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The limits of the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae, Aleocharinae, Athetini)

Jyrki Muona

Abstract

The phylogeny of the staphylinid beetle tribe Athetini is examined using morphological characters as data and parsimony analyses with both Equal and Implied Weights method. The results demonstrate that both the tribe Athetini and the genus *Atheta* Thomson should be dismembered. Dilacrini NEW TRIBE, type genus *Dilacra* Thomson, 1858 and two new genera, *Boreoatheta* NEW GENUS, type species *Atheta thulea* Poppius, 1909 and *Pseudodimetrota* NEW GENUS, type-species *Homalota marcida* Erichson, 1837 are described.

Fifteen subgenera of *Atheta* Thomson are erected as genera: *Alaobia* Thomson, 1858 NEW STATUS, *Badura* Mulsant & Rey, 1873 NEW STATUS, *Bessobia* Thomson, 1858 NEW STATUS. *Chaetida* Mulsant & Rey, 1873 NEW STATUS, *Coprothassa* Thomson, 1859 NEW STATUS, *Datomicra* Mulsant & Rey, 1874 NEW STATUS, *Microdota* Mulsant & Rey, 1873 NEW STATUS, *Mocyta* Mulsant & Rey, 1874 NEW STATUS, *Oreostiba* Ganglbauer, 1895 NEW STATUS, *Parameotica* Ganglbauer, 1895 NEW STATUS, *Paranopleta* Brundin, 1954 NEW STATUS, *Philhygra* Mulsant & Rey, 1873 NEW STATUS, *Rhagocneme* Munster, 1923 NEW STATUS, *Traumoecia* Mulsant & Rey, 1873 NEW STATUS and *Thinobaena* Thomson, 1859 NEW STATUS.

Fifteen species formerly included in *Atheta* Thomson s. str. are placed in new genera: *Atheta piligera* J. Sahlberg, 1876 and *Atheta thulea* Poppius to *Boreoatheta* new genus; *Homalota marcida* Erichson, 1837 to *Pseudodimetrota* new genus; *Homalota ravilla* Erichson, 1839, *Atheta harwoodi* B. S. Williams, 1930, *Atheta janssoni* Bernhauer, 1923 and *Homalota vaga* Heer, 1839 to *Traumoecia* Mulsant & Rey, 1873; *Homalota subglabra* Sharp, 1869, *Homalota dilaticornis* Kraatz, 1856, *Atheta pervagata* G. Benick, 1974, *Homalota subterranea* Mulsant & Rey, 1853 and *Homalota testaceipes* Heer, 1839 to *Alaobia* Thomson, 1858; *Homalota fallax* Kraatz, 1856 to *Dilacra* Thomson, 1858 and *Homalota autumnalis* Erichson, 1839 and *Homalota basicornis* Mulsant & Rey, 1852 to *Paranopleta* Brundin, 1954.

Introduction

The latest Palearctic Coleoptera catalogue (Schülke & Smetana, 2015) included forty-five subgenera with more than one thousand species in the genus *Atheta* Thomson alone. Putting aside works dealing with small groups – and there are many of those – the main sources this catalogue seemed to follow for the overall structure of the tribe Athetini were Lohse (1971) and Benick & Lohse (1974). In the earlier edition (Smetana, 2004), the family-group taxa were listed as being after Newton & Thayer (1991), but such a reference was not included in the bibliography. This reference most likely referred to Newton & Thayer (1992), but as this work contained all family-group taxa in alphabetical order, it was a listing of correctly applied names at that level, not an opinion about the detailed relationships of the taxa. In addition to Lohse (1971), several important early major studies on Athetini systematics exist, however. The most noteworthy were Brundin´s contributions (1943, 1944, 1953), Yosii & Sawada (1974), Sawada (1982) and Seevers (1978). The usefulness of these studies is somewhat limited as they all suffer from the lack of an objective analytical method. Muona (1997) reported some results based on a cladistics analysis, but as that study was never properly published, it was of little use as well. Some of the results from it were incorporated in Muona (1979), however.

Gusarov (2003) and Elven & al. (2010, 2012) delivered the early molecular studies on this subject and several papers have been published since, the most notable large-scale ones being Osswald (2013), Orlov et al. (2020) and Orlov et al. (2021). Interestingly, one major contribution seems to have been missed by all recent works. The German barcoding project published a NJ (=Neighbor Joining) tree of all sequenced samples (Hendrich et al., 2014). This huge dendrogram was not meant to be a phylogenetic tree and it is based on one half of one gene only, but it is of great interest nevertheless, especially because of the large number of species included.

The present paper is less ambitious, even if it has more detailed objectives than the above mentioned recent studies. It aims to define the monstrous genus *Atheta* in a strict sense and demonstrate the value of the rich morphological character information available in the material provided by Brundin (especially 1943, 1944, 1953)

as well as Sawada (especially Yosii et Sawada (1976). Special attention is directed to the "abdominal chaetotaxy pattern" character, discovered by Yosii & Sawada (1976) and inexplicably entirely ignored later on as well as the details of the internal structure of the aedeagus. The method of analysis chosen is discussed to some extent as well. This seems to be important presently, as most analytical papers today do not consider this subject worthwhile in spite of its fundamental role. Choosing between parsimony, maximum (average) likelihood and Bayesian methods is not only a question of comparing methods.

Material

Taxa

Ninety-four species were included in the analysis. In addition to these, about 98 further species were studied and placed in the genera as here defined on the basis of the results obtained in the analyses. These are added in the same listing with the analyzed taxa, but in a different style (Appendix 1).

All new combinations refer to the earlier placement of the taxon in question in Schülke et Smetana (2015).

Because restrictions of taxon name length, the names in the trees are partly difficult to connect with the correct present names in the appendices and – rarely – in the discussion. Because of this a code is provided (fig. 20). It shows the names used in the trees in alphabetical order indicating the valid name of the taxon today. The descriptions of taxa are listed in a written out version of the matrix including the correct names as well (Appendix 2).

Characters

The matrix includes 24 characters, corresponding to 54 characters if coded as binary (Appendix 3).

The nomenclature of the structures found in the male copulatory organ is based on the pioneer studies of Brundin (e.g. 1944, 1953). Yosii & Sawada (1976) provided a rich source of additional data, but these authors used partly different terms. This was probably a language question only as both authors used a language not native to them in these studies, Brundin German and Yosii et Sawada English. I have chosen to follow Brundin. The names of the structures are presented in fig. 12 and 13. Other terminology is standard for staphylinid beetles of the subfamily Aleocharinae..

0. Ligula: bifid halfway = 0; bifid deeply = 1; bifid at tip, elongated = 2; short, plump = 3; long, elongated,undivided = 4. The halfway bifid ligula has been used widely as an "*Atheta*" feature (e.g. Lohse, 1971), but this is an error as it is widespread in Oxypodini and definitely a plesiomorphy in Athetini.

1. Tarsal formula, number of segments in pro-meso-metatarsi: 5-5-5 = 0; 4-5-5 = 1.

2. Median lobe ductuslamells: tiny, simple = 0; large, simple = 1 (fig 10A-D); with lateral supports = 2 (10 J), L); with closed lateral supports = 3 (fig. 11 J, K); pointed, simple = 4 (fig. 10 F); pointed with lateral support = 5 (fig. 11 A-H, L; with tiny base and extremely elongated apex, flagellum = 6 (fig. 10 M, 14, 17 C).

3. Paramer condylit : small, normal = 0; as large as paramerite = 1.

4. Pronotal midline hairs: directed caudad = 0; "type 2 and 5" with midline hairs directed more caudad than hairs on lateral parts of disk = 1; "type 1", with midline hairs directed craniad = 2; "type 3" with midline hairs directed half-way craniad and halfway caudad = 3; "type 4" with midline hairs directed half-way to center from front and end = 4. As Seevers demonstrated (1978) many more possibilities exist in the Holarctic fauna. The Palearctic Athetini with few exceptions can be divided as done here. The present division is an attempt to classify these forms in a new way. The extremes of types 2 and 5 are quite different, but there is no clear division between them in many cases. The median row of types other than 5 can be very sharp and clear, but it can be vague and in some cases types can merge, especially 2 has often a small part of 1 in front suggesting 3. 2 and 5 are united here, but 1 and 3 might belong together as well. Most Oxypodini have type 2 and 5.

5. Elytral hair pattern: directed caudad = 0; towards lateral caudad corners = 1; with S-formed patch on disk= 2. This features is sometimes vague, but it appears to be useful (Muona, 2023a).

6. Ligula: without long setae = 0; both branches (divided ligula) or sides (undivided ligula) with long seta = 1. This feature is certainly independent of ligula form.

7. Abdominal sternites: with straight border = 0; with crenulate border = 1. This is another excellent feature discovered by Yosii & Sawada (1976), but totally ignored in later studies.

8. Macrochetotaxy: without anterior row from tergite 4 on = 0; without anterior rows on tergites 2 and 3 only = 1; formula 01 + 12 + 13 = 2; formula 02 + 13/23 = 3 (see Yosii & Sawada, 1976; also Muona, 2023a). NONADDITIVE or ADDITIVE, depending on analysis. As discussed in Yosii & Sawada (1976), this feature has much promise. Although sometimes requiring permanent mounts, it can in many cases be

seen with a stereomicroscope as well. According to Yosii & Sawada's (1976) scheme 0-2 type formed a monophyletic clade, 0-0-0-0 type was the plesiomorphic state and 0-1 types had developed several types. However, they did not discuss this in a purely phylogenetic sense nor did they perform an objective analysis.

9. Median lobe internal sack lateral hooks: not present = 0; elongate = 1; basally bulbous = 2; anchor shaped with median shallow tooth = 3.

10. Median lobe copulatory piece ductuslamells: not present = 0; about transparent =1; well sclerotized = 2.

11. Spermatheca: without strongly sclerotized narrow basal section = 0; with strongly sclerotized narrow basal section = 1 (Muona, 2023a).

12. Spermatheca: with open basal coil = 0; with rounded bundle, "*graminicola*" type= 1; with smaller triangular bundle, "*xanthopus*" type = 2; with extensive bundle, "*atramentaria*" type = 3; with primitive obscure bundle = 4; with unique bundle = 5; tubular, with expanded apex = 6.

13. Male tergite 8: simple = 0; with lateral ridges = 1.

14. Male tergite 8: simple = 0; with lateral teeth = 1; with lateral teeth and two median ones = 2; with lateral teeth and three or more median ones = 3; crenulate without lateral larger teeth = 4; excavated medially = 5; with chisel-shaped large lateral teeth = 6.

15. Male antennomeres 1 to 4 with: normal setae = 0; numerous unusually long and strong setae = 1. .

16. Pronotum: without special setae = 0; with conspicuous black extra setae on corners = 1. .

17. Median lobe internal sack apically with: simple lamells = 0; striated pair of lamells = 1; complex symmetrical structure of four parts = 2; lateral sets of complex four plates = 3.

18. Median lobe internal sack: without transverse serrate lamell = 0; with transverse serrate lamell = 1.

19. Median lobe internal sack: without basal spine bundle = 0; with basal spine bundle = 1.

20. Median lobe internal sack: without medial spine bundle = 0; with medial spine bundle = 1.

21. Athetine bridge : absent = 0; well-developed = 1; partly open = 2.

22. Mentum medially: narrow = 0; wide = 1.

23. Mentum laterally: with many pseudopores = 0; without pseudopores, with a few pores = 1. .

24. Median lobe capsule under ductus ejaculatoris opening: simple = 0; with strong transverse sclerotization = 1.

Analysis

The analyses were made with the Windows version of the program TNT (Goloboff & Morales, 2023), using sectorial searches, ratchet, drift and tree fusing with 800 initial adding sequences and waiting for ten hits for the best score before stopping the search for additional trees, saving up to 2000 trees. The results were obtained after 40 to 80 billion rearrangements, searches finding 15 to 165 optimal trees. IE (implied Weights) trees with concavity values from strongest to weakest (K= 3, 6, 10) and the EW (equal weights) trees (Goloboff, 2022) were calculated and group support was evaluated by calculating the GC-values with symmetrical resampling with standard TNT values (Goloboff et al., 2003). The GC-value refers to "the difference in frequency between the group, G , and the most frequent contradictory group, C and is a better indication of group support than absolute frequency" (Goloboff, 2022). As stated in Goloboff (2022): "A group being contradicted in every pseudoreplicate is clearly different from a group that is indifferent for every pseudoreplicate; both situations are perceived as the same by absolute frequencies, but clearly different from the perspective of GC". With GC, a completely non-contradicted value is 1, a totally contradicted being -1 and an indifferent one is 0. Thus all values between 0 and 1 are supported, relative to the amount, and all negative values indicate lack of support, again to the degree the value indicates. The values between 0 and 1 are given in full numbers, i.e. 63 denotes 0.63. Values from 1 to 10 are regarded as very low, even if above the indifferent 0.

Taking into consideration the apparemt importance of the main discovery in Yosii & Sawada (1976), the abdominal sternite chaetotaxy pattern (character 8), it was treated as additive in a separate set of analyses for comparison (see also Muona, 2024).

The trees discussed are majority rule consensus trees, but the decision whether a group is accepted or not is based on the GC-values obtained with strict consensus trees (fig. 1). An example is given using medium strength concavity 6 and an early stage of the complete matrix, with majority rule tree showing nodes present in 50 to 100 percent of the optimal trees, the strict consensus tree with only the nodes present in all optimal trees and the GC-values calculated with 1000 replicates. It is instructive to compare the majority rule and strict trees to each other and the resampling values (fig. 9). Considering the fact that these results are products of tens of billions of

studied possibilities it is easy to see why one could never reach an objective analysis by thinking alone.

The analysis here used is a cladistics one. Considering the widespread popularity of Maximum Likelihood (=ML) and Bayesian methods today, it is useful to explain this choice.

First thing to consider is the data, in this case morphology. As shown by Goloboff et al. (e.g. 2019) and Goloboff (2022), the existing Bayesian methods using Mk function acceptably with close to random sequence data, but with morphological data this is not the case. Interestingly Orlov et al. (2020) state: "*Bayesian Inference is used widely in molecular studies (Holder and Lewis, 2003; Yang and Rannala, 2012; De Bruyn et al., 2014) and to a lesser, but growing (Goloboff et al., 2019) extent, in morphological analyses"* and *"Our purpose is not to debate or study the performance of the methods. We applied both unweighted MP and with implied weights (MP-IW) as well as BI to explore our dataset and compare phylogenetic results as part of our sensitivity analysis"*. From these citations one might get the impression that Goloboff supports Bayesian methods in systematics and that the choice of analytical methods is a question of the performance of the methods. Whatever Goloboff thinks is best seen by reading Goloboff (2022), the first ever published analytical systematics textbook for morphologists, but the question of methods is not really a question of performance. It is whether the method produces an approximation of the reality or not and in this comparison Mk methods fail.

The second factor was the optimality criterion. In order to know that a certain value is best provides a way to compare results in an objective way. In ML it is the best score, in parsimony it is the answer requiring least extra changes, ad hoc statements, in practice the smallest number of steps. No such criterion exists for Bayesian analysis. Whatever model you use, the result you get is it.

All presently widely used ML programs calculate maximum average likelihoods, i.e. the overall likelihood of the best tree without optimizing the internal nodes of the tree. Simply put, all these nodes – the splits leading to different taxa – are without expressly recoverable synapomorphies. Their strength is usually measured with resampling and this is known to be a very complex subject (Goloboff, 2022), even if the problems are usually not even mentioned. There are ways to calculate ML for the paths and the nodes of the trees, but then the whole process becomes very time consuming and these options are not in use today because of this. The main reason is that parsimony does this in most cases as well and much faster. It is of course important to remember that even with parsimony, the strength of the clades must be evaluated and that is not simple either. Here it is done by searching for strong GC values.

Results

The searches with character number 8 (abdominal chaetotaxy pattern) coded as additive are marked throughout the text with "+" after the search type, i.e. EW = equal weights treated nonadditive for all characters and EW+ = equal weights with character 8 treated as additive. The majority rule consensus trees and the GC-values calculated from the resampling of the corresponding strict consensus trees are shown in figures 1 to 8.

Acrotona aterrima, *pseudotenera*, *pygmaea*, *Nehemitropia lividipennis* and *Lyprocorrhe anceps* are placed together in all analyses. In EW trees the support is moderate but with stronger concavity it becomes stronger. With trees treating character 8 additive, the support grows considerably stronger.

