

Notes on the Phylogenetic Relationships of Planthoppers of the Family Issidae (Hemiptera, Fulgoroidea) of the Western Palaearctic Fauna, with Descriptions of Two New Genera

V. M. Gnezdilov

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia
e-mail: vmgnezdilov@mail.ru, vgnездilov@zin.ru

Received February 7, 2016

Abstract—Seven groups of genera are distinguished in the subtribe Issina Spinola. The new genera *Apedalmus* gen. n. (the type species *Falcidius abruzicus* Dlabola, 1983) and *Thalassana* gen. n. (the type species: *Hysteropterum ephialtes* Linnavuori, 1971) are erected. The subgenera *Acrestia* Dlabola, 1980, *Montissus* Gnezdilov, 2003, and *Atticus* Gnezdilov, 2003 are upgraded to genera. The subgenus *Capititudes* Gnezdilov, Drosopoulos et Wilson, 2004 is transferred to the genus *Acrestia*, and the subgenus *Stygiata* Emeljanov, 1972 to *Celyphoma* Emeljanov, 1971. The subtribe Agalmatiina Gnezdilov, 2002 and the subfamily Hysteropterinae Melichar, 1906 are placed in synonymy under Issina Spinola, 1839. *Issus reticulatus* Herrich-Schäffer, 1835 is designated as the type species of the genus *Hysteropterum* Amyot et Serville, 1843.

DOI: 10.1134/S0013873816030106

The classification of the higher fulgoroid planthoppers and, in particular, the group of “issidoid” families (Gnezdilov, 2007, 2013a, 2013b, 2013d), has been perfected during the last years, which necessitates phylogenetic studies of these families. The cladograms of Fulgoroidea, based on analysis of the nucleotide sequences, were proposed by T. Bourgoïn with coauthors (Bourgoïn et al., 1997), V.B. Yeh with coauthors (Yeh et al., 1998, 2005), and D. Urban and D. Cryan (Urban and Cryan, 2007). The scheme of fulgoroid phylogeny based on analysis of the morphological characters was proposed by A.F. Emeljanov (1990). The results of molecular investigations of the phylogeny of the higher Fulgoroidea and, in particular, the family Issidae, published last year (Sun et al., 2015; Gnezdilov et al. 2015) have proved independence of Caliscelidae and a sister position of Trienopini Fennah in relation to Trypetimorphini Melichar (Tropiduchidae), which were substantiated by earlier morphological data (Emeljanov, 1999; Gnezdilov, 2007); the synonymy of Agalmatiina Gnezdilov, 2002, Hysteropterinae Melichar, 1906, and Issina Spinola, 1839 in the family Issidae was also revealed.

The fauna of the family Issidae of the Western Palaearctic Region is one of the most completely studied regional faunas of this planthopper group (Gnezdilov, 2003; Gnezdilov et al., 2014). Nevertheless, analysis of the morphological characters of the western Palaearctic species has shown that the composition

and status of some genera require revision, allowed differentiation of groups of closely related genera within the subtribe Issina, and showed the need to resurrect the subtribe Thioniina Melichar, 1906 for the taxa with developed 3-lobed hind wings.

The material used in the study is deposited in the Muséum National d’Histoire Naturelle in Paris (MNHN), the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (ZIN), the Zoological Museum in Hamburg (ZMH), the Zoological Museum in Munich (ZSM), and the Agricultural University in Athens (AUA).

Among the recent taxa of the family Issidae, the most primitive forms are found in the Neotropical, Afrotropical, and Oriental regions. These species possess developed 3-lobed hind wings. In particular, *Oronoqua deina* Fennah, 1947 inhabiting crowns of trees in South America possesses well-developed fore wings projecting considerably beyond the apex of the abdomen and developed 3-lobed hind wings without anastomoses between *CuA* and *CuP* and also between *Pcu* and *A₁* (Gnezdilov et al., 2010). The Afrotropical *Chimetopon camerunensis* Schmidt, 1910 and *Ikonza angolensis* Gnezdilov, 2016 are characterized not only by 3-lobed hind wings but also by a free (not merged at least partly with the postcubitus) two- or 3-branched first anal vein (Gnezdilov, 2016). The latter character, free *Pcu* and *A₁*, can be considered plesiomorphic, as such condition of the veins is also typical of an Issidae

species described (Grimaldi and Engel, 2005) from Miocene Mexican amber (this species may belong to the genus *Thionia* Stål, 1859) and of representatives of the families Tropicuchidae (Gnezdilov, 2013d) and Nogodinidae (Gnezdilov, 2012) from the “issidoid” group of families (Gnezdilov, 2013c). A partial merging of the postcubitus and anterior anal vein (its anterior branch) is very typical of the Oriental genera, being a rarity among the New World genera characterized by a branching of the second anal vein.

It is according to the degree of development of the hind wing with a moderately long anojugal area remained that the *Issus* group of genera occupies the basal position in the subtribe Issina, being a sister group in relation to the complex of all the other western Palaearctic genera—Hysteropterina plus Agalmatina *sensu* Gnezdilov (Gnezdilov, 2002, 2003). The sister relationships between the genera *Issus* and *Latisus* are beyond doubt, these taxa are related through a unique synapomorphy—the presence of paired digitate processes on the inner side of the dorsolateral lobes of the phallobase (Figs. 1–4).

Analysis of the morphological data has shown that the genus *Mulsantereum sensu* Gnezdilov (2004) and Gnezdilov, Wilson (2007) is clearly divided into two groups, the proper *Mulsantereum* Gnezdilov, 2002 with the type species *Mulsantereum maculifrons* (Mulsant et Rey, 1855) and the *M. abruzicum* species-group including the species *M. abruzicum* (Dlabola, 1983), *M. novaki* (Wagner, 1962), and *M. oculatum* (Linnavuori, 1965).

The *M. abruzicum* species-group differs from *M. maculifrons* in the following characters: the radius of the fore wing is 3-branched, the media 2–5-branched (in *M. maculifrons*, the radius is 2-branched and the media is 3-branched); the hypocostal lobe of the fore wing is narrow or absent (wide in *M. maculifrons*); the 1st metatarsomere bears an incomplete row of 2–5 intermedial spines (7 or 8 intermedial spines in *M. maculifrons*); each dorsolateral lobe of the phallobase bears a subapical margination of teeth (Figs. 5, 9) (in *M. maculifrons*, the lobe is triangular); the dorsoapical part of the phallobase appears as a slightly sclerotized protruding sac (in *M. maculifrons*, the dorsoapical part of the phallobase does not protrude); the ventral lobe of the phallobase is not narrowed towards the apex, emarginate (Figs. 6, 10) (narrowed towards the apex and not emargination in *M. maculifrons*); the anal tube of the male forms no emargination at the

