

Phylogeny of Diboliina inferred from a morphologically based cladistic analysis (Coleoptera: Chrysomelidae: Galerucinae)

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Abstract

A cladistic analysis of 14 genera of hemispheric flea beetles based on adult morphological characters is presented. A multiple origin of hemispheric body shape is concluded. The phylogenetic position of the hemispheric genus *Argopistes* Motschulsky, 1860 is studied and its attribution to the subtribe Diboliina is proposed. A phylogenetic analysis of subtribe Diboliina using cladistic methods and based on morphological characters is carried out. Inferred from the results of this analysis this subtribe retains four genera: *Argopistes*, *Dibolia* Latreille, 1829, *Megistops* Boheman, 1859, and *Paradibolia* Baly, 1875. A diagnosis of the subtribe Diboliina, a redescription, a key to genera, and an annotated list of genera are given. Trends in morphological transformations in Diboliina and other alticines are discussed.

Key words

Diboliina, *Argopistes*, *Dibolia*, *Megistops*, *Paradibolia*, flea beetles, phylogeny, cladistic analysis, morphology.

1. Introduction

The flea beetles Alticini is the most species rich taxon among family Chrysomelidae and comprises 534 genera and ca. 8 000 species (KONSTANTINOV & VANDENBERG 1996; NADEIN 2012). According to modern views (REID 1995; LINGAFELTER & KONSTANTINOV 2000; GÓMEZ-ZURITA et al. 2007) the flea beetles are treated here in the tribal rank within subfamily Galerucinae. A generally accepted classification of Alticini does not exist and the generic groups are in need of revision. The most recent works concerning phylogeny of Alticini (TAKIZAWA 2005; GÓMEZ-ZURITA et al. 2007; GE et al. 2012) are based on different sources of both morphological and molecular data.

The morphological approach gives useful criteria to revise existing generic groups. Alticini are morphologically diverse and represented by different forms. One of the most remarkable example is a hemispheric

body shape. Traditionally, based on the general body shape, the hemispheric alticines are grouped together (NADEIN 2013a). This refers to the first system of Alticini by CHAPUIS (1875) (subtribe Mniophilina) and to the so-called “catalogue phylogeny” (HEIKERTINGER & CSIKI 1939, 1940; SEENO & WILCOX 1982) which arranges together hemispheric and other flea beetle genera based on a phenetic rather than a phylogenetic approach.

As an example, in the classification of CHAPUIS (1875) the genus *Argopistes* Motschulsky, 1860 is placed in the subtribe Mniophilina together with *Argopus* Fischer von Waldheim, 1824, *Sphaeroderma* Stephens, 1831, *Mniophila* Stephens, 1831, *Minota* Kutschera, 1859, and *Apteropeda* Chevrolat, 1836. Comparative morphological analysis of over 130 alticine genera (NADEIN 2007, 2013a, and unpublished personal data) and larval morphological

and bionomical studies (TAKIZAWA 2005; ZAITSEV & MEDVEDEV 2009) resulted in a hypothesis on the affinity of *Argopistes* to *Dibolia* Latreille, 1829, *Megistops* Boheman, 1859 and *Paradibolia* Baly, 1875. The latter genera (excepting *Paradibolia*) were classified to the subtribe Diboliina (CHAPUIS 1875; SAVINI 1993).

The present work attempts to test the phylogenetic links of some hemispheric alticines with a special emphasis to the genus *Argopistes*.

2. Material and methods

2.1. Material examined

A comparative morphological analysis of over 130 genera of Alticini was carried out by NADEIN (2007 and unpubl. data). 42 species from 25 genera were examined in detail in the course of this study (Table 1). The latter set of taxa was chosen for analysis to test phylogenetic links of some hemispheric flea beetles and the hypothesis of an affinity of *Argopistes* to genera of the subtribe Diboliina and the genus *Paradibolia*. The set of taxa is based on previous phylogenetic studies of alticines (REID 1995; LINGAFELTER & KONSTANTINOV 2000; KIM et al. 2003; GE et al. 2012; NADEIN 2013a). The genera represent major generic groups and possibly some phylogenetic lineages: Oedionychina, Alticina, Aphthonina, Blepharidina, Chaetocnema, Psylliodina, Manobiina, Nonarthrina, Febraina.

The material treated in the paper is housed in the following collections: Natural History Museum, London (NHML); Museum für Naturkunde, Humboldt Universität, Berlin (MNHU); Senckenberg Deutsches Entomologisches Institut, Müncheberg (SDEI); Zoological Institute, Saint-Petersburg (ZIN); and A. Warchałowski collection, Wrocław (AW).

2.2. Examination of specimens and morphological terminology

Specimens of Alticini involved in this study were dry-pinned. At least one specimen of each species examined was cleared, rinsed in distilled water, and dissected. Some of the dry-pinned specimens were examined intact. Special emphasis was placed on the study of the sclerotized structures of the genitalia. Specimens or separated abdomens were boiled in 10% KOH solution for several minutes, after which they were rinsed in distilled water and dissected in water or glycerin. Finally, the structures were placed in glycerin slides and glass vials for study and storage. Photos were taken with a digital camera Nikon

D5100 attached to a light microscope (Nikon Eclipse 80i) and a dissecting microscope (Nikon SMZ800).

The morphological terminology follows the works of KONSTANTINOV (1994, 1998a,b), KONSTANTINOV & VANDENBERG (1996), LINGAFELTER & KONSTANTINOV (2000), BEUTEL & LESCHEN (2005), and HÜBLER & KLASS (2013).

2.3. Cladistic analysis

Twenty-five terminal taxa were scored for 50 characters of the adults (Table 2), with the majority of them discussed previously (NADEIN 2013a,b) or, otherwise, with comments supplemented to characters. The character matrix was constructed with Nexus Data Editor* (version 0.5.0 by R. Page, 1998). Characters are variously coded as binary or multistate. All character states were treated unordered and equally weighted. Inapplicability of a character to a taxon was coded with “-”.

Tree reconstruction was done with PAUP* 4.0b10 (SWOFFORD 2001) implementing heuristic tree searches that include the following settings: shortest trees were heuristically searched with 100 tree-bisection-reconnection (TBR) replications, swapping on all trees, random addition sequences (5000 replicates). Bootstrap values were calculated by resampling at 1000 replications using simple searches while holding 1 tree at each step and swapping on the best tree. Characters were optimized onto trees using ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimizations. Trees were rooted using the genus *Hyphasis* Harold, 1877 as outgroup taxon. A strict consensus tree was built to perform the results of analysis.

2.4. List of characters

Body

1. Body, length to width ratio: (0) >1.6; (1) 1.4–1.6; (2) <1.4 (hemispherical).

Head capsule

2. Head, dorsal view, length to width ratio: (0) ≤1; (1) > 1.
3. Head orientation: (0) hypognathous (NADEIN 2013b: figs. 1–9); (1) opisthognathous (Figs. 4, 12, 15); (2) intermediate position (Figs. 18, 19).
4. Eyes, distance: (0) shortest distance between eyes larger than transversal diameter (Fig. 22); (1) shortest distance between eyes smaller than transversal diameter (Fig. 20); (2) shortest distance between eyes smaller than diameter of antennal socket (Figs. 21, 23).
5. Ocular sulci: (0) present (NADEIN 2013b: figs. 19–23); (1) absent (Figs. 20–23).

Table 1. Taxa examined for phylogenetic analysis.

Species	Locality	Number of specimens, Depository
<i>Argopistes biplagiatus</i> Motschulsky, 1860	Russia (Far East), Korea, Japan	15, ZIN
<i>Argopistes simoni</i> (Baly, 1878)	Australia	3, NHML
<i>Argopistes tsekooni</i> Chen, 1934	Japan	3, SDEI
<i>Argopistes unicolor</i> Jacoby, 1885	Japan	2, SDEI
<i>Argopistes atricollis</i> Chen, 1934	India	1, SDEI
<i>Argopistes</i> sp.	Australia	1, NHML
<i>Dibolia femoralis</i> L. Redtenbacher, 1849	Germany	5, AW
<i>Dibolia cryptocephala</i> (Koch, 1803)	Ukraine, Russia	3, SDEI
<i>Dibolia tshatkalica</i> Palij, 1968	Uzbekistan	1, AW
<i>Dibolia schillingii</i> Letzner, 1847	Russia	1, ZIN
<i>Dibolia cynoglossi</i> (Koch, 1803)	Russia	1, ZIN
<i>Megistops fenestra</i> (Illiger, 1807)	Brazil, Paraguay	5, NHML
<i>Megistops vandepolii</i> (Duvivier, 1889)	Argentina	4, NHML
<i>Megistops decorata</i> (Blanchard, 1851)	Brazil	1, ZIN
<i>Megistops trinitatis</i> Bryant, 1944	Trinidad	3, NHML
<i>Megistops decemmaculata</i> Bryant, 1944	Paraguay	1, ZIN
<i>Paradibolia coerulea</i> Bryant, 1927	Camerun	1, ZIN
<i>Paradibolia indica</i> Baly, 1875	India	2, NHML
<i>Paradibolia robusta</i> Weise, 1912	Kenya	1, NHML
<i>Paradibolia ruficollis</i> Weise, 1911	Siam	1, NHML
<i>Paradibolia philippinensis</i> Chen, 1934	Philippines	1, MNHU
<i>Halticorcus platyceri</i> Lea, 1917	Australia	5, NHML
<i>Longitarsus luridus</i> (Scopoli, 1763)	Ukraine	11, ZIN
<i>Altica viridicyanea</i> (Baly, 1874)	Russia	2, AW
<i>Manobia parva</i> Chen, 1934	Vietnam, Japan	14, AW
<i>Sphaeroderma testaceum</i> (Fabricius, 1775)	Ukraine	3, ZIN
<i>Ophrida spectabilis</i> (Baly, 1862)	China, Taiwan	13, SDEI; 18, MNHU
<i>Sphaerometopa acroleuca</i> (Wiedemann, 1819)	Java, Sumatra	9, MNHU
<i>Psyllodes attenuata</i> (Koch, 1803)	Mongolia	10, ZIN
<i>Hyphasis parvula</i> Jacoby, 1884	Sumatra, Vietnam	5, MNHU; 3, AW
<i>Chaetocnema major</i> (Jacquelin du Val, 1852)	Ukraine	2, ZIN
<i>Nonarthra cyanea</i> (Baly, 1874)	China (Guangxi), Japan	4, AW; 2 SDEI; 4 MNHU
<i>Erystus banksi</i> Weise, 1910	Manila, Philippines	10, MNHU
<i>Bhamoina varipes</i> (Jacoby, 1884)	Myanmar, India, Vietnam	4, MNHU; 2, AW
<i>Chabria angulicollis</i> (Clark, 1865)	Sumatra	8, SDEI; 2, MNHU
<i>Amphimela mouhoti</i> Chapuis, 1875	Sri Lanka	1, SDEI
<i>Acrocrypta philippina</i> Döberl, 1999	Philippines	7, SDEI; 2, MNHU
<i>Pentamesa trifasciata</i> Chen, 1935	China (Sichuan)	2, MNHU
<i>Argopus unicolor</i> Motschulsky, 1860	Russia (Far East)	12, ZIN
<i>Euphitrea micans</i> Baly, 1875	China, Java, Sumatra, Vietnam	7, SDEI; 18, MNHU; 3, AW
<i>Homelea variabilis</i> Jacoby, 1885	Sumatra	2, MNHU
<i>Neocrepidodera obscuritarsis</i> (Motschulsky, 1859)	Russia (Far East)	7, ZIN

6. Antennal groove: (0) absent (NADEIN 2013a: SI 2, fig. 2); (1) present (Figs. 20–24).
 7. Antennal sockets: (0) not separated by frontal ridge (Figs. 20–23); (1) separated by frontal ridge (NADEIN 2013b: figs. 19–21).
 8. Antennal sockets, distance: (0) larger than diameter of socket; (1) equal to diameter of socket or smaller (Figs. 20, 23).
 9. Elevation on vertex: (0) absent (Figs. 20–23); (1) present. – A central area of the vertex in the genus *Euphitrea* is strongly convex and elevated, its sides delimited from the eyes by very broad and deep grooves.
 10. Frontal area: (0) with longitudinal convex ridge (Figs. 20, 21); (1) triangular, more or less convex (Figs. 22, 23); (2) flat, without convexities (NADEIN 2013b: fig. 22)
 11. Frontal setae: (0) pair of long setae present (NADEIN 2013b: figs. 19, 21–24); (1) pair of long setae absent.
 12. Frontogenal suture: (0) absent (NADEIN 2013b: figs. 19, 21); (1) present (Figs. 20–23).
 13. Frontal calli: (0) present (Figs. 20–23); (1) absent.
 14. Frontal calli, position: (0) contiguous (Figs. 20–23); (1) not contiguous.
 15. Genae: (0) equal to or longer than half of transversal diameter of eye (NADEIN 2013b: figs. 19, 21–24); (1) shorter than half of transversal diameter of eye (Figs. 20, 21).
- Mouthparts**
16. Labral setiferous pores: (0) three pairs; (1) two pairs.
- Antennae**
17. Antennomere 1: (0) not longer than two following combined (can be shorter) (NADEIN 2013b: figs. 45–47); (1) distinctly longer than two following combined (Figs. 26, 27).
 18. Number of antennomeres: (0) 11; (1) 10; (2) 9.