This group with unusual abdominal margin structure is characteristic. *Lyprocorrhe anceps* is placed within *Acrotona* in the IW3 search (fig. 7), but it remains basal in other ones. Five further species, including the type-species of *Colpodota*, *Homalota parens*, were included here after comparison of characters. There is no indication of a split between *Acrotona* and *Colpodota*. The *Acrotona* group is placed outside the major body of Athetini in most trees, but there is no GC support for this in the analyses. However, a position in a separate tribe might be the correct solution.

This group is identical with Yosii et Sawada's "*Acrotona* s. lat." lineage.

Alaobia with *pervagata, dilaticornis, testaceipes, scapularis, subterranea* and *gagatina* is found in all trees. Both *subglabra* and *pallidicornis* join here in all IW (fig. 3, 5, 7) and IW+ (fig. 4, 6, 8) searches with good GC-support and this is indicated in EW (fig. 1, 2) searches as well. The general morphology and internal aedeagus structure in the type-species of *Alaobia* (*scapularis*), *Neohilara* (*subterraneanea*) and *Ceritaxa* (*dilaticornis* as *spissata*) is close to identical. *Homalota pallidicornis* Mulsant & Ry, type species of *Mycota* Mulsant & Rey, appears similar enough to be left here as well. The extraordinary biology of *Alaobia scapularis* as a parasite of *Lampyris noctiluca* may offer an explanation for the rarity of the many pale colored species in this group (http://www.glowworms.org.uk/parasitic/parasitic.html).

Atheta with *euryptera, triangulum, xanthopus, castanoptera, graminicola, sexdentata, pfaundleri, contrista*a and *ebenina* has strong GC-support in all analyses (see also Muona, 2023a. In EW+ (fig. 2) and early IW+ searches (fig. 4, 6) *atramentaria* joins them and as the concavity becomes a factor *cinnamoptera* replaces it. This group has good GC-support and so does *cinnamoptera* in it in IW+ searches (fig. 4, 6, 8). Several other species not included in the analysis share the characters of this group and one of them, *nigritula,* type species of *Tetropla* Mulsant et Rey, is placed here in all IW+ searches as well.

The trees with character 8 treated as additive join *crassicornis*, *allocera and pilicornis*, but support joining these well-supported small groups to the main *Atheta* s.str. is not present in the GC-values. Many other species with relationships with these and the supported main group in the trees are placed here as well. Being the former huge genus *Atheta*, some latitude is given to its breadth (Muona, 2022). The decisive factors for joining all these together are the 0-2 abdominal chaetotaxy and lack of *Neodimetrota* synapomorphies (Muona, 2023b). The median lobe found in *Atheta* can be divided in two. The ones similar to the type species, *A. graminicola* with complex internal sack and doubled ductuslamells (fig. 11 C-H) and the ones with simple ductuslamells (fig. 10 G, H, K; 19 D-F)). The monophyly of the latter group I not proven as of yet.

Bessobia with *excellens* and *fungivora*, *Plataraea* with *elegans* and *nigrifrons* and *Traumoecia* with *ravilla* and *picipes* are all consistently placed close to the *Atheta-Neodimetrota* group in the majority rule trees but this connection has GC support only in the moderate to strong concavity results IW6+, IW3 and IW3+ (fig. 6-8). This may be the result of the influence of the additive 0-2 chaetotaxy, although in the IW3 tree this is not activated. The limits between *Traumoecia* and *Anopleta* are not clear and Yosii & Saewada synonymized them. *Anopleta* was not included in the analysis, so it is left as it is, but the only species checked, *wuorentausi* Bernhauer belongs clearly to *Traumoecia* (see fig. 15 D-F; 18 F).

Boreophilia with *munsteri*, *islandica* and *subplana* has constant good GC-support. It is one of the few groups that have lesser support with strong concavity and character 8 treated as additive. All studied other putative *Boreophilia* species shared the features of the analyzed ones.

Dilacra with *vilis* and *luteipes*, *Parameotica laticeps*, *Dochmonota clancula* and *Brundinia marina* form a well-supported group in all analyses, usually basally connected with *Hydrosmectina* as well, rarely and with low values also with *Tomoglossa*. This group is mostly placed among the basal dichotomy or polytomy with Athetini. The placement of *Tomoglossa* is unstable, probably due to its plesiomorphic features and it may not be closely related with *Dilacra-Docmonota-Brundinia-Hydrosmectina*. The plesiomorphic abdominal chaetotaxy and the characteristic aedeagus define these genera as a group (fig. 12, 13). A useful easily visible feature is the fine, dense vestiture covering even the abdomen. This complex is consistently placed basally in Athetini and is here separated from these as a separate tribe.
Dacrila fallax remains outside this clade in all searches and appears to be firmly placed with Tachyusini as suggested by Yosii et Sawada (1976) and Osswald et al. (2013) in spite of its superficial similarity with Dilacrini (fig. 1).

Amischa analis and *Pycnota nidorum* are always present as sister-groups with good support. The abdominal chaetotaxy is plesiomorphic, the inner structure of the median lobe is of simple type, ligula is undivided with lateral setae and body covered with dense, fine vestiture.

Neodimetrota with *aeneipennis, tenuiducta* and *lapponica* has strong GC-support in all trees. EW searches (fig. 1, 2) place *cinnamoptera* in *Neodimetrota* but all IW searches, both with and without character 8 as additive, place it either basally to *Atheta* and in IW3+ (fig. 8) between *Atheta* and *Neodimetrota*. Here it is moved to *Atheta*. *Neodimetrota* was treated in detail in Muona (2023b) and all putative members studied belong here. In trees with character 8 treated as nonadditive and with low concavity *Neodimetrota, Boreophilia, intermedia* and *Atheta* are placed close to each other, as placed in Brundin (1953) and as hypothesized in Muona (2023b) with the exclusion of *marcida*. Neodimetrota species have an anchor shaped spike in the median lobe internal sack (fig. 18 D, E). Somewhat similar structures occur commonly in other genera, but they are either basally enlarged as in *Boreoatheta* and *Atheta* s.str (fig. 19 A-E) or spike shaped as in *Alaobia* (fig. 19 F).

Paranopleta inhabilis is always combined with *Atheta basicornis* and *Atheta autumnalis* with strong GC-support. This connection was pointed out in Brundin (1943) but although he had produced the images of the aedeagi at the time, he never pursued the matter further (fig. 14). Externally the species are characterized by stout, pale antennae, large head and flat form (fig. 15). Besides morphology, these species are connected via biology as well. *P. autumnalis* lives under fallen pine tree bark on freshwater edges, in Finland the best known locality being the sandy beaches of the Oulanka river in Kuusamo, where continuing meandering forces pine trees to fall on the riverbanks. *P. autumnalis* swarms there in early summer over the sandy banks, but even though sampling has been strong, it has never been taken in any other habitat in the region, including beaches with small stones instead of sand. *P. inhabilis* is strictly tied to forests as well living under bark of burnt coniferous trees. The least rare species, *P. basicornis* is known to live under bark of deciduous trees, also in fallen trunks in wet conditions and it is also taken from bracket fungi.

In both EW and IW trees *Geostiba circellaris, Microdota orosana* (=*trebinjensis*), Liogluta *pagana* and *longiuscula, Alpinia carpathica, Oreostiba tibialis, Thinobaena vestita* and Alconota *insecta* and *gregaria* form a large group with good support, but the order of the taxa varies within it. These same taxa were included in Elven et al. (2012), but formed two groups about as distant as they could be, placing *Geostiba* and *Aloconota* in Geostibini and *Liogluta, Alpinia, Oreostiba* and *Thinobaena* inside the Athetini. In Yosii et Sawada (1976) both these

groups are present as well and the *Aloconota* section is hypothesized as being derived from the *Liogluta* group. The connections between *Liogluta, Alpinia, Oreostiba*, *Thinobaena* are close and especially *Liogluta* and *Oresostiba* could be united as *Oreostiba tibialis* seems to be the only "Oreostiba" left from the time Brundin (1940) did his first revision (fig. 16, 17 A, D). The median lobe structure of *Aloconta* (fig. 17 B, C) is very different from that of the *Liogluta* group. *Aloconota* (type species *languida*) and *Disopora* (type species *gregaria*) have quite differen median lobes and this old division may have merit. In gregaria the ductudlamells form an elongated tip (fig. 17 B) but in *Disopora* the tip is drawn to an extraordinary long virgo (as in *sulcifrons*, 17 C). This combined with *gregaria's* strange pronotal hair pattern appears significant.

On the basis of the structures of the median lobe the connection between *Aloconota* group and *Liogluta* group appears weak and it is here considered questionable. *Atheta orosana* (Scheerpeltz) (= *trebinjensis*) is placed in *Microdota* in Schülke et Smetana (2015). It does not combine with the type species *M. amicula* and remains in the same group as other taxa related to *Oreostiba* in the analyses. However, on the basis of the median lobe it does not belong to the *Oreostiba* group either (fig. 18 A).

Tachyusa constricta, Falagria caesa, Cordalia obscura, Gnypeta carbonaria and *Halobrecta flavipes* form a group with some support in EW and EW+ trees. In EW searches this group is connected with *Dacrila fallax*, in IW6+ (fig. 6) with *Xenota myrmecobia*, but in IW10 (fig. 3) this group is broken and in IW10+ (fig. 4) it is joined with *Amischa analis*, *Pycnota nidorum* , *Xenota myrmecobia* and *Dacrila fallax* and in IW3+ (fig. 8) finally with *Datomicra nigra*. In spite of this instability, the group remains together and appears to be a natural one. In Hendrich et al. (2014) *Cordalia* and *Falagria* are closely related but *Gnypeta* and *Tachyusa* far removed from them, whereas in Orlov et al. (2020) Falagrini is the sister-group of a huge clade including Tachyusini. Yosii & Sawada (1976) treated *Gnypeta, Cordalia* and *Falagria* as two different lineages with independent origin. It seems that the one thing all studies agree on is that these taxa do not belong to Athetini. The views presented in Osswald (2013) and Brundin (1943) appear reasonable. In any case these taxa do not belong to Athetini according to the present data either.

Monotypic taxa

Twenty-four genus group taxa remained without well supported ties to any of the already mentioned ones. None of these belong to the main target of this study, Athetini *sensu stricto*, marked as the "FIRST GROUP" (Appedix 1). Genera belonging to the Athetini "SECOND GROUP" with (0-1) chaetotaxy are clearly members of Athetini as well on the basis of their morphology. These include *Alianta, Amidobia, Badura, Chaetida, Dadobia, Dalotia, Dimetrota, Dinaraea, Rhagocneme, Schistoglossa and Trochanterella.*

Species with plesiomophic chaetotaxy (0-0-0-0-0-0 or 0-0 chaetotaxy) should probably be placed outside Athetini and certainly outside *Atheta*, but the tribal question cannot be solved here. These genera include *Amischa, Coprothassa, Tomoglossa* and *Datomicra, Dimetrotina, Hydrosmecta, Lundbergia, Lypoglossa, Microdota, Mocyta, Philhygra, Pycnota,* and *Xenota.* Many of these genera are highly characteristic and their placement earlier in *Atheta* as subgenera had no basis whatsoever. The very large genus *Microdota* is a special case as it appears to be a completely unnatural assemblage of small species with stout antennae.

Homalota intermedia has been placed both in *Atheta* and *Neodimetrota*, but it lacks the diagnostic features of both. In IW6 (fig. 5) *intermedia* + *Chaetida* had low GC support and in IW10 (fig. 3) very low GC support tied *intermedia* with *Boreophilia*. Considering general habitus, elytral vestiture pattern and punctation and unusual antennae *intermedia* does resemble *Chaetida*. On the other hand, *intermedia* has unusually short body setae and *Chaetida* unusually long ones, so this solution does not appear convincing either. *Homalota intermedia* is placed in *Neodimetrota* with a question mark for the time being.

New taxa

Dilacrini NEW TRIBE, type genus *Dilacra* Thomson, 1858.

The main features of this tribe are primitive 0-0-0-0-0-0 abdominal chaetotaxy (plesiomorphy), strong transverse sclerotizations under the ductus ejaculatoris opening in median lobe (synapomorphy), very small but well-developed ductuslamells (synapomorphy) and prominent crista apicalis section of the median lobe (synapomorphy) (fig. 13).

Boreoatheta NEW GENUS, type species *Atheta thulea* Poppius, 1909.

This genus is related to *Boreostiba*, but it has powerful, robust basally wide aedeagial hooks (fig. 19) contrary to *Boreostiba* (fig. 18 C), proportionately large ductuslamells and complex apical median lamells (fig. 19) contrary to Boreostiba (fig. 18 C) and different elytral hair pattern. *Boreostiba* has parallel-sided body with slightly caudad widening abdomen, whereas *Boreoatheta* is wide and less parallel-sided. Pronotal vestiture patterns are different, type 3 in *Boreostiba* and type 1 in *Boreoatheta*.

Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochaetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil;

male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sack without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Pseudodimetrota NEW GENUS, type species *Homalota marcida* Erichson, 1837.
Two apomorphies characterize this genus: parameres with a separate large extension and median lobe with a narrow ventral spike (Muona, 2023b). *Pseudodimetrota* is externally somewhat similar to *Neodimetrota* species, but antennae are very long, elytra conspicuously longer and wider than pronotum, tibial setae are fairly short and male has basal antennomeres flattened and considerably stouter than in females.

Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochaetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sack without transverse serrate lamell;

Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Discussion

As expected, the inclusion of the characters available in the contributions of Brundin (1940, 1943, 1944, 1953) and Yosii et Sawada (1976) offered new insight in the systematics of Athetini when used in an analytical framework. Many useful characters could be gathered from the published and many previously unpublished illustrations Brundin made in the 1940s and 1950s. Yosii et Sawada (1976) discovered several important features as the analyses here demonstrated. Their observations of *Geostiba* and allies turned out to agree with molecular results later on and the abdominal structure observations were of great importance. The discovery of the crenulate sternites in the *Acrotona* group may indicate tribal status and the chaetotaxy patterns as a whole appear to reflect Athetini evolution. Although the terms were no used, it is readily visible in the scheme (Yosii & Sawada, 1976: Fig. 1) that their 0-2 type defined the only monophyletic group as a synapomorphy and the outgroup type 0-0-0-0 found in Oxypodini was seen as a plesiomorphy. The different 0-1 types had evolved several times independently and even one reversal was present. It appears that most of the system was produced by Sawada. In the postscript Yosii (1976) discussed another option for the observations taking into account material not used in the published main result of Yosii & Sawada (1976: Fig. 1). He hypothesizes that the various 0-0-0-0 groups has evolved separately from *Aleochara* type ancestors, which he regarded as the most basal group. He also pointed out that *Meotica* Mulsant & Rey, in a subtribe of Oxypodini presently also had cernulate sternite margins similar to the Acorona group. In essence he suggested that the entire order within Athetini started from *Atheta* s.str. and evolved towards 0-1 types. The only molecular studies with fair (Elven et al., 2012) or good sampling of taxa (Hendrich et al., 2014) do not support these views, however. The results of the present analyses agree with this.

The different IW concavity values produced different results with one character treated either as additive or not. Treating the abdominal chaetotaxy as additive increased its importance. The most derived 0-2 state seemed to be a synapomorphy in the first place, and weighting the additive character strengthened this result further. However, taxa like *Boreophilia* seemed to get less support during weighting having the apparently homoplastic state 0-1 chaetotaxy. All the other characters in combination could not overrun this effect so all in all this appears to support the main conclusions in Yosii et Sawada (1976). The 0-2 clade is unique and several separate 0-1 clades exist.

It remains open whether all of the 0-1 clades belong to Athetini. On the basis of this study and Yosii et Sawada (1976) *Acrotona* s. lat., *Liogluta* series and *Taxicera* do not. With the possible exception of *Acrotona* s. lat. this result agrees with those of Elven et al. (2012). Osswald et al. (2013) found Tachyusini as "birds" together with Athetini "as the rest of reptiles" but the branches unitimg these two groups were in fact without support and should have been collapsed. As their main target was Oxypodini, they did not include any *Acrotona* or *Liogluta* species in the data.