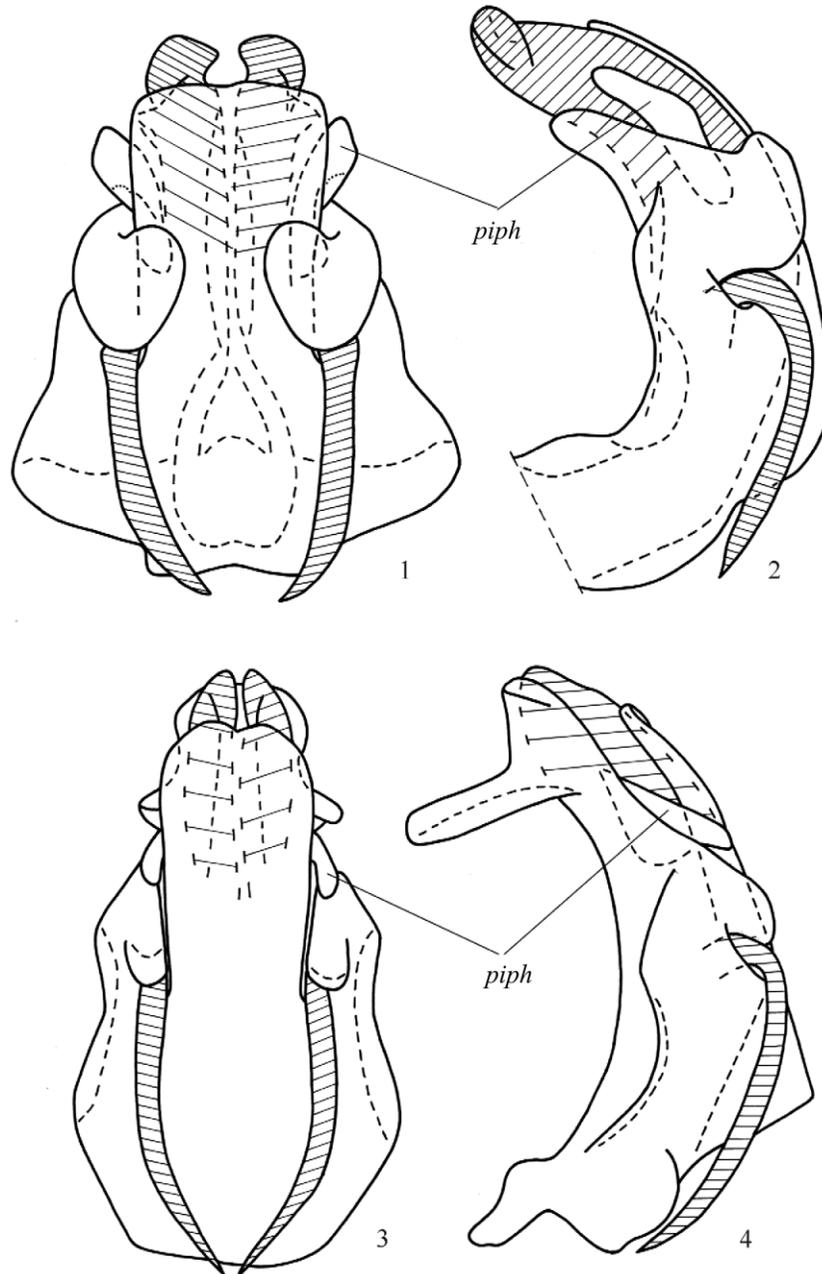
apex (Figs. 7, 12) (with a distinct emargination in *M. maculifrons*); the stylus is very shallowly emarginate posteriorly (Figs. 8, 11) (convex in *M. maculifrons*); the posterior margin of sternite VII of the female with a sharp cuneiform emargination medially (widely emarginate in *M. maculifrons*); the median area (median field) of gonapophyses IX (Figs. 13, *ma*) is formed by partly fused lobes (in *M. maculifrons*, the lobes are completely fused).

Thus, the genus *Mulsantereum* Gnezdilov, 2002 (the type species *Hysteropterum maculifrons* Mulsant et Rey, 1855) should be considered monotypical, and the genus *Apedalmus* gen. n. is erected here for the *M. abruzicum* species-group.

The genus *Bubastia sensu* Gnezdilov et al. (2014) can be divided into 4 groups, the proper *Bubastia* Emeljanov, 1975 (subgenus *Bubastia* s. str.) and three complexes of species: the subgenera *Acrestia* and *Capititides* and the *Bubastia ephialtes* species-group. Analysis of the morphological characters of these groups has confirmed their independence. *Bubastia* s. str. is the largest complex comprising 17 species; it is characterized by the presence of a pair of ventral hooks of the aedeagus directed towards its base (except for *B. olympica* Dlabola, 1982), by the phallobase entirely concealing the aedeagus, and by completely fused lobes of the median area of gonapophyses IX (Figs. 14–16).

The subgenera *Acrestia* Dlabola, 1980 and *Capititides* Gnezdilov, Drosopoulos et Wilson, 2004 differ from *Bubastia* s. str., being similar to each other in the absence of ventral hooks of the aedeagus, in the apical processes of the aedeagus projecting beyond the upper margin of the phallobase, and in only partly fused lobes of the median area of gonapophyses IX (Figs. 17, 18, 23–25, 29). Thus, *Acrestia* comprising two species differs from the monotypical *Capititides* in a transverse coryphe, in a very peculiar stylus with a serpentine neck, and also in the ventral lobe of the phallobase formed by two long processes (Figs. 18, 21, 22). *Capititides* in turn possesses an elongate coryphe, its stylus also has a neck (but not serpentine), and the ventral lobe of its phallobase is truncate apically (Figs. 23, 28). The anal tube in the males of *Acrestia* and *Capititides* is long and narrow (Figs. 19, 20, 26, 27).

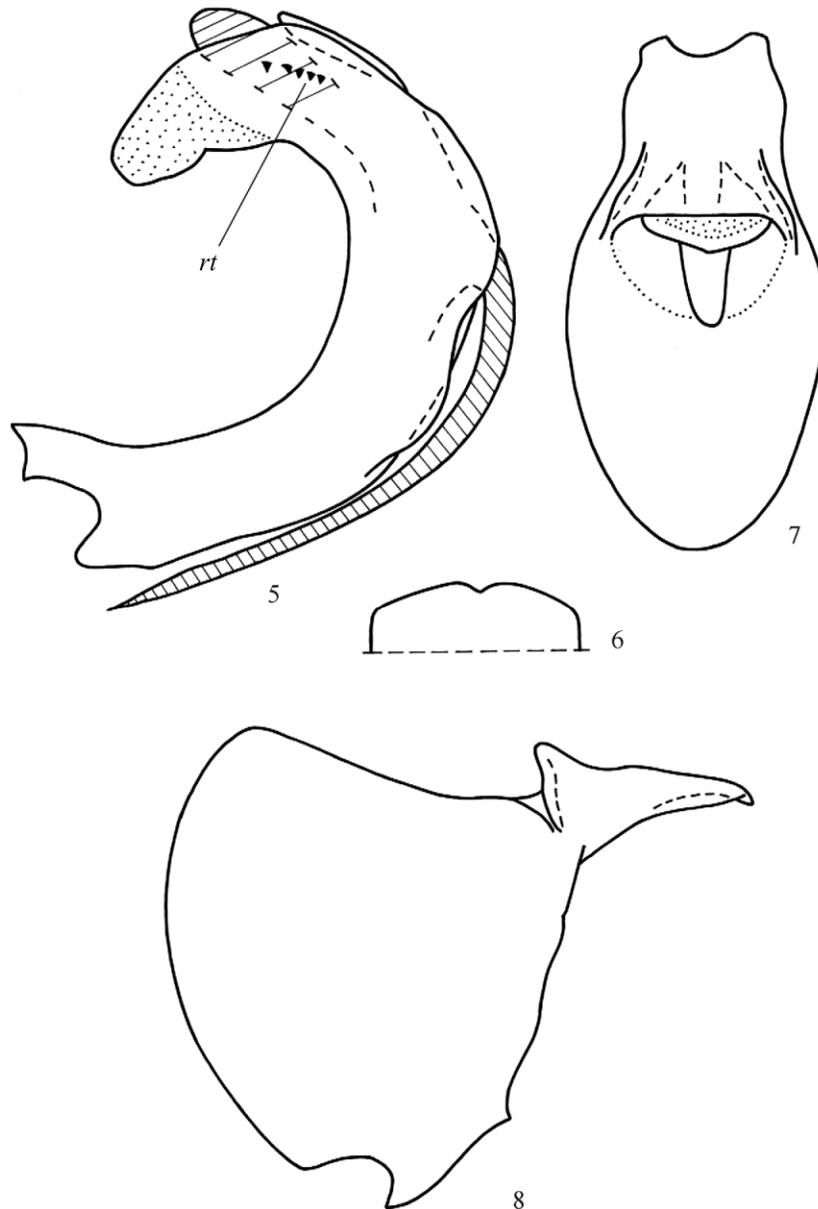
The species of the *B. ephialtes* group, including *B. ephialtes* (Linnavuori, 1971) and *B. cyrenaica* (Linnavuori, 1965), differ from the other species of the



Figs. 1–4. *Issus muscaeformis* (Schrank) (1–2) and *Latissus dilatatus* (Fourcroy) (3–4), male: (1, 3) penis, ventral view; (2, 4) penis, lateral view; *piph*, processes of inner walls dorsolateral lobes of phallobase.

genus *Bubastia* in the following characters: the apical processes of the aedeagus project beyond the upper margin of the phallobase; the short ventral hooks of the aedeagus are directed upwards; the dorsolateral lobes of the phallobase are widely truncate apically and have a serrate margin (similarly to *Capititudes*); the posterior margin of the stylus is sharply emarginate; the anal tube of the male is long and narrow; and the lobes of the median area of gonapophyses IX are not completely fused (Figs. 30–35). Thus, this species-

group is closely related to *Acrestia* and *Capititudes* rather than to *Bubastia* s. str. and should be erected as a genus. Molecular analysis also clearly shows that *B. ephialtes* and *B. obsoleta* (Fieber, 1877), a representative of the subgenus *Bubastia* s. str., diverge towards different, far distant clusters (Gnezdilov et al., 2015). Consequently, the scope of the genus *Bubastia* should be restricted to the nominotypical subgenus, *Capititudes* should be considered in the rank of a subgenus of the genus *Acrestia*, and the *B. ephialtes* spe-



Figs. 5–8. *Apedalmus abruzicus* (Dlabola), male: (5) penis, lateral view; (6) apex of ventral lobe of phallobase; (7) anal tube, dorsal view; (8) stylus, lateral view; *rt*, row of teeth.

