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SIMILARITY OF THE *BLEPHARIDA*-GROUP GENERA USING LARVAL AND ADULT CHARACTERS (COLEOPTERA: CHRYSOMELIDAE: ALTICINAE)

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Abstract.—Adult and mature larval characters of *Blepharida atripennis, B. rhois, B. sacra, Diamphidia* sp., *Euplectroscelis xanti, Ophrida marmorea Podontia affinis, P. lutea* and *P. dalmani,* were studied as representatives of their respective genera or subgenera from the *Blepharida*-Group of approximately 16 genera worldwide, presumed to be related. The similarities and relationships of these and other genera based on adult and larval morphology and biology are discussed. The mature larvae of these nine species are illustrated in detail, three for the first time (*Ophrida marmorea, Euplectroscelis xanti,* and *Diamphidia* sp.). Adult external morphology and the metafemoral spring were compared and indicated several overlapping similarities. Some discussion of the classification of the Galerucinae and Alticinae is provided.

Alticinae larvae, including forest and agricultural pests, have been studied by workers from morphological and biological perspectives. Ogloblin and Medvedev (1971), Kimoto and Takizawa (1994) and Steinhausen (1994) studied some genera of alticine larvae taxonomically using the chaetotaxy of the anal plate. Some other workers conducted a variety of studies, but the majority of the studies have been done relatively recently (i.e., since 1970). For a review of many of the publications on chrysomelid larvae see Steinhausen (1996) and Lee and Furth, (2000).

The larval morphology of *Blepharida* Chevrolat, *Podontia* Dalman, *Euplectroscelis* Crotch, *Ophrida* Chapuis and *Diamphidia* Gerstaecker are still relatively unknown, except for: *Blepharida atripennis* Horn, *B. sacra* (Weise) (Lee, 1999a); *B. rhois* (Forster) (Böving & Craighead, 1931; Lee, 1999a); *B. nigrotesselata* Baly (Paterson, 1943); *Podontia affinis* (Gröndal); *P. lutea* (Olivier) (Lee, 1999b); and *P. dalmani* Baly (Medvedev, 1992; Lee, 1999b). The present authors illustrate and/or describe the mature larvae belonging to nine genera or subgenera of the *Blepharida*-group from various parts of the world: *Blepharida atripennis* Horn; *B. rhois*; *B. sacra* (Weise); *Diamphidia* sp.; *Euplectroscelis xanti* Crotch; *Ophrida marmorea* (Wiedemann); *Podontia affinis* (Gröndal); *P. lutea* (Olivier); and *P. dalmani.*

Since Henriksen (1927), Böving (1927, 1929), and Böving and Craighead (1931) studies of chrysomelid larvae have indicated that there are very few detectable differences between Galerucinae and Alticinae larvae (see also Marshall, 1980 and Lawrence & Britton, 1991, but see Lawson, 1991, who lists some differences) and so these two largest chrysomelid subfamilies often have been lumped together when discussing chrysomelid larvae. Böving (1927), apparently following the classification scheme of Leng (1920), suggested that if the Diabroticini and Phyllobroticini (whose

Table 1. The *Blepharida*-group genera and their biogeographic affinities.

Blepharida-Group: (alphabetical)	Biogeography
Acrocyum Jacoby, 1885	Neotropical (Caribbean)
Blepharida Chevrolat, 1836	
(*Blepharida* Chevrolat *sensu stricto*)	Neotropical
(*Blepharidina* Bechyne, 1968)	Afrotropical
(*Blepharidella* Weise, 1909)	Afrotropical
(*Calotheca* Heyden, 1887)	Afrotropical
Blepharoides Jacoby, 1893	Oriental (Sumatra)
Chrysogramma Jacoby, 1885	Neotropical (C. America)
Crimissa Stål, 1858	Neotropical (S. America)
Diamphidia Gerstaecker, 1855	Afrotropical
Elithia Chapuis, 1875	Neotropical (S. America)
Euplectroscelis Crotch, 1873	Neoarctic (Baja Calif., Mexico)
Notozona Chevrolat, 1836	Neotropical
Ophrida Chapuis, 1875	Oriental
Parophrida Chen, 1934	Oriental (Philippines)
Podontia Dalman, 1824	Oriental
Polyclada Chevrolat, 1833	Afrotropical
Procalus Clark, 1865	Neotropical (Chile)
Sphaerophrida Chen, 1934	Oriental (Philippines)
Xanthophysca Fairmaire, 1901	Afrotropical (Madagascar)

larvae were easily separated from the rest of the Galerucinae) were removed from the subfamily Galerucinae and placed with the Systenini, Crepidoderini, and Psylliodini of the subfamily Alticinae, then it would be possible to separate the rest of the larvae into the traditional two subfamilies of Galerucinae and Alticinae as with the adults. Later in order to solve this problem, Böving and Craighead (1931) used a classification with the family Galerucidae containing three subfamilies: Galerucinae; Diabroticinae (containing *Phyllobrotica* Chevrolat); and Halticinae; see more detailed treatment below in the Discussion.

Furth (1992) discussed many of the genera in the *Blepharida*-group based on adult morphology, including genitalia and the metafemoral spring, concentrating especially on the New World members. Furth (1992) also provided a key to the 11 New World genera and suggested a more appropriate catalogue arrangement than previously used in Heikertinger and Csiki (1940) or Seeno and Wilcox (1982), based on morphology. Furth (1992) pointed out that morphologically *Pseudorthygia* Csiki and *Phydanis* Horn should not be placed with the *Blepharida*-group in catalogues (e.g., Seeno and Wilcox, 1982) and that *Crimissa* Stål, *Elithia* Chapuis, and *Procalus* Clark should be grouped with each other, but their relationship with the other *Blepharida*-group genera is still unclear. Furth (1992) also distinguished between Afrotropical and New World *Blepharida* with bifid tarsal claws by grouping them into the two subgenera, *Blepharidina* and *Blepharida*. Furth (1998) synonymized *Blepharonycha* Fall with *Blepharida* (*sensu stricto*) and reviewed the known biological information for all the New and Old World *Blepharida*-group genera (see Tables 1 and 2).

Most of the Old World genera and subgenera usually have been grouped in cat-

Table 2. The *Blepharida*-group genera for which there are any reliable host plant information.

Blepharida-group: (alphabetical)	Host plant family
Blepharida	
(Blepharida sensu stricto)	Burseraceae; Anacardiaceae
(Blepharidina)	Anacardiaceae
Crimissa	Anacardiaceae (?)
Diamphidia	Burseraceae
Elithia	Anacardiaceae
Euplectroscelis	Burseraceae
Notozona	Burseraceae; Anacardiaceae (?)
Ophrida	Anacardiaceae; Burseraceae
Podontia	Anacardiaceae; Burseraceae
Polyclada	Anacardiaceae (?)
Procalus	Anacardiaceae

alogues together with the majority of the New World genera; however, for some unapparent reason two Afrotropical genera (*Diamphidia* and *Polyclada* Clark, formerly *Cladocera* Hope) were placed in a completely different part of the Heikertinger and Csiki (1940) catalogue between Oedionychines and Monoplatines; this was later corrected by Seeno and Wilcox (1982). The placement of genera in catalogues is a non-alphabetical, non-random arrangement and is presumably based on some shared morphological similarities; however, there is never any accompanying explanation for this. Therefore, these "catalogue phylogenies" (see Furth, 1992) or catalogue classifications are sometimes confusing or misleading and become perpetuated for many years.

The chitinized jumping apparatus of Alticinae (flea beetles), the metafemoral spring, has been a useful character to demonstrate morphological grouping of Alticinae genera because of its consistent shape within each genus (Furth, 1980, 1982a, 1985, 1988, 1989; Furth and Suzuki, 1994, 1998). The metafemoral spring morphology has been included in the present study of the *Blepharida*-group.

FOODPLANT BIOLOGY

Of the 19 genera/subgenera of the *Blepharida*-group the biology of more than half (ca. 11) is known or suspected at least as to what food plant family they feed on (see Furth, 1998 for details) (Table 2)

MATERIALS AND METHODS

All larval specimens used in this study were collected and preserved in 70% ethyl alcohol. The final instar larvae were exposed to KOH solution for 30 minutes, rinsed in water and dissected under an Olympus stereoscopic microscope. For morphological studies of the minute structures, the parts were mounted on slides and observed through the compound microscope (Leitz). The terminology of setae in this study is adopted from Anderson (1947). For larval descriptions the number of specimens

Table 3. Adult morphological characters of the *Blepharida*-group genera/subgenera considered in this study.