In the present analysis Dilacrini is separated from Athetini and I am in full agreement with Osswald et al (2013) about the multiple reductions of the Athetine bridge – actually its lateral flanks – in Athetini and related taxa. In its pure form the plesiomorphic lack of this bridge is associated with a uniform compression plate whereas at least most of the apomorphic reduced bridge types have a jointed compession plate as a remnant of the full bridge (fig. 14 A).

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The late Professor Lars Brundin donated his Aleocharinae drawings to me in 1986. I am immensely thankful for this generous gift, a small part of which made this paper possible. He produced all the illustrations in this

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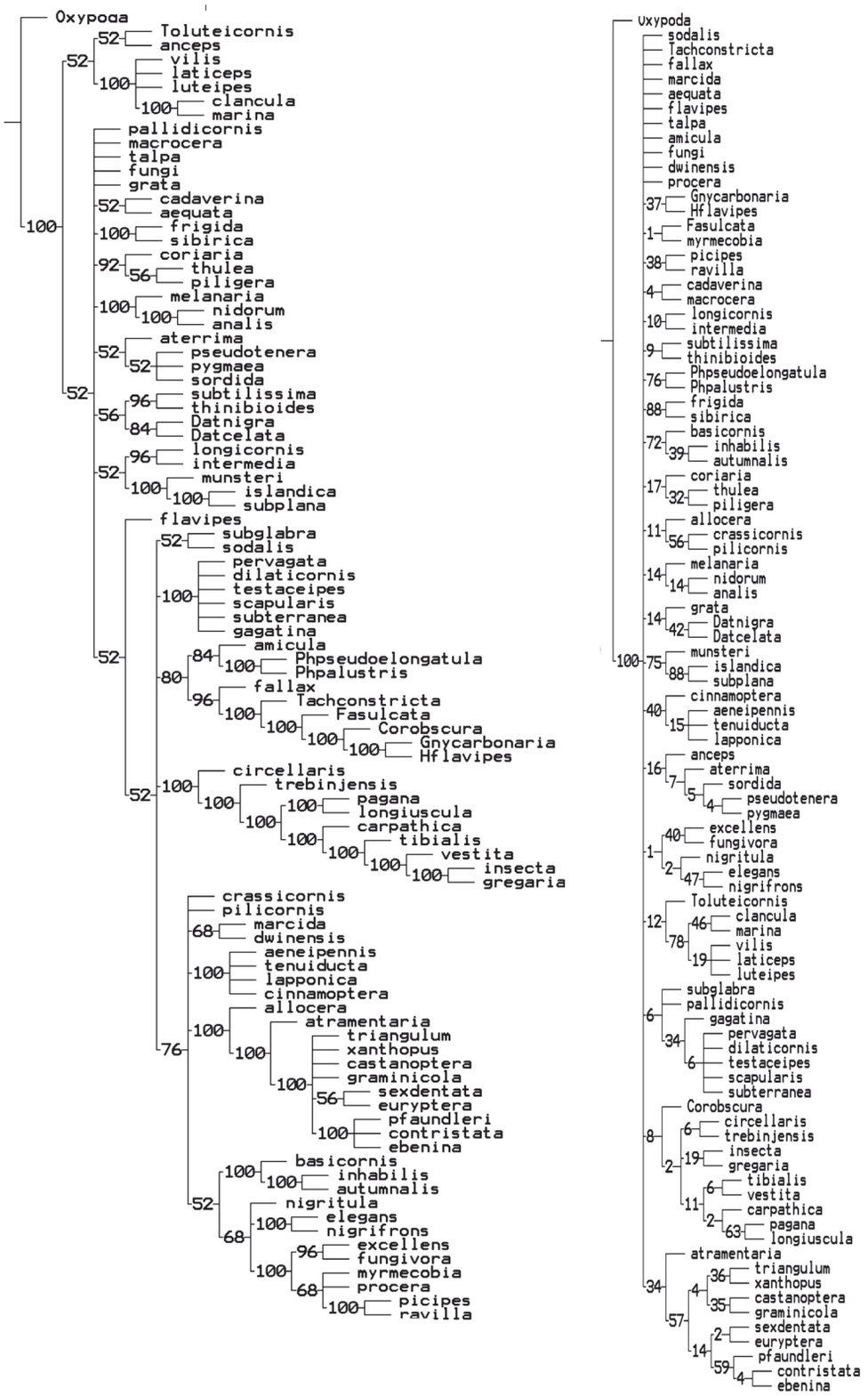
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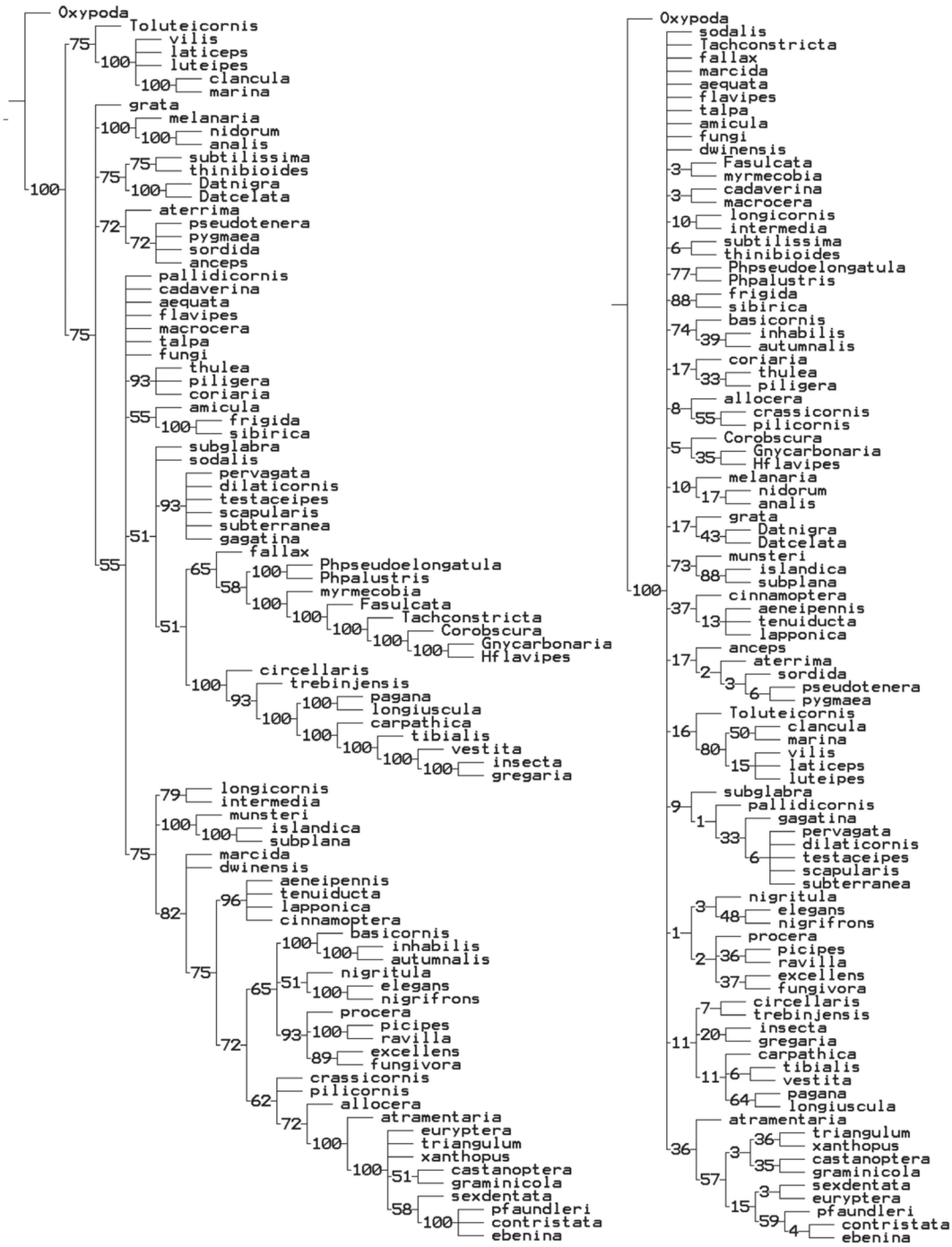
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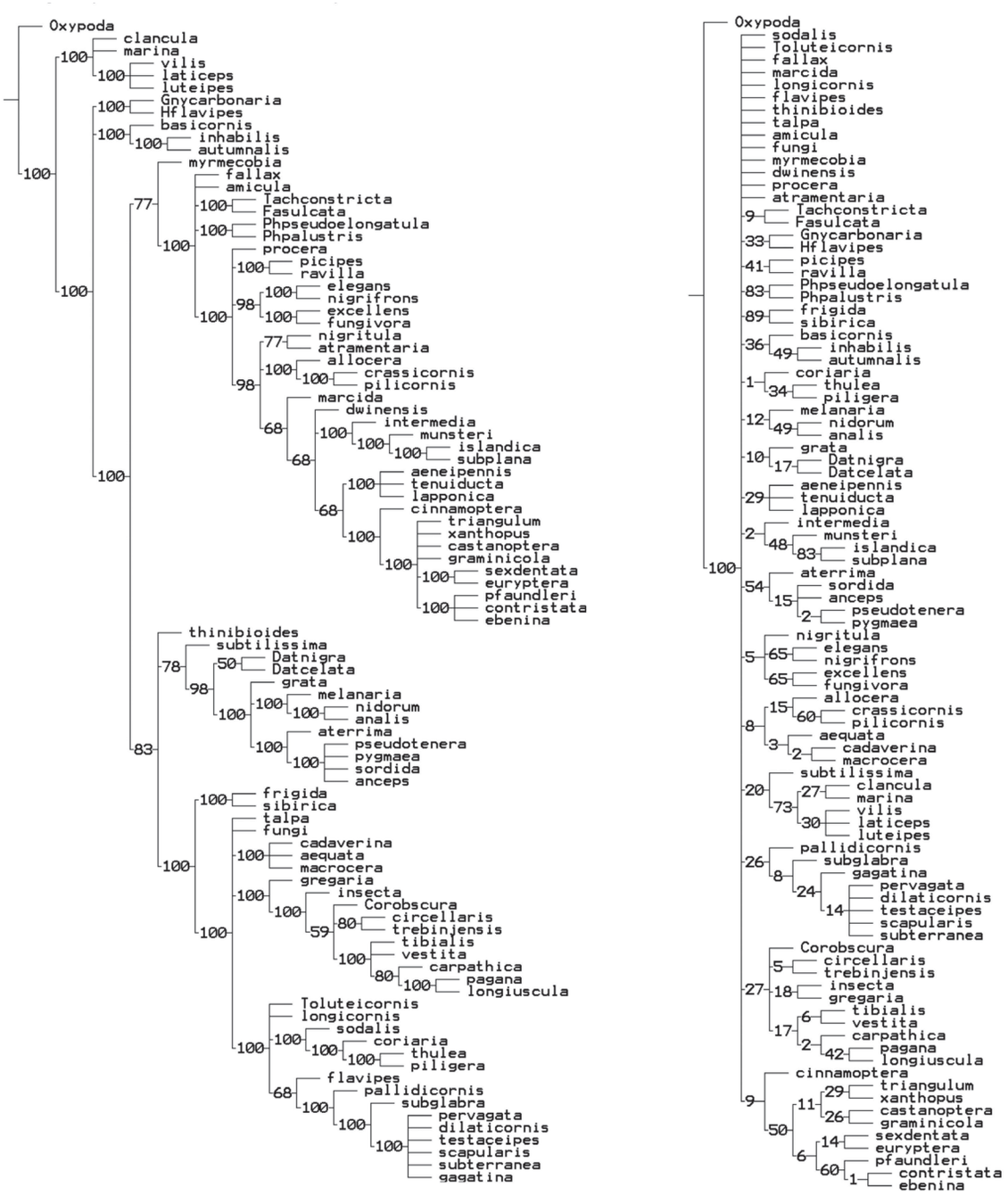
Majority rule EW tree of 25 trees and GC-values for strict consensus EW trees

Fig. 1. EW Majority rule consensus tree and GC values



Majority rule EW+tree of 29 trees and GC-values for strict consensus EW+trees

Fig. 2. EW+ Majority rule consensus tree and GC values



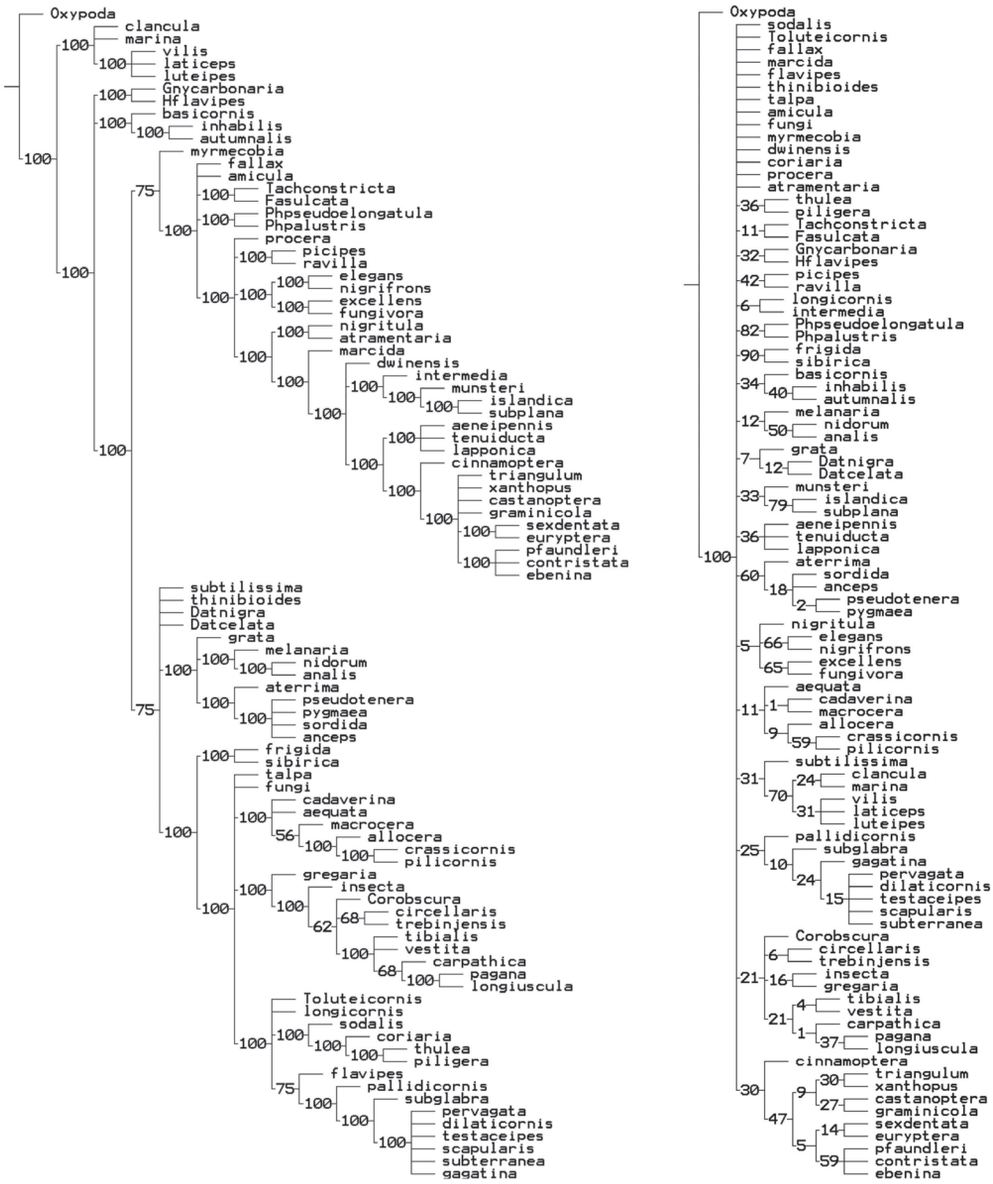
Majority rule IW10 tree of 61 trees and GC-values for strict consensus IW10 trees