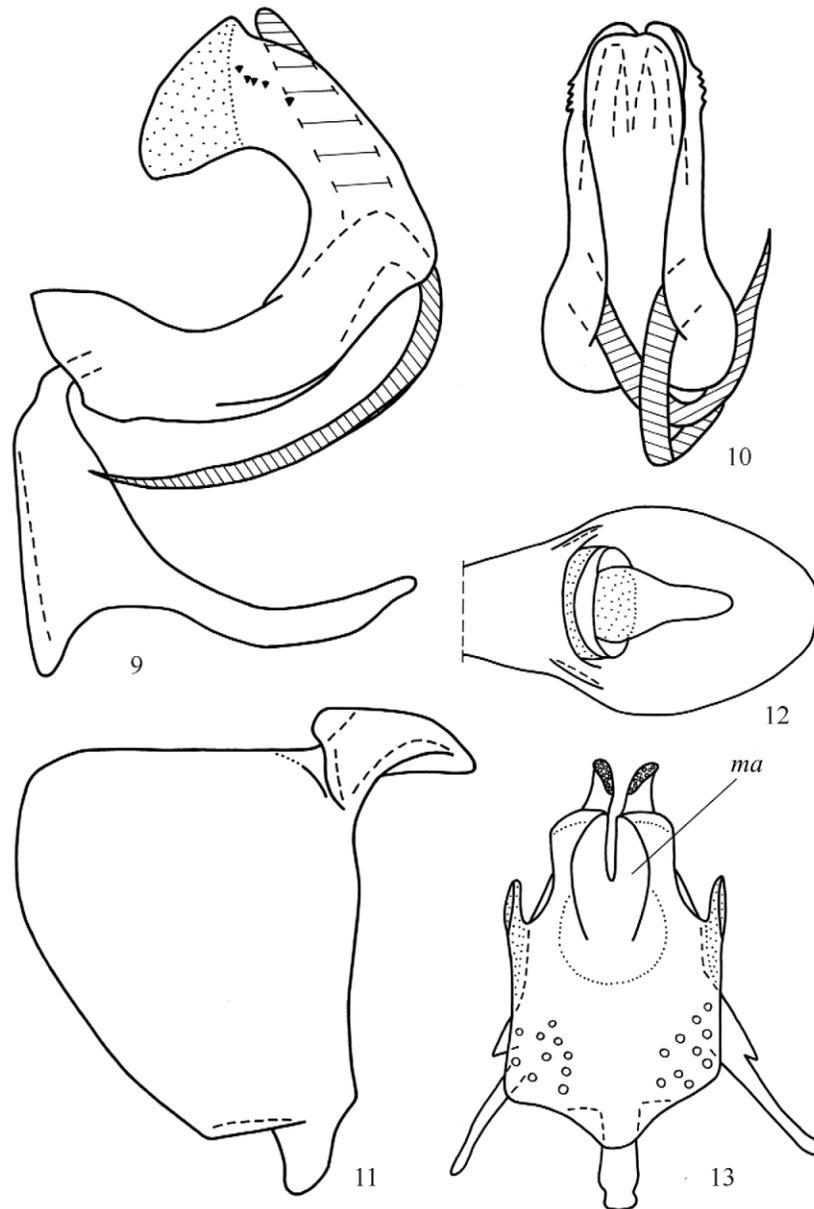
cies-group should be distinguished into a genus, *Thalassana* gen. n.

In addition to the *Issus* group of genera, the *Conosimus* monotypical group and 5 more groups of genera can be distinguished within the subtribe *Issina* Spinola (Fig. 43).

(1) The compact complex of the genera *Alloscelis* Kusnezov, 1930, *Tshurtshurnella* Kusnezov, 1927, *Zopherisca* Emeljanov, 2001, and *Mycterodus* Spinola, 1839 adjoins the *Acrestia-Thalassana* group considered above and forms a common group of genera,

Mycterodus. The representatives of this group are similar in the structure of the penis with the aedeagus not concealed entirely by the phallobase and with the dorsal part of the aedeagus clearly visible from the outside.

The monophyly of the genus *Mycterodus* with 5 subgenera (*Mycterodus* Spinola, 1839, *Aconosimus* Dlabola, 1987, *Comporodus* Kocak, 1982, *Aegaeum* Gnezdilov, 2003, and *Semirodus* Dlabola, 1987) is supported by 2 synapomorphies: the 1st metatarsomere bears an interrupted row of intermedial spines (3 + 1 or 4 + 1) at the apex, and the metope frequently bears



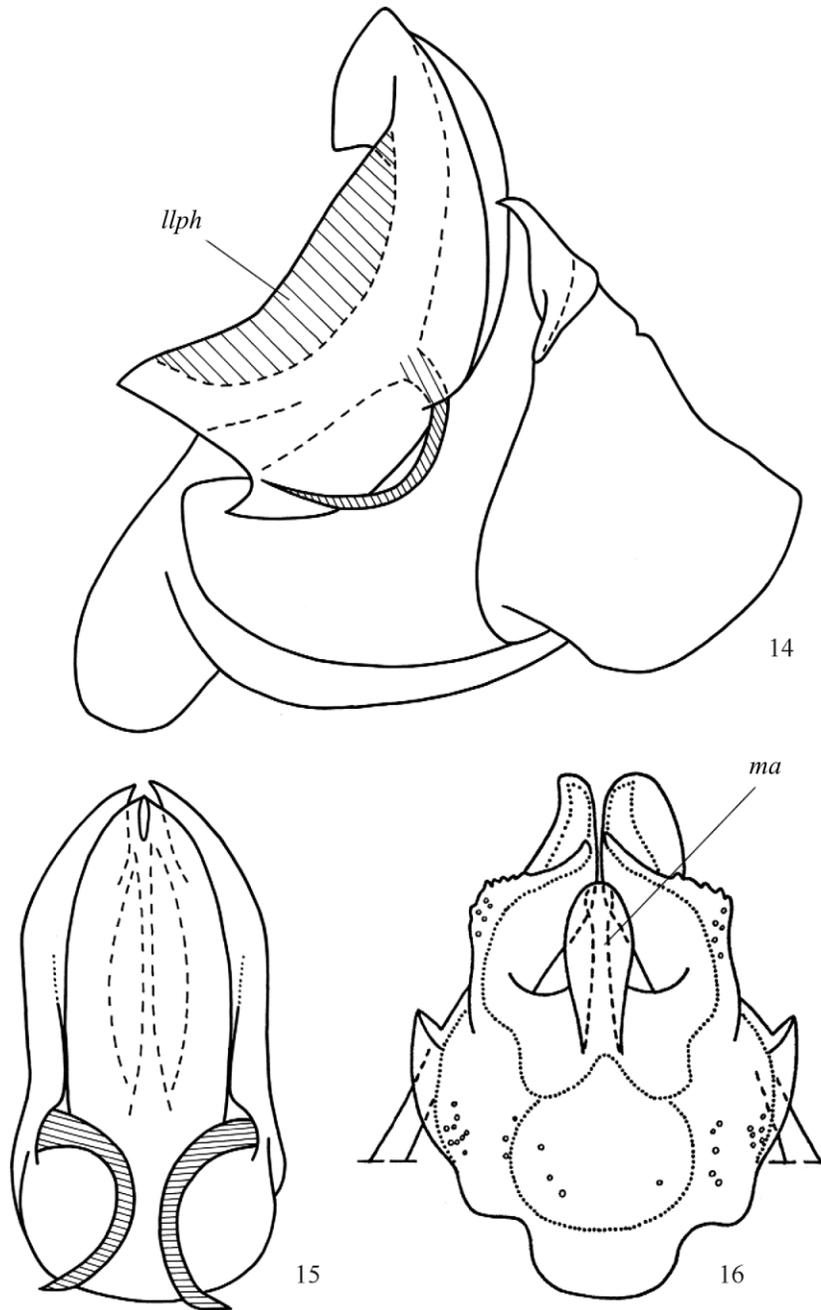
Figs. 9–13. *Apedalmus oculatus* (Linnavuori): (9) penis and connective, lateral view; (10) penis, ventral view; (11) stylus, lateral view; (12) male anal tube, dorsal view; (13) gonapophyses IX, ventral view; *ma*, median area.

a pale V-shaped stripe. The subgenus *Aconosimus* is characterized by a smooth margin of the dorsolateral lobes of the phallobase, by flat lateral areas of gonapophyses IX, and by the absence of ventral hooks of the aedeagus, which distinguishes *Aconosimus* from the other subgenera. The sister relationships between *Comporodus* and *Aegaeum* can be substantiated by developed hind wings and by the presence of a ventral lobe of the aedeagus (Gnezdilov, 2015, fig. 11).