CHARACTER	*Blepharida (s.s.)*	*Blepharidina*	*Diamphidia*	*Euplectroscelis*	*Ophrida*	*Podontia*
TARSAL CLAWS	bifid	bifid	toothed	simple	bifid	toothed
PROCOXAL CAVITIES	closed	closed	open	closed	closed	closed
FRONS/VERTEX PUNCTATION	fine	coarse	fine	coarse	coarse	coarse
FRONS/VERTEX SCULPTURE	none	grooves	none	none	grooves	grooves
PRONOTUM SHAPE	U-shaped	lyre-shaped	U-shaped	U-shaped	lyre-shaped	lyre-shaped
PRONOTUM PUNCTATION	fine punctures	fine punctures	fine punctures	coarse punctures	fine punctures	fine punctures
PRONOTUM SCULPTURE	no grooves	weak grooves	no grooves	no grooves	deep grooves	deep grooves
METAFEMUR SHAPE	swollen	swollen	tapered	swollen	swollen	tapered
EYE SHAPE	elongate-oval	elongate-oval	oval	elongate-oval	elongate-oval	oval
EYE SIZE	large	large	small	large	large	small
PROEPIMERON GROOVE	absent	present	absent	absent	present	present
METATIBIAL APEX	emarginate	emarginate	emarginate	emarginate	weak emarginate	emarginate

examined is indicated in the Body Length description by (N = #). Figures for the larvae are composites with the same nine body parts consistently numbered within each figure. Adult specimens were studied using a Leica MZ APO dissecting microscope. The metafemoral spring was dissected out of the metafemur after the latter was placed into 10% Potassium Hydroxide for 24–72 hours to allow a gradual and consistent elimination of attached musculature and clearing of the chitinized spring. All specimens are deposited at the U. S. National Museum of Natural History, Washington, D. C., except *Diamphidia* sp. which is deposited at the Plant Protection Research Institute (Pretoria, South Africa). Figures 10–16 were photographed with a Sony DKC-5000 Digital Photo Camera attached to a Leica MZ APO dissecting microscope.

RESULTS

LARVAL DESCRIPTIONS

Genus Blepharida Chevrolat, 1836

Blepharida (Blepharida) atripennis Horn, 1895
(Fig. 1)

For a detailed description of this species see Lee (1999a).
Body length. 11.2 mm (N = 5). Head width: 1.4 mm (N = 5).
Material examined. MEXICO, **Baja California Sur,** East of Todos Santos, 17 Sept. 1988, larvae collected on the leaves of *Bursera epinnata* (Rose) Engler (Burseraceae) and determined by E. Riley.

Blepharida (Blepharida) rhois (Forster, 1771)
(Fig. 2)

For a detailed description of this species see Lee (1999a).
Body length. 10.5 mm (N = 5). Head width: 1.2 mm (N = 5).
Materials examined. USA, **Missouri,** St. Louis, 25 April 1944, larvae collected by Mayer. Larvae with excrements on back on *Rhus copalina* (Linnaeus) (Anacardiaceae).

Blepharida (Blepharidina) sacra (Weise, 1897)
(Fig. 3)

For a detailed description of this species see Lee (1999a).
Body length. 8.5 mm (N = 5). Head width: 1.5 mm (N = 5).
Material examined. ISRAEL, **Judean Desert,** Ein Qilt., 16 January 1984, larvae collected on the leaves of *Rhus tripartita* (Bernard da Ucria) Grande and determined by D. G. Furth.

Genus *Diamphidia* Gerstaecker, 1655

Diamphidia sp.
(Fig. 4)

Description. *Mature larva* (Fig. 4a). Body pale reddish brown, strongly convexed, C-shaped; mandibles dark brown, head, legs, pronotum and spiracles pale brown.

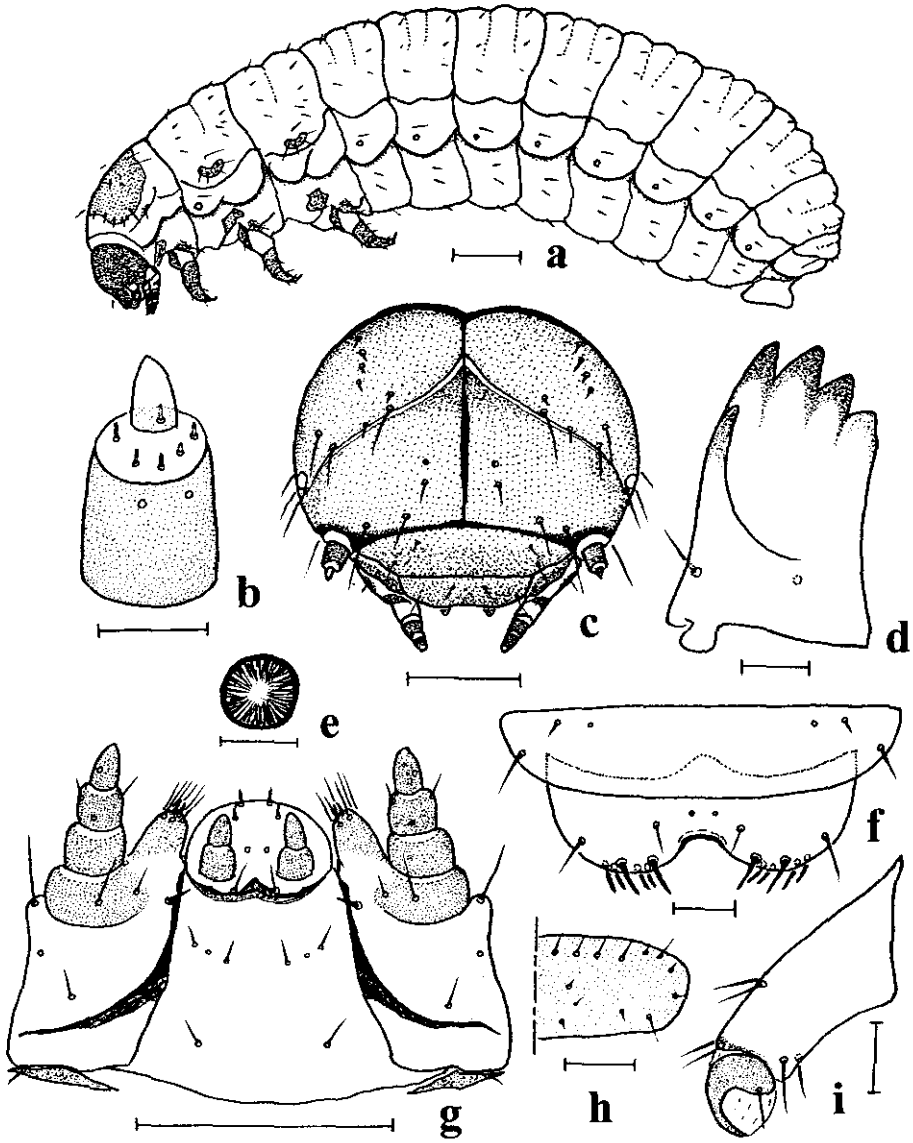

Fig. 1. *Blepharida atripennis*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