Fig. 3. IW10 Majority rule consensus tree and GC values



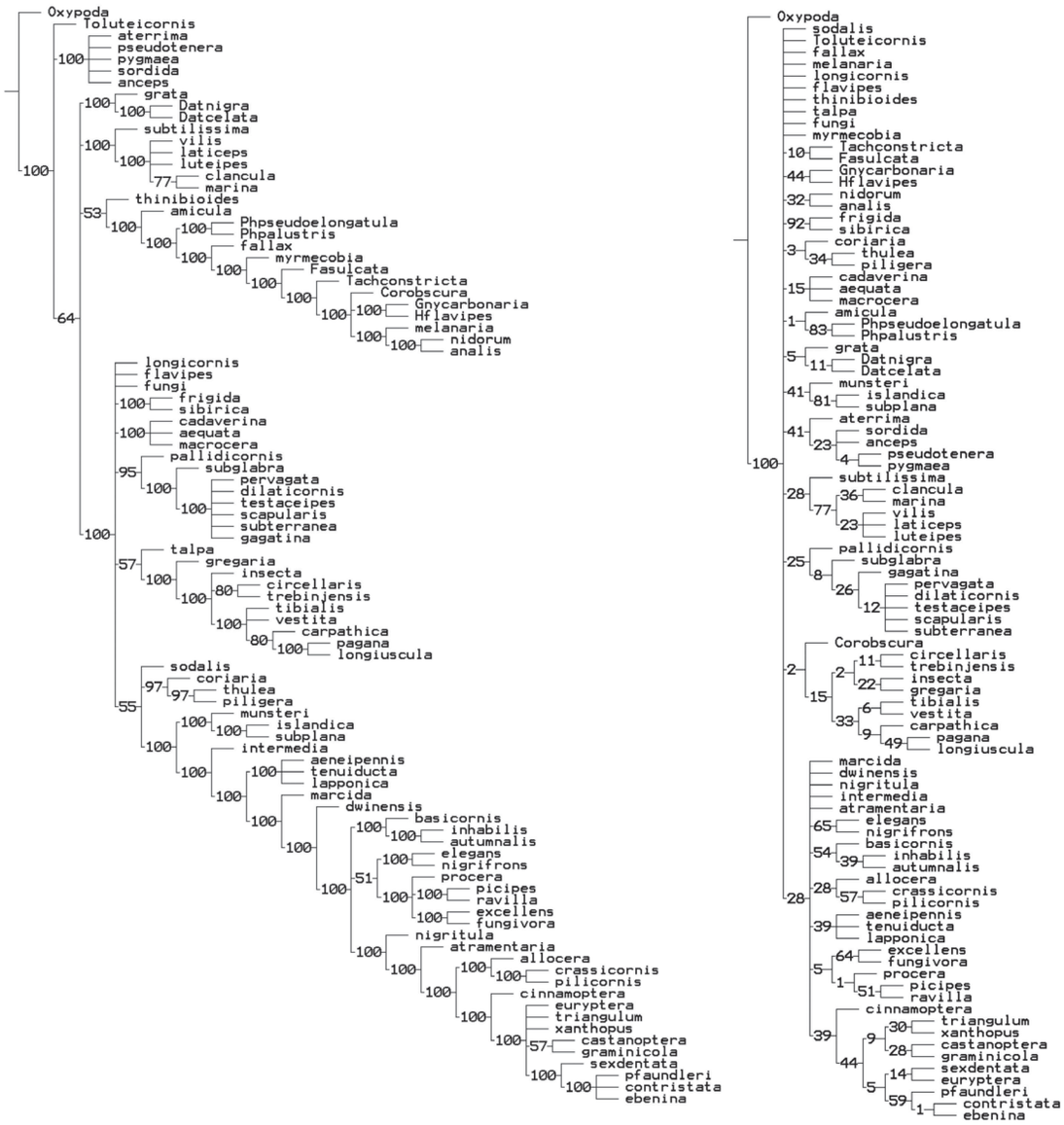
Majority rule IW10+tree of 15 trees and GC-values for strict consensus IW10+trees

Fig. 4. IW10+ Majority rule consensus tree and GC values



Majority rule IW6 tree of 16 trees and GC-values of strict IW6 tree

Fig. 5. IW6 Majority rule consensus tree and GC values



Majority rule IW6+ tree of 45 trees and GC-values of strict IW6+ tree

Fig. 6. IW6+ Majority rule consensus tree and GC values



Majority rule tree of IW3 15 trees and GC-values for IW3 strict consensus tree

Fig. 7. IW3 Majority rule consensus tree and GC values



Majority rule tree of IW3+135 trees and GC-values for IW3+ strict consensus tree

Fig. 8. IW3+ Majority rule consensus tree and GC values

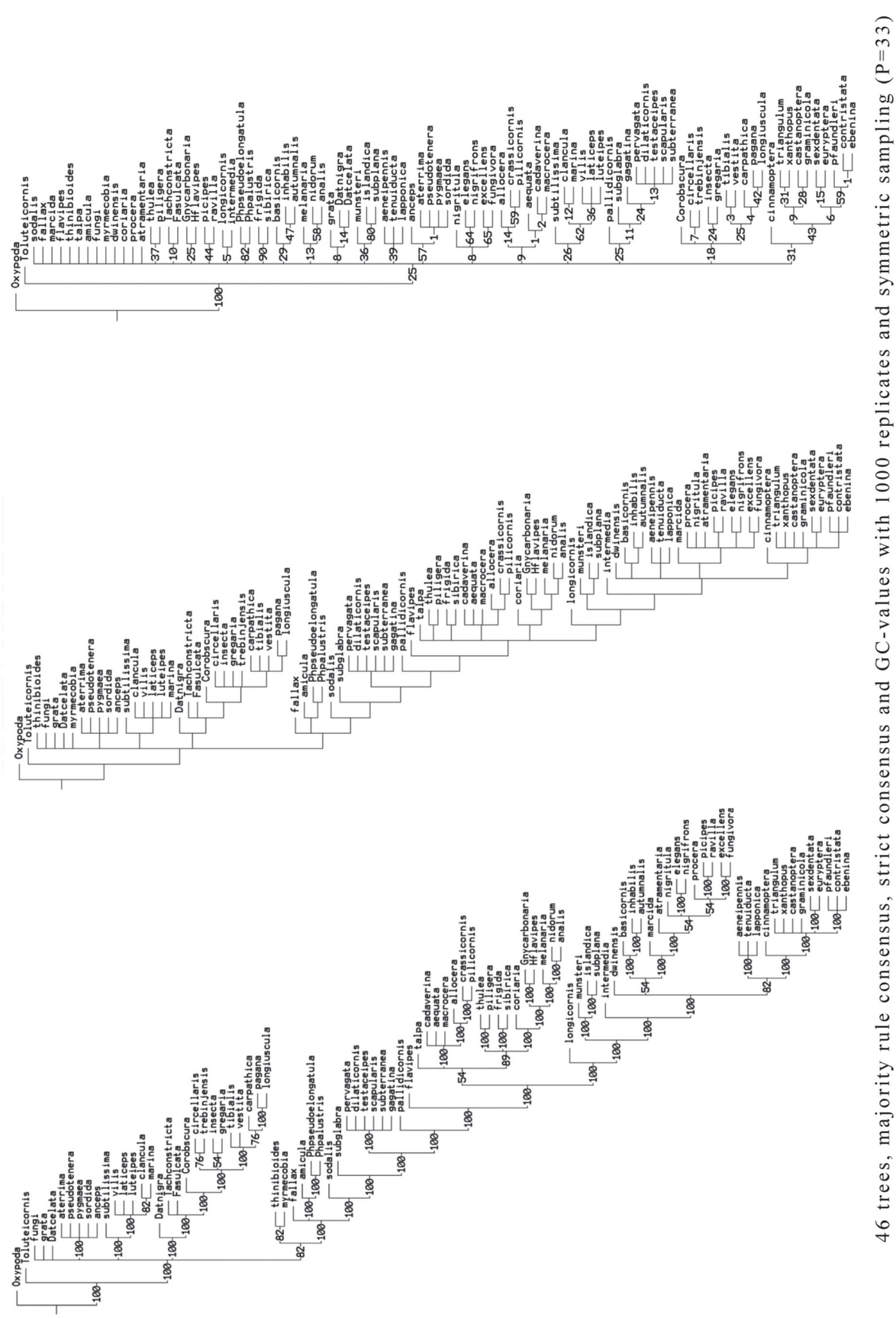


Fig. 9. Early IW6 version Majority rule consensus tree, strict consensus and GC values

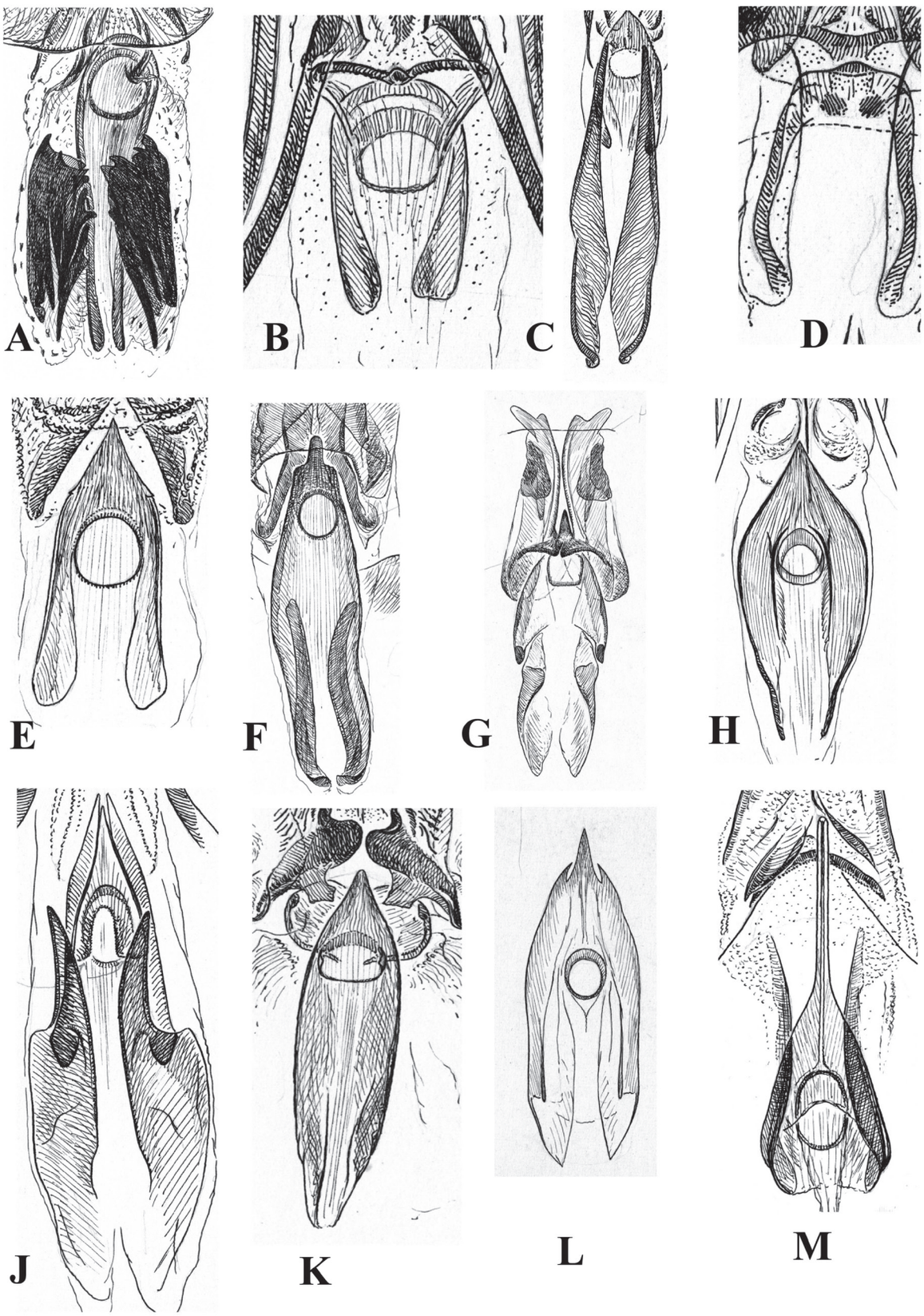


Fig. 10. Details of median lobe showing eound to oval entrance opening of ductus ejaculatoris and the ductuslamells surrounding it as a support structure. Various other features may or may not be discernable.
A. *Traumoecia vaga*; B. *Ousipalia* sp.; C. *Dadopora zosterae*; D. *Parameotica ?epirotica*; E. *Traumoecia taxiceroides*; F. *Alaobia trinotata*; G. *Atheta pilicornis*; H. *Atheta liturata*; J. *Rhagocneme dwinensis*; K. *Atheta nidicola*; L. *Dacrila fallax*; M. *Paranopleta inhabilis*.

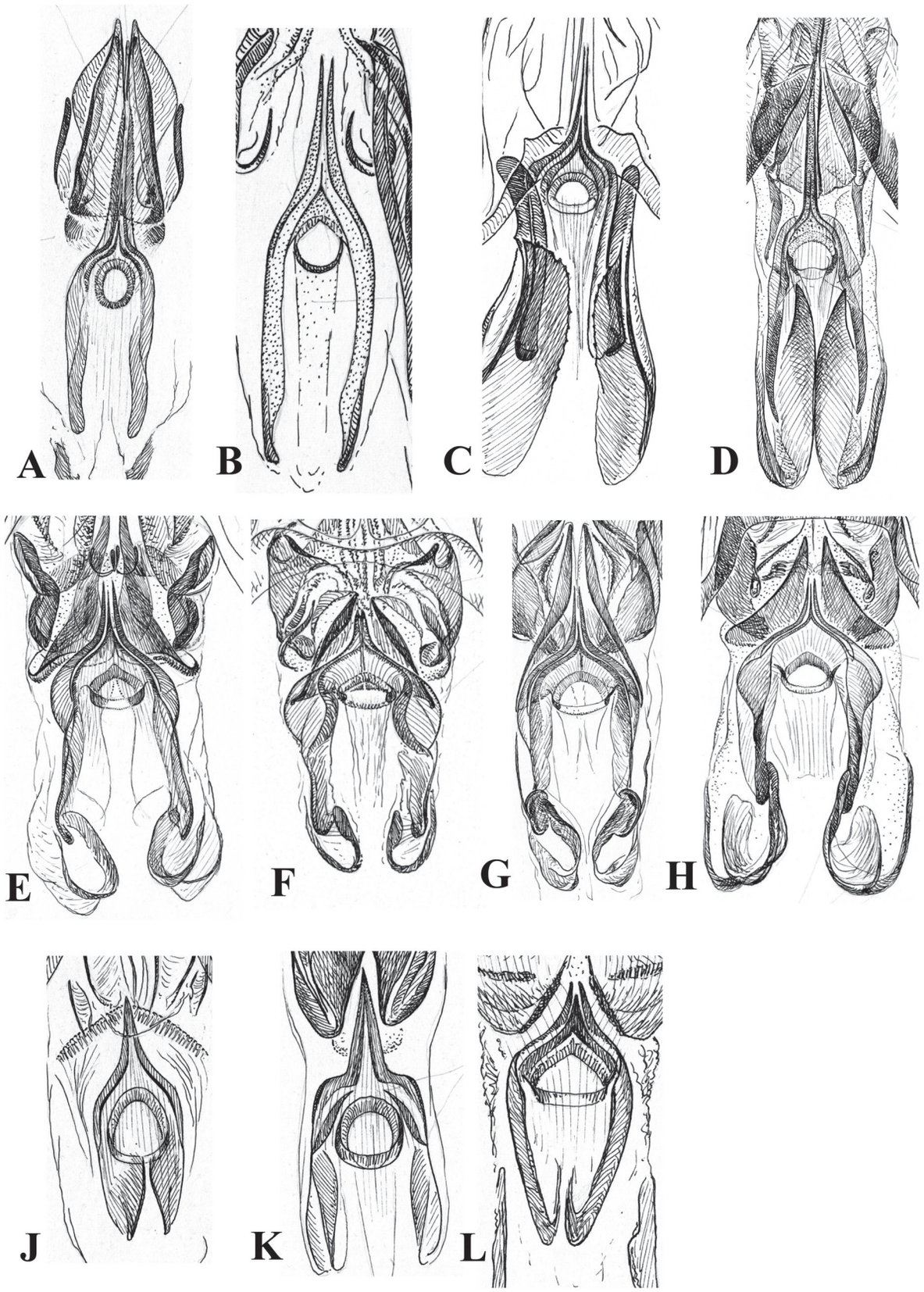


Fig. 11. Details of median lobe showing round to oval entrance opening of ductus ejaculatoris and the ductuslamells surrounding it as a support structure. Various other features may or may not be discernable.
A. *Plataraea nigrifrons*; B. *Chaetida longicornis*; C. *Atheta boleticola*; D. *Atheta nigritula*; E. *Atheta ebenina*; F. *Atheta euryptera*; G. *Atheta hypnorum*; H. *Atheta brunneipennis*; J. *Thinobaena vestita*; K. *Atheta oblita*; L. *Atheta procera*.

