

Pselaphinae of the Russian Far East (Coleoptera: Staphylinidae) with comments about the current taxonomic status of the subfamily

Жуки-ощупники Дальнего Востока России (Coleoptera: Staphylinidae: Pselaphinae) с замечаниями об их современном таксономическом статусе в качестве подсемейства

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КЛЮЧЕВЫЕ СЛОВА: Coleoptera, Staphylinidae, Omaliine-group, Pselaphinae, *Protopselaphus*, таксономический статус, морфология, распространение, определительные ключи, Дальний Восток России.

ABSTRACT: This study is devoted to the fauna of Pselaphinae of the Russian Far East, which currently includes 83 described species with one subspecies, distributed in 32 genera. The study provides a brief characterisation of the natural conditions of the region, a comprehensive critical analysis of the current taxonomic position of the subfamily and the accepted classification, information on some aspects of morphology, geographical and biotopic distribution and peculiarities of the biology of the Far Eastern Pselaphinae, identification keys to the genus and species levels, and an annotated list of species. The work is illustrated with 388 figures and pictures.

РЕЗЮМЕ: Данное исследование посвящено фауне жуков-ощупников Дальнего Востока России, которая на данный момент включает в свой состав 83 описанных вида с одним подвигом, распределённых по 32 родам. В исследовании приводится краткая характеристика природных условий региона, даётся всесторонний критический анализ современного таксономического положения этой группы и принимаемая классификация, приводятся сведения по некоторым аспектам морфологии, географическому и биотопическому распространению и особенностях биологии дальневосточных ощупников, определительные ключи до рода и до вида, составлен аннотированный список видов. Работа иллюстрирована 388 рисунками и фотографиями.

Introduction

The Pselaphinae are a large taxonomic group distributed throughout the world, with the exception of the polar regions. Currently, about 10000 species are known, distributed in more than 1200 genera. In reality, the subfamily undoubtedly contains many more (apparently, several times) taxa. But their study is constrained primarily by the lack of the necessary number of specialists who could treat the extensive material on this group, stored in many museums around the world. These beetles are rather small, usually not exceeding 1.5–2.0 mm, however, for its size class the group presents a striking variety of forms and structures.

Knowledge of the lifestyle of these Coleoptera is almost non-existent and in the vast majority of cases is limited to label data indicating where exactly the beetle was collected. The large majority of species are associated with forests and inhabit mainly litter and dead wood, sometimes reaching high abundances and diversity. Beetles are predators (with the exception of a fairly large group of myrmecophiles and termitophiles) and feed on a variety of mites, Collembola and many other small soil invertebrates. The preimaginal stages are very poorly studied.

The fauna of Pselaphinae of the Russian Far East remained practically unknown for a long time. Until 1984, only 6 species were known from this vast territory. In this regard it is interesting to cite the state-

ment of Jeannel [1958: 4], who in his *Révision des Psélaphides du Japon* wrote (in French) that "...except for *Tmesiphorus crassicornis* Sharp, collected in Nanaye, Lewis did not find any more pselaphid beetles in Hokkaido, where he conducted a long research in the summer of 1880. It is probable that the fauna of the Japanese Pselaphidae is localized in the central and southern parts of the archipelago, and that these beetles are almost entirely absent from the north." However, studies in recent decades have disproved this idea. On the Kuril island of Kunashir, neighboring with Hokkaido, 37 species of Pselaphidae from 22 genera are now known, and in total 84 species (including one not yet described) with one subspecies belonging to 32 genera have already been registered from the Russian Far East. And these are likely not final numbers. For example, this is indicated by the recent discovery of a large (2.8 mm) pselaphine beetle *Dendrolasiophilus subitus* Kurbatov et Kovalev, 2022, in the relatively well-studied Southern Primorye.

In 1989 the first identification keys of Pselaphinae (as Pselaphidae) of the Far East of the USSR were published [Kurbatov, 1989]. They included 56 species from 30 genera, of which about half were known only from neighboring countries, and it was only supposed that theoretically they could inhabit our Far East. Just a few years after publication, these keys are already obsolete. Although new discoveries can still be expected, author decided to systematize all the information on the Pselaphinae of the region accumulated to date, including illustrated identification keys and an annotated list of species recorded from this territory.

This work is based primarily on the author's own materials collected in the Far East: Amur Region (1978), Jewish Autonomous Region (1978), Primorsky Krai (1987–1993, 2009, 2019, 2024), Kunashir Island (1989–1992, 2011), Sakhalin Island (2011, 2021). The author studied the collections of Pselaphinae of Zoological Museum of Moscow State University, Moscow Pedagogical State University, Zoological Institute of the Russian Academy of Sciences (St. Petersburg), Federal Scientific Centre of Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences (Vladivostok), Muséum d'histoire naturelle (Geneva, Switzerland), and those of various entomologists. First of all, it is necessary to mention A.B. Ryvkin (Moscow), who for many years collected extensive material in the Amur Region, as well in the Jewish Autonomous Region and Primorsky Krai. N.B. Nikitski (Moscow), V.V. Belov (now Texas, USA), S.V. Saluk (Minsk, Belarus), I.V. Melnik (Moscow), A.V. Kovalev (St. Petersburg), Ya.N. Kovalenko (Moscow Region) also provided the author with Pselaphinae collected by them in various regions of the Far East. Many species of Pselaphinae from other regions of the globe were also used in this study. They were both collected by the author himself and obtained from his colleagues D. Chandler (USA), A.K. Tishechkin (USA), D.N. Fedorenko (Russia), R. Telnov (Latvia), Sh. Nomura (Japan), P. Hlaváč (Slovakia), D. Bekchiev (Bulgaria), G. Sabella (Italy), V. Grebennikov (Canada), G. Coulon (Belgium, †), F. Angelini (Italy, †).