The subgenus *Montissus* Gnezdilov, 2003 is a sister group of the genus *Tshurtshurnella* Kusnezov, 1927 and stands apart within the genus *Mycterodus* Spinola

sensu Gnezdilov (Gnezdilov, 2003). These taxa are similar in the absence of ventral hooks of the aedeagus, in the presence of a dentiform projections of the apical processes of the aedeagus (Gnezdilov, 2015, figs. 9, 10), and in a small (1 or 2) number of intermedial spines of the 1st metatarsomere; however, the species of *Montissus* differ from the representatives of *Tshurtshurnella* in a narrow and elongate fore wing, which allows me to consider *Montissus* a separate genus.

(2) The *Bubastia* group of genera comprises *Bubastia* s. str., *Palmallorcus* Gnezdilov, 2003, *Webbisanus*

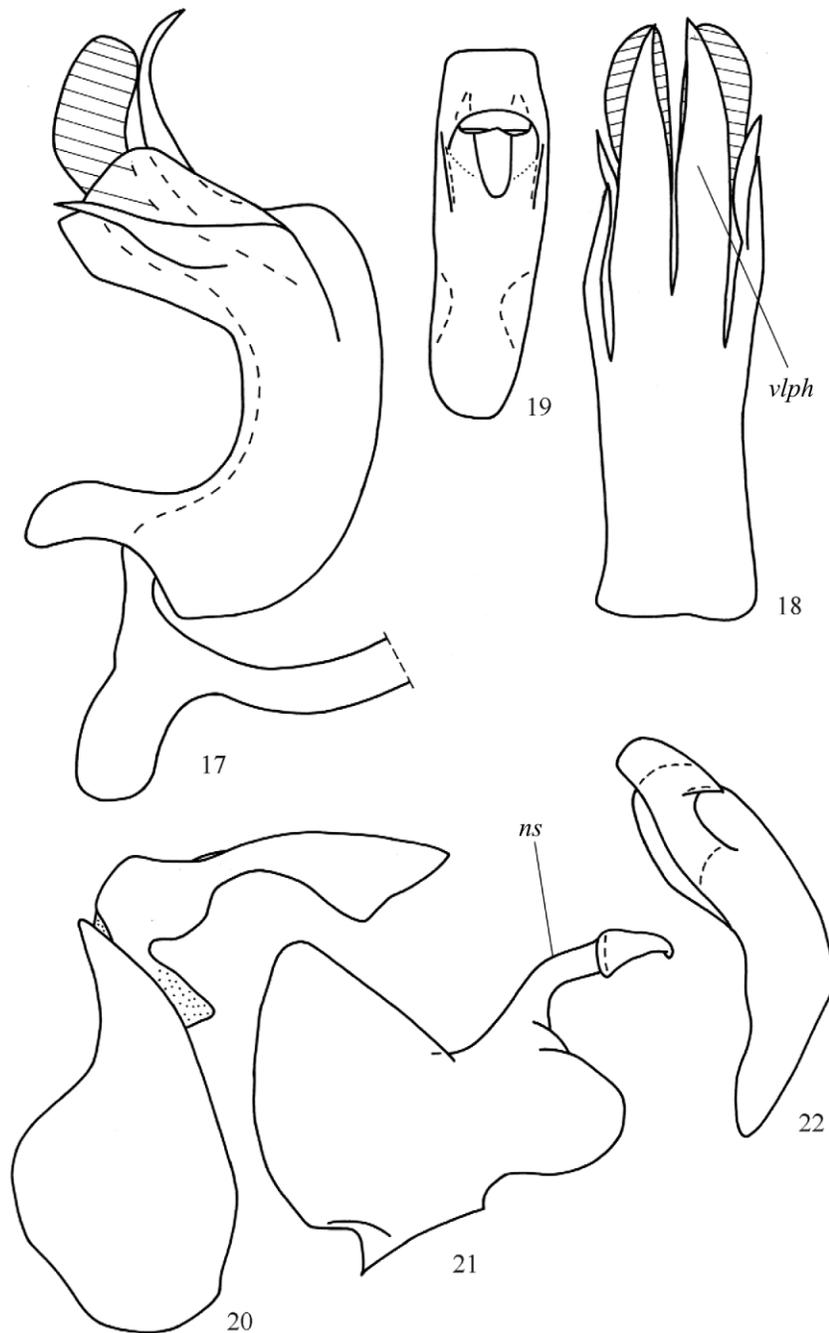


Figs. 14–16. *Bubastia taurica* (Kusnezov): (14) penis, connective, and stylus, lateral view; (15) penis, ventral view; (16) gonapophyses IX, ventral view; *llph*, lateral lobes of phallobase; *ma*, median area.

Dlabola, 1983, *Apedalmus* gen. n., *Falcidius* Stål, 1866, *Numidius* Gnezdilov, Guglielmino et D'Urso, 2003, *Semissus* Melichar, 1906, *Latilica* Emeljanov, 1971, and *Kovacsiana* Synave, 1956. Within this group, the genera *Numidius*, *Semissus*, *Latilica*, and *Kovacsiana* are characterized by a multibranch radius (with at least 3 branches), while the overwhelming majority of the genera of Issidae possess a 2-branched radius. *Semissus* and *Falcidius* are similar in the struc-

ture of clearly bifurcate apical processes of the aedeagus, and the close relationship between *Latilica*, *Semissus*, and *Kovacsiana* is confirmed by the presence of a furcate subapical process of the phallobase. The sister position of the genera *Kovacsiana* and *Latilica* is substantiated by a well-developed one- or two-lobed hind wing.

(3) The following group comprises genera with one lateral spine on the hind tibia (*Anatonga* Emeljanov,