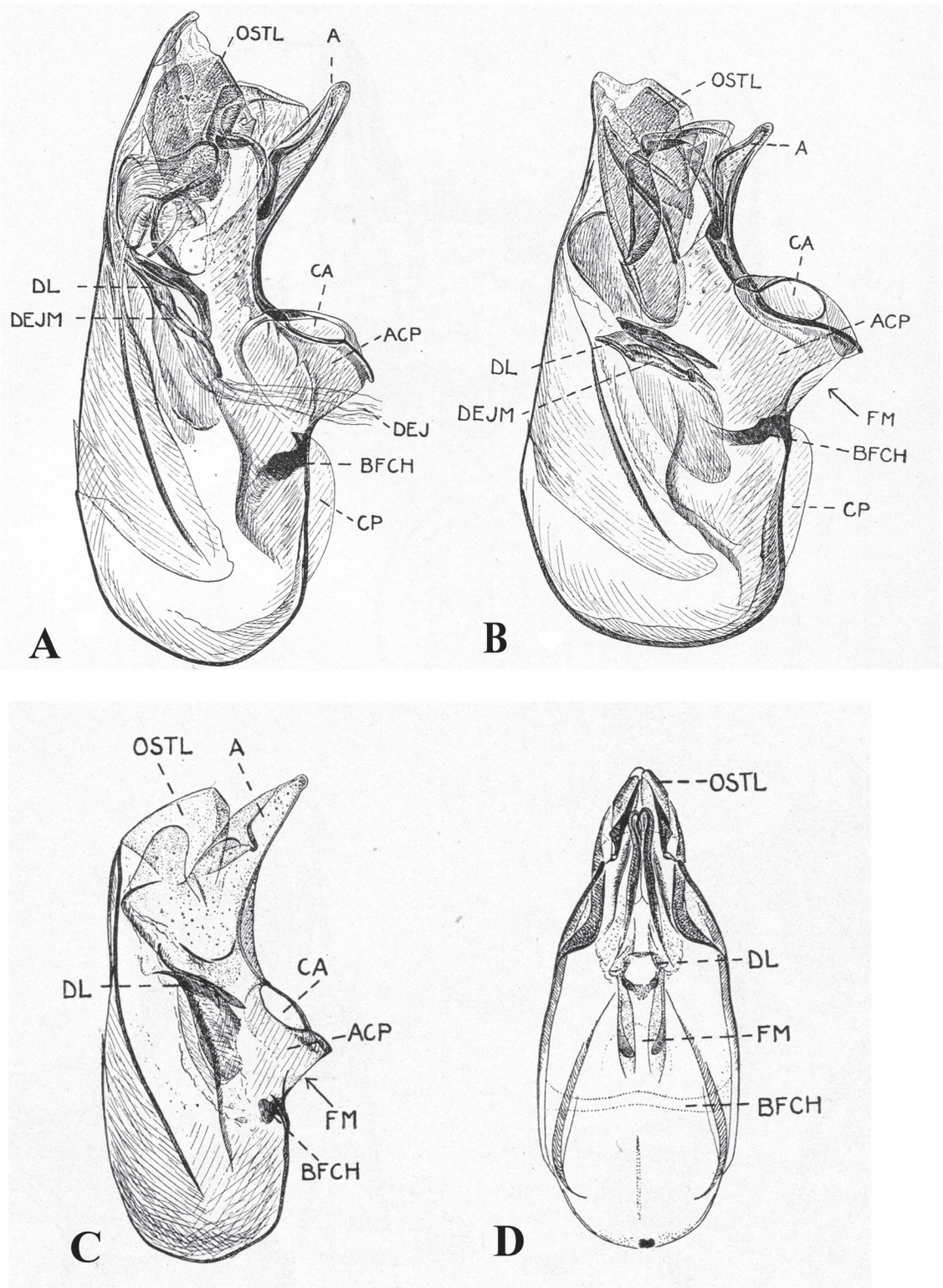


Fig. 12. Median lobe, A-C. Lateral view. D. Dorsal view. A. *Brundinia marina*; B. *Dochmonota clancula*; C-D. *Dilacra vilis*. A = Apex of capsule, ACP = Apical central wall of capsule, BFCH = lateral sclerotization under DEJ, CA = Crista apicalis of the capsule, CP = Crista proximalis of the capsule, DEJ = Ductus ejaculatoris, DEJM = opening in internal sack for entrance for DEJ, DL = ductuslamells, FM = foramen mediale in capsule, HK = hook-shaped sclerotizations in internal sack, OSTL = Apical lamells.

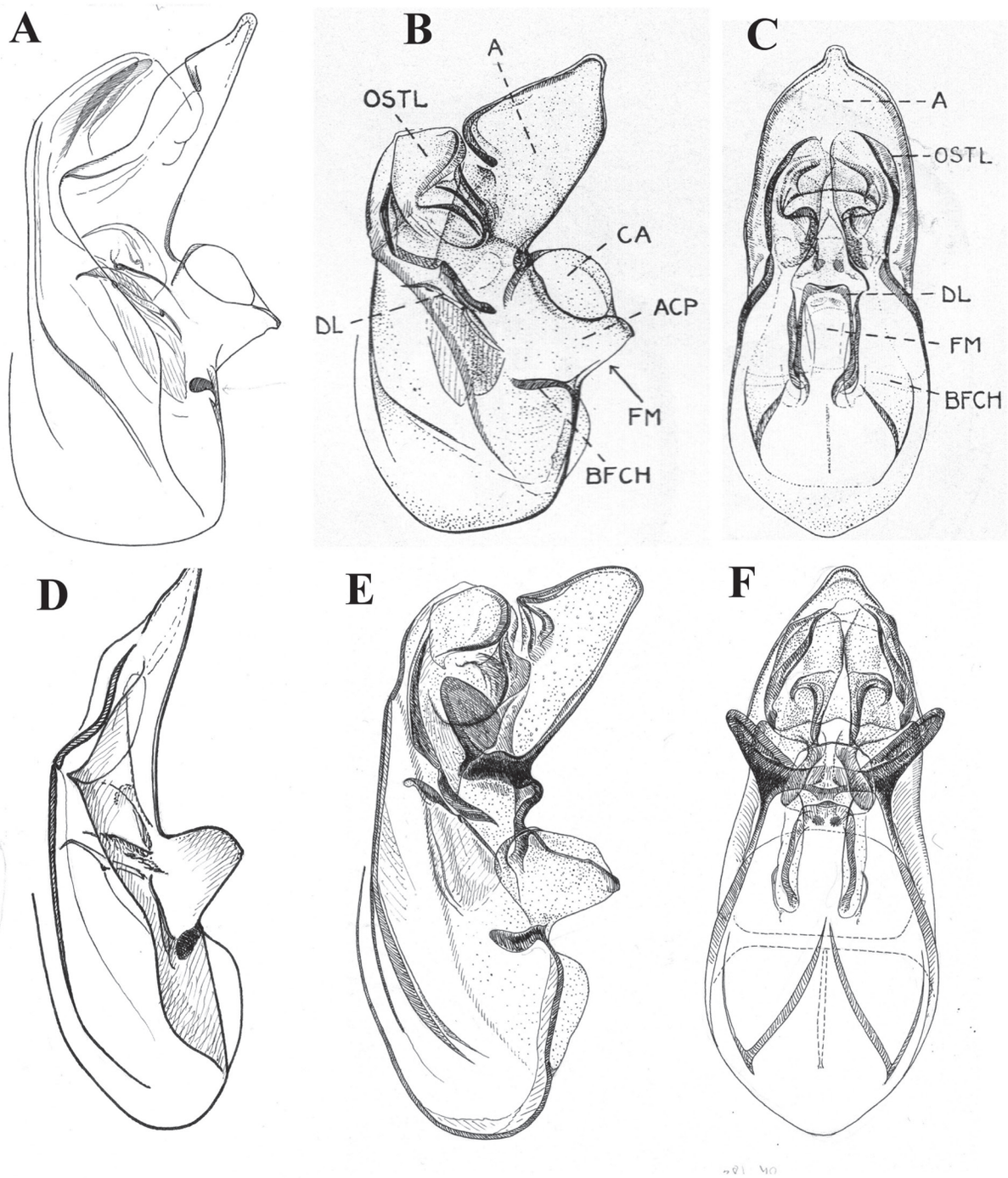


Fig. 13. Median lobe. A, B, D, E. Lateral view. C. Dorsal view. F. Ventral view. A. *Dilacra luteipes*; B-C. Parameotica laticeps; D. *Hydrosmectina subtilissima*; E-F. *Parameotica ?epirotica* Benick. A = Apex of capsule, ACP = Apical central wall of capsule, BFCH = lateral sclerotization under DEJ, CA = Crista apicalis of the capsule, DL = ductuslamells, FM = foramen mediale in capsule, OSTL = Apical lamells.

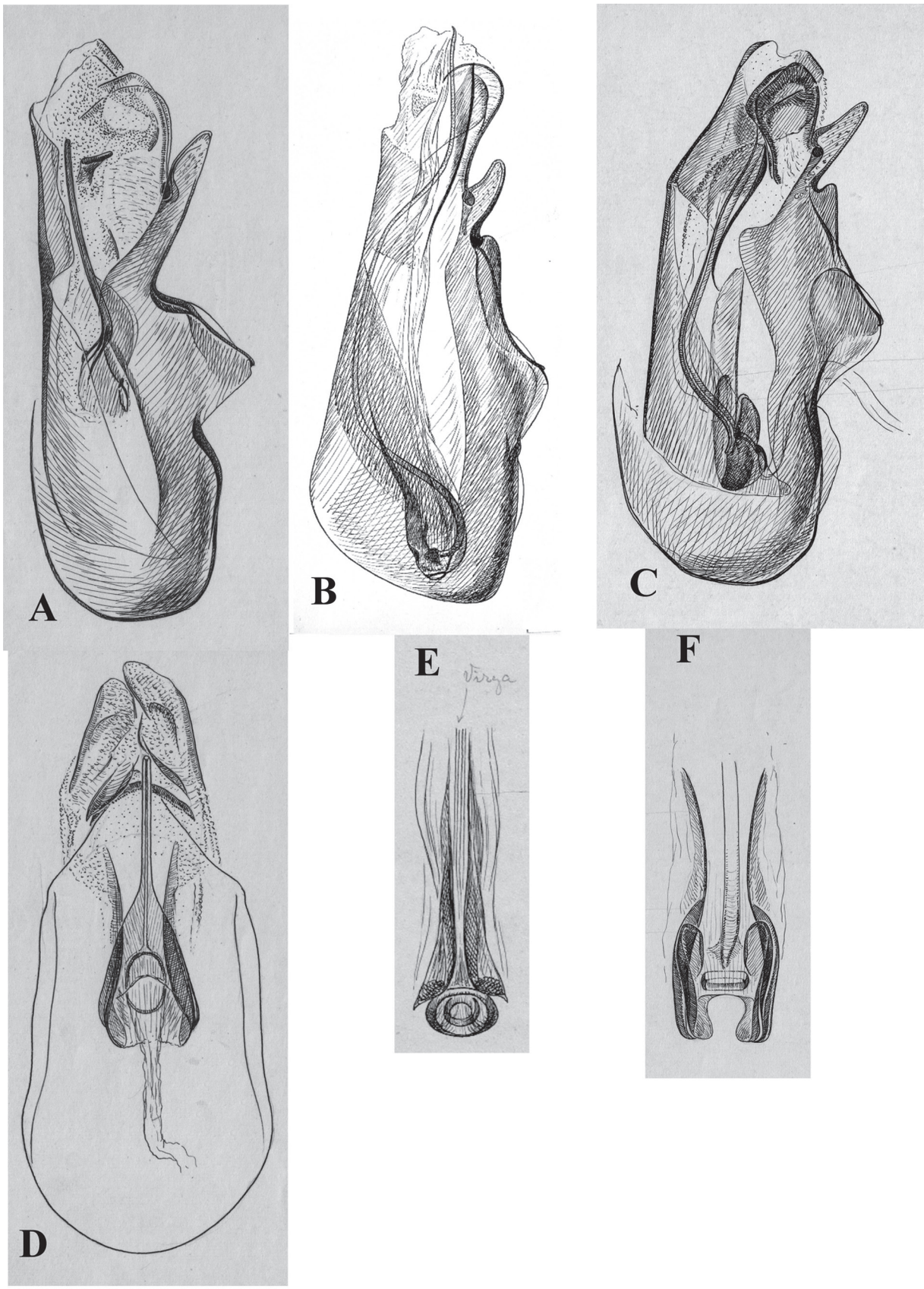


Fig. 14. *Paranopleta* sp. A, D. *P. basicornis*; B, E. *P. autumnalis*; C, F. *P. inhabilis*. A-D. Median lobe, E-F. Ductuslamells and opening for ductus ejaculatoris.

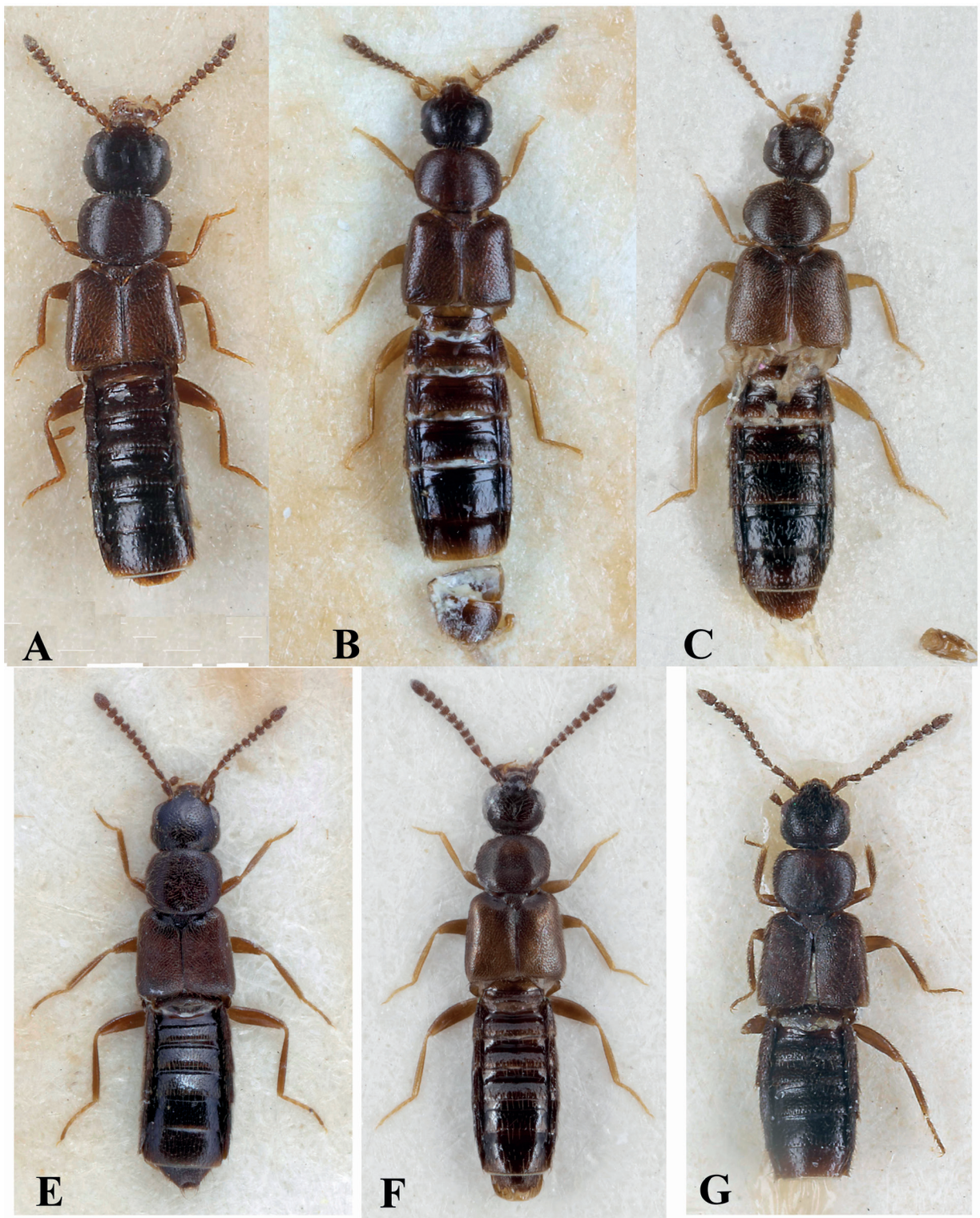


Fig. 15. A-C. *Paranopleta* species. E-G *Traumoecia* species. A. *P. inhabilis*; B. *P. basicornis*; C. *P. autumnalis*; E. *T. janssoni*; F. *T. taxiceroides*; G. *T. wuorentausi*.