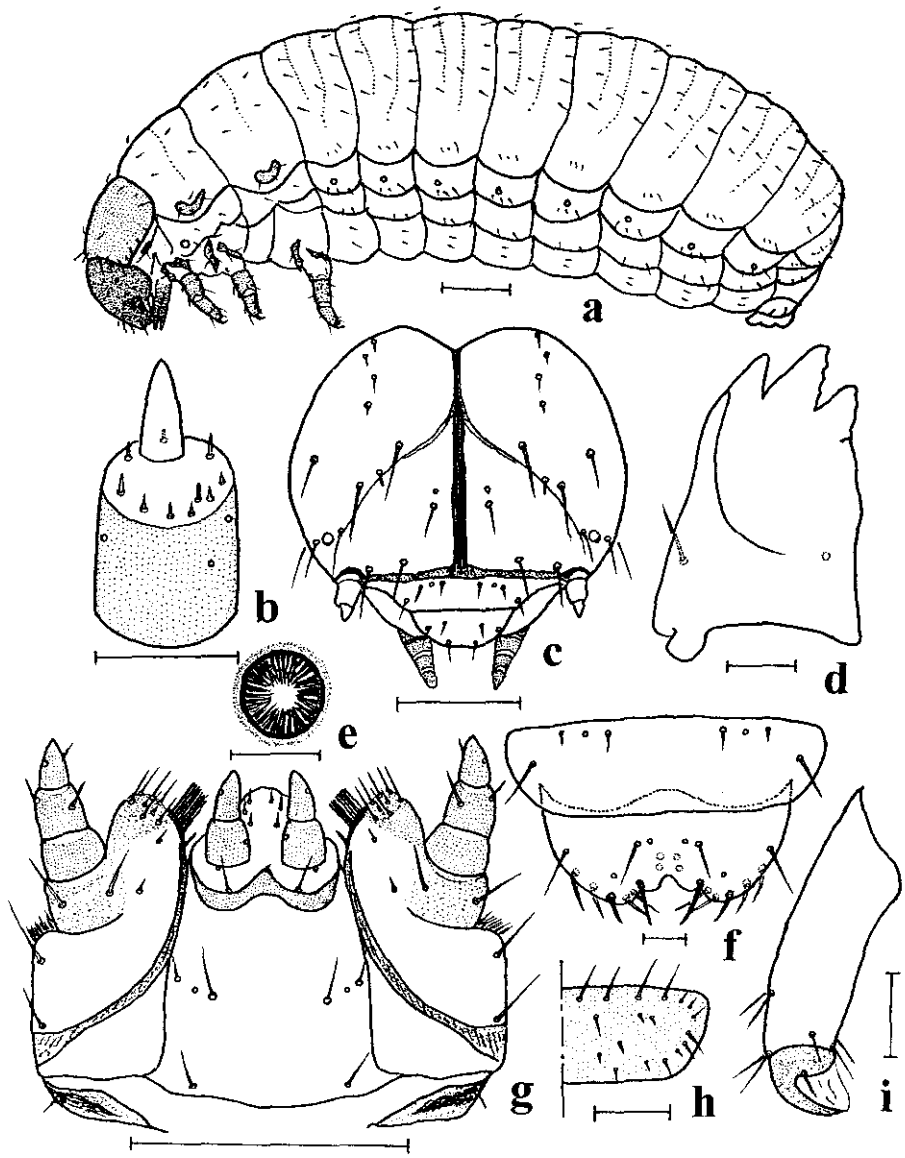

Fig. 2. *Blepharida rhois*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

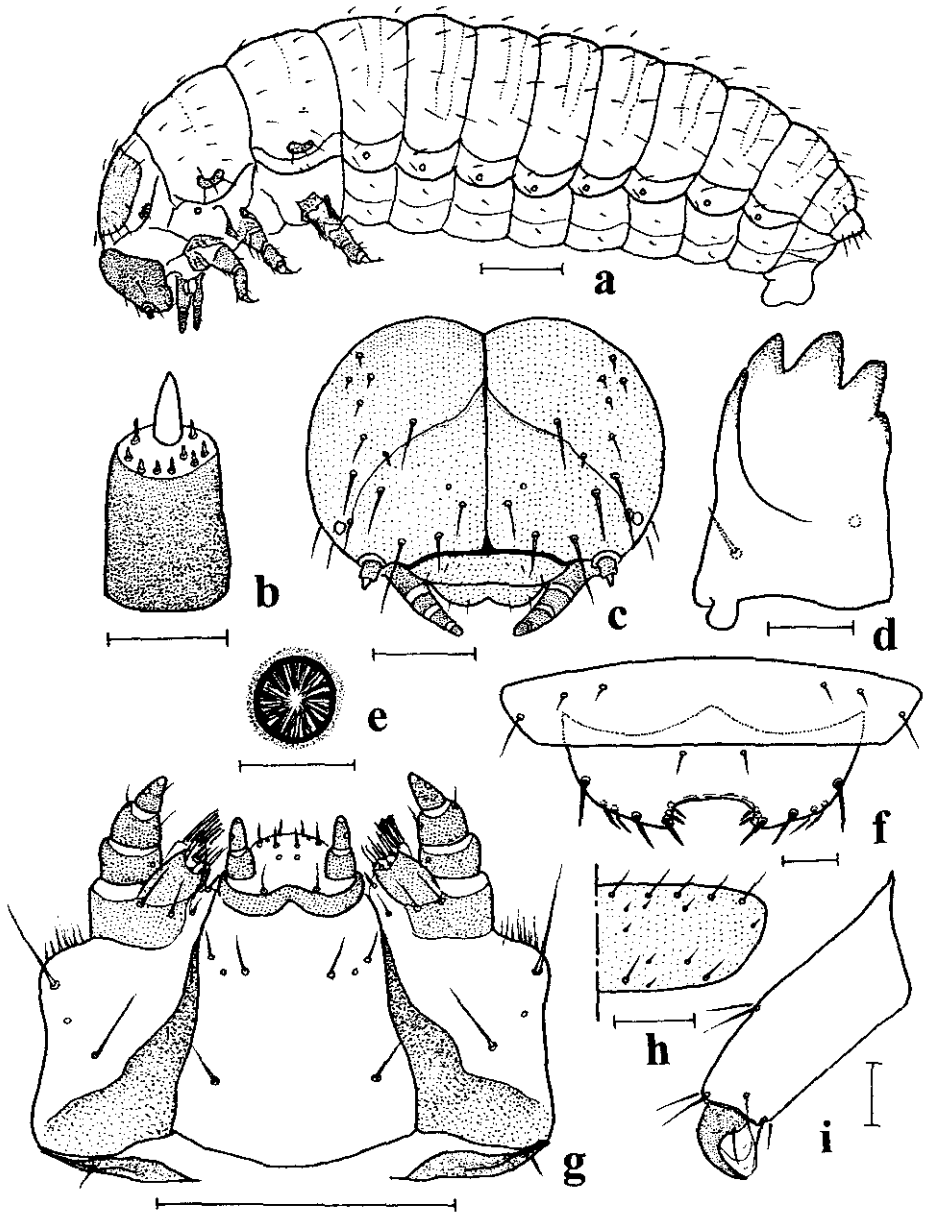

Fig. 3. *Blepharida sacra*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

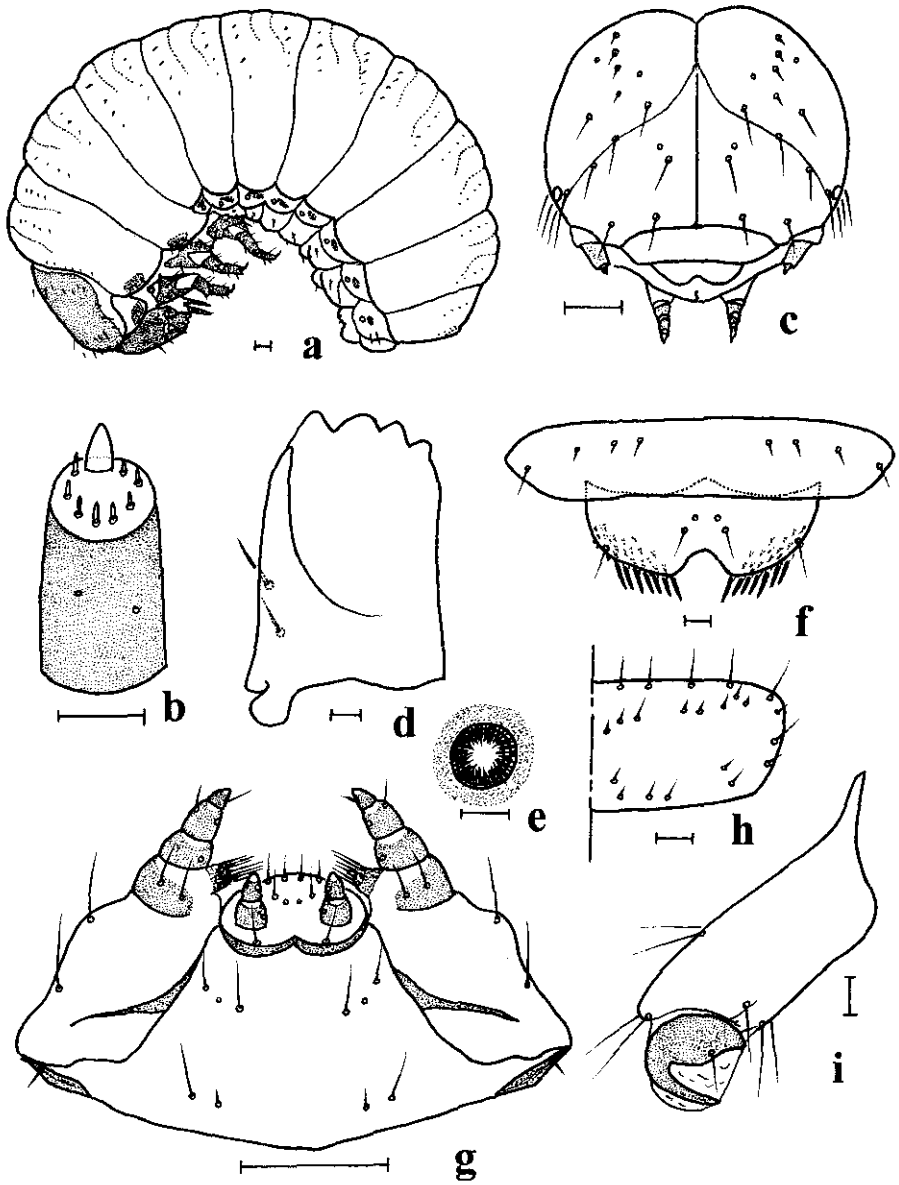

Fig. 4. *Diamphidia* sp.: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

Head (Fig. 4c). Hypognathous, rounded, strongly sclerotized; frontal suture broadly divergent and sinuate; frons with 4 pair of frontal setae and 1 pair of frontal sensilla; endocarina (i.e., crista frontalis is located between the frontal sutures) developed; coronal suture well-developed; epistomal suture developed; stemmata 1 in number on each side; antenna (Fig. 4b) 1-segmented, segment rather long, with a rather short conical sensory papilla, 8 setae and 2 sensilla; clypeus (Fig. 4f) with 4 pair of clypeal setae; labrum (Fig. 4f) strongly incised in the middle of anterior margin, W-shaped, with 2 pair of labral setae and 1 pair of labral sensilla; epipharynx with 7 pair of epipharyngeal setae; hypopharynx with numerous spines on the antero-lateral side; mandible (Fig. 4d) palmate, well-sclerotized, with 5 distal teeth, 3rd to 5th teeth short and dull, 2 mandibular setae; maxillary palp (Fig. 4g) 3-segmented, segment 1 with 1 sensillum, segment 2 with 1 seta and 1 sensillum, segment 3 with 1 seta; palpifer with 2 setae; stipes with 2 setae; cardo with 1 seta; galea with 9 setae; labial palp 2-segmented, segment 1 with 1 sensillum, segment 2 with 1 sensillum; prementum and postmentum separated by sclerotized membrane; prementum with 4 pair of setae and 1 pair of sensilla, postmentum with 3 pair of setae and 1 pair of sensilla. *Thorax.* Pronotum (Fig. 4h) reddish brown, strongly sclerotized, with 22 pair of setae; mesothoracic spiracles (Fig. 4e) annuliform, situated on epipleural anterior part; epipleuron with 3 setae; peritreme strongly sclerotized; legs rather long and stout; tibia with 7 setae; tarsungulus (Fig. 4i) falciform, strongly curved at anteriorly, enlarged base with 1 seta; pulvillus whitish, bladder-like, as long as tarsungulus. *Abdomen.* Typical abdominal segments with three folds; abdomen with 8 pair of spiracles, the peritremes circular, adjacent area broadly sclerotized; pygopod developed.

Body length. 16 mm (N = 5). Head width: 2.4 mm (N = 5).

Material examined. SOUTH AFRICA, **Transvaal,** Lapalala Nat. Res. 22 January 1987, larvae collected on the leaves of *Sclerocarya caffra* Sond. (Anacardiaceae) and determined by B. Grobbelaar.