Table 2. Morphological data matrix.

Taxon name	00000	00001	11111	11112	22222	22223	33333	33334	44444	44445
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890
<i>Argopistes biplagiatus</i>	20111	10100	11001	12000	10011	10101	21010	01011	10011	10100
<i>Dibolia femoralis</i>	10001	10100	11001	11000	00010	10100	21110	00011	10012	10100
<i>Megistops fenestra</i>	10211	10100	11001	12000	10010	10100	21110	00011	10011	10100
<i>Paradibolia coerulea</i>	10221	10100	11001	12000	10010	10121	21110	00011	10011	10100
<i>Longitarsus luridus</i>	00000	01100	10000	00010	00100	00000	00000	00112	20010	00000
<i>Altica viridicyanea</i>	00000	01100	10000	00011	00100	00000	00000	00000	00000	00101
<i>Manobia parva</i>	01000	01100	00000	10011	10000	00020	00000	00000	00102	00100
<i>Ophrida spectabilis</i>	10000	11001	101-0	00001	11100	01120	00010	10000	00000	10110
<i>Psylliodes attenuata</i>	00000	01000	10001	00110	00000	10200	00011	00112	20010	00000
<i>Hyphasis parvula</i>	10000	01100	10000	10000	11010	00100	01010	00000	01110	01100
<i>Chaetocnema major</i>	00000	01000	10001	00011	00100	11020	20010	10002	20000	00000
<i>Nonarthra cyanea</i>	10001	01002	10011	00200	11011	01101	01010	00000	00010	11010
<i>Halticorcus platycerii</i>	20110	10101	10001	12000	10011	10101	01010	00100	00012	00100
<i>Sphaeroderma testaceum</i>	20000	01100	10001	01000	11010	10110	00010	00100	00102	01100
<i>Sphaerometopa acroleuca</i>	10000	11101	10001	01000	10110	00100	10000	00000	00012	10010
<i>Erystus banksi</i>	20000	11001	10001	01000	11111	11101	10010	00000	00000	00010
<i>Bhamoina varipes</i>	20200	01100	10001	01000	11010	10110	00010	00100	00102	11100
<i>Chabria angulicollis</i>	10000	11001	10000	01000	10110	01100	10010	00000	00000	00110
<i>Amphimela mouhoti</i>	20200	1-002	101-1	01000	11011	00120	21010	00000	00000	00001
<i>Acrocrypta philippina</i>	10000	11001	10011	01000	10110	01101	10000	00000	00010	00010
<i>Pentamesa trifasciata</i>	20000	01000	10010	00000	11010	10100	00010	00100	00100	00100
<i>Argopus unicolor</i>	20000	01100	10000	00000	11010	10100	00010	00100	00102	11100
<i>Euphitrea micans</i>	10000	11011	10011	01000	11110	01100	10010	00000	00002	00111
<i>Neocrepidodera obscuritarsis</i>	00000	01100	10000	00011	01000	01020	00000	00100	00102	00000
<i>Homelea variabilis</i>	20000	01001	10011	01000	11110	01101	10000	00000	00000	10011

Thorax

- 19.** Pronotum, breadth: (0) as wide as base of elytra or nearly so (Figs. 3–19); (1) much narrower than base of elytra (NADEIN 2013b: figs. 1–18).
- 20.** Pronotum, dorsal surface: (0) without transversal and/or longitudinal grooves and furrows (Figs. 3–14); (1) transversal and/or longitudinal grooves or furrows present (NADEIN 2013b: figs. 48, 49, 51, 52).
- 21.** Pronotum, base: (0) not sinuate (NADEIN 2013b: figs. 1, 3, 7, 8); (1) sinuate (Figs. 35, 36).
- 22.** Pronotum, anterior margin: (0) straight; (1) emarginate. – In some genera of flea beetles, e.g. *Acrocrypta*, *Sphaerometopa*, *Chabria*, *Erystus*, the anterior angles of the pronotum are elongated forward forming a deep emargination between them when viewed from above.
- 23.** Pronotum, carina at posterior margin: (0) absent; (1) present.
- 24.** Pronotum, shape: (0) sides weakly converging anteriorly or nearly parallel-sided (NADEIN 2013b: figs. 6–10); (1) sides strongly converging anteriorly (Figs. 35–38).
- 25.** Hypomera, shape: (0) flat or weakly concave, not arcuate (NADEIN 2013b: figs. 50, 53, 55); (1) strongly concave, arcuate (Figs. 35–38).
- 26.** Prosternal process: (0) narrower than half of procoxal cavity (NADEIN 2013b: figs. 50, 55); (1) as wide as half of procoxal cavity or wider (Figs. 35–38).
- 27.** Procoxal cavity: (0) open (Figs. 35–38); (1) closed (NADEIN 2013b: fig. 53).
- 28.** Metendosternite, length of furcal arms: (0) long and narrow (NADEIN 2013b: figs. 66, 68, 69); (1) short and broad (Figs. 47–49).

Elytra

- 29.** Punctuation of the elytra: (0) confused (Fig. 3); (1) partially confused with traces of regular rows (Fig. 12); (2) regular (Fig. 4).
- 30.** Epipleura: (0) horizontal or nearly so; (1) inclined inward.

Legs

- 31.** Metatibia, shape of ventral edge: (0) straight (NADEIN 2013b: figs. 94–97); (1) weakly curved; (1) distinctly curved (Figs. 75–77, 79–83).
- 32.** Metatibia, length: (0) as long as metafemur or longer (NADEIN 2013b: figs. 95, 102); (1) shorter than metafemur (Figs. 15, 16).
- 33.** Metatibial spur: (0) simple (Figs. 75, 76); (1) bifid (Figs. 78–83).
- 34.** Metafemur: (0) three or more times longer than wide (NADEIN 2013b: fig. 95); (1) two times longer than wide or shorter (Figs. 15, 16).
- 35.** Metatarsal articulation: (0) apically on the tip of tibia (Figs. 75–83); (1) articulated at some distance from the tip of tibia (KONSTANTINOV & VANDENBERG 1996: fig. 84).
- 36.** Meso- and metatibial apices, emargination: (0) absent (Figs. 75–83); (1) present (BIONDI & D’ALESSANDRO 2012: figs. 22, 23, 25, 28).
- 37.** Metatibial apex, angular projection: (0) absent (Figs. 78–80); (1) present (Figs. 75–77).
- 38.** Tarsomere 3: (0) bilobate (Fig. 81); (1) not bilobate (NADEIN 2013a: SI 2, fig. 77).
- 39.** Metatarsomere 1, length: (0) shorter than following tarsomeres combined (NADEIN 2013b: figs. 95–98);

(1) as long as following tarsomeres combined or longer (Figs. 75, 76).

40. Metatarsomere 1, ventral surface: (0) densely setose on whole surface (NADEIN 2013a: figs. 67, 69); (1) densely setose in apical half or two thirds (Figs. 78, 80–82); (2) not densely setose (NADEIN 2013b: figs. 94, 96, 97).
41. Metatarsomere 1, shape: (0) gradually widened apically; (1) thin basally, abruptly widened apically (Figs. 75, 76, 80–83); (2) narrow along whole length.
42. Metatarsus apical tarsomere: (0) not swollen (Fig. 76, 80, 83); (1) swollen (KONSTANTINOV & VANDENBERG 1996: fig. 80).

Abdomen

43. Ventrite V (male): (0) without longitudinal ridge on inner surface; (1) with longitudinal ridge on inner surface (NADEIN 2013b: fig. 161).
44. Metacoxal process of ventrite 1: (0) obtuse (NADEIN 2013b: fig. 161); (1) angular.

Genitalia

45. Median lobe of aedeagus: (0) dorsoventrally depressed (NADEIN 2013b: fig. 159); (1) tubular and straight; (2) tubular and curved (NADEIN 2013b: figs. 157, 158).
46. Spiculum ventrale: (0) membranous (NADEIN 2013b: figs. 144–148); (1) well sclerotized (Figs. 66–68).
47. Spiculum ventrale, process: (0) long and thin (NADEIN 2013b: figs. 144–148); (1) short and thick (Figs. 66–68).
48. Vaginal palps, shape: (0) long and narrow (NADEIN 2013b: figs. 132–136); (1) short and broad (Figs. 72–74).
49. Vaginal palps, structure: (0) not joined basally (Figs. 72–74); (1) joined basally (NADEIN 2013b: fig. 132).
50. Spermatheca pump: (0) distinctly delimited from receptacle (Figs. 69–71); (1) weakly or not delimited from receptacle (NADEIN 2013b: figs. 123, 131).

3. Results and discussion

3.1. Phylogenetic relationships

Analyses were done with and without character 1 (body shape) to test the sensitivity of the results to this character. The strict consensus tree of the cladograms obtained from each analysis is shown on Figs. 1 and 2 respectively. The statistics for consensus tree 1 (with character 1; Fig. 1) is as follows: strict consensus of 5 trees; tree length = 160; CI = 0.38; RI = 0.64; RCI = 0.24; HI = 0.61. Statistics for consensus tree 2 (without character 1; Fig. 2) is:

strict consensus of 2 trees; tree length = 152; CI = 0.38; RI = 0.64; RCI = 0.25; HI = 0.61.

A bootstrap analysis based on data matrix without character 1 demonstrates high support of 89% to Clade A (terminals *Argopistes*, *Dibolia*, *Megistops*, *Paradibolia*); and 93% to Clade B (terminals *Argopistes*, *Dibolia*, *Megistops*, *Paradibolia*, and *Halticorcus*). Clade D has low support of 65% while clade C has support of less than 50%.

The hemispheric body shape is defined here with parameters of body length/width ratio 1.0–1.4 and body length/height ratio 1.6–2.3. In details the phenomenon of hemisphericity was discussed in NADEIN (2013a). Hemispheric body shape is found in some Galerucini (e.g., *Oides* Weber, 1801), Chrysomelinae (many genera, especially *Paropsis* Olivier, 1807 and allies). Among Alticini species with more or less hemispheric body shape are presented in following genera (Figs. 3–15): *Acrocrypta* Baly, 1862, *Amphimela* Chapuis, 1875, *Apteropeda*, *Argopistes*, *Argopus*, *Bhamoina* Bechyné, 1958, *Borneocycla* Medvedev, 2007, *Bubiscus* Savini, Furth & Joly, 2009, *Chabria* Jacoby, 1887, *Chilocoristes* Weise, 1895, *Clavicornaltica* Scherer, 1974, *Erystus* Jacoby, 1885, *Euphitrea* Baly, 1875, *Glaucosphaera* Maulik, 1926, *Halticorcus* Lea, 1917, *Homelea* Jacoby, 1884, *Ivalia* Jacoby, 1887, *Jacobyana* Maulik, 1926, *Maaltica* Samuelson, 1969, *Nonarthra* Baly, 1862, *Normaltica* Konstantinov, 2002, *Pentamesa* Harold, 1876, *Sesquisphaera* Bechyné, 1958, *Sphaeroderma*, *Sphaerometopa* Chapuis, 1875, *Sphaeropleura* Jacoby, 1887, and some others. From these, 14 genera were included in the current analysis (Table 2) to test the phylogenetic links of *Argopistes* and other hemispheric flea beetles.

The topologies of consensus trees 1 and 2 generally resemble each other meaning that the character of hemispheric body shape (character 1) has a little influence on the topology. The results of cladistic analysis show that hemispheric alticines represent different phylogenetic lineages. Three major clades including hemispheric flea beetles are recognizable on the cladogram. One (Clade B) includes the hemispheric genera *Argopistes* and *Halticorcus*. Two other clades include generic groups – genera allied to *Chabria* (Clade C) and to *Sphaeroderma* (Clade D), respectively. The results correspond with molecular data analysis by GE et al. (2012) – not in all detail, but in general in that hemispheric flea beetles do not represent a natural group. Notably, there is agreement with molecular data in grouping *Pentamesa*, *Bhamoina*, and *Argopus* (“*Pentamesa* group” sensu GE et al. 2012) while *Argopistes* and *Dibolia* are placed together in their “*Dibolia* group”.

As a conclusion, hemispheric alticines are similar in body shape but differ in many other morphological characters, e.g. structure of the head, prothorax, legs, male and female genitalia (see also NADEIN 2013a). As revealed in the course of this study and previous (NADEIN 2013a), many of them are quite distant morphologically and phylogenetically. Apparently, this habitual similarity is of independent origin.