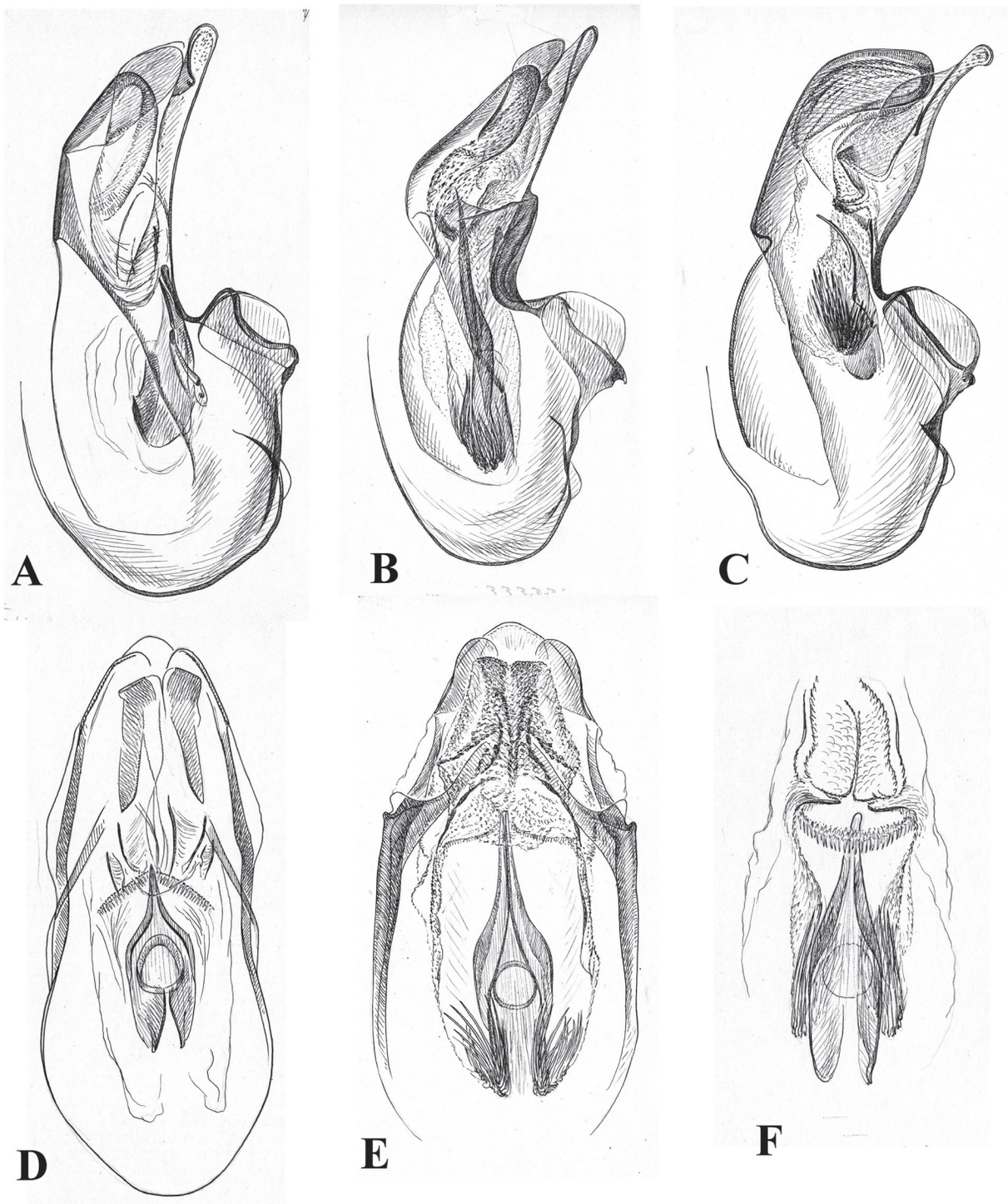


Fig. 16. Median lobe. A-C lateral view. D-F dorsal view. A, D. *Thonobaena vestita*; B, E. *Liogluta roettgeni*; C, F. *Oreostiba tibialis*. All species with transverse serrate belt across at the tip of ductuslamells, *Liogluta* and *Oreostiba* with bundle of spines at base of ductuslamells.

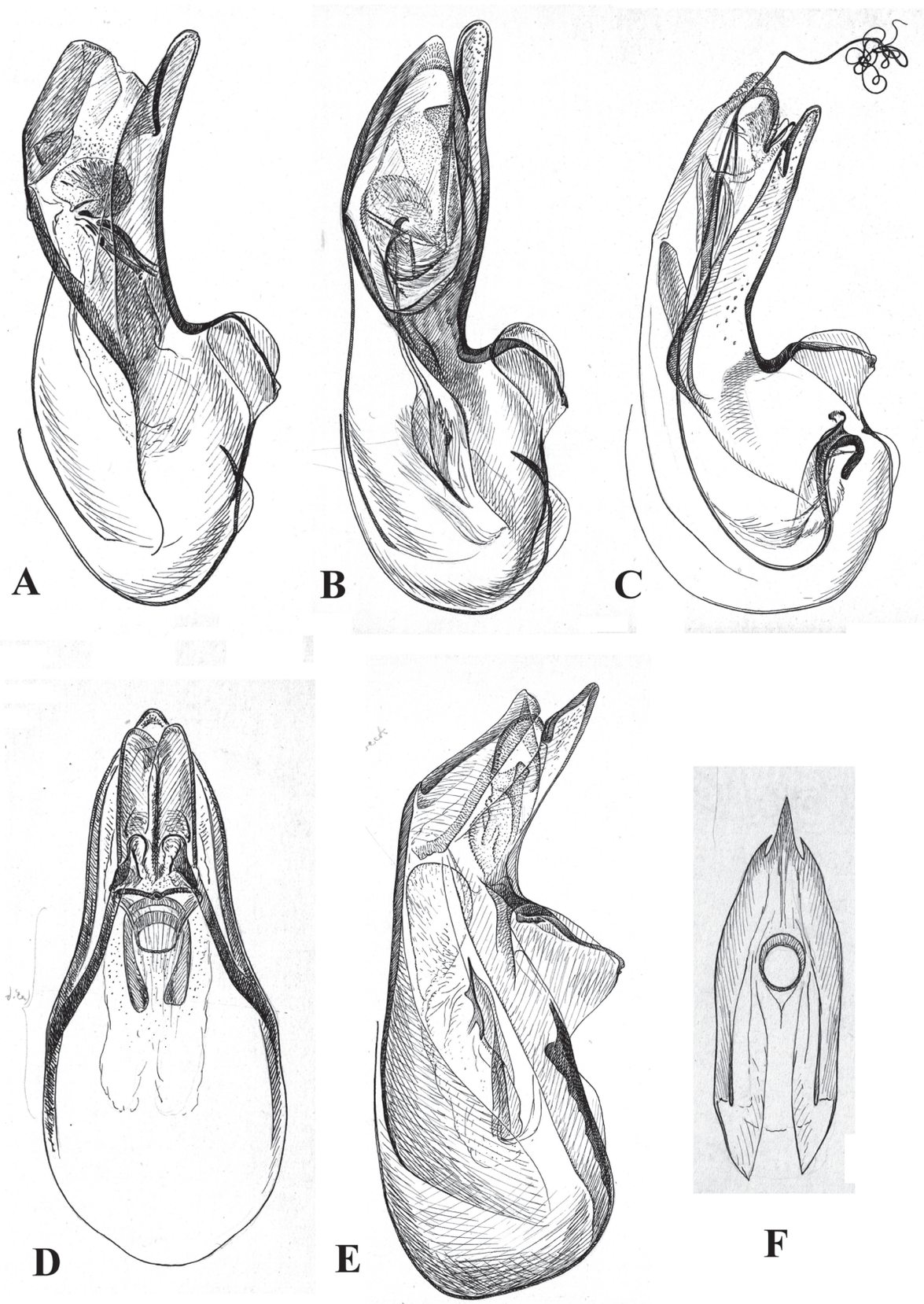


Fig. 17. Median lobe. A-C, E. Lateral view. D. Ventral view, F. Ductuslamells and opening for ductus ejaculatoris, ventral view. A, D. *Alpinia ?alpicola* with transverse serrate belt across at the tip of ductuslamells; B. *Aloconta* (s.str.) *gregaria*; C. *Aloconota* (*Disopora*) *sulcifrons*; E-F. *Dacrila fallax*.

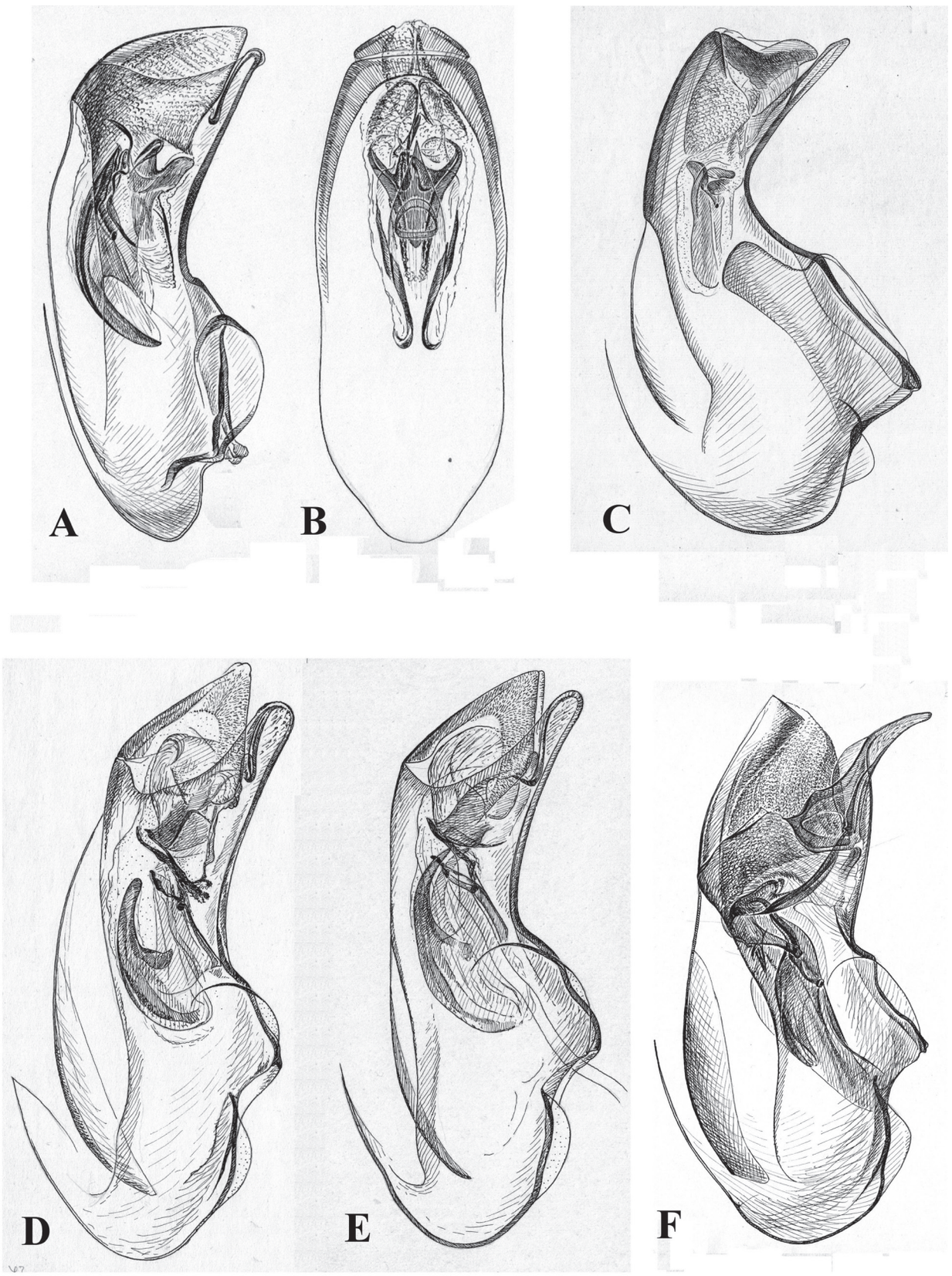


Fig. 18. Median lobe. A, C, D, E, F. lateral view. B. Dorsal view. A, B. *Atheta orosina*; C. *Boreostiba frigida*; D. *Neodimetrota* ***aeneipennis*** (Thomson) (= *parapicipennis* Brundin); E. *Neodimetrota picipennoides* Hanssen: F. *Traumoecia* picipes.

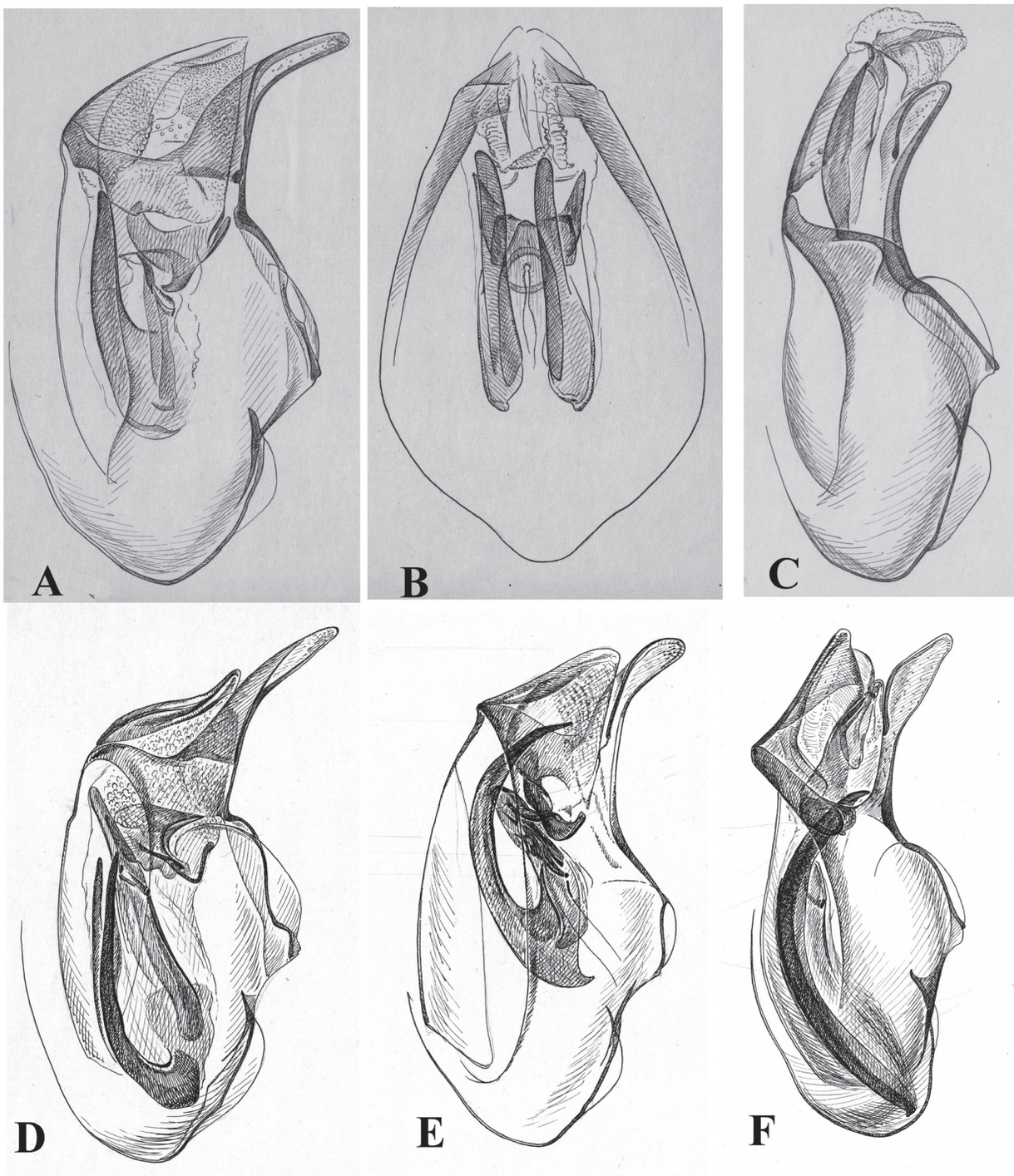


Fig. 19. Median lobe. A, C-F. Lateral view. B. Dorsal view. A-B. *Boreoatheta thulea*; C. *B. piligera*; D. *Atheta diversa*; E. *A. allocera*; F. *A. hybrida*.