Genus *Euplectroscelis* Crotch, 1873

Euplectroscelis xanti Crotch, 1873
(Fig. 5)

Description. *Mature larva* (Fig. 5a). Body creamy yellow, slightly convex; head and legs brown, mandibles dark brown, pronotum and spiracles pale brown. *Head* (Fig. 5c). Hypognathous, rounded, slightly sclerotized; frontal suture broadly divergent and nearly straight; frons with 3 pair of frontal setae and 1 pair of frontal sensilla; endocarina (i.e., crista frontalis is located between the frontal sutures) developed; coronal suture well-developed; epistomal suture developed; stemmata 1 in number on each side; antenna (Fig. 5b) 1-segmented, segment with a large conical sensory papilla, 8 setae and 2 sensilla; clypeus (Fig. 5f) with 2 pair of clypeal setae and 2 pair of clypeal sensilla; labrum (Fig. 5f) slightly incised in the middle of anterior margin, W-shaped, with 2 pair of labral setae and 1 pair of labral sensilla; epipharynx with 6 pair of epipharyngeal setae; mandible (Fig. 5d) palmate, well-sclerotized, with 5 distal teeth and 1 mandibular seta and 1 sensillum; maxillary palp (Fig. 5g) 3-segmented, segment 1 with 1 sensillum, segment 2 with 2 setae and 1 sensillum,

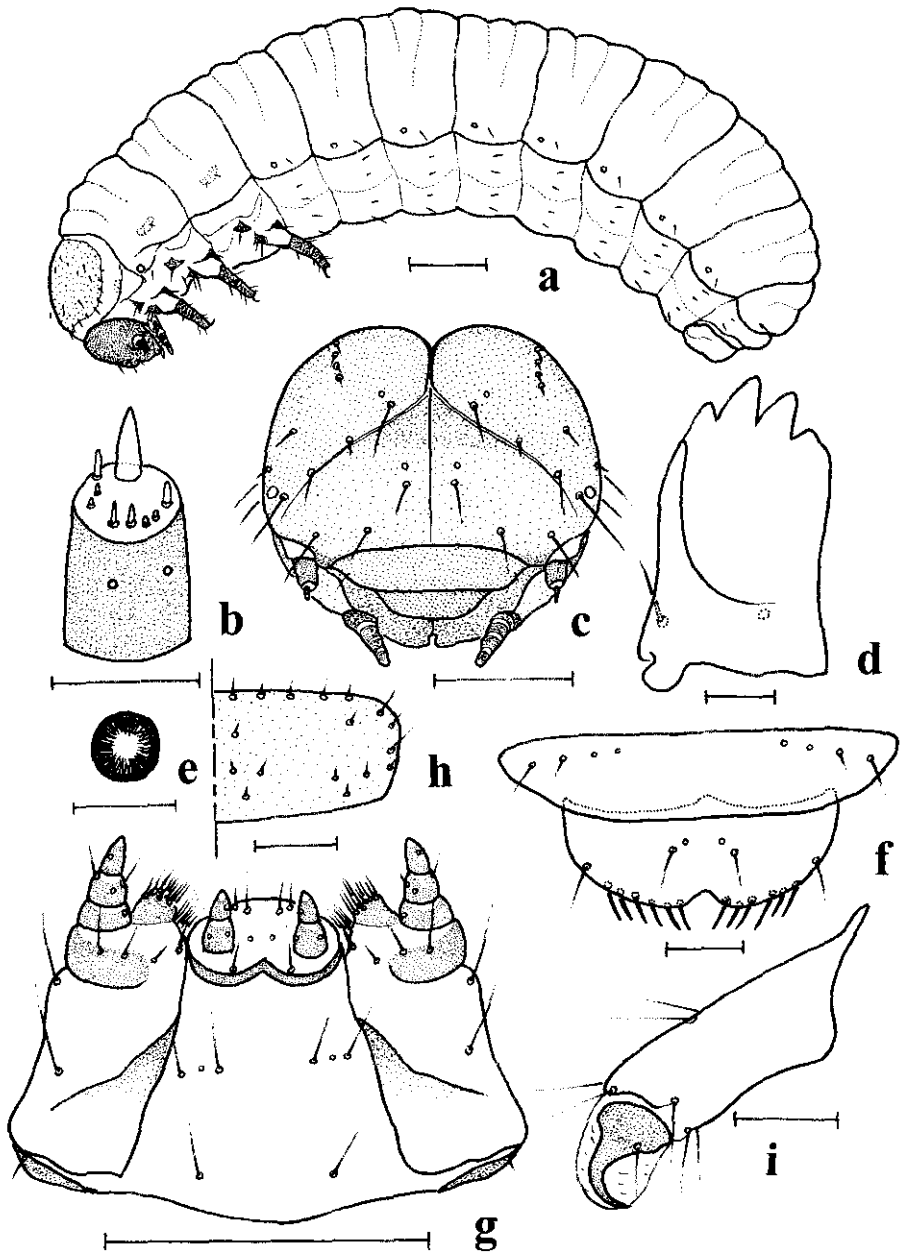

Fig. 5. *Euplectroscelis xanti*: (1) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

segment 3 with 1 sensillum; palpifer with 3 setae; stipes with 3 setae; cardo with 1 seta; galea with 9 setae; lacinia with tightly bunched group of 6 setae located behind galea; labial palp 2-segmented, segment 1 with 2 sensilla, segment 2 with 1 sensillum; prementum and postmentum separated by sclerotized membrane; prementum with 3 pair of setae and 1 pair of sensilla, postmentum with 3 pair of setae and 1 pair of sensilla. *Thorax.* Pronotum (Fig. 5h) pale brown, weakly sclerotized, with 17 pair of setae; mesothoracic spiracles (Fig. 5e) annuliform, situated on epipleural anterior part; epipleuron with 2 setae; peritreme strongly sclerotized; legs rather long and stout; tibia with 7 setae; tarsungulus (Fig. 5i) falciform, moderately curved at anteriorly, enlarged base with 1 seta; pulvillus whitish, bladder-like, as long as tarsungulus. *Abdomen.* Typical abdominal segments with three folds; abdomen with 8 pair of spiracles, the peritremes circular; pygopod developed.
Body length. 9.5 mm (N = 5). Head width: 1.2 mm (N = 5).
Material examined. MEXICO, **Baja California Sur,** East of Todos Santos, 17 Sept. 1988, larvae collected on the leaves of *Bursera odorata* Brandegee and determined by E. Riley.