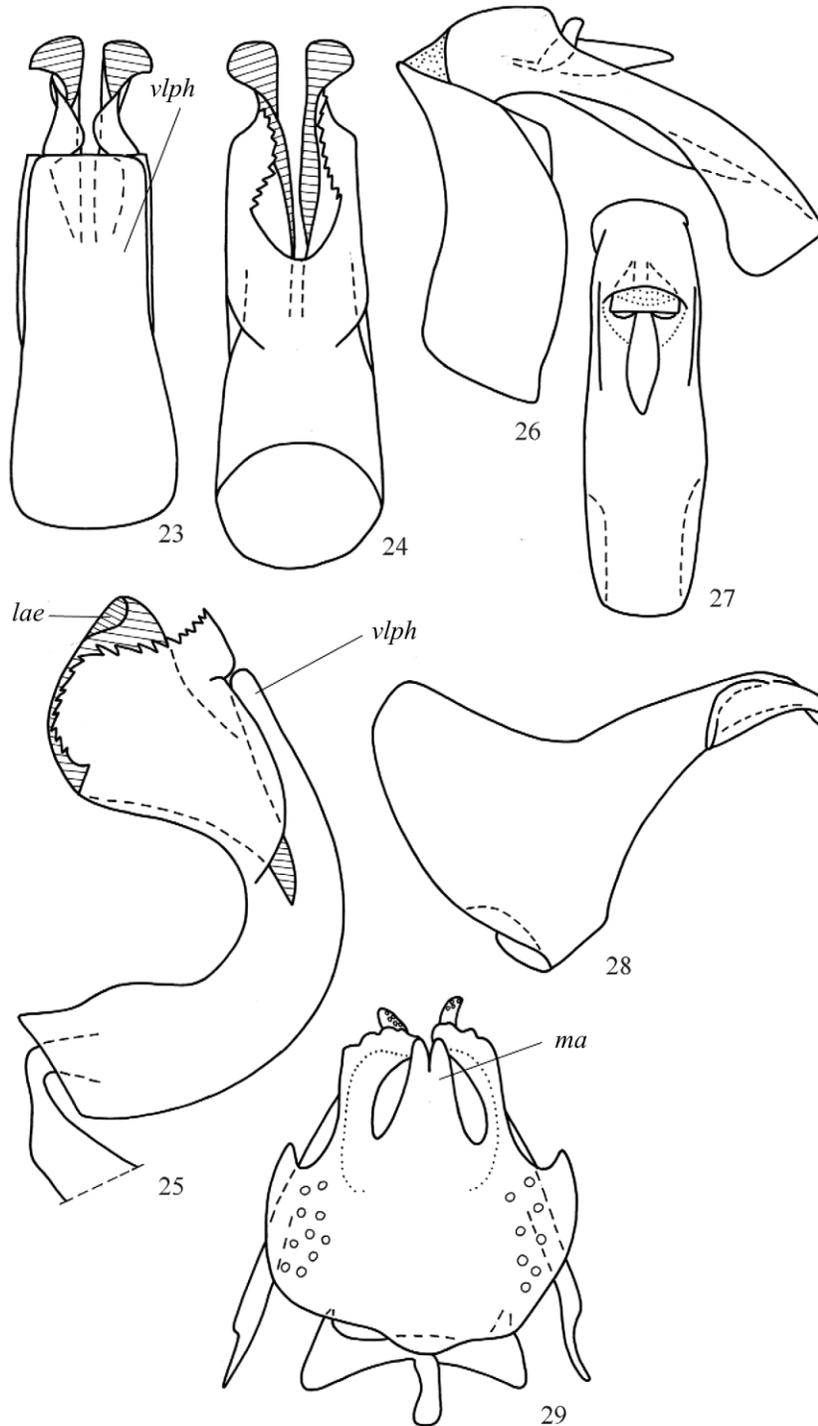


Figs. 17–22. *Acrestia (Acrestia) suturalis* (Fieber), male: (17) penis and connective, lateral view; (18) penis, ventral view; (19) anal tube, dorsal view; (20) pygophore and anal tube, lateral view; (21) stylus, lateral view; (22) stylus, dorsal view; *ns*, neck of stylus; *vlph*, ventral lobe of phallobase.

2001, *Brachyprosopa* Kusnezov, 1929, *Caepovultus* Gnezdilov et Wilson, 2007, *Celyphoma* Emeljanov, 1971, *Pentissus* Dlabola, 1980, *Phasmena* Melichar, 1902, *Iranodus* Dlabola, 1980, *Inflatodus* Dlabola, 1982, *Cavatorium* Dlabola, 1980, *Quadriya* Ghauri, 1965, *Tautoprosopa* Emeljanov, 1978, *Bergevinium* Gnezdilov, 2003, and *Lethierium* Dlabola, 1980) and also *Sfaxia* Bergevin, 1917 without lateral spines. This

group includes all the genera with the center of diversification in the Irano-Turanian Region and on the Arabian Peninsula and also two genera with the center of diversification on the Iberian Peninsula and in Northwestern Africa—*Phasmena* group of genera.

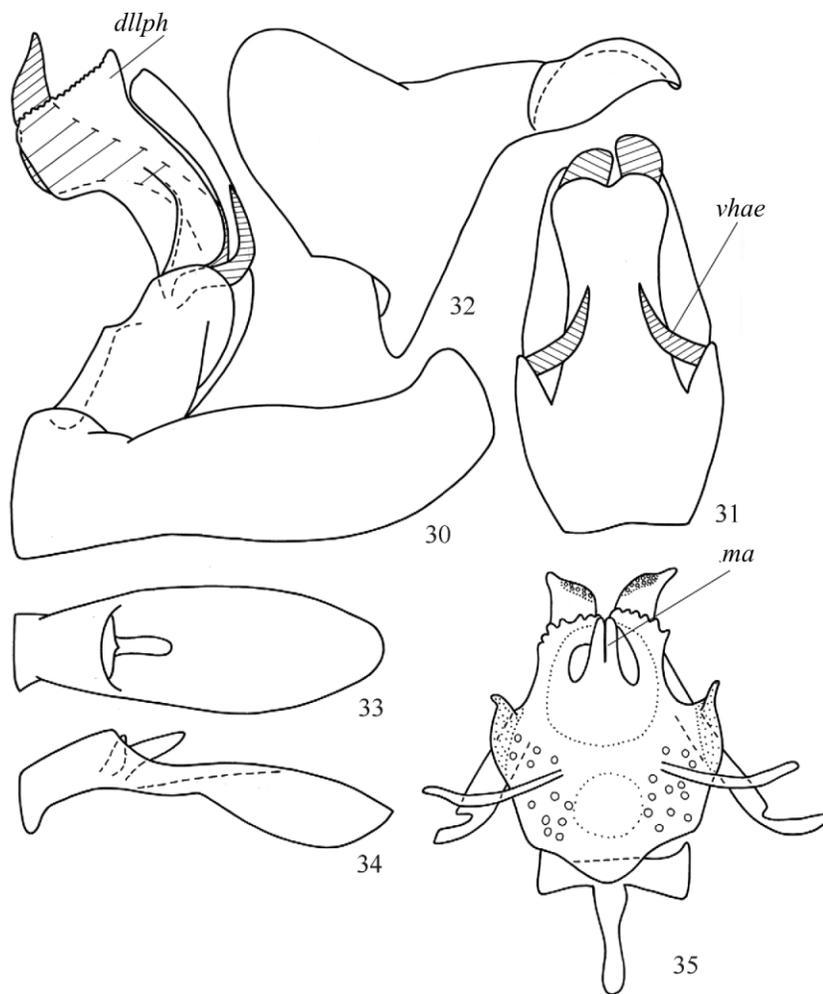
In this group, *Sfaxia* is similar to the genera *Pentissus* and *Caepovultus* in the presence of simple trans-



Figs. 23–29. *Acrestia (Capititudes) jatagana* (Dlabola): (23) penis, ventral view; (24) penis, posterior view; (25) penis, lateral view; (26) pygophore and anal tube, lateral view; (27) male anal tube, dorsal view; (28) stylus, lateral view; (29) gonapophyses IX, ventral view; *vlph*, ventral lobe of phallosome; *lae*, lobes of aedeagus; *ma*, median area.

verse carinae of the gonopods and in weakly arcuately curved or nearly straight distal parts of gonapophyses IX. The genera of the sister pair *Pentissus*–*Caepovultus* are related based on the 2-branched anterior cubitus (*CuA* 2) of the fore wing, which, however,

is a not unique synapomorphy, being also characteristic of the genera of the *Issus* group. *Caepovultus* exhibits autapomorphy unique among the western Palearctic genera, an unbranched media of the fore wing (*M* 1). The monotypical genus *Pentissus* in turn is



Figs. 30–35. *Thalassana ephialtes* (Linnavuori): (30) penis and pygophore, lateral view; (31) penis, ventral view; (32) stylus, lateral view; (33) male anal tube, dorsal view; (34) male anal tube, lateral view; (35) gonapophyses IX, ventral view; *dllph*, dorsolateral lobes of phallobase; *ma*, median area; *vhae*, ventral hooks of aedeagus.

characterized by reduced hind wings and by considerably shortened, approximately rounded fore wings. The shape of the ventral hooks of aedeagus sharply narrowed before the apex also relates this genus to *Celyphoma*.