aeneipennis > *Neodimetriota*
aequata > *Dinaraea*
allocera > *Atheta*
amicula > *Microdota*
analis > *Amischa*
anceps > *Lyprocorrhe*
aterrima > *Acrotona*
atramentaria > *Atheta*
autumnals > *Paranopleta*
basicornis > *Paranopleta*
cadaverina > *Dimetrota*
carpathica > *Alpinia*
castanoptera > *Atheta*
cinnamoptera > *Neodimetrota*
circellaris > *Geostiba*
clancula > *Dochmonota*
contristata > *Atheta*
coriaria > *Dalotia*
Corobscura > *Cordalia obscura*
crassicornis > *Atheta*
Datcelata > *Datomicra celata*
Datnigra > *Datomicra nigra*
dilaticornis > *Alaobia*
dwinensis > *Rhagocneme*
ebenina > *Atheta*
elegans > *Plataraea*
euryptera > *Atheta*
excellens > *Bessobia*
fallax > *Dilacra*
Fasulcata > *Falagria caesa*
flavipes > *Nothotecta*
frigida > *Boreostiba*
fungi > *Mocyta*
fungivora > *Bessobia*
gagatina > *Alaobia*
Gnycarbonaria > *Gnypeta carbonaria*
graminicola > *Atheta*
grata > *Dimetrotina*
gregaria > *Aloconota*
Hflavipes > *Halobrecta flavipes*
inhabilis > *Paranopleta*
insecta > *Aloconota*
intermedia > *UNKNOWN GENUS 1*
islandica > *Boreophilia*
lapponic > *Neodimetrota*
laticeps > *Parameotica*
longicornis > *Chaetida*
longiuscula > *Liogluta*
luteipes > *Dilacra*
macrocera > *Badura*
marcida > *Pseudodimetrota* NG
marina > *Brundinia*
melanaria > *Copropthassa*
munsteri > *Boreophilia*
myrmecobia > *Xenota*
nidorum > *Pycnota paradoxa*
nigrifrons > *Plataraea*
nigritula > *Atheta*
Oxypoda > *Oxypoda spectabilis*
pagana > *Liogluta*
pallidicornis > *Alaobia*
pervagata > *Alaobia*
pfaundleri > *Atheta*
Phpalustris > *Philhygra palustris*
Phpseudoelongatula >*Philhygra pseudoelongatula*
picipes > *Traumoecia*
pilicornis > *Atheta*
piligera > *Boreoatheta* NG
procera > *Atheta*
pseudotenera > *Acrotona*
pygmaea > *Acrotona*
ravilla > *Traumoecia*
scapularis > *Alaobia*
sexdentata > *Atheta*
sibirica > *Boreostiba*
sodalis > *Alaobia*
sordida > *Nehemitropia lividipennis*
subglabra > *Alaobia*
subplana > *Boreophilia*
subterranea > *Alaobia*
subtilissima > *Hydrosmectina*
Tachconstricta > *Tachyusa constricta*
talpa > *Amidobia talpa*
tenuiducta > *Neodimetrota*
testaceipes > *Alaobia*
thinibioides > *Hydrosmecta longula*
thulea > *Boreoatheta* NG
tibialis > *Oreostiba*
Toluteicornis > *Tomoglossa luteicornis*
trebinjensis > *Microdota orosana*
triangulum > *Atheta*
vestita > *Thinobaena*
vilis > *Dilacra*
xanthopus > *Atheta*

Fig. 20 Code giving the valid names for the taxa in the trees, in alphabetical order.

Appendix 1

Tribes, genera and species included in the matrix **(in bold bold font)** and those examined for the characters needed for placement (in standard font). Genera not included in the matrix are marked as **NOT ANALYZED.** All new taxa, combinations and changes in status are marked accordingly. Many species placed in *Atheta* subgenera in Schülke et Smetana (2015) appear now as if representing new combinations because subgenera are treated as genera. They are not marked as new combinations because most of them have been treated this way in some source or other earlier and some, e.g. *Philhygra* back and forth many times.

tribe Athetini Casey, 1910

FIRST GROUP (0-2 chaetotaxy with aedeagial synapomorphies, a monophyletic group, clade)

***Atheta* Thomson, 1858** type species *Aleochara graminicola* Gravenhorst, 1806
***castanoptera* Mannerheim, 1830 (*Bolitochara*)**
***graminicola* Gravenhorst, 1806 (*Aleochara*)**
***triangulum* Kraatz, 1856 (*Homalota*)**
***xanthopus* Thomson, 1856 (*Homalota*)**
***contristata* Kraatz, 1856a (*Homalota*)**
***ebenina* Mulsant & Rey, 1873 (*Homalota*)**
***pfaundleri* G. Benick, 1940**
***euryptera* Stephens, 1832 (*Aleochara*)**
***sexdentata* Jansson, 1929**
***cinnamoptera* Thomson, 1856 (*Homalota*) NEW COMBINATION**
***atramentaria* Gyllenhal, 1810 (*Aleochara*)**
***nigritula* Gravenhorst, 1802 (*Aleochara*)**
***allocera* Eppelsheim, 1893**
***procera* Kraatz, 1856 (*Homalota*)**
***crassicornis* Fabricius, 1792 (*Staphylinus*)**
***pilicornis* Thomson, 1852 (*Homalota*)**
aeneicollis Sharp, 1869 (*Homalota*)
aquatica Thomson, 1852 (*Homalota*)
aquatilis Thomson, 1867 (*Liogluta*)
brunneipennis Thomson, 1852 (*Homalota*)
diversa Sharp, 1869 (*Homalota*)
heymesi Hubenthal, 1913
hypnorum Kiesenwetter, 1850 (*Homalota*)
incognita Sharp, 1869a (*Homalota*)
laevicauda J. Sahlberg, 1876
minarzi Bernhauer, 1936
woerndlei Bernhauer, 1917
laevana Mulsant & Rey, 1852 (*Homalota*)
setigera Sharp, 1869 (*Homalota*)
nidicola Johannsen, 1914 (*Homalota*)
oblita Erichson, 1839 (*Homalota*)
acutangula Hanssen, 1937: 189
boleticola J. Sahlberg, 1876
britanniae Bernhauer & Scheerpeltz, 1926
paracrassicornis Brundin, 1954
strandiella Brundin, 1954
fungicola Thomson, 1852 (*Homalota*)
divisa Märkel, 1844 (*Homalota*)
boletophila Thomson, 1856 (*Homalota*)
?liturata Stephens, 1832 (*Aleochara*)

***Anopleta* Mulsant & Rey, 1874 NOT ANALYZED**
corvina Thomson, 1856 (*Homalota*)
depressicollis Fauvel, 1875 (*Homalota*)
kochi Roubal, 1937 (*Atheta*)
nitella Brundin, 1948 (*Atheta*)
puberula Sharp, 1869 (*Homalota*)
sodermani Bernhauer, 1931 (*Atheta*)

***Bessobia* Thomson, 1858 NEW STATUS**
***excellens* Kraatz, 1856 (*Homalota*)**
***fungivora* Thomson, 1867**
monticola Thomson, 1852 (*Homalota*)
occulta Erichson, 1837 (*Homalota*)

***Neodimetrota* Muona, 2023**
***aeneipennis* Thomson, 1856 (*Homalota*)**
***lapponica* J. Sahlberg, 1876 (*Atheta*)**
***tenuiducta* K. Sawada, 1970 (*Ischnopoda*)**
***?intermedia* ThomSon, 1852 (*Homalota*)**
altaica Bernhauer, 1901 (*Atheta*)
episcopalis Bernhauer, 1910 (*Atheta*)
europaea Likovský, 1984 (*Atheta*)
knabli G. Benick, 1938 (*Atheta*)
leonhardi Bernhauer, 1911 (*Atheta*)
nigripes Thomson, 1856 (*Atheta*)
picipennoides Hanssen, 1932 (*Atheta*)
putrida Kraatz, 1856 (*Homalota*)
subrugosa Märkel & Kiesenwetter, 1848 (*Homalota*)

***Paranopleta* Brundin, 1954 NEW STATUS**
***autumnalis* Erichson, 1839 (*Homalota*)**
NEW COMBINATION
***basicornis* Mulsant & Rey, 1852 (*Homalota*)**
NEW COMBINATION
***inhabilis* Kraatz, 1856 (*Homalota*)**

***Plataraea* Thomson, 1858**
***elegans* G. Benick, 1935 (*Atheta*)**
***nigrifrons* Erichson, 1839 (*Homalota*)**
brunnea Fabricius, 1798 (*Staphylinus*)
dubiosa G. Benick, 193 (*Atheta*)

***Pseudodimetrota* NEW GENUS**
***marcida* Erichson, 1837 (*Homalota*)**
NEW COMBINATION

***Traumoecia* Mulsant & Rey, 1873**
NEW STATUS
***ravilla* Erichson, 1839 (*Homalota*)**
NEW COMBINATION
***picipes* Thomson, 1856 (*Homalota*)**
harwoodi B. S. Williams, 1930 (*Atheta*
NEW COMBINATION
janssoni Bernhauer, 1923
NEW COMBINATION
taxiceroides Munster, 1932 (*Atheta*)
vaga Heer, 1839 (*Homalota*)
NEW COMBINATION
wuorentausi Bernhauer, 1926 /Atheta)
NEW COMBINATION

SECOND GROUP (0-1 chaetotaxy, homoplastic character state, probably not a clade)

***Alpinia* Brundin, 1948**
***carpathica* L. Miller, 1868 (*Homalota*)**

***Alaobia* Thomson, 1858 NEW STATUS**
***gagatina* Baudi di Selve, 1848 (*Homalota*)**
***pallidicornis* Thomson, 1856 (*Homalota*)**
***scapularis* C. R. Sahlberg, 1831 (*Aleochara*)**
***?sodalis* Erichson, 1837 (*Homalota*)**
***subglabra* Sharp, 1869 (*Homalota*)**
NEW COMBINATION
***dilaticornis* Kraatz, 1856 (*Homalota*)**
NEW COMBINATION
***pervagata* G. Benick, 1974 (*Atheta*)**
NEW COMBINATION
***subterranea* Mulsant & Rey, 1853 (*Homalota*) NEW COMBINATION**
***testaceipes* Heer, 1839 (*Homalota*)**
NEW COMBINATION
hybrida Sharp, 1869 (*Homalota*)
pandionis Scheerpeltz, 1958 (*Atheta*)
trinotata Kraatz, 1856 (*Homalota*)
sparreschneideri Munster, 1923
flavipes Hochhuth, 1860 (*Oxypoda*)
NEW COMBINATION
voeslauensis Bernhauer, 1944 (*Atheta*)
NEW COMBINATION

***Alianta* Thomson, 1858: 35**
NOT ANALYZED
incana Erichson, 1837 (*Homalota*)

***Amidobia* Thomson, 1858**
***talpa* Heer, 1841 (*Homalota*)**

***Badura* Mulsant & Rey, 1873**
NEW STATUS
***macrocera* Thomson, 1856 (*Homalota*)**
puncticollis Benick, 1938

***Boreophilia* G. Benick, 1973**
***insecuta* Eppelsheim, 1893 (*Atheta*)**
***subplana* J. Sahlberg, 1880 (*Atheta*)**
eremita Rye, 1866 (*Homalota*)
fusca C. R. Sahlberg, 1831 (*Aleochara*)
hyperborea Brundin, 1940b (*Atheta)*
islandica Kraatz, 1857 (*Homalota*)
munsteri Bernhauer, 1902 (Atheta)

***Boreostiba* Lohse, 1990**
***frigida* J. Sahlberg, 1880 (*Atheta*)**
***sibirica* Mäklin, 1880 (*Homalota*)**

***Boreoatheta* NEW GENUS**
***piligera* J. Sahlberg, 1876 (*Atheta*)**
NEW COMBINATION
***thulea* Poppius, 1909 (*Atheta*) NEW COMBINATION**

***Chaetida* Mulsant & Rey, 1873**
NEW STATUS
***longicornis* Gravenhorst, 1802 (*Aleochara*)**

***Dadobia* Thomson, 1858 NOT ANALYZED**
immersa Erichson, 1837 (*Homalota*)

***Dalotia* Casey, 1910**
***coriaria* Kraatz, 1856 (*Homalota*)**

***Dimetrota* Mulsant & Rey, 1873**
***cadaverina* Brisout de Barneville, 1860 (*Homalota*)**

***Dinaraea* Thomson, 1858**
***aequata* Erichson, 1837 (*Homalota*)**
angustula Gyllenhal, 1810 (*Aleochara*)
arcana Erichson, 1839 (*Homalota*)
linearis Gravenhorst, 1802 (*Aleochara*)

***Liogluta* Thomson, 1858**
***longiuscula* Gravenhorst, 1802 (*Aleochara*)**
***pagana* Erichson, 1839 (*Homalota*)**
alpestris Heer, 1839 (*Homalota*)
granigera Kiesenwetter, 1850(*Homalota*)
micans Mulsant & Rey, 1852 (*Homalota*)
microptera Thomson, 1867
wuesthoffi G. Benick, 1938 (*Atheta*)

***Nototheca* Thomson, 1858**
***flavipes* Gravenhorst, 1806 (*Aleochara*)**

***Oreostiba* Ganglbauer, 1895 NEW STATUS**
***tibialis* Heer, 1839 (*Homalota*)**

***Rhagocneme* Munster, 1923 NEW STATUS**
***dwinensis* Poppius, 1908 (*Atheta*)**
subsinuata Erichson, 1839 (*Homalota*)

***Schistoglossa* Kraatz, 1856 NOT ANALYZED**
aubei Brisout de Barneville, 1860 (*Homalota*)
bergvalli Palm, 1968: 248
curtipennis Sharp, 1869a: 173 (*Homalota*)
gemina Erichson, 1837: 330 (*Homalota*)
pseudogemina G. Benick, 1981a: 11
viduata Erichson, 1837: 330 (*Homalota*)

***Thinobaena* Thomson, 1859 NEW STATUS**
***vestita* Gravenhorst, 1806 (*Paederus*)**

***Trochanterella* Brundin, 1954 NOT ANALYZED**
cribripennis J. Sahlberg, 1890 (*Atheta*)

(0-0-0-0-0-0 chaetotaxy)

***Amischa* Thomson, 1858**
***analis* Gravenhorst, 1802 (*Aleochara*)**
bifoveolata Mannerheim, 1830 (*Bolitochara*)
decipiens Sharp, 1869 (*Homalota*)

***Coprothassa* Thomson, 1859 NEW STATUS**
***melanaria* Mannerheim, 1830 (*Oxypoda*)**

***Pycnota* Mulsant & Rey, 1873**
***paradoxa* Mulsant & Rey, 1861 (*Homalota*)**

***Tomoglossa* Kraatz, 1856**
***luteicornis* Erichson, 1837 (*Homalota*)**
laeta Eppelsheim, 1884

(0 – 0 chaetotaxy)

***Datomicra* Mulsant & Rey, 1874 NEW STATUS**
***celata* Erichson, 1837 (*Homalota*)**
***nigra* Kraatz, 1856 (*Homalota*)**