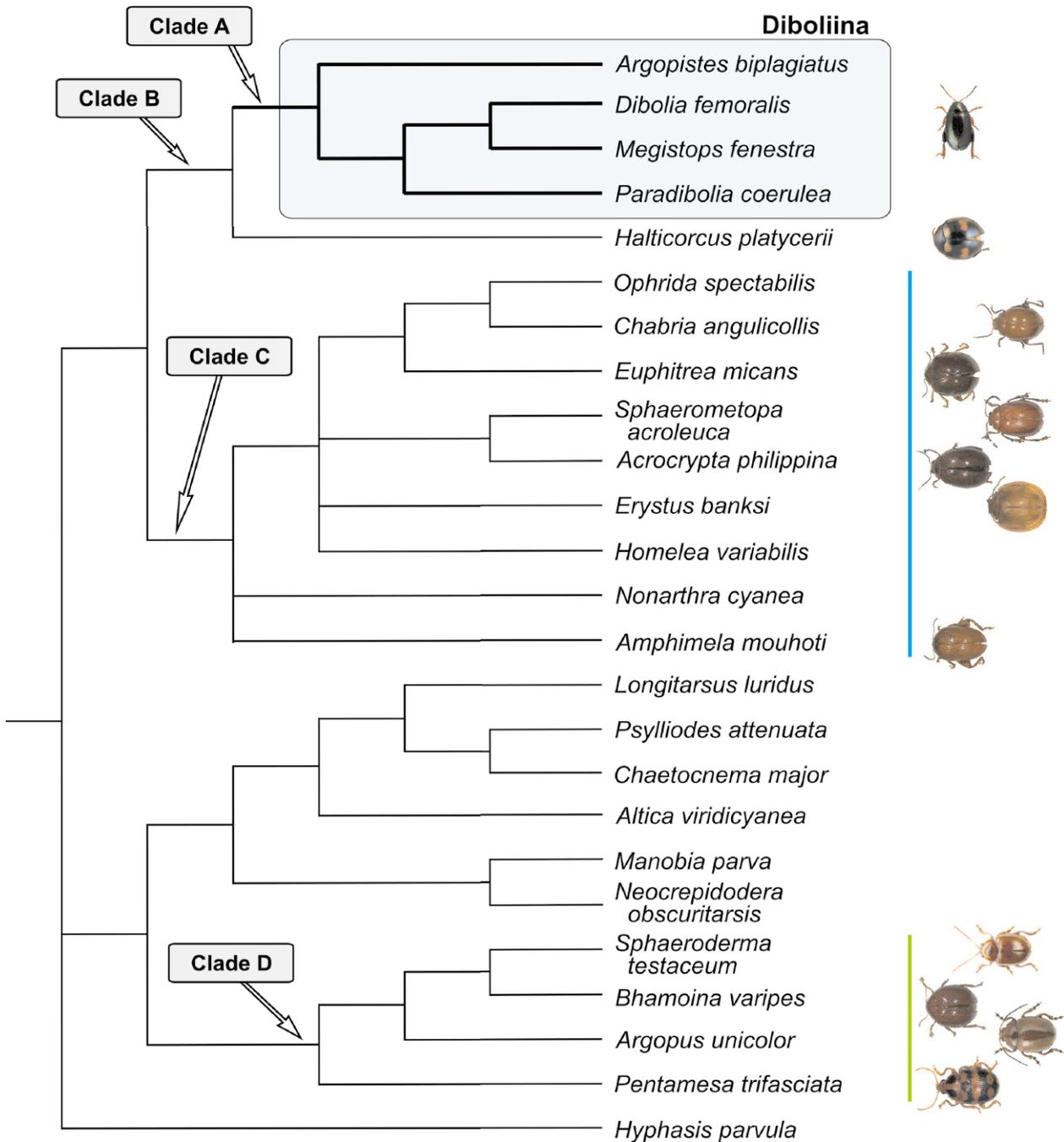


Fig. 1. Strict consensus tree 1 based on the heuristic analysis of unweighted morphological characters (with character 1: body shape). Terminal taxa with hemispheric body shape are with corresponding images (excepting *Homelea variabilis* and *Nonarthra cyanea*). Blue bar refers to clade C; green bar refers to clade D.

3.2. Revision of subtribe Diboliina

Type genus *Dibolia* Latreille, 1829.

3.2.1. Phylogeny of Diboliina

Diboliina Chapuis, 1875

Diboliites Chapuis 1875: 137 (original spelling).

Diboliae: Horn, 1889: 167.

Diboliini: Heikertinger & Csiki, 1939; Seeno & Wilcox, 1982.

The results of the cladistic analysis successfully tested the hypothesis on the affinity of *Argopistes* to genera of the subtribe Diboliina and the genus *Paradibolia*. The position of the genus *Argopistes* in Mniophilina has not been supported. The bootstrap value is 89%, which confirms the high support and possible monophyly. The result corresponds well with recent studies based on molecular data (GE et al. 2012) excepting inclusion of

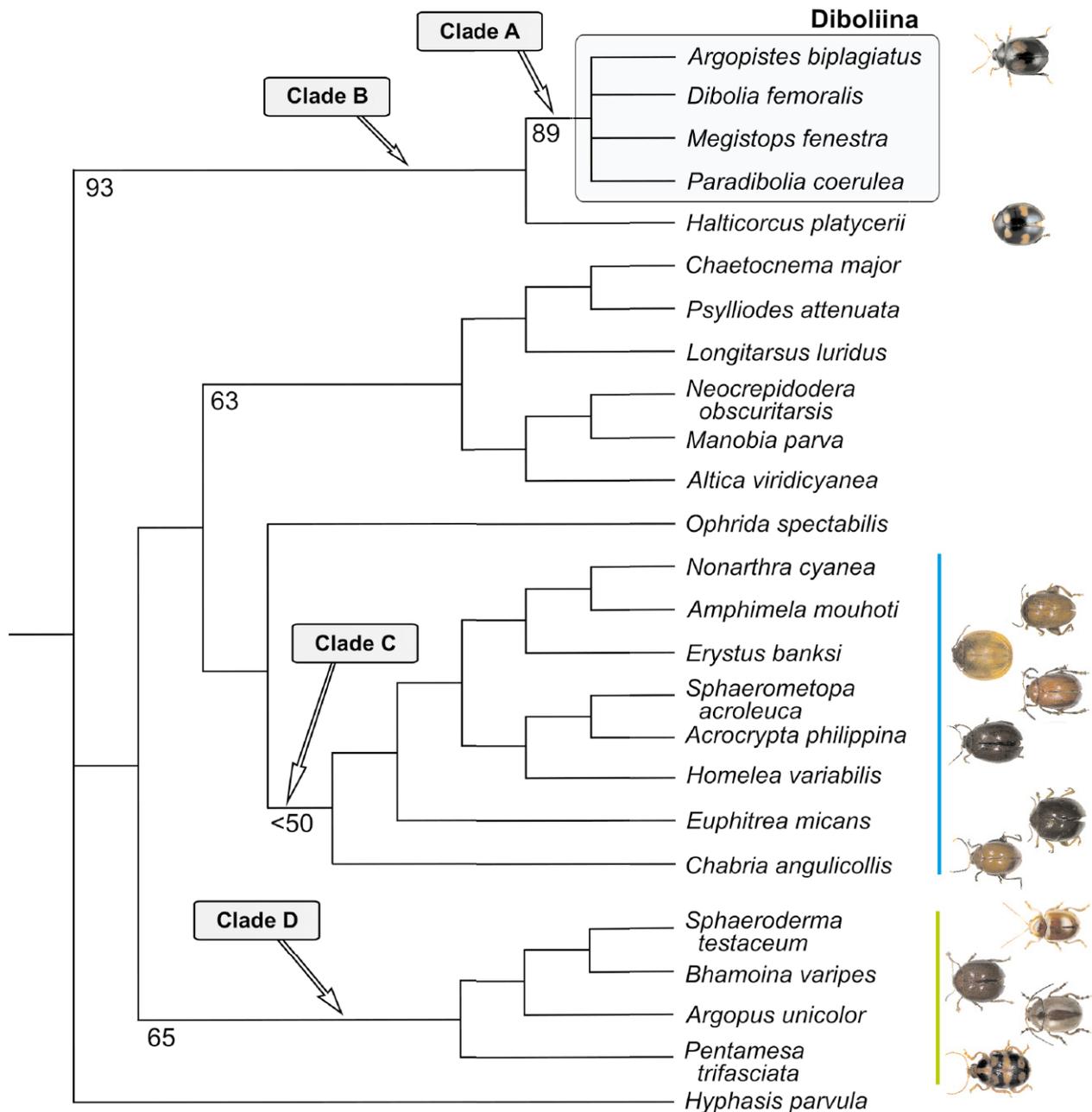
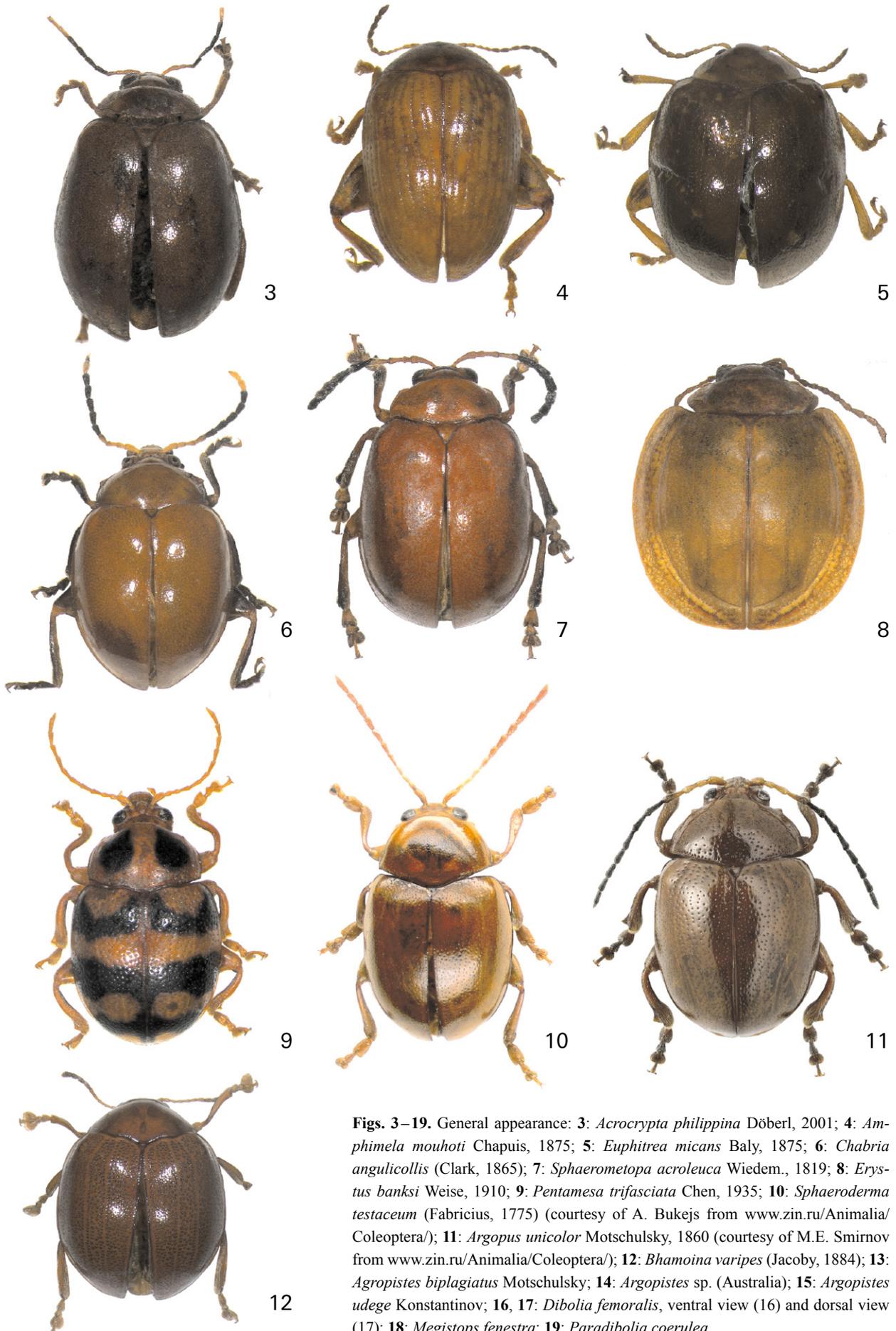


Fig. 2. Strict consensus tree 2 based on the heuristic analysis of unweighted morphological characters (without character 1: body shape). Terminal taxa with hemispheric body shape are with corresponding images (excepting *Homelea variabilis* and *Nonarthra cyanea*). Blue bar refers to the clade C; green bar refers to the clade D. Numbers indicate the bootstrap value.