Genus *Ophrida* Chapuis, 1875

Ophrida marmorea (Wiedemann, 1819)
(Fig. 6)

Description. *Mature larva* (Fig. 6a). Body yellowish brown, strongly convex, C-shaped; head, mandibles, legs, and spots dark brown, pronotum and spiracles pale brown. *Head* (Fig. 6c). Hypognathous, rounded, strongly sclerotized; frontal suture broadly divergent and sinuate; frons with 4 pair of frontal setae; endocarina (i.e., crista frontalis is located between the frontal sutures) developed; coronal suture well-developed; epistomal suture developed; stemmata 1 in number on each side; antenna (Fig. 6b) 1-segmented, segment with a large conical sensory papilla, 10 setae and 2 sensilla; clypeus (Fig. 6f) with 4 pair of clypeal setae; labrum (Fig. 6f) strongly incised in the middle of anterior margin, W-shaped, with 2 pair of labral setae and 1 pair of labral sensilla; epipharynx with 4 pair of epipharyngeal setae; mandible (Fig. 6d) palmate, strongly sclerotized, with 5 distal teeth, 5th tooth broad, 2 mandibular setae and 1 sensillum; maxillary palp (Fig. 6g) rather long and stout, 3-segmented, segment 1 without seta, segment 2 with 2 setae and 1 sensillum, segment 3 with 1 sensillum; palpifer with 3 setae; stipes with 3 setae; cardo with 1 seta; galea with 8 setae; lacinia with tightly bunched group of 8 setae located behind galea; labial palp 2-segmented; prementum and postmentum separated by narrow sclerotized membrane; prementum with 3 pair of long setae and 1 pair of sensilla, postmentum with 8 pair of setae. *Thorax.* Pronotum (Fig. 6h) pale brown, strongly sclerotized, with 48 pair of setae; mesothoracic spiracles (Fig. 6e) annuliform, situated on epipleural anterior part; epipleuron with 2 long and 2 short setae; peritreme strongly sclerotized; legs rather long and stout; tibia with 7 setae; tarsungulus (Fig. 6i) falciform, strongly curved at anteriorly, enlarged base with 1 seta. *Abdomen.* Typical abdominal segments with two folds; abdomen with 8 pair of spiracles and with long setae laterally, the peritremes circular; pygopod developed.
Body length. 9.0 mm (N = 5). Head width: 1.6 mm (N = 5).

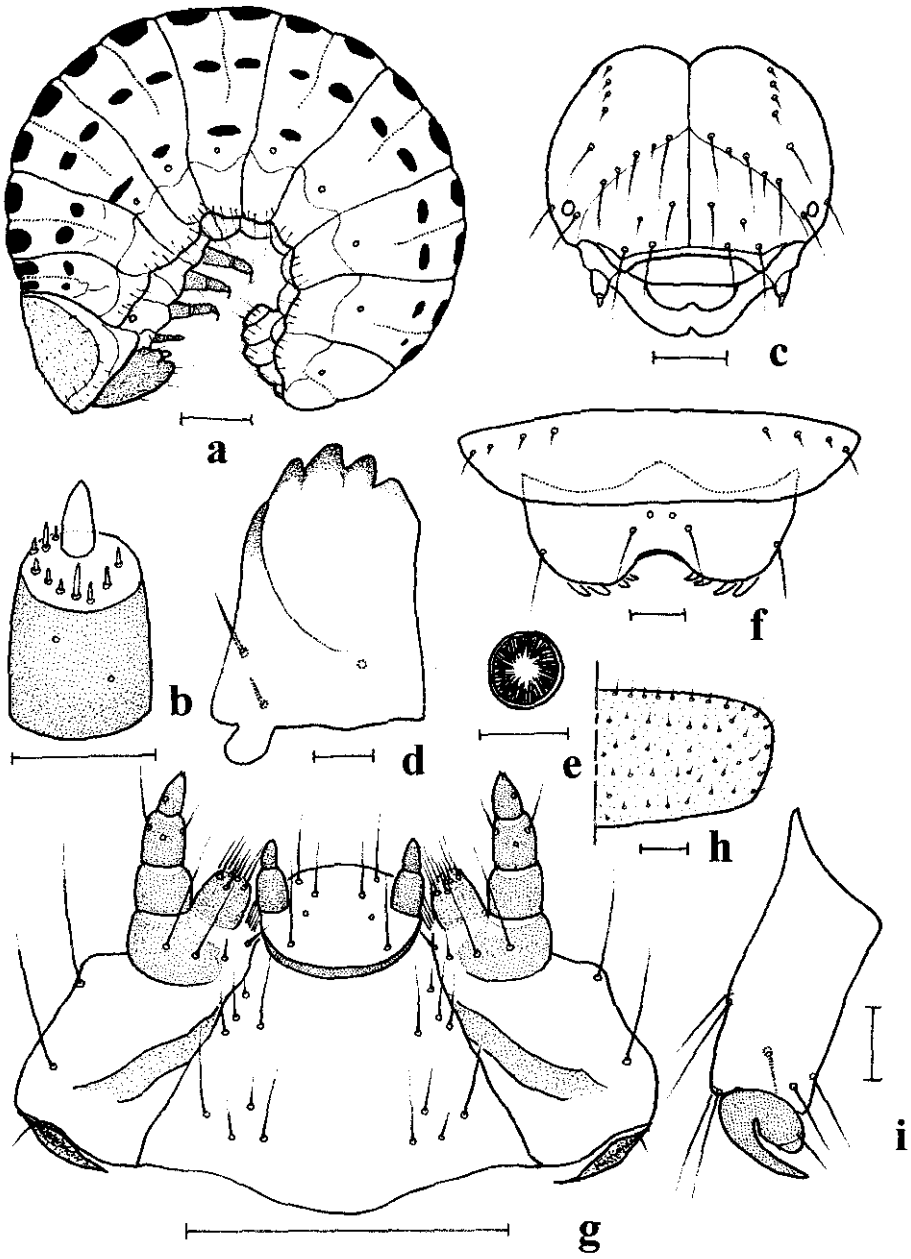

Fig. 6. *Ophrida marmorea*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

Material examined. INDIA, **Mormugao,** Goa Port, 25 April, 1945, larvae collected on the leaves of *Spondias* sp. (Anacardiaceae) and determined by J. C. Bridwell.

Genus *Podontia* Dalman, 1824

Podontia affinis (Gröndal, 1808)
(Fig. 7)

For a detailed description of this species see Lee (1999b).
Body length. 12.0 mm (N = 5). Head width: 2.0 mm (N = 5).
Material examined. VIETNAM, Boun-Coi, 30 June 1981, larvae collected and determined by L. N. Medvedev.

Podontia dalmani Baly, 1865
(Fig. 8)

For a detailed description of this species see Lee (1999b).
Body length. 20.0 mm (N = 5). Head width: 2.1 mm (N = 5).
Material examined. VIETNAM, Uadlen, 22 March 1987, larvae collected and determined by L. N. Medvedev.

Podontia lutea (Olivier, 1790)
(Fig. 9)

For a detailed description of this species see Lee (1999b).
Body length. 18.0 mm (N = 5). Head width: 2.7 mm (N = 5).
Material examined. VIETNAM, Tam-dao, 3 May 1985, larvae collected and determined by L. N. Medvedev.

Shared Larval Morphology

Common characters of the 9 species of the *Blepharida*-group:
1. Antenna 1-segmented
2. Mandible without penicillus
3. Anterior margin of labrum incised (notched)
4. Stemmata 1 in number on each side
5. Endocarina developed
6. Coronal suture well-developed
7. Frontal suture Y-shaped

ADULT MORPHOLOGY

There are a number of adult external morphological characters shared by most of the genera in what is considered the *Blepharida*-group (see Table 3); however, most of these characters are shared either by most (not all) of the genera or by several genera within this group (i.e., subgroups).
The following are characters shared by almost all the genera in this group:

1) general body shape is robust, chrysomeline-like, with the pronotum and elytra dorsally very convex, and with a strong humerus.