***Dimetrotina* Casey, 1911**
***grata* Cameron, 1933 (Atheta)**
laticollis Stephens, 1832 (*Aleochara*)

***Hydrosmecta* Thomson, 1858**
***longula* Heer, 1839 (*Homalota*)**
tenella Mannerheim, 1830 (*Bolitochara)*

***Lundbergia* Muona, 1975 NOT ANALYZED**
trybomi J. Sahlberg, 1880

***Lypoglossa* Fenyes, 1918 NOT ANALYZED**
lateralis Mannerheim, 1830 (Oxypoda)

***Microdota* Mulsant & Rey, 1873 NEW STATUS**
***amicula* Stephens, 1832: 132 (*Aleochara*)**

***?orosana* Scheerpelts, 1931 (as *tebinjensis* Brundin, 1940)**

***Mocyta* Mulsant & Rey, 1874 NEW STATUS**
***fungi* Gravenhorst, 1806 (*Aleochara*)**

***Philhygra* Mulsant & Rey, 1873**
NEW STATUS
***pseudoelongatula* Bernhauer, 1907 (*Atheta*)**
***palustris* Kiesenwetter, 1844 (*Homalota*)**
arctica Thomson, (*Homalota*)
hygrotopora Kraatz, 1856 (*Homalota*)
hygrobia Thomson, 1856 (*Homalota*)
melanocera Thomson, 1856 (*Homalota*)
britteni Joy, 1913 (*Atheta*)

***Xenota* Mulsant & Rey, 1873**
***lativentris* J. Sahlberg, 1875 (*Atheta*)**

THIRD GROUP (serrate caudal margins of abdominal segments, probably a seprate tribe)

***Acrotona* Thomson, 1859**
***aterrima* Gravenhorst, 1802 (*Aleochara*)**
***pseudotenera* Cameron, 1933 (*Atheta*)**
***pygmaea* Gravenhorst, 1802 (*Aleochara*)**
convergens A.Strand, 1958 (*Atheta*)
parens Mulsant & Rey, 1852 (*Homalota*)
parvula Mannerheim, 1830 (*Bolitochara*)
piceorufa Mulsant & Rey, 1873 (*Colpodota*)
pilosicollis Brundin, 1952 (*Atheta*)

***Lyprocorrhe* Thomson, 1859**
***anceps* Erichson, 1837 (*Homalota*)**

***Nehemitropia* Lohse, 1971**
***lividipennis* Mannerheim, 1830 (*Oxypoda*)**

tribe Geostibini Seevers, 1978

***Alevonota* Thomson, 1858**
NOT ANALYZED
gracilenta Erichsen, 1839 (*Homalota*)

***Aloconota* Thomson, 1858**
***gregaria* Erichson, 1839 (*Homalota*)**
insecta* Thomson, 1856 (*Homalota9
planifrons G.Waterhouse, 1863 (*Homalota*)

***Geostiba* Thomson, 1858**
***circellaris* Gravenhorst, 1806**

tribe Dilacrini NEW TRIBE (chaetotaxy 0-0-0-0-0-0, synapomorphic aedeagus)

***Brundinia* Tottenham, 1949**
***marina* Mulsant & Rey, 1853b: 39 (*Homalota*)**
meridionalis Mulsant & Rey, 1853

***Dochmonota* Thomson, 1859**
***clancula* Erichson, 1837 (*Homa*lota)**

rudiventris Eppelsheim, 1886 (*Homalota*)

***Dilacra* Thomson, 1858**
***luteipes* Erichson, 1837 (*Homalota*)**
***vilis* Erichson, 1837 (*Homalota*)**

***Hydrosmectina* Ganglbauer, 1895**
NEW STATUS
subtilissima Kraatz, 1854 (Homalota)

***Parameotica* Ganglbauer, 1895**
***laticeps* Thomson, 1856 (*Homalota*)**

tribe Tachyusini Thomson, 1859 (chaetotaxy 0-0-0-0-0-0)

***Brachyusa* Mulsant & Rey, 1874**
NOT ANALYZED
***concolor* Erichson 1839 (Homalota)**

***Dacrila* Mulsant et Rey, 1874**
fallax Kraatz, 185

***Gnypeta* Thomson, 1858**
***carbonaria* Mannerheim, 1830: 75 (*Aleochara*)**

***Tachyusa* Erichson, 1837**
***constricta* Erichson, 1837: 307**

tribe Taxicerini Lohse, 1989

***Halobrecta* Thomson, 1858**
***flavipes* Thomson, 1861 (*Homalota*)**

tribe Falagrini Mulsant et Rey, 1873

***Cordalia* Jacobs, 1925**
***obscura* Gravenhorst, 1802 (*Aleochara*)**

Falagria Leach, 1819
caesa Erichson, 1837

tribe Oxypodini Thomson, 1859

***Oxypoda* Mannerheim, 1830**
spectabilis Märkel, 1844

APPENDIX 2. Taxa in the order of matrix and with correct present names.

Outgroup. Oxypoda spectabilis:
Ligula bifid halfway; tarsi 555; ductuslamells tiny simple; condylit small normal; pronotal hair directed caudad; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge absent; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 1. Atheta graminicola:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with rounded bundle, graminicola; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 2. Atheta castanoptera:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with rounded bundle, graminicola; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; metum laterally with many pseudopores; capsule under opening simple.

Terminal 3. Atheta xanthopus:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with smaller triangular bundle, xanthopus; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; in-

ternal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 4. Atheta triangulum:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with smaller triangular bundle, xanthopus; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 5. Atheta euryptera:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with primitive rounded bundle; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 6. Atheta sexdentata:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with primitive rounded bundle; male tergite 8 simple; male tergite 8 with chisel-shaped large lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 7. Atheta atramentaria:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with extensive bundle, atramentaria; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 8. Atheta ebenina:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with primitive rounded bundle; male tergite 8 state4; male tergite 8 with chisel-shaped large lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well

developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 9. Atheta contristata:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with primitive rounded bundle; male tergite 8 state4; male tergite 8 with chisel-shaped large lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 10. Atheta pfaundleri:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca with sclerotized narrow basal section; spermatheca with primitive rounded bundle; male tergite 8 state4; male tergite 8 with chisel-shaped large lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 11. Atheta intermedia:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 12. Atheta nigritula:
Ligula state9; tarsi 455; ductuslamells with lateral supports; condylit small normal; pronotal hair type 3; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 13. Atheta procera:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 14. Atheta pilicornis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 15. Atheta crassicornis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 16. Bessobia fungivora:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 with lateral ridges; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 17. Bessobia excellens:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 3; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 with lateral ridges; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 18. Boreostiba sibirica:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit as larg as paramerite; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 19. Boreostiba frigida:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit as larg as paramerite; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sterni-

tes with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 20. Atheta cinnamoptera:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca with sclerotized narrow basal section; spermatheca with unique bundle; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 21. Neodimetrota lapponica:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 22. Neodimetrota tenuiducta:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 23. Nwodimetrota aeneipennis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 24. Boreophilia subplana:
Ligula bifid deeply; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with numerous unusually long and strong setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack

without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 25. Boreophilia islandica:
Ligula bifid deeply; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with numerous unusually long and strong setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 26. Boreiphilia munsteri:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks anchor shaped; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with numerous unusually long and strong setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 27. Plataraea nigrifrons:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 3; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum with conspicuous black extra setae on corners; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 28. Plataraea elegans:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 3; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open baal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum with conspicuous black extra setae on corners; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 29. Dalotia coriaria:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 30. Rhagocneme dwinensis:
Ligula bifid halfway; tarsi 455; ductuslamells with lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks basally bulbous; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 31. Xenota myrmecobia:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 32. Datomicra celata:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 33. Datomicra nigra:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 34. Dimetrotina grata:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 35. Mocyta fungi:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized nar-

row basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 36. Microdota amicula:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 37. Philhugra palustris:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack with basal spine bundle; internal sack with medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 38. Philhygra pseudoelongatula:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type 3; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack with basal spine bundle; internal sack with medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 39. Amidobia talpa:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 40. Hydrosmecta longula (thinobioides):
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells;

internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 41. Hydrosmectina subtilissima:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 3; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks basally bulbous; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 42. Brundinia marina:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 43. Dilacra luteipes:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 44. Paraneotica laticeps:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 45. Dilacra vilis:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 46. Dochmonota clancula:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening with strong transverse sclerotization.

Terminal 47. Badura macrocera:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 48. Notothecta flavipes:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 49. Chaetida longicornis:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 50. Dinaraea aequata:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 4; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 51. Cadaverota cadaverina:
Ligula bifid halfway; tarsi 455; ductuslamells with lateral supports; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section;

spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 52. Pseudodimetrota marcida:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 53. Traumoecia ravilla:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks elongate; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 54. Traumoecia picipes:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks elongate; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 55. Lyprocorrhe anceps:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with crenulate border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with striated pair lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 56. Nehemitropia lividipennis (sordida):
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with crenulate border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athe-

tine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 57. Acrotona pygmaea:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with crenulate border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 58. Acrotona pseudotenera:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with crenulate border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 59. Acrotona aterrima:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with crenulate border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 60. Liogluta longiuscula:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern With S-formed patch; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 61. Liogluta pagana:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 62. Thinobaena vestita:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 4; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 63. Oreostiba tibialis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack with basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 64. Alpinia carpathica:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack with medial spine bundle; Athetine bridge well-developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 65. Microdota orosana (trebinjensis):
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks elongate; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 66. Aloconota gregaria:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type 3; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 67. Aloconota insecta:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type 4; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca

without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 68. Geostiba circellaris:
Ligula bifid halfway; tarsi 455; ductuslamells with lateral supports; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 69. Amischa analis:
Ligula short, plump; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks elongate; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 70. Cordalia obscura:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially wide; mentum laterally without pseudopores, with a few pores; capsule under opening simple.

Terminal 71. Coprpthassa melanaria:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 72. Fakagria caesa (sulcate):
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennom-

eres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 73. Halobrecta flavipes:
Ligula bifid at tip, elongated; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair directed caudad; elytral hair pattern towards lateral caudad corners; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 74. Pycnota paradoxa (nidorum):
Ligula short, plump; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 75. Dilacra fallax:
Ligula bifid deeply; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type 4; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 76. Gnypeta carbonaria:
Ligula bifid halfway; tarsi 455; ductuslamells pointed with lateral support; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula both branches with long seta; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 77. Tachyusa constricta:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior rows on tergite 2 and 3 only; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures;

internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 78. Tomoglossa luteicornis:
Ligula state5; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy without anterior row from tergite 4 on; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 79. Atheta allocera:
Ligula bifid halfway; tarsi 455; ductuslamells with closed lateral supports; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks basally bulbous; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with extensive bundle, atramentaria; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk with transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 80. Boreoatheta piligera:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 81. Boreoatheta thulea:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type1; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 82. Paranopleta autumnalis:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 83. Paranopleta inhabilis:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 02 + 13/23; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca tubulat, with expanded apex; male tergite 8 simple; male tergite 8 with lateral teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 84. Paranopleta basicornis:
Ligula bifid halfway; tarsi 455; ductuslamells with tiny base and extremely elongated apex, flagellum; condylit small normal; pronotal hair type1; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy state4; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with simple lamells; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge partly open; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 85. Alaobia sodalis:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks basally bulbous; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 excavated medially; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with complex symmetrical structure of four structures; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 86. Alaobia gagatina:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria about transparent; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 87. Alaobia pallidicornis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern caudad; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria slerotized; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 crenulate without lateral larger teeth; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 88. Alaobia subterranea:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal ster-

nites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 89. Alaobia scapularis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 90. Alaobia testaceipes:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 91. Alaobia dilaticornis:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 92. Alaobia pervagata:
Ligula bifid halfway; tarsi 455; ductuslamells pointed simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; spermatheca with open basal coil; male tergite 8 simple; male tergite 8 with lateral teeth and two median ones; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

Terminal 93. Alaobia subglabra:
Ligula bifid halfway; tarsi 455; ductuslamells simple; condylit small normal; pronotal hair type 2 to 5; elytral hair pattern towards lateral caudad corners; ligula without long setae; abdominal sternites with straight border; macrochetotaxy formula 01 + 12 + 13; internal sack lateral hooks not present; ductuslamell suspensoria not present; spermatheca without strongly sclerotized narrow basal section; sper-

matheca with open basal coil; male tergite 8 simple; male tergite 8 simple; male antennomeres 1 to 4 with normal setae; pronotum without special setae; internal sack apically with with lateral sets of complex four plates; internal sackk without transverse serrate lamell; Internal sack without basal spine bundle; internal sack without medial spine bundle; Athetine bridge well-developed; mentum medially narrow; mentum laterally with many pseudopores; capsule under opening simple.

APPENDIX 4. Character matrux.

	0 5 10 15 20
	| | | | |
Oxypoda	00000000000000000000000000
graminicola	01302200302110100200010 00
castanoptera	01302200302110100200010 00
xanthopus	01302200302120100200010 00
triangulum	01302200302120100200010 00
euryptera	01303200302140100200010 00
sexdentata	01303200302140600200010 00
atramentaria	01302200302030200200010 00
ebenina	01302200302144600200010 00
contristata	01302200302144600200010 00
pfaundleri	01302100302144600200010 00
intermedia	01302000330060000100010 00
nigritula	91203100302000200200010 00
procera	01502100301000400200010 00
pilicornis	01402100302000100210010 00
crassicornis	01402100302000100210010 00
fungivora	01503200301001000200010 00
excellens	01503100301001500200010 00
sibirica	01413200201000000000010 00
frigida	01413200201000000000010 00
cinnamoptera	01502100330150100100010 00
lapponica	01402100330000100100010 00
tenuiducta	01402100330000100100010 00
aeneipennis	01402100330000100100010 00
subplana	11102000230000010100011 00
islandica	11102000230000010100011 00
munsteri	01102000230000410100010 00
nigrifrons	01503100300000001200010 00
elegans	01503100300000201200010 00
coriaria	01402010221000100200010 00
dwinensis	01202100320000000100010 00
myrmecobia	01502100101000500000010 00
Datcelata	01102000102000200000010 00
Datnigra	01102000102060200000010 00
grata	01401000102000200000010 00
fungi	01101000200000000000010 00
amicula	01401200101000400200010 00
Phpalustris	01101100101000000201110 00
Phpseudoelongatula	01603100101000000201110 00
talpa	01602000200000000000010 00
thinibioides	01102200100000000000010 00
subtilissima	01103200122000000000011 01
marina	01102000000000000200020 01
luteipes	01101000000000000200020 01
laticeps	01101000000000000200020 01
vilis	01101000000000000200020 01
clancula	01102000000000000200020 01
macrocera	01402000200000000011001 000
flavipes	01401000200000000200010 00
longicornis	01302000200060000200010 00
aequata	01104000220000020001001 000
cadaverina	01201000201000000011001 000
marcida	01102100302000000100010 00
ravilla	01502100311000500200010 00
picipes	01501200311000500200010 00
anceps	01101201002000500100010 00
sordida	01501001002000000000010 00
pygmaea	01401001002000000000010 00
pseudotenera	01401001002000000000010 00
aterrima	01401001102000000000010 00
longiuscula	01501200201000400210011 10
pagana	01501100201060400210011 10
vestita	01504100200000000011001 10
tibialis	01501100200000000011011 10
carpathica	01101100201000000011011 10
trebinjensis	01401100211000000200011 10
gregaria	01603000200000000000011 10
insecta	01604100200000200000011 10
circellaris	01201100200000000200011 10
analis	31401010010000500000010 00
Corobscura	01501110002060000000011 10
melanaria	01401010102000000000010 00
Fasulcata	01501100101060000000010 00
Hflavipes	21500110102000000000020 00
nidorum	31101010102000000000010 00
fallax	11504100100000000200010 00
Gnycarbonaria	01502110102060000200020 00
Tachconstricta	01301100102060000200010 00
Toluteicornis	51101000002000000200010 00
allocera	01302100320030100210010 00
piligera	01102000221000000000010 00
thulea	01102000221000000000010 00
autumnalis	01602100300060200000020 00
inhabilis	01602100300060100000020 00
basicornis	01602100300000200000020 00
sodalis	01101100220000500200010 00
gagatina	01401100201000200300010 00
pallidicornis	01401000202000400300010 00
subterranea	01401100200000200300010 00
scapularis	01401100200000200300010 00
testaceipes	01401100200000200300010 00
dilaticornis	01401100200000200300010 00
pervagata	01401100200000200300010 00
subglabra	01101100200000000300010 00