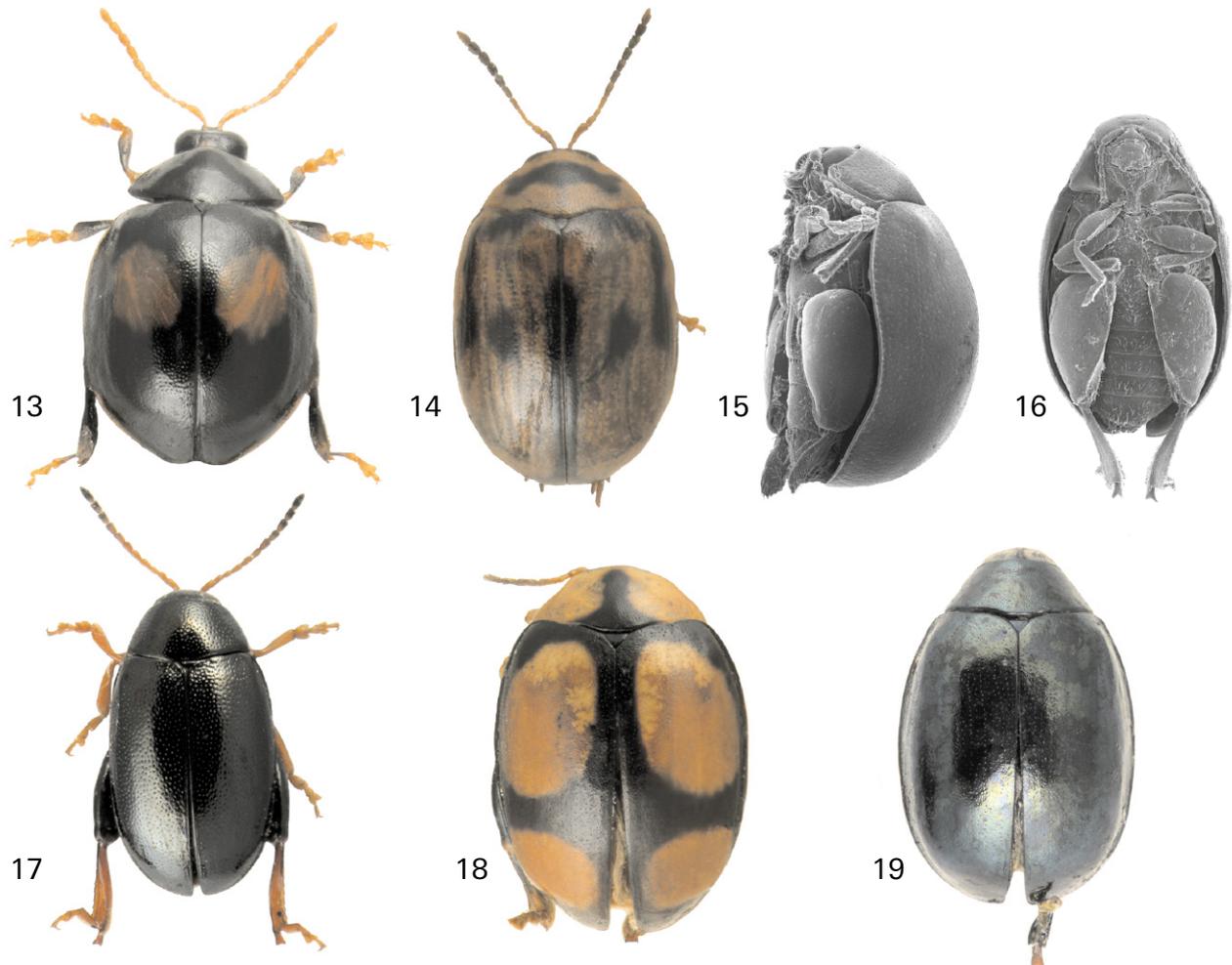
Jacobyana Maulik, 1926 to “*Dibolia* group”. The latter is morphologically distant from *Diboliina* genera in the structure of the head, legs, and genitalia. It corresponds in general with data obtained by TAKIZAWA (2005) based on larval morphology. His “Genus group *Sphaeroderma*” contains both *Argopistes* and *Dibolia*, along with *Argopus*, *Schenklingia* (= *Halticorcus*), and *Sphaeroderma*. This combined group embraces genera with leaf-mining larvae. The latter three genera are considered being in different clades in the present analysis.

The cladistic analysis reveals the possible sister group of *Diboliina*, namely the subtribe *Febrina* (NADEIN

2013a). Clade B with genera of *Diboliina* and genus *Halticorcus* has a high bootstrap support of 93%. *Halticorcus* is a representative of the subtribe *Febrina* whose affinity to *Diboliina* has previously been supposed (NADEIN 2013a). The subtribe *Febrina* comprises *Febra* Clark, 1864, *Profebra* Samuelson, 1967, *Halticorcus*, *Chilocoristes*, *Axillofebra* Samuelson, 1969, *Setsaltica* Samuelson, 1971, and *Maaltica* Samuelson, 1969 distributed in the Indo-Malayan Region, Australia, and Oceania. Remarkably, the genera of *Diboliina* and *Febrina* both have leaf-mining larvae, which seems to be an additional criterion supporting their phylogenetic affinity.



Figs. 3–19. General appearance: **3:** *Acrocrypta philippina* Döberl, 2001; **4:** *Amphimela mouhoti* Chapuis, 1875; **5:** *Euphitrea micans* Baly, 1875; **6:** *Chabria angulicollis* (Clark, 1865); **7:** *Sphaerometopa acroleuca* Wiedem., 1819; **8:** *Erystus banksi* Weise, 1910; **9:** *Pentamesa trifasciata* Chen, 1935; **10:** *Sphaeroderma testaceum* (Fabricius, 1775) (courtesy of A. Bukejs from www.zin.ru/Animalia/Coleoptera/); **11:** *Argopus unicolor* Motschulsky, 1860 (courtesy of M.E. Smirnov from www.zin.ru/Animalia/Coleoptera/); **12:** *Bhamoina varipes* (Jacoby, 1884); **13:** *Agropistes biplagiatus* Motschulsky; **14:** *Argopistes* sp. (Australia); **15:** *Argopistes udege* Konstantinov; **16, 17:** *Dibolia femoralis*, ventral view (16) and dorsal view (17); **18:** *Megistops fenestra*; **19:** *Paradibolia coerulea*.



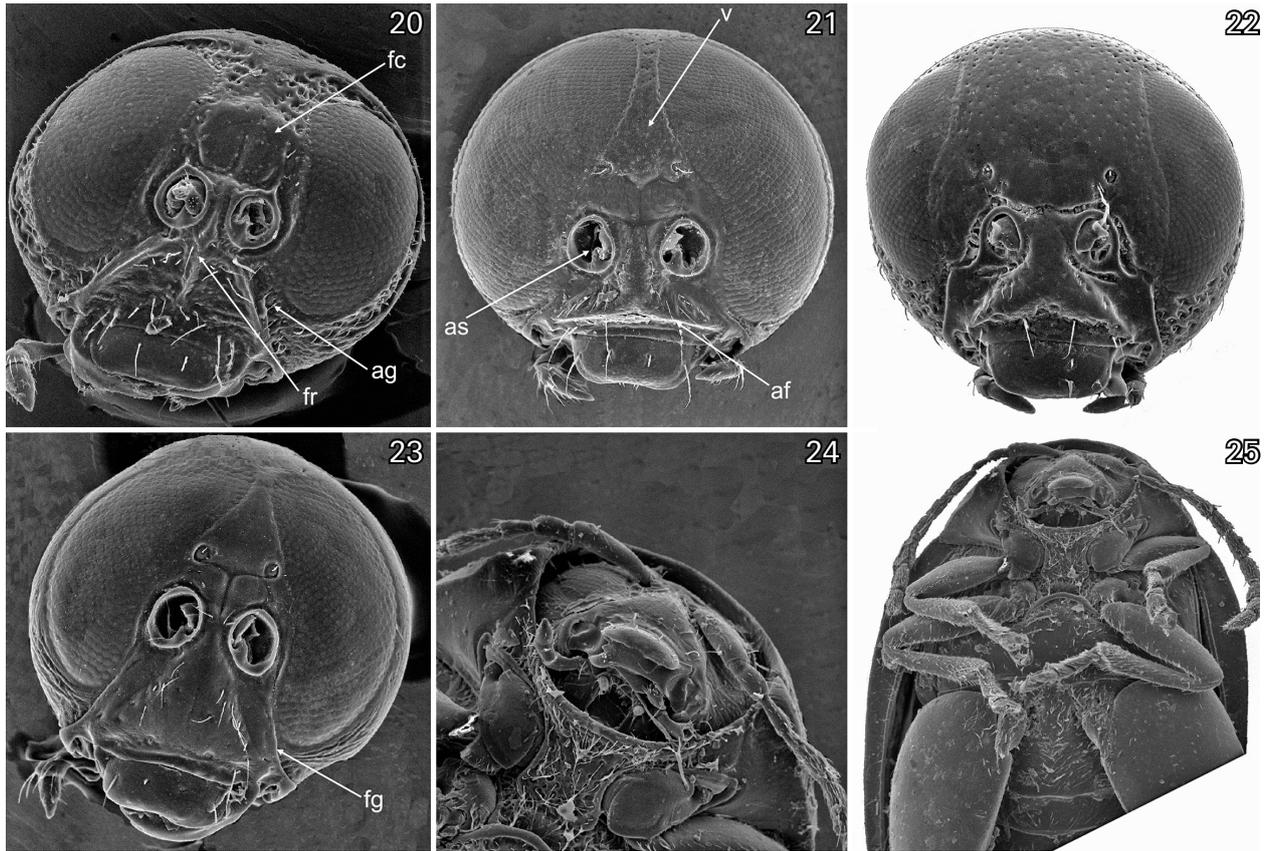
3.2.2. Diagnosis and redescription of Diboliina

Diagnosis. Body wide-oval to hemispherical; head hypognathous to opistognathous; first antennomere as long as the two or three following combined; eyes very large, kidney-shaped; frontal calli contiguous; frontal ridge and antennal grooves present; labrum with two pairs of setiferous pores; antennae 11-segmented, filiform; pronotal base rounded or bisinuate, hypomera arcuate-concave; prosternum broad; procoxal cavities open behind; metaventricle shorter than first abdominal segment; epipleura horizontal to subvertical; median lobe of aedeagus tubulate; tegmen Y-shaped; vaginal palpi short and thick, not fused basally; spiculum ventrale T-shaped and well sclerotized, its process long; metafemora greatly swollen; metafemoral spring large, rectangular-oval; posterior tibiae curved; first metatarsomere as long as following segments combined; its ventral side densely setose in apical two thirds or half, tarsus attached to tibia apically; spur of metatibia large, bifid or simple.

The possibly related subtribe Febraina differs from Diboliina distinctly in the absence of frontogenal suture, another structure of the frontal area, usually long and curved last antennomere, straight metatibiae lacking an acute tip and having a small and simple spur, and non-bilobed third tarsomere.

Redescription. *Body* ovate, cylindrical to rounded, hemispherical, head weakly visible from above or invisible (Figs. 13–19).

Head (Figs. 20–25): Deeply drawn into prothorax, its orientation hypognathous or opistognathous, shape of head rounded in form in frontal view; vertex (area above frontal calli and between eyes, Fig. 21: v) small or very small, covered with small punctures and a pair of large setiferous pores; frontal calli quadrate or rectangular (Fig. 20: fc), usually well separated from vertex, separated from antennal sockets by deep and thin sulcus-like impression; antennal sockets large (Fig. 21: as), distance between sockets not exceeding the diameter of sockets, usually less, sockets separated by frontal ridge, and well separated from eyes by deep and thin sulcus-like impression, this impression usually evident from behind each socket and separate from frons; frontal ridge typically T-shaped, elevated, in *Argopistes* frontal ridge looks triple (Fig. 20: fr), but lateral ridges are edges of antennal grooves, sometimes anterior part of frons (anterofrontal ridge, Fig. 21: af) not convex, ridge in some cases large, broad and widened anteriorly, therefore appearing triangular (Fig. 23); area between lower margin of eye and frontal ridge appears more or less as impressed groove for first segment of antenna (Fig. 20: ag); frontal area including mouth region separated from genae by thin line



Figs. 20–25. Head: **20:** *Agropistes biplagiatus*; **21:** *Paradibolia coerulea*; **22:** *Dibolia femoralis*; **23:** *Megistops decorata*; **24:** *Megistops vandepolii*; **25:** ventral view of *Megistops vandepolii*. – **Abbreviations:** ag – antennal groove; af – anterofrontal ridge; as – antennal socket; fc – frontal calli; fg – frontogenal suture; fr – frontal ridge; v – vertex.