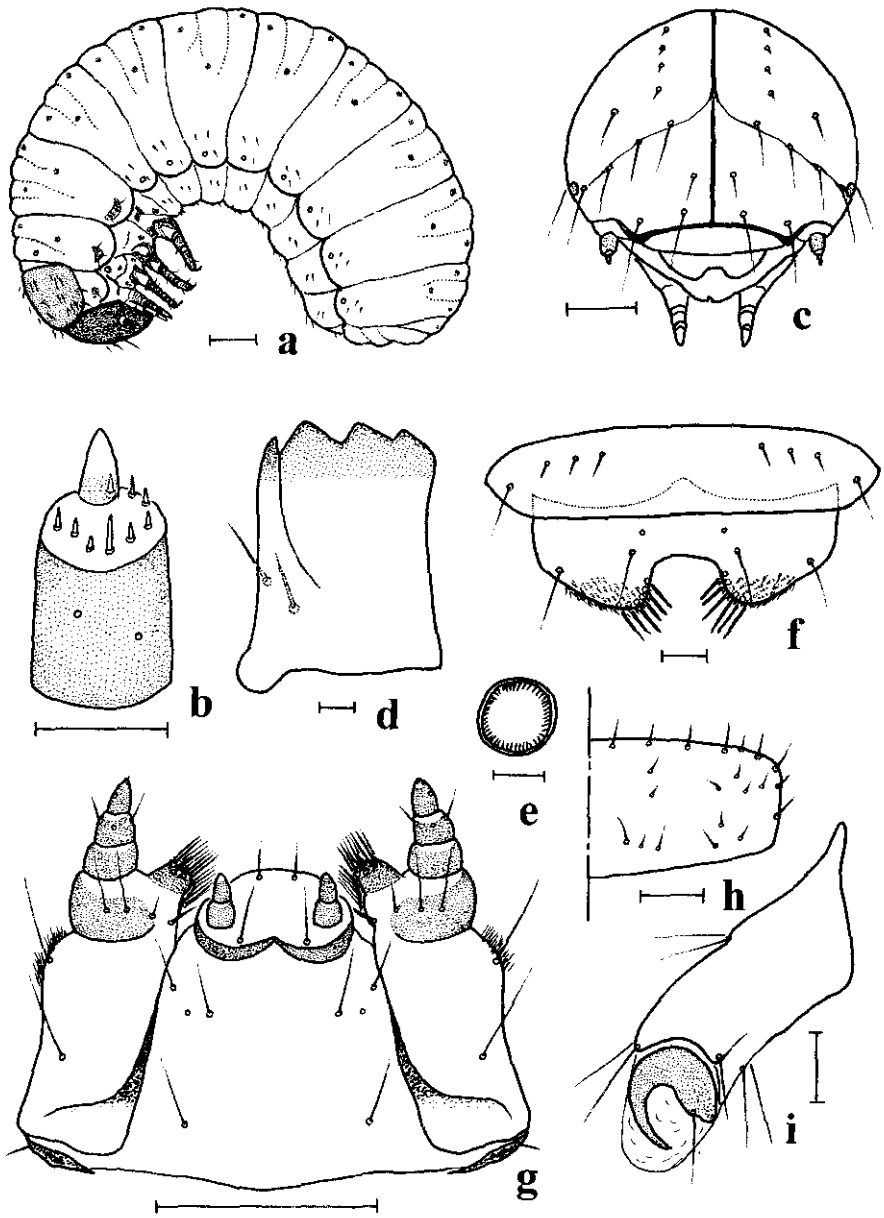

Fig. 7. *Podontia affinis*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

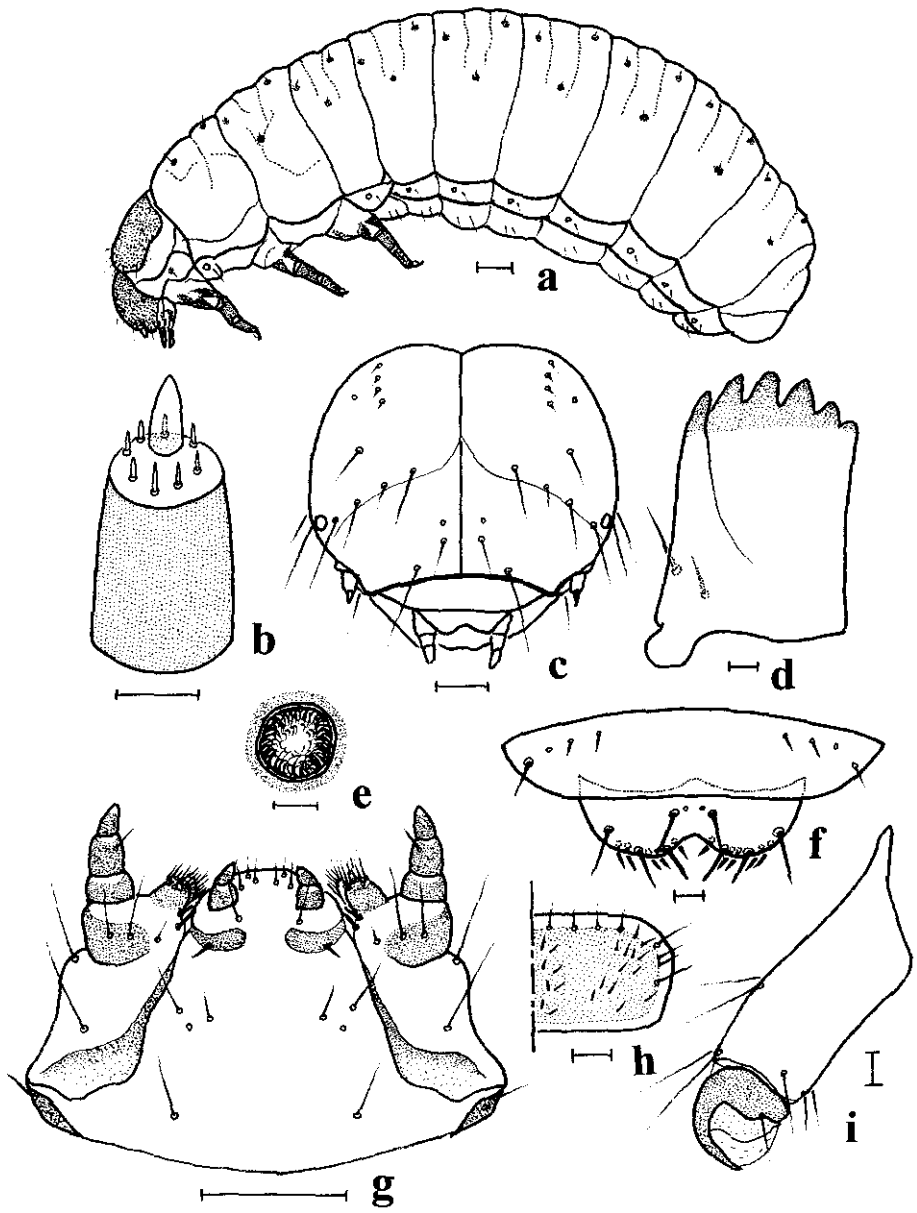

Fig. 8. *Podontia dalmani*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

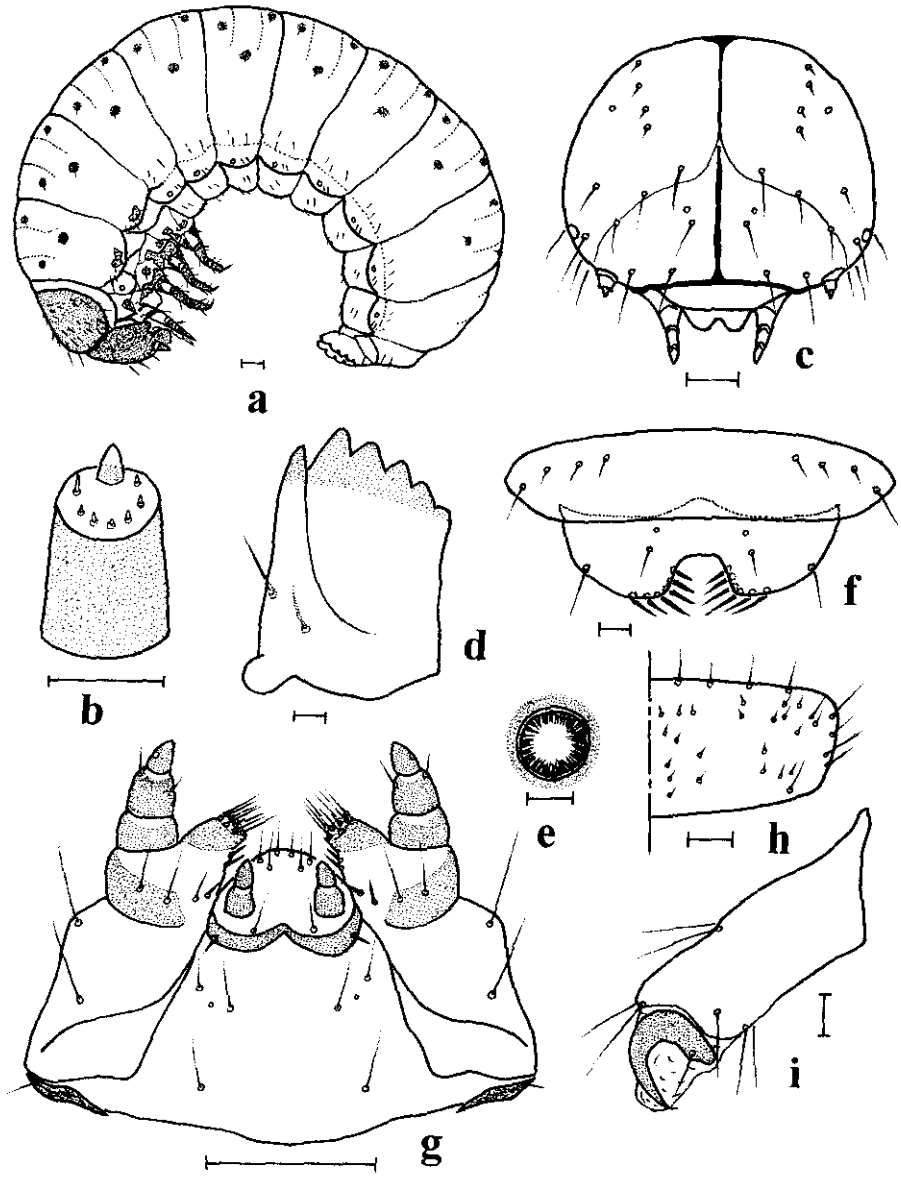

Fig. 9. *Podontia lutea*: (a) mature larva, lateral view; (b) antenna, dorsal view; (c) head, dorsal view; (d) mandible, buccal view; (e) spiracle, dorsal view; (f) clypeus, labrum and epipharynx, dorsal view; (g) lower mouth parts, ventral view; (h) pronotum, dorsal view; (i) left hind leg, dorsal view.

Scale line—1.0 mm (Fig. 1a); 0.5 mm (Fig. 1c, g, h); 0.1 mm (Fig. 1b, d, e, f, i).

2) eye shape is elongate-oval vertically and usually converging dorsally with the dorsal inter-ocular distance approximately equal to or less than the maximum vertical eye length.
3) metatibia with apex of dorsum usually emarginate/excavated or depressed and flattened often creating the appearance of a preapical tooth (Figs. 13–16).
4) metafemoral spring morphology (*Blepharida* Morpho-group) (cf. Furth and Suzuki, 1998) (Figs. 10–12).

The following character states are shared by different subgroups within the *Blepharida*-group (Table 3):

1) tarsal claws bifid (separate teeth); bifid (small basal tooth); simple; or appendiculate
2) procoxal cavities open or closed
3) frons and vertex with either few and fine punctures or coarse punctation
4) frons and vertex sculpture with either no/few impressed lines or deeply impressed lines
5) pronotal shape either transverse with anterior margin U-shaped or lyre-shaped with lateral margins sinuate and anteriorly widened
6) pronotal punctation either fine and confused or with some deeply impressed puncture lines or puncture rows
7) pronotal sculpture with either no/few impressions or with distinct deep impressions
8) metafemoral shape either greatly inflated and evenly rounded or club-like/eumolpine-like with distinct basal/apical tapering
9) eye shape usually elongate-oval and oriented dorso-medially or more oval and more vertical
10) eye size large relative to the front and inter-antennal distance or distinctly smaller
11) proepimeron laterally separated from the pronotum by a distinct groove or suture
12) metatibial apex dorsally strongly emarginate on outer edge or weakly emarginate almost flattened
12) elytral pattern (if bicolored) asymmetrical (most with a mottled pattern) or symmetrical (not in Table 3)

The metafemoral spring form of all 9 species falls into the *Blepharida* Morpho-group (see Furth and Suzuki, 1998). The spring's dorsal extended arm reaches noticeably beyond the ventral lobe and is only slightly slanted downward apically, the spring basal angle is acute and pointed basally and without a chitinized recurve flange. These 9 species in 5 genera were represented by two forms, one with the dorsal extended arm as long as or longer that the ventral lobe (*Diamphidia* and *Podontia*) (Figs. 10, 12), and the other with the dorsal extended arm much shorter than the ventral lobe (*Blepharida, Euplectroscelis, Ophrida*) (Fig. 11).

