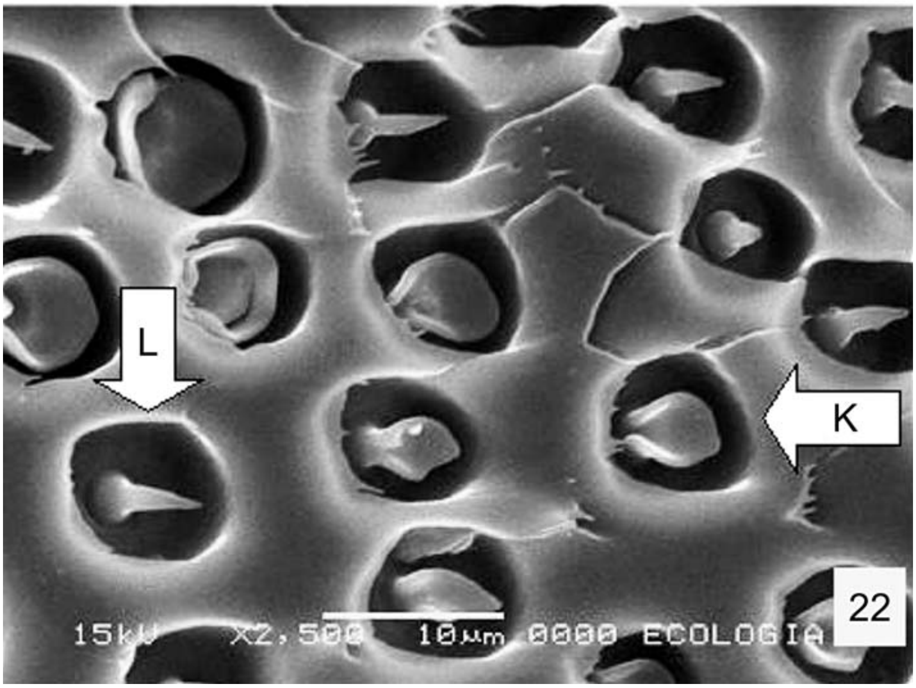
Figs. 17–18. Sensilla on inner surface of penultimate antennal segment, 2,500×. 17. *Cotinis mutabilis*. 18. *Euphoria basalis*. Placoid sensilla types ''A'', ''F'' and basiconical sensilla type ''L''.



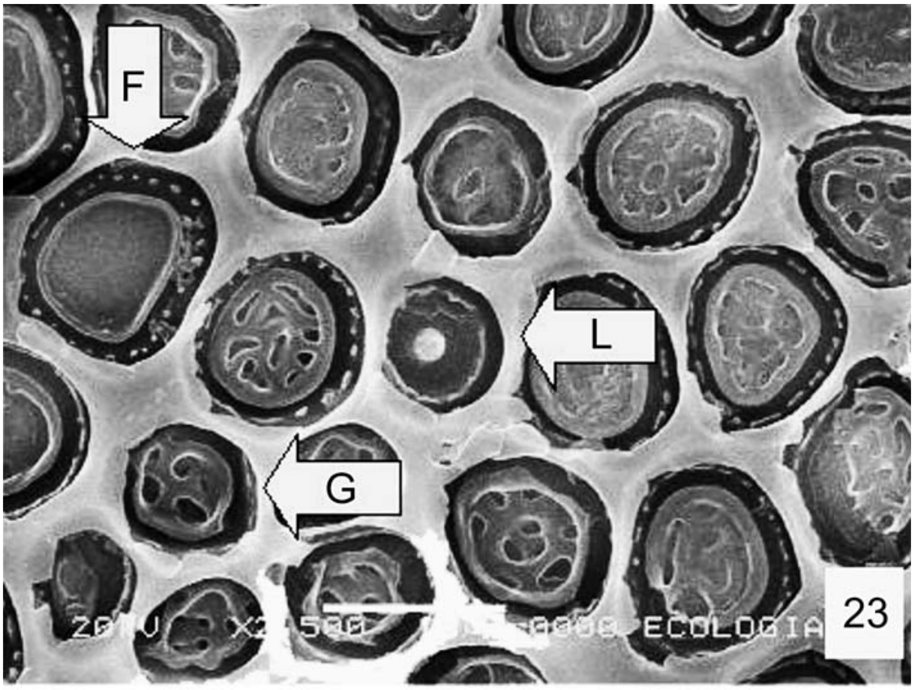


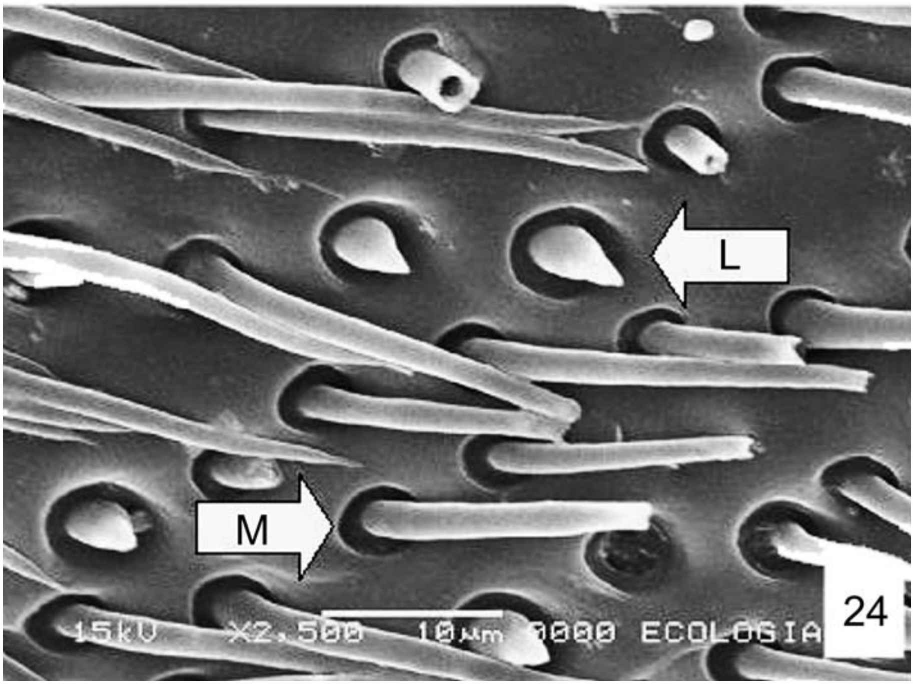
Figs. 19–20. Sensilla on inner surface of penultimate antennal segment, 2,500×. 19. *Pelidnota virescens*. 20. *Callirhinus metallescens*. Placoid sensilla types "G", "H" and basiconical sensilla type "L".