(frontogenal suture, Fig. 23: fg); eyes very large, kidney-shaped, embracing greater part of visible side of head, distance between eyes and vertex small, at least not exceeding length of eye (*Dibolia*), usually not exceeding diameter of antennal socket, eyes not delineated by sulci from rest of vertex and frons, only in *Argopistes* some impressions around outer side of eyes present, facets of eye numerous, small, flat.

Antennae (Figs. 26, 27): filiform; comparatively short, their length not exceeding half of body length; 11 antennomeres; antennomere 1 as long as 2 or 2.5 following antennomeres combined, apical 4–5 antennomeres except last thick, two times longer than wide or even nearly as long as wide.

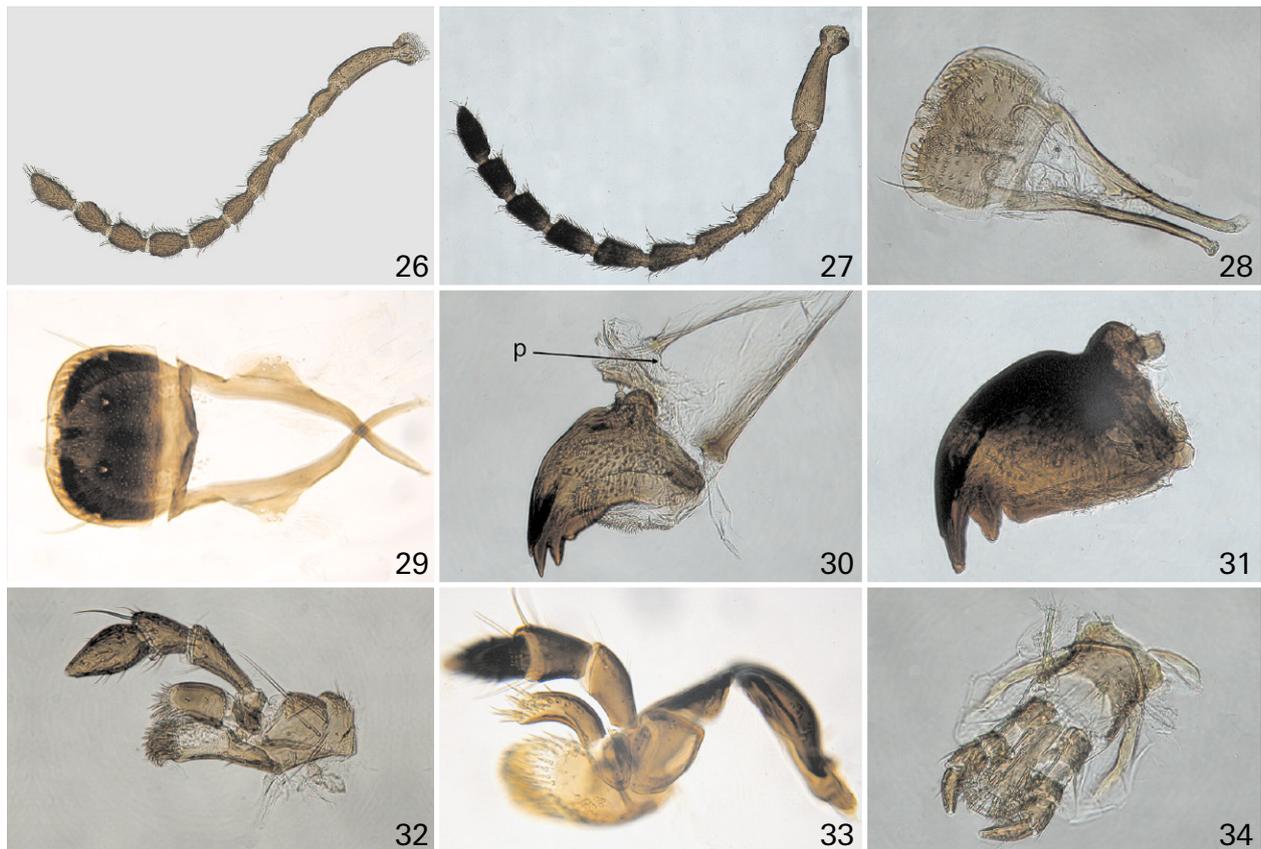
Mouthparts: Labrum rectangular (Figs. 28, 29), without medial incision of anterior edge, dorsal surface with two pairs of large setiferous pores; mandibulae (Figs. 30, 31) triangular, protheca (Fig. 30: p) weakly to well developed, inner edge and apex with 5 teeth; maxillae of typical shape (Figs. 32, 33), palpus with narrow palpomeres; labium (Figs. 34, 39) with prementum elongate, reaching last labial palpomere, its apical part widened, labial palpomeres narrow.

Prothorax (Figs. 35–38): Pronotum always covered with punctures, without grooves, furrows and impressions, posterior edge of pronotum simple, rounded

(*Megistops*, *Dibolia*), weakly bisinuate (*Paradibolia*) to clearly bisinuate (*Argopistes*); prothorax distinctly wider than long; hypomera (Fig. 35: h) enlarged, triangular, arcuate-concave, hypomerical sutures visible (Fig. 38: hs); prosternum (Fig. 37: p) above procoxal cavities narrow, at least not wider than width of cavities, intercoxal prosternal process comparatively wide (Fig. 36: ipp), its anterior edge straight; procoxal cavities (Fig. 37: pc) widely open behind, transversely elongate; coxae deeply drawn into cavities, barely projecting.

Mesothorax: Mesonotum (Figs. 40–43) of typical shape (KONSTANTINOV & VANDENBERG 1996), highly sclerotized, prealar (Fig. 42: pp) and postmedial projections (Fig. 43: pmp) well developed, elongate; scutellar shield triangular (Fig. 42: s), visible between elytra. Mesoventrite very short, distance between pro- and mesocoxae much smaller than their longitudinal diameter, distance between mesocoxae as large as distance between procoxae; mesanepimera and mesanepisterna narrow; visible surface of mesoventrite between intercoxal prosternal process and metaventral process very small, intercoxal prosternal process may partially cover mesoventrite.

Metathorax: Metanotum (Figs. 44–46) well sclerotized, has all well developed and typical structures for alticines (KONSTANTINOV & VANDENBERG 1996); prescutum and postnotum wide (Fig. 44: psc and Fig. 46:



Figs. 26–34. Antennae: **26:** *Agropistes biplagiatus*; **27:** *Dibolia femoralis*. Labrum: **28:** *Agropistes biplagiatus*; **29:** *Dibolia femoralis*. Mandibula: **30:** *Agropistes biplagiatus*; **31:** *Dibolia femoralis*. Maxilla: **32:** *Agropistes biplagiatus*; **33:** *Dibolia femoralis*. Labium: **34:** *Agropistes biplagiatus*. – **Abbreviation:** p – prostheca.

pn). Metaventricle shorter than first abdominal segment, metaventral process wide, elongate, rounded at apex, not reaching prosternal intercoxal process, metacoxal area not projecting, feebly bent inward or straight, posterior edge of metaventricle medially with deep incision; metanepisterna of typical shape, narrow; distance between metacoxae nearly as large as between mesocoxae. Met-endosternite (Figs. 47–49): branches of anterior part of ventral process (Fig. 47: avp) well sclerotized, long or short, furcal arms thick (Fig. 47: fa), poorly sclerotized, sometimes wider, anterior tendon and tendon of apical edge of furcal arm present (Fig. 47: at, tat), tip of furcal arm usually elongated (Fig. 47: ta) anterior and ventral laminae (Fig. 47: al, vl) more or less broad, stalk (Fig. 47: s) wide and comparatively short.

Elytra: Ovate or rounded in shape, convex, glabrous, covered with punctures of various sizes and density, randomly placed in regular striae; epipleura wide, their orientation horizontal (*Dibolia*, *Megistops*), sloping (*Paradibolia*) to concave and subvertical (*Argopistes*). Elytral binding patch (Figs. 57–62) covered with numerous dense scales rounded in shape, ventral surface of elytra (Figs. 63–65) covered with dense and thin spines.

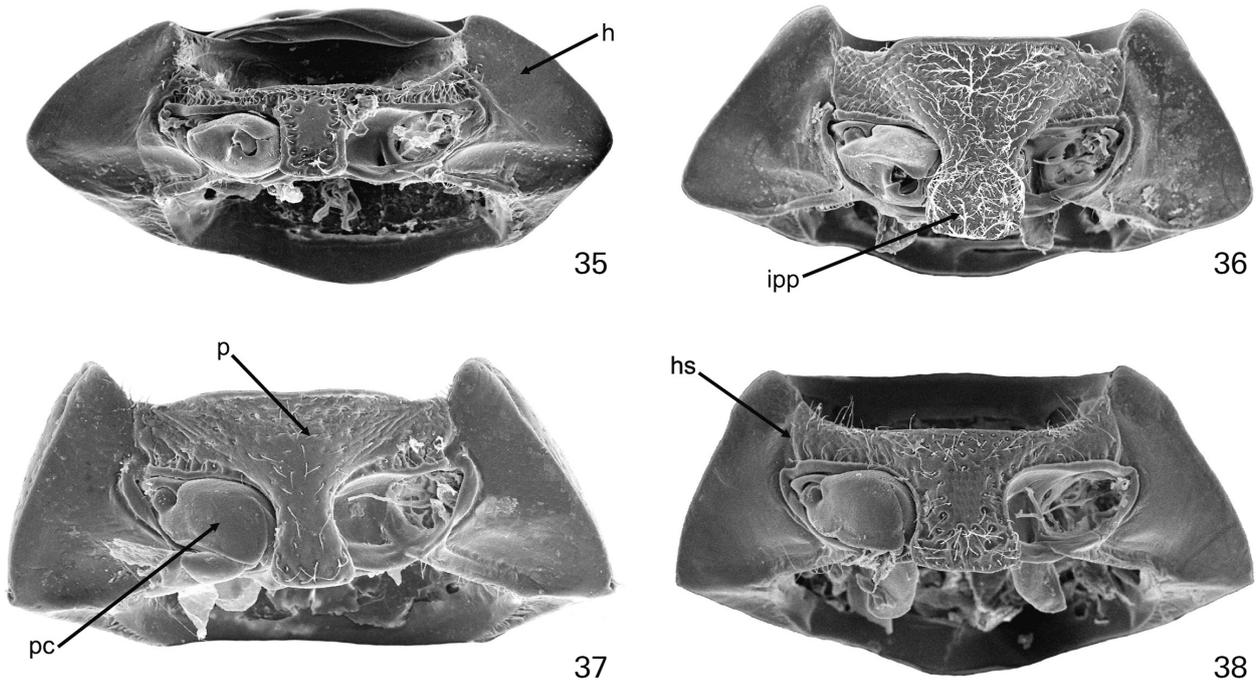
Hind wings (Figs. 84, 85): Wing venation is typical for alticines (KONSTANTINOV & VANDENBERG 1996), all genera with completely developed wings with no ten-

dency to reduction. Typical set of veins is present: radius, sector of radial vein, medial veins 1 and 2, cubital, and precubital.

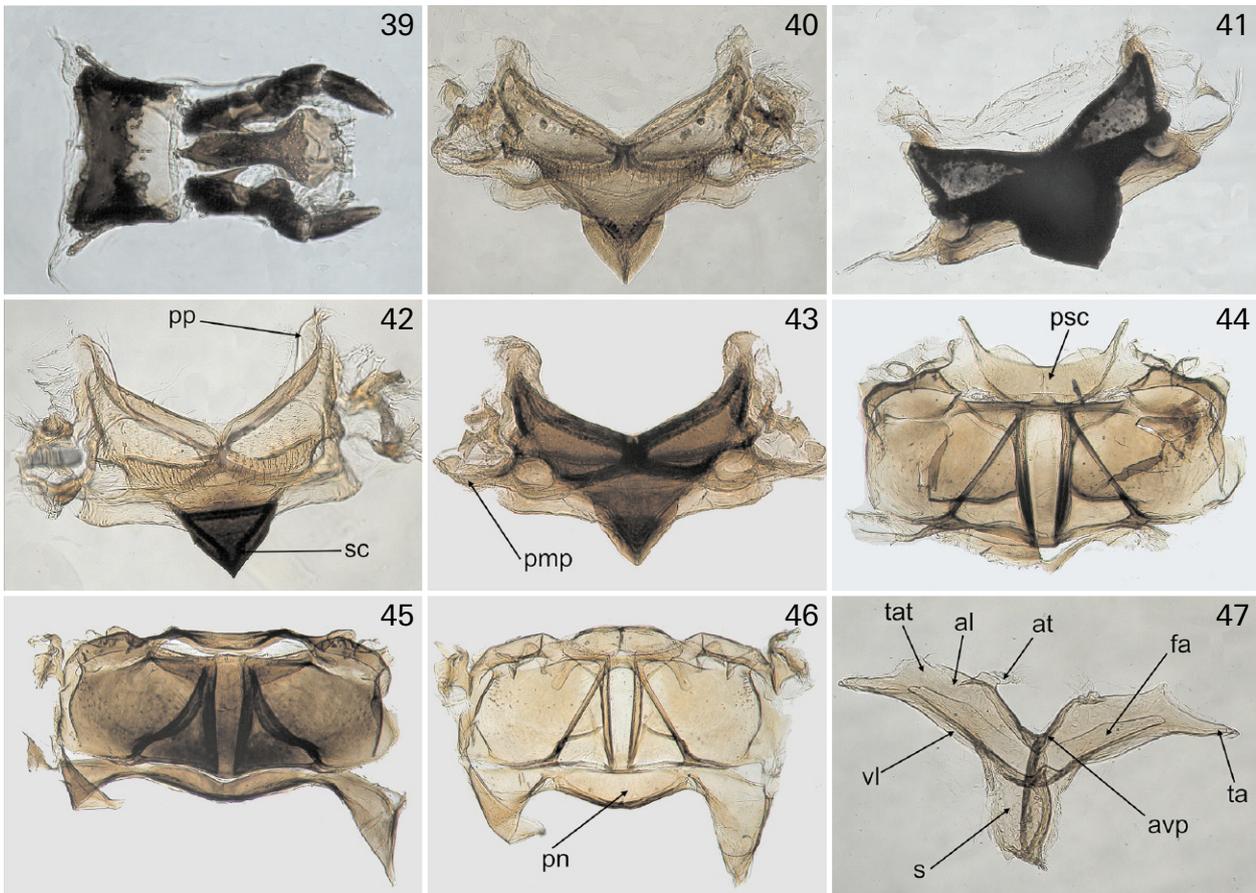
Abdomen: Ventriles short, wide, without projections or convexities, first visible ventrite (= third sternite) longer than metasternum; medial projection comparatively long; sexual dimorphism present in the shape of last visible ventrite (VII); pygidium with medial longitudinal groove (Figs. 53–55: lg); tergite VIII well-developed (Fig. 56).