DISCUSSION

Recently there has been considerable interest in constructing phylogenies using cladistic methodology. Interestingly there have not been many attempts to analyze the adult and larval forms of single groups even though such analysis seems to be

Fig. 10. *Diamphidia* sp.: metafemoral spring (actual size, length = 1.55 mm).

logical because the adults and larvae of a taxon must have a common evolution. However, this exercise is more difficult than it seems because for many groups of Coleoptera the larvae are very poorly known. Such is the case for Chrysomelidae, especially Alticinae and the closely-related subfamily Galerucinae which together contain about 1,000 genera. Besides the huge diversity in these groups, this lack of knowledge is primarily because most groups within these subfamilies have root-feeding larvae which are very difficult to rear.

Lawrence and Britton (1991) combined the Alticinae and Galerucinae into one subfamily (Galerucinae) based primarily on the fact that there were no apparent differences between the larvae of these subfamilies (an old idea, see Introduction above), they stated "Alticine larvae are not separable from those of other galerucines, and transitional forms occur among the adults as well." However, they did not give any data, further details or references for either part of this statement. Lawrence and Newton (1995) proposed a comprehensive new/revised classification of the Co-

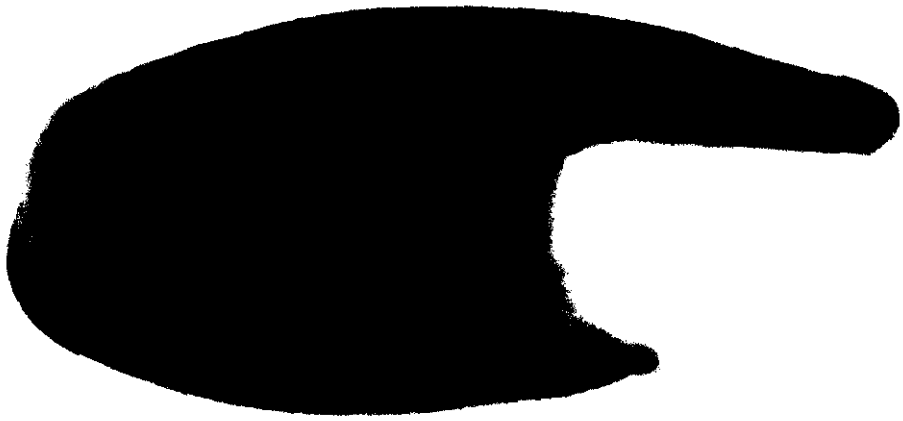

Fig. 11. *Ophrida marmorea*: metafemoral spring (actual size, length = 1.58 mm).

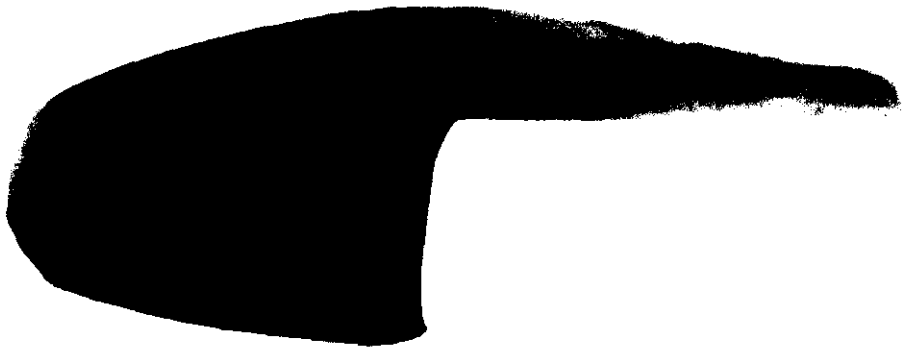

Fig. 12. *Podontia dalmani*: metafemoral spring (actual size, length = 1.75 mm).

leoptera and their treatment of the Chrysomeloidea was based on the cladistic phylogenetic analysis of Reid (1995) who lumped the Galerucinae and Alticinae (no data given) even before he did his phylogenetic analysis. Reid's phylogenetic analysis was based on 19 chrysomelid taxa purporting to represent the approximately 2,300 genera and using 71 characters (48 adult and 23 larval). Reid (1995) used the exemplar approach which assumed that less that 1% of the genera accurately represented the character states of all genera and that the species used from each genus were true representatives (of the characters used) for all species in each genus; the species used in that study were not given, so it is difficult to confirm that the latter was true. In addition to some new data, Reid (1995) took his character data from many different studies which had used a variety of techniques to study these characters. Although this was the first attempt of cladistic phylogeny of the Chrysomeloidea it could not possibly represent an accurate classification of this prodigious group. Because Lawrence and Newton (1995) provided a new and comprehensive

Fig. 13. *Blepharida sacra*: apex of metatibia (actual size, length = 1.33 mm).