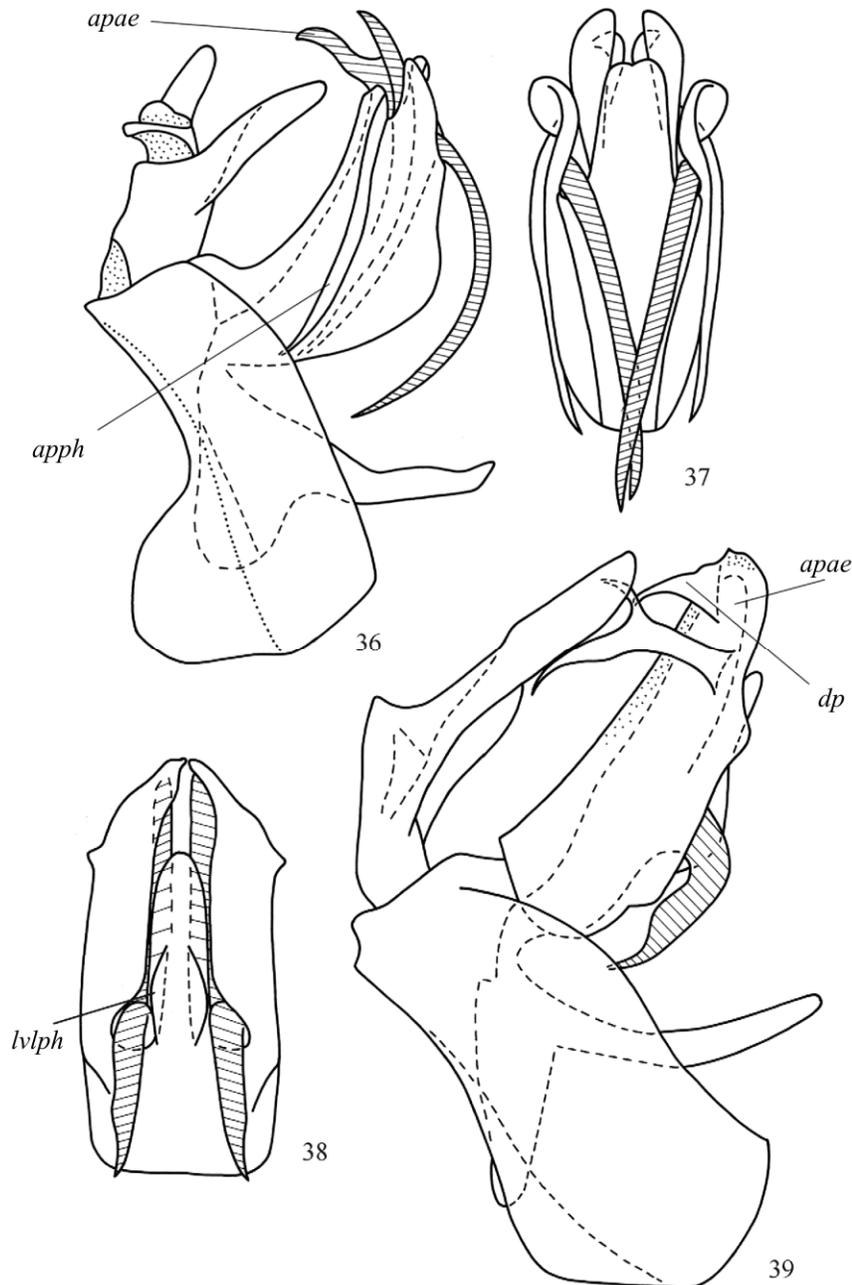
The genera *Celyphoma* and *Brachyprosopa* are similar in the presence of a dentiform apical process of the dorsolateral lobe of the phallobase; however, the presence of distinctive vertical lobes of the ventral lobe of the phallobase also relates the genus *Celyphoma* to *Tautoprosopa*.

The sister relationships between *Anatonga* and *Phasmena* are beyond doubt. These genera are similar in the dorsolateral lobes of the phallobase bearing long pointed apical processes directed towards the phallobase base. The proper *Anatonga* is a peculiar monotypical genus characterized by the absence of ventral

hooks of the aedeagus and by the presence of a deep emargination of the ventral lobe of the phallobase; its unique autapomorphy is a large up-directed process of the median area of the posterior connective laminae of gonapophyses IX.

Quadriva is related to *Iranodus* in a unique synapomorphy: the presence of a flattened process on the dorsal surface of the phallobase.

The species of the genera *Phasmena* and *Celyphoma* examined by me demonstrate two types of the structure of the male genitalia, which allows me to reconsider the scope of these genera. The genus *Phasmena* is characterized by a distinctly bifurcate apical processes of the aedeagus and by the presence of a long narrow (occasionally bifurcate) apical process situated at each side of the phallobase and directed towards its base (Figs. 36, 37). In the species of the



Figs. 36–39. *Phasmena nigrodorsalis* Siderski (36, 37) and *Celyphoma fruticulina* (Emeljanov) (38, 39), male: (36, 39) penis, pygophore and anal tube, lateral view; (37, 38) penis, ventral view; *apae*, apical processes of aedeagus; *apph*, apical processes of phallobase; *dp*, dentiform process; *lvlph*, lobes of ventral lobe of phallobase.

genus *Celyphoma*, the apices of the apical processes of the aedeagus are simple, and the phallobase can bear 1 or 2 (one of them can be branched) processes directed sideways or towards the base of the phallobase (Figs. 38, 39).

According to these details of the structure, I suggest that only 7 species should be attributed to the genus *Phasmena*: *Ph. adyoungi* Dlabola, 1982, *Ph. breviscula* Emeljanov, 1978, *Ph. cardinalis* Emeljanov,

1978, *Ph. nasuta* Melichar, 1902, *Ph. nigrodorsalis* Siderski, 1938, *Ph. tardiviva* Emeljanov, 1978, and *Ph. telifera* Melichar, 1902.

The genus *Celyphoma* should be considered as one comprising two subgenera: the proper *Celyphoma* to which the species *Phasmena spiraeae* Mitjaev, 1967, *Ph. gobica* Emeljanov, 1982, *Ph. tumida* Emeljanov, 1982, and *Ph. petrensis* Emeljanov, 1972 should also be added and the subgenus *Stygiata* Emeljanov, 1972,

which, in addition to the type species (*Ph. ephedrae* Emeljanov, 1972), should also include *Ph. contigua* Emeljanov, 1982 from Mongolia (Emeljanov, 1982) and *Celyphoma quadrupla* Meng et Wang, 2012 from China (Meng and Wang, 2012), since these species, similarly to the type species of the subgenus, are characterized by the ventral hooks of the aedeagus crossing on the dorsal side of the phallobase.

(4) The *Kervillea sensu* Gnezdilov group of genera (Gnezdilov, 2002, 2003) comprises *Kervillea* Bergevin, 1918, *Pseudohemisphaerius* Melichar, 1906, *Latematium* Dlabola, 1979, *Corymbius* Gnezdilov, 2002, *Bootheca* Emeljanov, 1964, *Rhissolepus* Emeljanov, 1971, and *Scorlupella* Emeljanov, 1971. This group is distinguished based on the structure of the phallobase, gonapophyses IX, and gonoplares.

The monotypical genus *Pseudohemisphaerius* Melichar, 1906 differs from all the western Palaearctic genera of the subtribe Issina in a loss of the posterior cubitus (*CuP*) and in smoothed fore-wing veins. However, *Pseudohemisphaerius* is closely related to the genera *Kervillea* and *Latematium* in a peculiar structure of the phallobase: a pair of long folds frequently conceals ventrally the ventral lobe of the phallobase. In the contour of the phallobase angularly widened in the lower third, *Pseudohemisphaerius* is similar to the genus *Bootheca*.

Analysis of the morphological characters has shown the necessity of revision of the status of the monotypical subgenus *Atticus* Gnezdilov, 2003 established in the genus *Latematium* (Gnezdilov, 2003). The proper *Latematium* is characterized by the anal tube of the male widened towards the apex (in dorsal view), by the absence of processes of the dorsolateral lobes of the phallobase, by the complete ventral lobe of the phallobase, and by the aedeagus without ventral hooks. *Atticus* differs in the anal tube of the male distinctly narrowed apically (in dorsal view), in the presence of processes on the dorsolateral lobes of the phallobase, in a 3-lobed ventral lobe of the phallobase, and in the aedeagus with a pair of short curved ventral hooks (Figs. 40–42). Thus, the weight of evidence suggests that *Atticus* is a separate genus.