Male genitalia consist of median lobe of aedeagus, Y-shaped tegmen, and pair of thin and long spicules. Median lobe usually thick and short, its apex bears various projections.

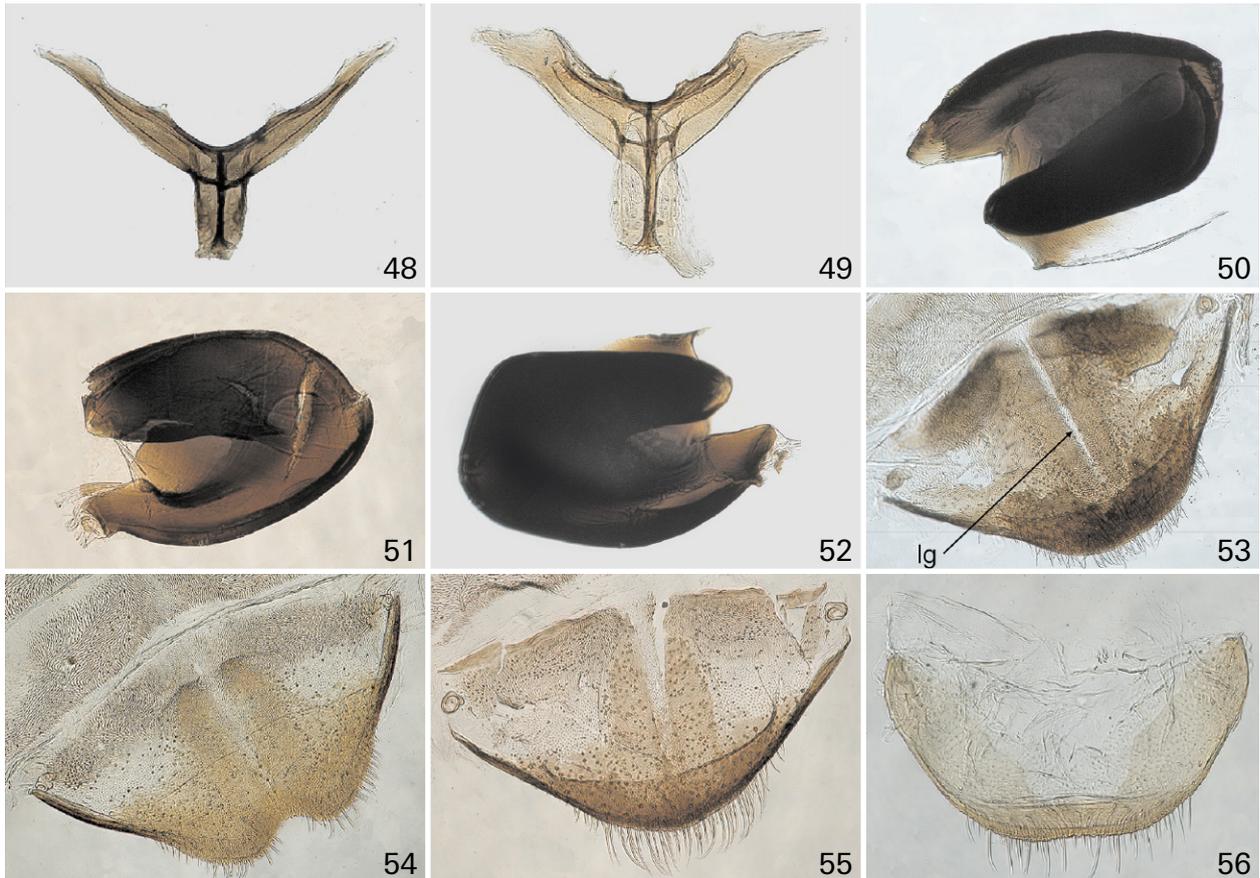
Female genitalia consist of spiculum ventrale, spermatheca, and vaginal palpi. Spiculum ventrale T-shaped (Figs. 66–68), process (Fig. 66: psv) much longer than width, base of spiculum ventrale (Fig. 66: bsv) well sclerotized, has the form of transparent membranous blade or short membranous blade, its apical edge covered with a row of setae. Spermatheca (Figs. 69–71) of various shapes, pump (Fig. 69: p) and receptacle (Fig. 69: r) usually thick, not strongly elongate, duct thick (Fig. 69: d), short or longer and coiled. Vaginal palpi short and thick (Figs. 72–74), 2.5 times longer than width or nearly equal in length to width, not closely joined, separated



Figs. 35–38. Prothorax, ventral view: **35:** *Agropistes biplagiatus*; **36:** *Paradibolia coerulea*; **37:** *Dibolia femoralis*; **38:** *Megistops decorata*. – **Abbreviations:** h – hypomeron; hs – hypomeral suture; ipp – intercoxal prosternal process; p – prosternum; pc – procoxal cavity.



Figs. 39–47. Labium: **39:** *Dibolia femoralis*. Mesonotum: **40:** *Agropistes biplagiatus*; **41:** *Dibolia femoralis*; **42:** *Paradibolia coerulea*; **43:** *Megistops decorata*. Metanotum: **44:** *Agropistes biplagiatus*; **45:** *Dibolia femoralis*; **46:** *Paradibolia coerulea*. Metendosternite: **47:** *Agropistes biplagiatus*. – **Abbreviations:** al – anterior lamina; at – anterior tendon; avp – anterior part of ventral projection; fa – furcal arm; pp – prealar projection; pmp – postmedial projection; pn – postnotum; psc – prescutum; s – stalk; sc – scutellum; ta – tip of furcal arm, tat – tendon of apical edge of furcal arm; vl – ventral lamina.



Figs. 48–56. Metendosternite: **48:** *Dibolia femoralis*; **49:** *Paradibolia coerulea*. Metafemoral extensor tendon: **50:** *Dibolia femoralis*; **51:** *Megistops decorata*; **52:** *Paradibolia coerulea*. Pygidium: **53:** *Dibolia femoralis*; **54:** *Agropistes biplagiatus*; **55:** *Megistops decorata*. Tergite VIII: **56:** *Agropistes biplagiatus*. – **Abbreviation:** lg – longitudinal groove.

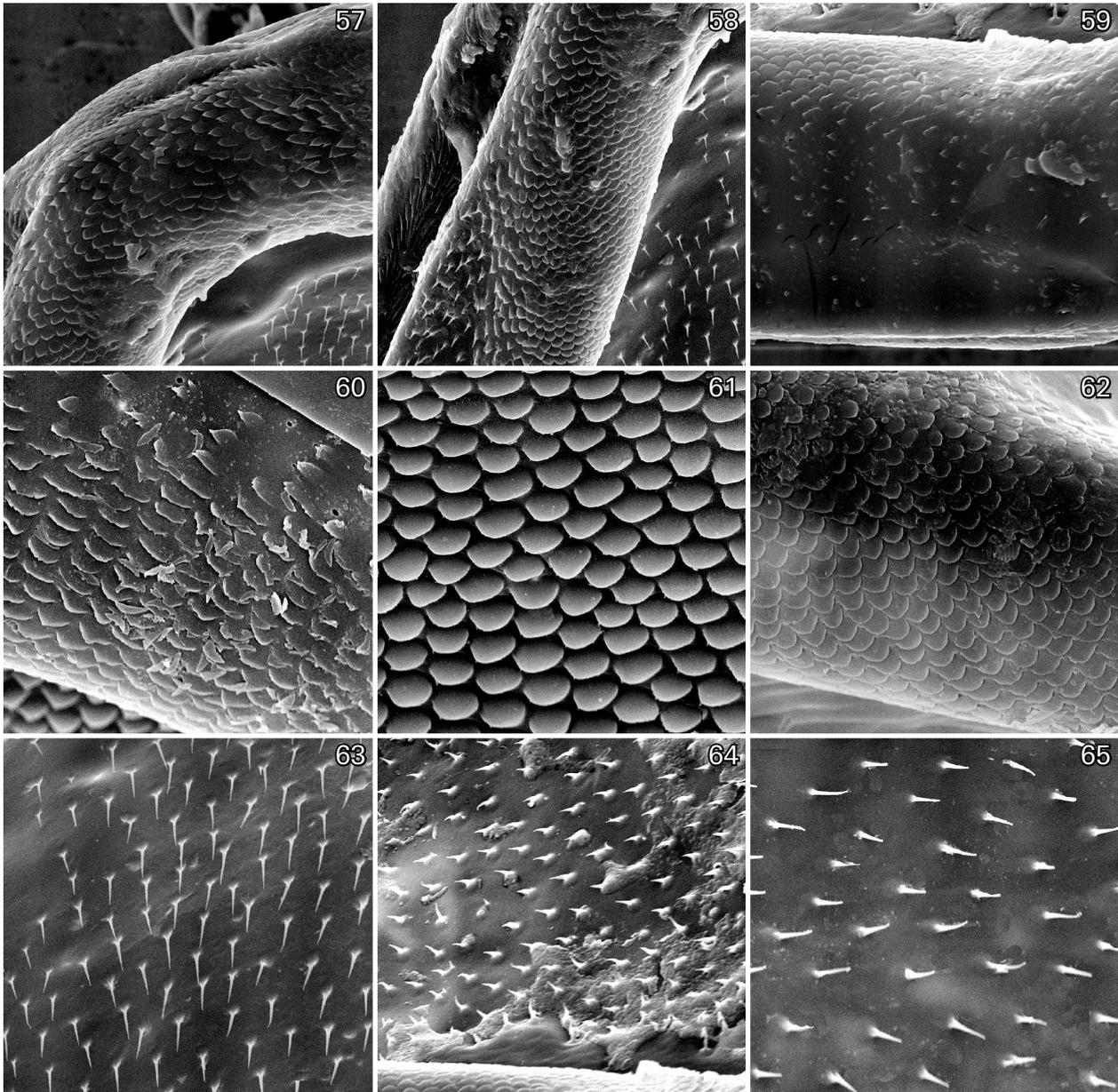
from each other, their apices conical, covered with small setae, outer setae denser and longer.

Legs (Figs. 75–83): Anterior and middle legs of typical shape, without modifications; posterior and middle tibiae with short apical spurs, without furrows, grooves, ridges or excavations; protarsomere 1 of male enlarged. Posterior femora greatly swollen, elongate-triangular; posterior tibiae comparatively short, not longer than length of femora; posterior tibiae thick, curved, apically widened, dorsal surface of tibia at least at distal half concave, outer side with ridge, apical third dorsally usually with large teeth of each side; posterior tarsus attached to tibia apically or subapically; tarsus as long as half of tibia or longer; metatarsomere 1 as long as three following tarsomeres combined, ventrally with short and very dense setae (Fig. 82: sa) concentrated in apical half of tarsus (Figs. 75, 76, 80–83), basal half with single hairs or glabrous; apex of posterior tibia with large spur, bifid in *Dibolia*, *Megistops* and *Paradibolia*, simple in *Agropistes* (Fig. 75: s); bifid spur thick (Figs. 78–83: bs), wide, long, sometimes equal to half of metatarsomere 1, rarely spur very short, not projecting far from socket, attached medially at the apex of tibia, simple spur shorter (Figs. 75–77), triangular, conical, attached at inner side of tibial apex, outer side of tibial apex sharply and angu-

larly projecting (Fig. 76: ap), shape of projection similar to spur. Metafemoral extensor tendon large, rectangular-oval (Figs. 50–52).