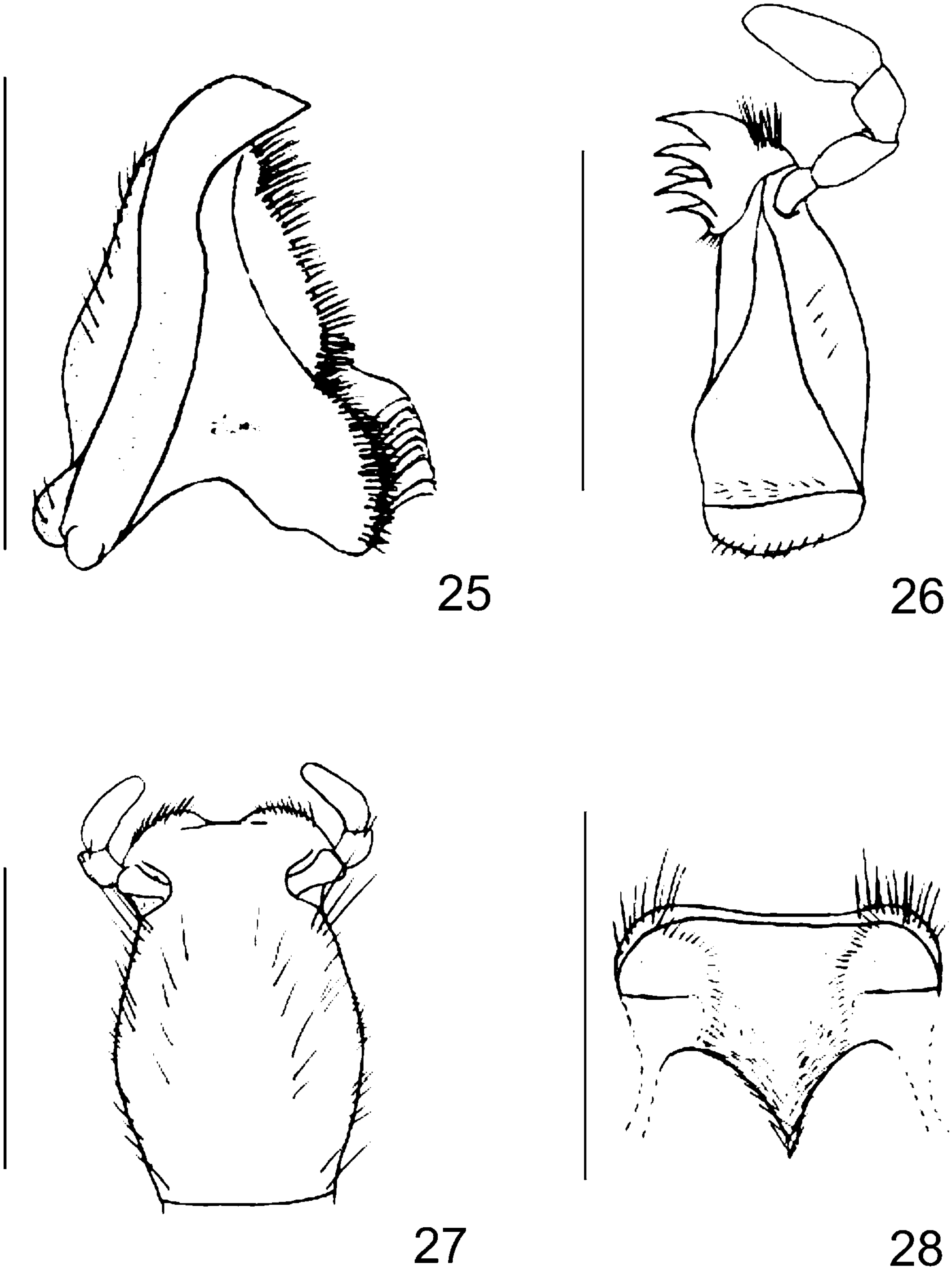


Figs. 21–22. Sensilla on inner surface of penultimate antennal segment, 2,500×. 21. *Isonychus ocellatus*. 22. *Hoplia dispar*. Placoid sensilla types ''J'', ''K'' and basiconical sensilla type ''L''.





Figs. 23–24. Sensilla on inner surface of penultimate antennal segment, 2,500×. 23. *Tomarus sallei*. 24. *Aegidium cribratum*. Placoid sensilla types ''F'', ''G'', basiconical sensilla type ''L'', and trichoid sensilla type ''M''.



Figs. 25–28. Mouth parts of *Hoplia festiva* Bates. 25. Left mandible, dorsal view. 26. Left maxilla, ventral view. 27. Labium, ventral view. 28. Labrum, ventral view. Scale bar =1 mm.