Fig. 14. *Diamphidia* sp.: apex of metatibia (actual size, length = 1.53 mm).

classification of beetles, many workers have tended to accept and use this classification without careful attention to the problems with Reid's analysis of the chrysomelids. Lingafelter and Konstantinov (2000) also attempted an exemplar approach to resolve the alticine-galerucine problem, but their "major lineages" were greatly under-representative and certain character states may not have been correctly represented by the exemplars chosen (e.g., the coding of *Blepharida* for the absence of vaginal palpi, which was shown by Furth, 1998, not to be the case).

The lumping of Galerucinae and Alticinae just because of the lack of larval dif-

Fig. 15. *Ophrida marmorea*: apex of metatibia (actual size, length = 1.75 mm).

Fig. 16. *Podontia affinis*: apex of metatibia (actual size, length = 1.75 mm).

ferences is very premature (pun intended) and is primarily based on studies done by Böving (Böving, 1927, 1929; Böving and Craighead, 1931) which only studied relatively few Galerucinae and Alticinae (6 of the 12 Galerucinae tribes and only 14 genera of Alticinae, primarily of species from the USA and a few from Denmark). Böving and Craighead (1931) stated that there needs to be considerably more comprehensive studies of the larvae of these two groups before an accurate classification can be constructed (see details below). As discussed elsewhere (Furth and Suzuki, 1994, 1998; Konstantinov, 1998) there are a variety of reasons for continuing the classification of the Galerucinae and Alticinae as separate subfamilies as listed in Seeno and Wilcox (1982). The lumping of Galerucinae and Alticinae into a single subfamily (Galerucinae) is an old idea; however, because the cladistic treatment by Reid (1995) did not actually analyze this question (i.e., no data-based analysis), no valid or useful purpose can be served by reverting to this classification as proposed in Lawrence and Newton (1995), which did not analyze or explain such a change. In the present study we continue to follow the concept of Galerucinae and Alticinae as separate subfamilies.

Larvae

Böving (1927) said that "in general aspect and structural details the Halticini larvae [*Altica* Geoffroy, etc.] are more similar to the main bulk of the Galerucinae larvae than these latter [Galerucinae] are to the Diabroticini and Phyllobroticini larvae and more than the Halticini larvae themselves are to the Halticinae tribes Systenini, Crepidoderini, and Psylliodini." Unlike most other Alticinae (root feeders), *Blepharida* [Blepharidini- *sensu* Leng (1920) and Böving (1927)] are external leaf feeders and are generally quite easy to rear. In the western Palearctic only 19% of the Alticinae species larvae are known (Steinhausen, 1996) and many of these are either external leaf feeders, leaf miners (e.g., *Argopus* Fisher, *Dibolia* Latreille, *Mantura* Stephens, *Sphaeroderma* Stephens, etc.—relatively easy to rear) or species of significant agricultural importance (e.g., *Phyllotreta* Chevrolat, *Psylliodes* Latreille,

etc.). Böving (1927) also stated: "If, however, it is deemed advisable on account of the characters of the imagines to retain the two subfamilies Galerucinae and Halticinae, the Diabroticini and Phyllobroticini should be removed from the first and placed in the second, and at least one tribe, the Blepharidini, should be excluded from the Halticinae." Paterson (1943) stated "The larval anatomy of *Haltica cuprea* is similar to that of other Halticinae, but the larvae of *Blepharida nigrotesselata* bear little superficial resemblance to those of other species in the subfamily." Paterson (1943) also noted various unique features of *Blepharida* larvae such as the "soft-bodied, shiny moist appearance with longitudinal whitish stripes which seem to be the Malpighian tubules showing through the translucent skin"; the arched body during feeding conceals the blackish, head and legs and the anal proleg forms a strong sucking disc, the anus is located dorsal to the anal proleg, normal alticine tubercles are lacking, "even the 'egg-burster' tubercle, which occurs in the first-instar of most Chrysomelid larvae, is also lacking," certain of the ventral setae are missing, and it differs from *Altica* by having a single large ocellus. Furth (1982b) also described living *Blepharida* larvae and noted that the longitudinal whitish stripes were apparently fat bodies rather than Malpighian tubules as mentioned by Paterson (1943).

In the present study of the species of the *Blepharida*-group seven larval characters are shared: 1-segmented antenna; mandible without penicillus; anterior margin of labrum incised (notched); one stemmata on each side; endocarina developed; coronal suture well-developed; and frontal suture Y-shaped. Many Alticinae larvae have 2-segmented antenna, especially leaf feeders in the genus *Altica,* as well as leaf miners (e.g., *Mantura* Stephens, *Argopus* Fischer, *Sphaeroderma* Stephens, *Chaetocnema* Stephens, except *Argopistes* Motschulsky, *Dibolia* Latreille) and soil dwellers (e.g., *Systena* Chevrolat, *Sangariola* Jacobson, *Epitrix* Foudras, *Hermaeophaga* Foudras, *Longitarsus* Latreille).

Most leaf mining Alticinae have no coronal suture, but do have a V-shaped frontal suture. The larval morphology of certain Alticinae larvae is quite different from others because of their feeding habitats. Leaf miners and stem borers are similar to Hispinae larvae and are characterized by having a flat body form, coronal suture absent, reduced labial palp, first to eighth abdominal segments each with a triangular projections, labial palp 1-segmented and strongly reduced and sparse setae. Characters of soil dwelling alticine larvae are very similar to those of external leaf feeders, but are easily distinguished by their very long and slender body shape.

These nine *Blepharida*-group species are external leaf feeders and are similar to some Galerucinae larvae in a few features (antennae 1-segmented, 1 stemmata on each side of head, general shape of lower mouth parts), but they differ in other significant characters (body with short and sparse setae, anterior margin of labrum somewhat incised (notched), postmentum with 3 pair of setae and 1 pair of sensilla).

Adults

Although there is no single easily discernable external morphological character which separates adult members of the many genera of the *Blepharida*-group, there is a combination of several characters which help define this group. However, probably the best shared characters concern the biology of these genera, especially their

shared food plant families (Anacardiaceae and Burseraceae) and their larval morphology.

Based on the morphological characters of the adults it appears that there are different subgroups within the *Blepharida*-group. This is particularly true for the shape of the apex of the metatibia, tarsal claws, pronotal shape and sculpturing, and eye shape and size. This probably indicates different lineages within the group which share broader biological characters. Until a comprehensive phylogenetic study of these genera is conducted it will be difficult to speculate further about the relationships within the *Blepharida*-group of genera. Some phylogenetic studies which use one taxon to represent many (i.e., the exemplar approach) have a high risk of error as increasingly larger numbers of genera are represented by only one species. On the contrary, we believe that such a phylogenetic analysis should be done using representatives of most or at least a majority of the member genera and by studying the characters used from a majority of the species in order to be certain the characters are coded in a representative manner.

The adult characters which best define the *Blepharida*-group are: the emarginate dorsum of the metatibial apex (except *Ophrida* which is more depressed or flattened); the elongate-oval eye shape, converging dorsally (except *Diamphidia* and *Podontia*); the general convex, chrysomeline appearance of the body; bifid tarsal claws (except *Euplectroscelis*); *Blepharida* Morpho-group form of the metafemoral spring (two subgroups of *Blepharida*/*Euplectroscelis*/*Ophrida* and *Podontia*/*Diamphidia*); and procoxal cavities closed (except *Diamphidia* and a few *Blepharida* (*sensu stricto*)). The two subgenera studied here (*Blepharida sensu stricto* and *Blepharidina*) also have adult character differences.

There are a variety of characteristics that strongly suggest a close (monophyletic) relationship of the 19 *Blepharida*-group taxa worldwide. These characteristics range from the morphological similarities of adults and larvae to a variety of factors of their biology, behavior, and foodplant relationships. As stated in Furth (1992) there is still considerable study needed of the Old World *Blepharida*-group genera in order to clearly resolve their morphological and phylogenetic relationships. Even the phylogenetic relationship of the New World genera are in need of analysis, especially genera such as *Acrocyum* Jacoby, *Chrysogramma* Jacoby, *Crimissa* Stål, *Elithia* Chapuis, and *Procalus* Clark. Therefore, it is obvious that the *Blepharida*-group is unique within the Alticinae and that considerably more study of the larvae and the adults needs to be conducted in order to resolve the questions and ranking of Galerucinae and Alticinae.

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