3.2.3. Some morphological features in Diboliina and their analysis

The genera of the subtribe have a distinct tendency towards a widening of the body. This involves changes in the structure of different body parts and is well traced in the transformation series (Fig. 86) from *Dibolia* to *Agropistes* (Fig. 87), where *Megistops* and *Paradibolia* occupy an intermediate position. The head orientation changes from hypognathous to opisthognathous; the eyes are enlarged because the head is more strongly bent under the pronotum; accordingly there is an elongation of the first antennomere and formation of deep antennal grooves on the frontal side of the head; the antennal sockets are drawn together as a consequence of eye enlargement. The base of the pronotum becomes sinuate; the epipleura wider and their orientation changes from horizontal to nearly vertical; posterior femora became more swollen and horizontally oriented; hind tibiae become shorter and thicker. The analogous transformation

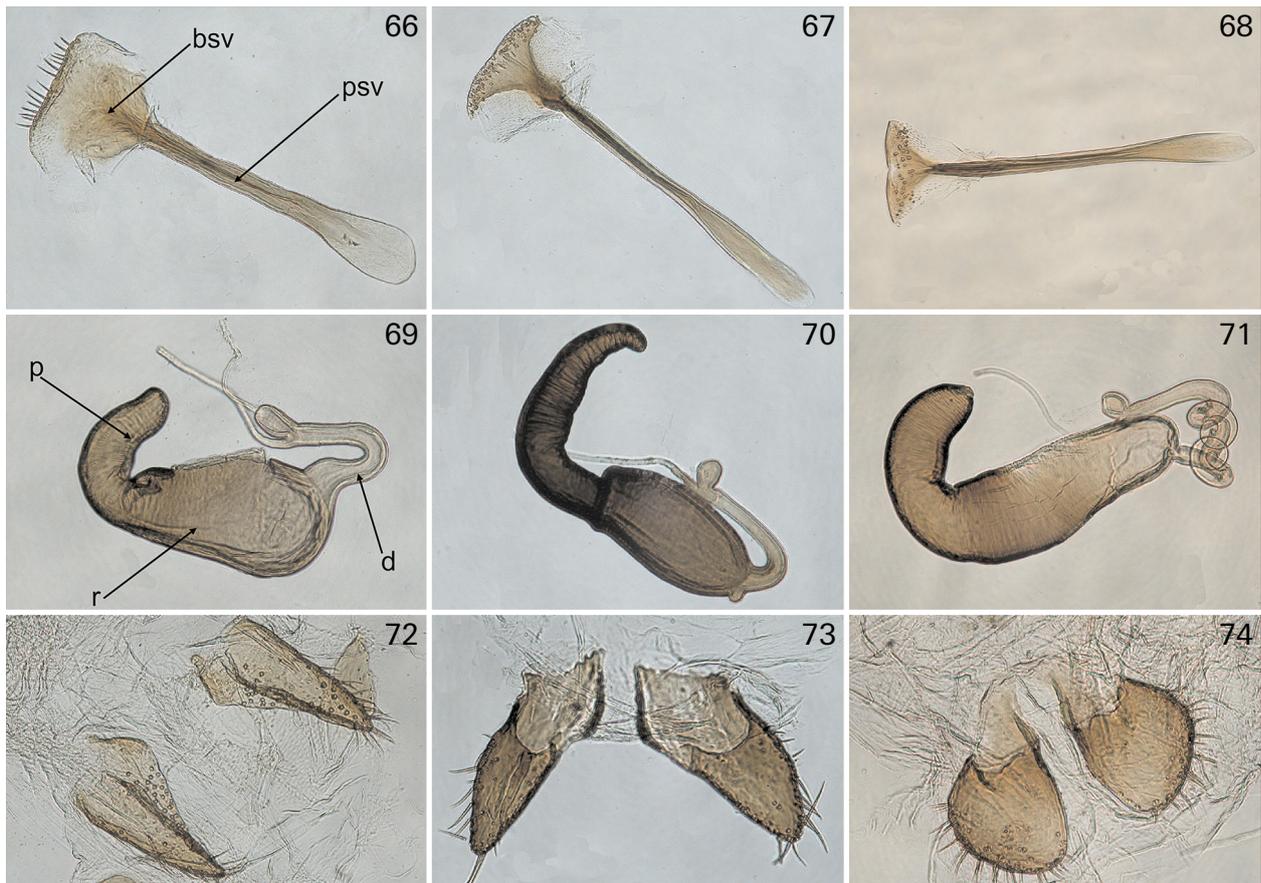


Figs. 57–65. Elytral binding patch: 57, 58: *Agropistes biplagiatus*; 59: *Dibolia femoralis*; 60, 61: *Megistops decorata*; 62: *Paradibolia coerulea*. Elytral ventral surface: 63: *Agropistes biplagiatus*; 64: *Dibolia femoralis*; 65: *Paradibolia coerulea*.

series can be traced in the genera from *Febra* to *Halticoriscus* and *Chilocoristes* (NADEIN 2013a) and from *Neocrepidodera* to *Sphaeroderma* (K. Nadein, unpubl. data).

The bifid spur (Figs. 78–83) of the posterior tibia is a peculiar feature of Diboliina except in *Argopistes*. A bifid spur is also present in the genus *Leptodibolia* Chen, 1941, which, however, is quite different from the genera of Diboliina in many characters. During a jump the beetle pushes off the body by extension of the metatibia that contacts the substrate by its tip bearing apical spur (K. Nadein, unpubl. data). Supposedly, the enlarged and bifid spur is necessary for more effective contact with the substrate for jumping. The absence of the bifid spur in posterior tibia in *Argopistes* (Figs. 75–77) can be explained in the following way. A bifid spur cannot be effective

in a hemispherical body, due to the loss of full contact with the substrate by tip of a hind tibia. The position of the posterior legs in *Argopistes* in comparison with *Dibolia* and others is considerably changed. In *Argopistes* the metatibial apical spur is also large and long (Figs. 75–77), located and oriented submedially outward; the tip of tibia is acute and prolonged into a short spur-like process. The spur and the acute tibial tip together form the “fork” for better contact with the substrate. As a result there is a similar structure like a bifid spur but adapted to another body shape. There is an analogous case in *Megistops fenestra* (Illiger, 1807): the bifid spur (Fig. 81) is short and broadly forked, and does not exceed the limit of the upper margin of the tibia. This morphology works functionally as the tibial apex in *Argopistes*.



Figs. 66–74. Spiculum ventrale (tignum): **66:** *Agropistes biplagiatus*; **67:** *Dibolia femoralis*; **68:** *Megistops decorata*. Spermatheca: **69:** *Agropistes biplagiatus*; **70:** *Dibolia femoralis*; **71:** *Megistops decorata*. Vaginal palps: **72:** *Agropistes biplagiatus*; **73:** *Dibolia femoralis*; **74:** *Megistops decorata*. – **Abbreviations:** bsv – base of spiculum ventrale; d – duct; p – pump; psv – process of spiculum ventrale; r – receptacle.

Metatarsomere 1 in the genera of Diboliina is also of peculiar structure. Because the spur of the metatibia is long, the metatarsomere 1 is elongate as well. The ventral side of metatarsomere 1 is not entirely setose, but the setose area is limited to the apical half or two thirds (Figs. 75, 76, 80–83).

Vaginal palps are short and broad, which possibly corresponds with leaf-mining oviposition.

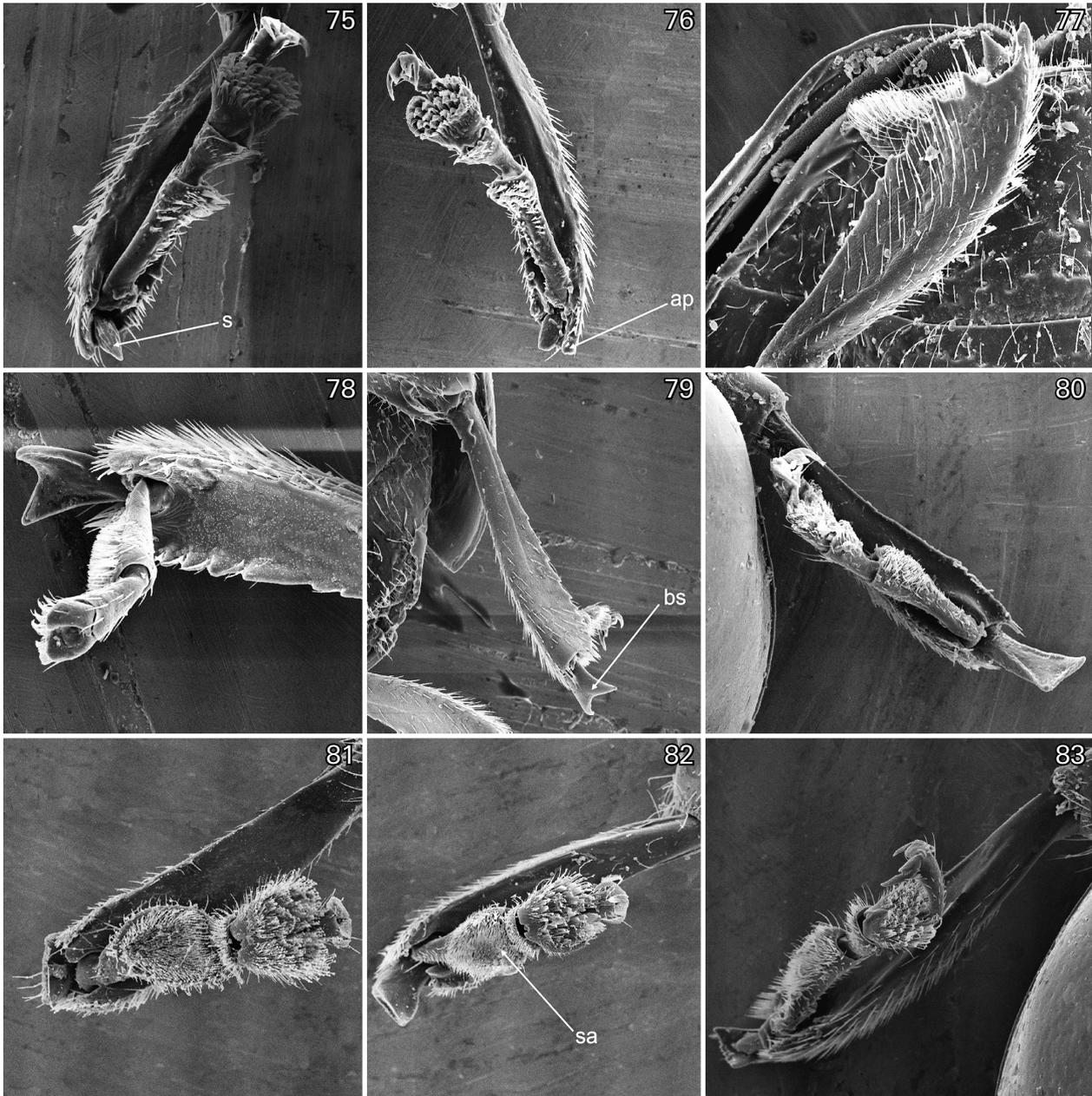
3.2.4. Larval way of life

The preimaginal stages are described for *Argopistes*, *Dibolia*, and *Megistops* (LINZMEIER et al. 2007; ZAITSEV & MEDVEDEV 2009). The life history of some species has also been observed (REED 1927; INOUE 1996; LINZMEIER et al. 2007). Leaf-mining of larvae is a peculiar feature for all four genera of Diboliina (by personal communication from C. Reid larvae of *Paradibolia* in Australia are leaf-mining). Leaf-mining is rare among alticines and this way of life is strongly specialized and significantly affects the structure of the larvae (SANTIAGO-BLAY 2004). Supposedly, leaf-mining in Diboliina is not the result of convergence, but this similarity in larval way of life is

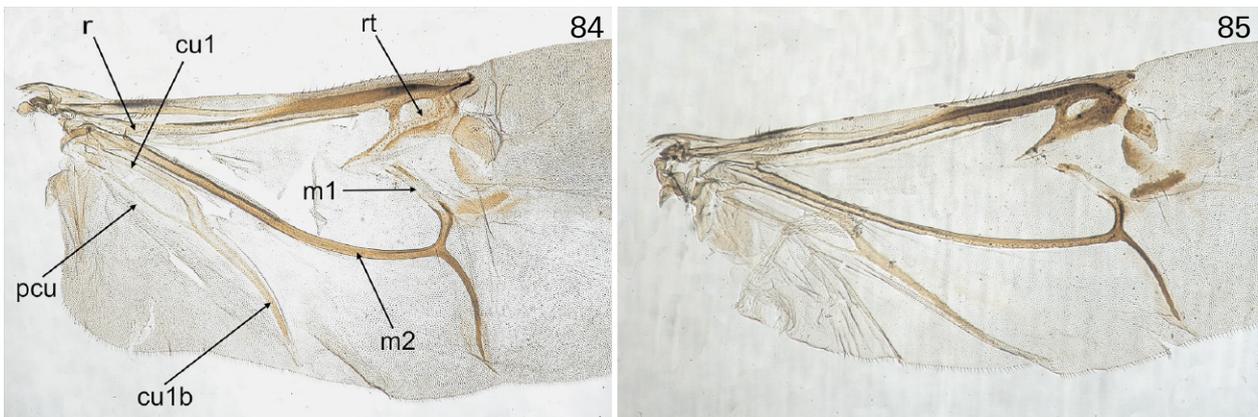
additional evidence of the relationship of the genera of Diboliina.