Kervillea, *Latematium*, *Atticus*, *Corymbius*, *Bootheca*, *Rhissolepus*, and *Scorlupella* are grouped according to the structure of the sectioned gonoplares (lobes Gp 1 and Gp 2 are not completely fused). However, the monotypical *Corymbius* can be also related to the oligotypical genus *Pamphylium* Gnezdilov et Wil-

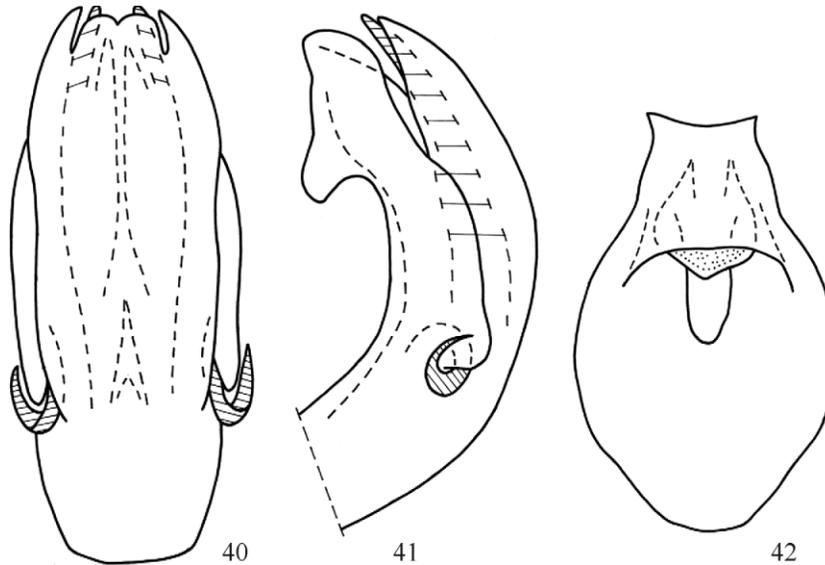
son, 2007 on the grounds of two characters: the fore wing widened towards the apex (in lateral view) and the presence of a pair of vertical lobes or carinae on the ventral lobe of the phallobase. Within this group, the sister relationships between *Scorlupella* and *Rhissolepus* are substantiated by gonapophyses IX similar in structure: the lobes of the median area are approximate or turned in the shape of folds) (Gnezdilov, 2002), by the metope bearing transverse carina, by a similar structure of the convex sac of the dorsal surface of the phallobase, and by the aedeagus without ventral hooks.

(5) In the cladogram based on molecular data, the subtribe Agalmatiina is not separated at one level with the subtribe Hysteropterina but included in the latter (Gnezdilov et al., 2015). AgNoR-bending also shows that *Hysteropterum albaceticum* Dlabola, 1983 (a representative of the type genus of the subtribe Hysteropterina) and *Agalmatium bilobum* (Fieber, 1877) (a representative of the type genus of the subtribe Agalmatiina) are similar in the subterminal localization of the nucleolar organizer (NOR) in the largest pair of autosome (Kuznetsova and Aguin-Pombo, 2015). The facts mentioned allow me to consider the names of these subtribes as synonyms.

The group of genera corresponding to the subtribe Agalmatiina *sensu* Gnezdilov (Gnezdilov, 2002, 2003) and comprising *Agalmatium* Emeljanov, 1971, *Clybeccus* Gnezdilov, 2003, *Iberanum* Gnezdilov, 2003, *Lindbergatium* Dlabola, 1984, *Tingissus* Gnezdilov, 2003 plus the sister pair *Fieberium* Dlabola, 1980 and *Palaolithium* Gnezdilov, 2003 is characterized by the ovipositor in which the median area of gonapophyses IX is convex and bears a distinct process; however, this process varies in shape between genera of this group. *Hysteropterum* Amyot et Serville, though possessing an only slightly convex median area of gonapophyses IX, is also attributed to this group based on the data of the molecular studies mentioned above—*Hysteropterum* group of genera.

The sister relationships of the genera *Agalmatium* and *Lindbergatium* are substantiated by a variety of characters: a small lateral tooth of the stylus, triangular subapical processes of the dorsolateral lobes of the phallobase, and triangular processes of the apical angles of the anal tube of the males (in lateral view).

The sister relationships of the genera *Palaolithium* and *Fieberium* are confirmed by the unique structure of the median area of gonapophyses IX with a pair of



Figs. 40–42. *Atticus graecicus* (Dlabola), male: (40) penis, ventral view; (41) penis, lateral view; (42) anal tube, dorsal view.

earlike processes (Gnezdilov, 2003, figs. 45, 46), by the presence of long and narrow subapical processes of the dorsolateral lobes of the phallobase, by an angularly projecting posterior margin of gonocoxite VIII, and by the presence of transverse carinae of gonoplasts.

Tribe **ISSINI** Spinola

Subtribe **ISSINA** Spinola

Issoides Spinola, 1839 : 204. Type genus: *Issus* Fabricius, 1803.

Hysteropterinae Melichar, 1906 : 3, **syn. n.** Type genus: *Hysteropterum* Amyot et Serville, 1843.

Agalmatiina Gnezdilov, 2002 : 609, **syn. n.** Type genus: *Agalmatium* Emeljanov, 1971.

Genus *Issus* Fabricius, 1803

Issus muscaeformis (Schrank, 1781) (Figs. 1, 2)

Material. Hungary: 1 ♂, “Mehadia” (ZIN).

Genus *Latissus* Dlabola, 1974

Latissus dilatatus (Fourcroy, 1785) (Figs. 3, 4)

Material. Slovenia: 1 ♂, “Simonov Bay, Jagodje vill., 22.VI.2001” (V.M. Gnezdilov leg.) (ZIN).

Genus *Hysteropterum* Amyot et Serville, 1843

The type species *Hysteropterum reticulatum* Herrich-Schäffer, 1835 is designated here according to

article 70.3.2 of the International Code of Zoological Nomenclature (2000).

The genus *Hysteropterum* was described by C.J.B. Amyot and J.G.A. Serville (Amyot and Serville, 1843) without designation of the type species which was later fixed for this genus by G.W. Kirkaldy (1903)—“*Hysteropterum t mmaculatum*.” As seen from the given citation, Kirkaldy did not indicate in which genus “*immaculatum*” was originally described and who was the author of this name.

Actually *Cercopis immaculata* was described by I. Fabricius (1794) and nowadays it is the type species of the genus *Mycterodus* Spinola, 1839, which is characterized by an elongate coryphe. It was this character (“tete protuberante”) to which M. Spinola turned attention when he established the genus *Mycterodus* (Spinola, 1839). In Spinola’s publication, this species appears under the name *Issus nasutus* Herrich-Schäffer, 1835. However, under the name *Issus immaculatus* F., Herrich-Schäffer pictured and described a representative of the genus *Hysteropterum*, a species with a transverse coryphe: “vertice quadrato-transverso” (Herrich-Schäffer, 1836). Z.P. Metcalf (1958) noticed this misidentification and gave a new name to this species, *Hysteropterum schaefferi* Metcalf, 1958. Thus, Amyot and Serville, establishing the genus *Hysteropterum*, understood its differences from *Mycterodus* Spinola. However, following Fabricius, the “*immaculata*” species name was erroneously interpreted in the literature, and it is unknown whose treatment was meant by Kirkaldy when he designated

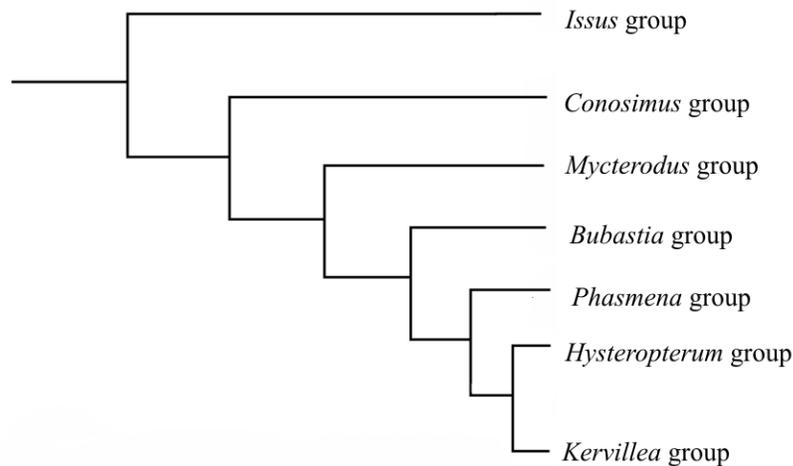


Fig. 43. Simplified cladogram based on morphological data on the phylogeny of the subtribe Issina.¹

the type species for the genus *Hysteropterum*. Recently W. Holzinger with coauthors (Holzinger et al., 2003) distinguished neotype for *Issus reticulatus* Herrich-Schäffer, 1835 and reduced *H. shaefferi* Metcalf, 1958 to a synonym of *I. reticulatus*.