3.2.5. Key to genera of Diboliina

- 1 Body hemispherical, apical spur of posterior tibia simple, not bifid ***Argopistes***
- 1' Body ovate, apical spur of posterior tibia bifid **2**
- 2 Body with variable metallic colouration or purely black **3**
- 2' Body without metallic colouration, yellowish-brown with black pattern or vice versa [only in the New World] ***Megistops***
- 3 Eyes widely separated from each other at vertex, pair of supraocular setiferous pores separated from each other by more than diameter of pore, body ovate-cylindrical, dorsal punctures comparatively large and deep ***Dibolia***
- 3' Eyes very close to each other at vertex, pair of supraocular setiferous pores separated from each other by no more than diameter of pore, body widely ovate, dorsal punctures comparatively small and shallow ***Paradibolia***



Figs. 75–83. Metatibia: **75–77:** *Agropistes biplagiatus*; **78, 79:** *Dibolia femoralis*; **80:** *Megistops decorata*; **81:** *Megistops fenestra*; **82:** *Megistops decemmaculata*; **83:** *Paradibolia coerulea*. – **Abbreviations:** ap – apical projection; bs – bifid spur; s – spur; sa – setose area.



Figs. 84, 85. Hind wings: **84:** *Paradibolia coerulea*; **85:** *Dibolia femoralis*. – **Abbreviations:** cu1 – cubital vein 1; cu1b – cubital vein 1b; m1 – medial vein 1; m2 – medial vein 2; r – radial vein; rt – sector of radial vein; pcu – precubital vein.

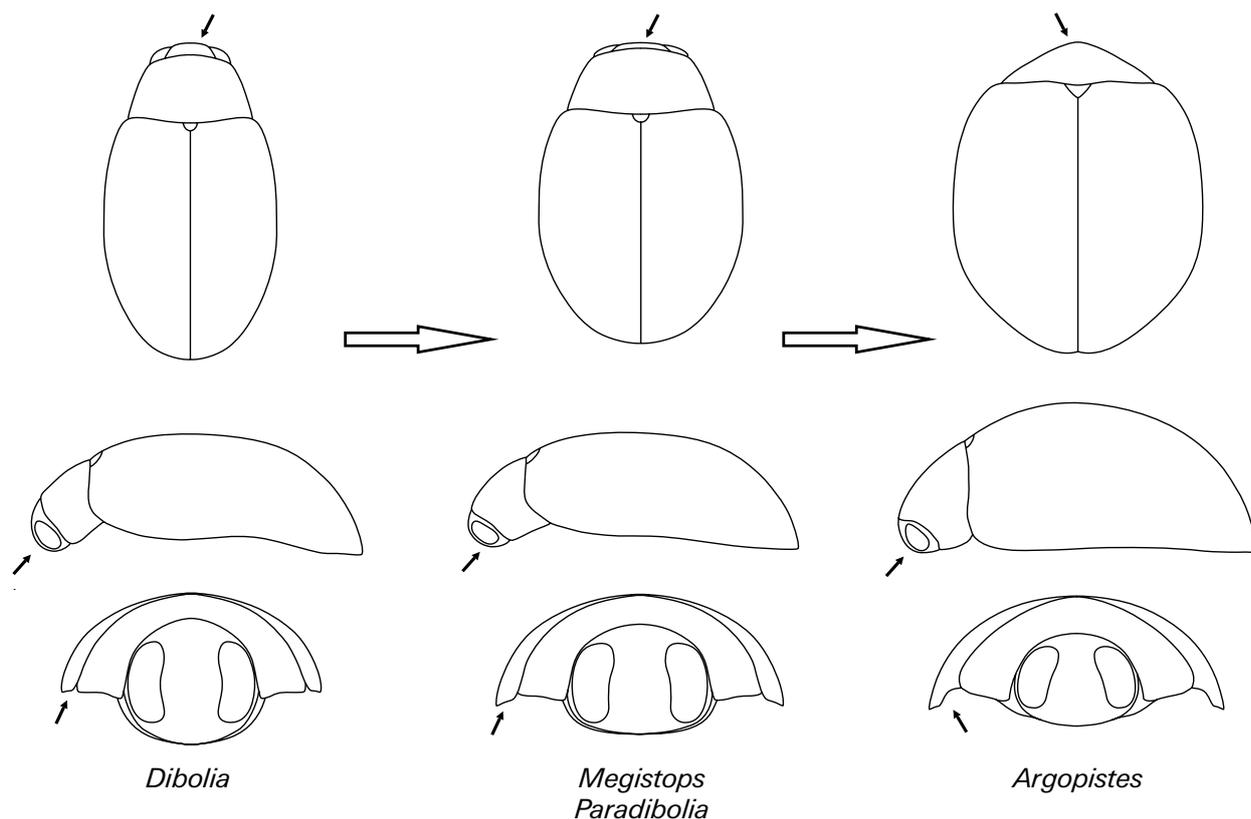


Fig. 86. Transformation series of body shape in Diboliina (see explanation in text).

3.2.6. Annotated list of genera

***Argopistes* Motschulsky**

- *Argopistes* Motschulsky, 1860: 236. Type species: *Argopistes biplagiatus* Motschulsky, 1860, by monotypy.
- *Sphaerophyma* Baly, 1878: 478. Type species: *Sphaerophyma simoni* Baly, by monotypy (SAMUELSON 1973; synonymized).

Comments: The genus is comprised of about 45 species with worldwide distribution. Host plants: Oleaceae, rarely Rutaceae and Verbenaceae; the larva is a leaf-miner (MEDVEDEV & ROGINSKAYA 1988; JOLIVET & HAWKESWOOD 1996).

***Dibolia* Latreille**

- *Dibolia* Latreille, 1829: 155. Type species: *Haltica occultans* Koch, 1803, by subsequent designation of CHŪJÓ (1936).
- *Petalopus* Motschulsky, 1845: 107. Type species: *Petalopus metallica* Motschulsky, by subsequent designation of KONSTANTINOV & VANDENBERG (1996).
- *Pseudodibolia* Iablokoff-Khnzorian, 1968: 269. Type species: *Dibolia zangezurica* Iablokoff-Khnzorian, 1968, by original designation; proposed as subgenus (KONSTANTINOV & VANDENBERG 1996; synonymized).
- *Eudibolia* Iablokoff-Khnzorian, 1968: 270. Type species: *Dibolia schillingi* Letzner, 1846, by original designation; proposed as subgenus (KONSTANTINOV & VANDENBERG 1996; synonymized).

Comments: The genus is comprised of about 60 species widely distributed in the Palearctic, Nearctic, and Afrotropical Regions, also in Central America. Host plants: Lamiaceae, Boraginaceae, Scrophulariaceae, Asteraceae, rarely Brassicaceae, Cistaceae, Apiaceae, Rosaceae; the larva is a leaf-miner (MEDVEDEV & ROGINSKAYA 1988; JOLIVET & HAWKESWOOD 1996).

***Megistops* Boheman**

- *Megistops* Boheman, 1859: 186. Type species: *Megistops quadrinotatus* Boheman, 1859.

Comments: The genus is comprised of 27 species distributed in South and Central America, and the Caribbean: Costa Rica, Ecuador, Bolivia, Argentina, Paraguay, Brazil, Chile, and Venezuela; Cuba, Trinidad, Haiti, West Indies. Host plants: Bignoniaceae, Clusiaceae, Cyperaceae, Rubiaceae, Buddlejaceae; the larva is a leaf-miner (JOLIVET & HAWKESWOOD 1996; LINZMEIER et al. 2007).

***Paradibolia* Baly**

- *Paradibolia* Baly, 1875: 31. Type species: *Paradibolia indica* Baly, 1875, by monotypy.

Comments: The genus is comprised of about seven species distributed in the Oriental, Afrotropical, and Australian Regions. Host plants are Lamiaceae; the larva is a leaf-miner (BIONDI & D'ALESSANDRO 2010; C. Reid, pers. comm.).

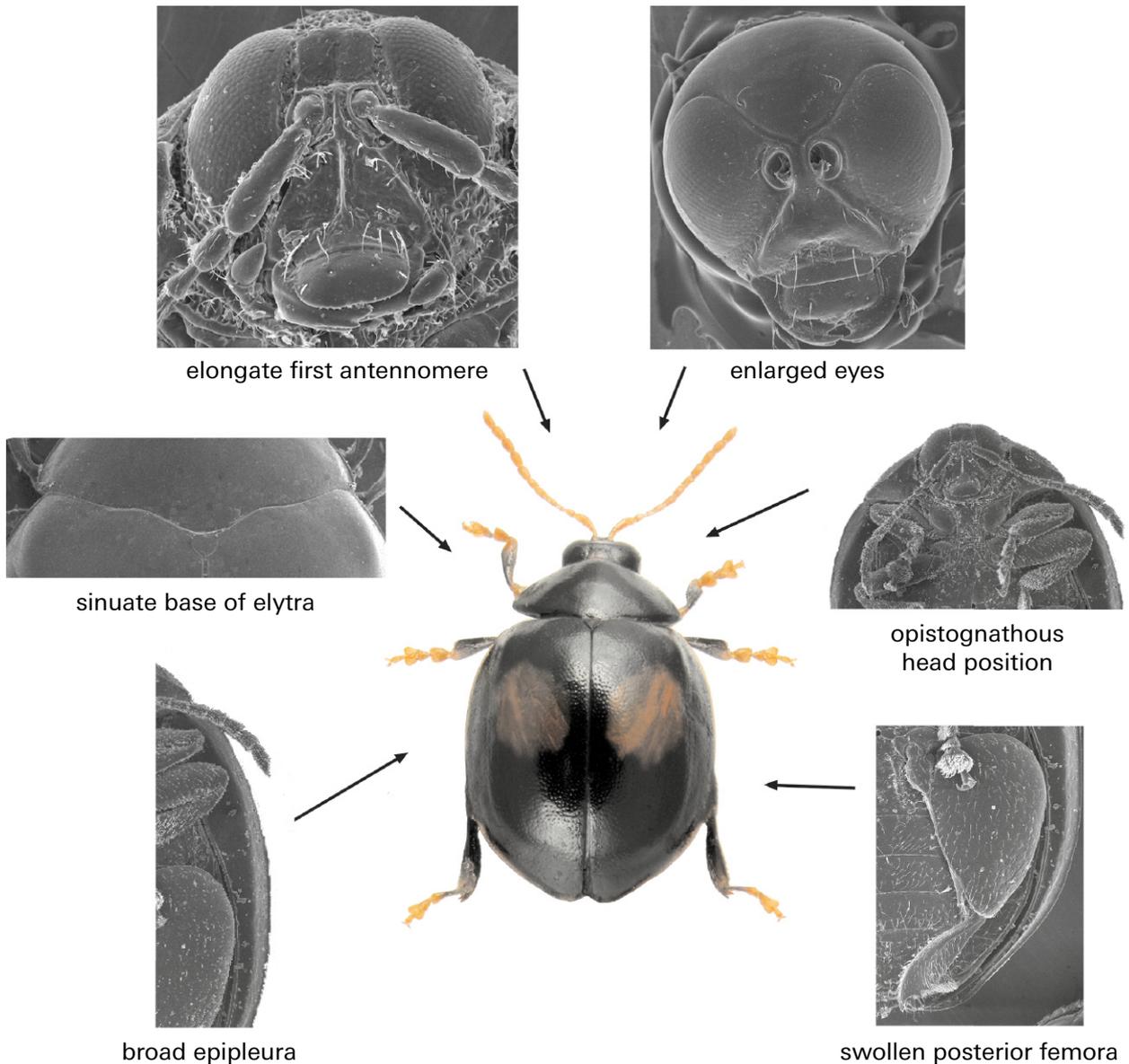


Fig. 87. Hemisphere and corresponding characters (*Agropistes biplagiatus* centrally).

4. Acknowledgements

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