Therefore, none of the designations of the type species of the genus *Hysteropterum* can be considered valid at present. According to article 70.3.2 of the International Code of Zoological Nomenclature (2000), in order to avoid further errors caused by erroneous interpretation of the species names mentioned and to preserve the name *Hysteropterum* as a valid generic epithet, the name *Issus reticulatus* Herrich-Schäffer, 1835 is fixed in the present study as the type species of the genus *Hysteropterum* Amyot et Serville, 1843.

Genus *Apedalmus* Gnezdilov, gen. n.

The type species: *Falcidius abruzicus* Dlabola, 1983.

Diagnosis. Metope with weak median and sublateral carinae fused on its upper margin. Coryphe transverse. Patterns of venation of fore wings: *R* 3 *M* 2–5 *CuA* 1. Hind wing rudimentary. Hind tibia with 2 lateral spines. 1st metatarsomere with 2 lateroapical and 2–5 intermedial spines. Phallobase with weakly sclerotized protruding dorsoapical part and with subapical row of teeth at each side (in lateral view). Aedeagus

with pair of long (half as long as phallobase) ventral hooks narrowed apically and directed towards base of aedeagus. Apical processes of aedeagus long, simple apically, reaching apices of dorsolateral lobes of phallobase. Gonoplocs with or without weak carinae; lobes (Gp 1 and Gp 2) completely fused. Distal parts of posterior connective laminae of gonapophyses IX (*dPCL*) curved at obtuse or nearly right angle. Lateral areas of posterior connective laminae of gonapophyses IX (*Lf*) appearing as processes. Lobes of median area (*Mf*) of posterior connective laminae of gonapophyses IX not fused. Anterior connective laminae of gonapophyses VIII (*ACL*) with 3 teeth in apical group and with 3 or 4 teeth in lateral group. Triangular sclerotized lamina of gonapophyses VIII (*TPL*) with short process-shaped lobe. Gonocoxite VIII with posterior margin lobiform projecting proximally. Endogonocoxal process with simple apex. Posterior margin of sternite VII of female with weak cuneiform median emargination.

Etymology. The generic name is formed by the words “Apennines” and “Dalmatia.”

Apedalmus abruzicus (Dlabola, 1983), comb. n.
(Figs. 5–8)

Falcidius abruzicus Dlabola, 1983 : 123.

Mulsantereum abruzicum: Gnezdilov, 2004 : 80.

Material. Italy: 1 ♂, 2 ♀, “Massafra, N of Taranto, 30.V.2008, grass in forest with *Quercus*,” 1 ♂, 5 ♀, “Matera, 02.VI.2008, dry grass” (leg. A. Maryńska-Nadachowska) (ZIN).

¹ Fig. 43 was erroneously omitted in the Russian text—Ed.

Apedalmus novaki (Wagner, 1962), comb. n.

Hysteropterum novaki Wagner, 1962 : 48 (after Novak, Wagner, 1962).

Falcidius novaki: Dlabola, 1980 : 214.

Mulsantereum novaki: Gnezdilov, Wilson, 2007 : 302.

Material. Croatia: 1 ♂, paratype, “Dalmatien” (P. Novak leg.) (ZMH); 1 ♀, “Susac D., Novak 8.5.51, Dalmatien” (ZMH); 3 ♀, “Dalmatia, Kopist (Caziol), 8.V–3.VIII.1956” (Novak leg.) (MNHN).

Apedalmus oculatus (Linnavuori, 1965), comb. n.
(Figs. 9–13)

Hysteropterum oculatum Linnavuori, 1965 : 64.

Falcidius oculatus: Dlabola, 1983 : 125.

Mulsantereum oculatum: Gnezdilov, 2004 : 80.

Material. Italy: 1 ♀, “I., Volterraio, 10.VI.1998” (K. Schoenitzer leg.) (ZSM).

Genus *Montissus* Gnezdilov, 2003, stat. n.

Type species: *Mycterodus batathen* Gnezdilov, 2003.

Species included. *Montissus batathen* (Gnezdilov, 2003), *M. bernhaueri* (Dlabola, 1997).

Genus *Bubastia* Emeljanov, 1975

Bubastia taurica (Kusnezov, 1926) (Figs. 14–16)

Material. Russia: 1 ♂, syntype, Crimea, Feodosiya, 31.VIII.1925 (F.K. Lukjanovich) (ZIN).

Genus *Acrestia* Dlabola, 1980, stat. n.

Type species: *Bubastia quadracuta* Dlabola, 1980 [= *A. suturalis* (Fieber, 1877), synonymy after Gnezdilov et al., 2004].

Subgenus *Acrestia* Dlabola, 1980

Species included. *Acrestia suturalis* (Fieber, 1877), *A. spartica* (Dlabola, 1982).

Acrestia (Acrestia) suturalis (Fieber, 1877), comb. n.
(Figs. 17–22)

Material. Greece: 1 ♂, Crete Island, 5.VII.2002 (A. Patshumas leg.) (ZIN).

Subgenus *Capititudes* Gnezdilov, Drosopoulos et Wilson, 2004

Type species: *Bubastia jatagana* Dlabola, 1980.

Acrestia (Capititudes) jatagana (Dlabola, 1980), comb. n. (Figs. 23–29)

Material. Greece: 1 ♂, Samos Island, “Pythagorion, 12–15.VII.1997” (S. Drosopoulos leg.) (ZIN).

Genus *Thalassana* Gnezdilov, gen. n.

Type species: *Hysteropterum ephialtes* Linnavuori, 1971.

Diagnosis. Metope widened above clypeus, with shallowly emarginate upper margin. Coryphe transverse. Caudodorsal margin of fore wing nearly straight (in lateral view). Apical processes of aedeagus narrowed apically, projecting beyond upper margin of phallobase (in lateral view). Ventral hooks of aedeagus short, curved, directed upwards. Dorsolateral lobes of phallobase widely truncate apically and with serrate margin. Ventral lobe of phallobase wide, long. Anal tube of male long, narrow. Stylus emarginate posteriorly; lateral tooth well developed.

Distal parts of posterior connective laminae of gonapophyses IX (*dPCL*) curved at obtuse or nearly right angle. Lobes of median area of gonapophyses IX approximate but not completely fused. Lateral areas of gonapophyses IX appearing as processes.

Etymology. The generic name is formed by the Greek words “θάλασσα” (the Mediterranean Sea) and “ανατολή” (the East).

Thalassana ephialtes (Linnavuori, 1971), comb. n.
(Figs. 30–35)

Hysteropterum ephialtes Linnavuori, 1971 : 71.

Bubastia ephialtes: Dlabola, 1980 : 226 (= *Bubastia libanotica* Dlabola, 1987, synonymy after Gnezdilov et al., 2004).

Material. Lebanon: 1 ♂, “Balaa (Jbeil), 1600 m, 20.VIII.1995” (H. Abdul-Nour leg.) (ZIN).

Thalassana cyrenaica (Linnavuori, 1965), comb. n.

Hysteropterum cyrenaicum Linnavuori, 1965 : 18.

Bubastia cyrenaica: Dlabola, 1984 : 58.

Genus *Phasmena* Melichar, 1902

Phasmena nigrodorsalis Sidorski, 1938
(Figs. 36, 37)

Material. Georgia: 1 ♂, Kumurskhevi, Vashlovan-skii Nature Reserve, 28.VIII.1984 (A.F. Emeljanov) (ZIN).

Genus *Celyphoma* Emeljanov, 1971

Celyphoma fruticulina (Emeljanov, 1964)
(Figs. 38, 39)

Material. Kazakhstan: 1 ♂, Karaganda Prov., Koksengir Mts., 12.V.1959 (A.F. Emeljanov) (ZIN).

Genus *Atticus* Gnezdilov, 2003, stat. n.

Type species: *Latematium graecicum* Dlabola, 1982.

Atticus graecicus (Dlabola, 1982) (Figs. 40–42)

Material. Greece: 1 ♂, “Steni, 22.V.1995” (J. Lykoskoufis leg.) (AUA).

ACKNOWLEDGMENTS

The study was performed within the frame of the state theme no. 01201351189 with support of the Russian Foundation for Basic Research (grant no. 16-04-01143).

I am grateful to Dr. A. Tsagkarakis (Athens, Greece), Dr. K. Schütte (Hamburg, Germany), and Prof. Dr K. Schönitzer (Munich, Germany) for the opportunity to examine the necessary material and also to D.A. Dmitriev (Champaign, Illinois, the USA) who directed my attention to the problem of the type species of the genus *Hysteropterum* and made useful comments on the text.

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