The author also considered it appropriate to publish here his comments on the modern taxonomic status of the Pselaphinae.

Brief characterization of natural conditions of the Far East

By the Russian Far East we understand here, following Parmuzin [1964], the territory directly adjacent to the Pacific Ocean, and the depth of the spread of oceanic influence on the continent serves as a criterion for finding the natural boundary between the Far East and Eastern Siberia (Fig. 1). While in the north the sphere of action of the eastern sea air masses is limited to a 50–250 km strip without a clearly pronounced monsoon regime, in the south it expands up to 700 km from the coast, and the climate here acquires typical monsoon features.

The area of the Far East is over 3 million square kilometers, and the region extends 4,500 kilometers from north to south, including many islands such as Sakhalin (Fig. 1). The territory of the region is mountainous, but the mountains are predominantly medium-high or low, not exceeding 2000 m (some volcanoes of Kamchatka and Kuril Islands have more significant heights).

The main feature of the climate is its monsoon regime. The monsoon of the cold half of the year is caused by the steady transport of continental cold air to the south and east. In contrast, during summer the sea air from the south is carried in north-western and northern directions. This atmospheric regime smooths the temperature contrasts between the north and south of the Far East, leading to anomalously cold winters in the south, the severity of which is mitigated by the warming influence of the sea only in a narrow coastal strip. Annual precipitation ranges from 900–1000 mm in the south and southeast to 300 mm in the north.

The differences between the extreme types of ecosystems in the region are very significant: the indicator of the total stock of plant mass increases a hundredfold from the Arctic deserts to the liana coniferous-broadleaf forests of southern Primorye. The unique specificity and richness of the flora and fauna of the southern Far East is due to the fact that East Asia is the only place on the globe where the tropical zone smoothly passes into the temperate zone without intermediate impoverishment [Darlington, 1957, cited in Matyushkin, 1985].

Materials and methods

Reliable identification of many species requires making preparations of the genitalia of males and sometimes other body parts. Author prefers to use Canada balsam for this purpose. The following is a modification of the method of making preparations described by Besuchet [1974] with comments on some useful techniques to simplify certain operations.

The dry specimen is soaked in water for 1–2 hours. If a few drops of ammonia are added to the water, the soaking process is reduced to 15–20 minutes. Then in a



Fig. 1. Map of the Russian Far East.
Рис. 1. Карта Дальнего Востока России.

drop of water under a microscope with the help of two pins the aedeagus or other necessary part of the body is extracted from the beetle and placed in isopropanol for 20–30 minutes or for a longer time until air bubbles disappear from the inner space of the aedeagus. A drop of Canada balsam is applied to a small plate of transparent plastic 0.2–0.3 mm thick (it is important that the plastic does not react with xylene!) about 10x20 mm in size, and the desired body part is transferred into this drop. The transfer of the aedeagus from isopropanol to Canada balsam is easily accomplished with a pin, on the tip of which a very small drop of Canada balsam is placed. This drop should be allowed to thicken a little, and then with a quick movement transfer the aedeagus adhering to it into the preparation. During the next 2–3 days, the orientation of the aedeagus can be easily changed; for this purpose, a very small drop of xylene is placed over it with the blunt end of a pin, which immediately liquefies the balsam locally, allowing the preparation to be given the desired orientation. The plate with the preparation is placed on a slide and examined under the microscope. Then the preparation is pinned under the beetle and thus the beetle and its preparation are kept in the collection on one pin. The balsam can be quickly dissolved by dripping ethyl acetate on it and then remounting the insect parts it contains onto a new plate in case the preparation needs to be reoriented later after the final solidification of the Canada balsam. The preparation does not degrade with time; the author has studied preparations made in the late 1950's of the last century, and they were no different from freshly prepared ones.

Comments on the status of Pselaphinae

Here we would like to focus in more detail on the problem of the taxonomic status of Pselaphinae.

During the 19th and 20th centuries, Pselaphidae were almost invariably considered as an independent family (sometimes they were divided into two families: Pselaphidae and Clavigeridae), although their relationships within the staphylinoid complex have always been the subject of discussion. Different views on this issue have been expressed, for example, by Raffray [1890, 1908], Böving & Craighead [1931], Crowson [1955], Tikhomirova [1973], Lawrence & Newton [1982] and many others. However, Pselaphidae was relatively recently reclassified as a subfamily within Staphylinidae based on phylogenetic analysis [Newton, Thayer, 1995]. We will analyze this research; in some cases, for a better understanding of the researchers' logic, we will refer to a similar study by Grebennikov & Newton [2009], in which the same fate befell the Scydmaenidae.

1. First of all, let us note that in both articles the phylogenetic analysis was carried out by the authors according to the same scheme, namely: the relationships between Staphylinidae, Pselaphidae and Scydmaenidae were not investigated, but the latter two taxa were *a priori* (before the analysis) included by the authors not just in the family Staphylinidae, but directly in one of the four informal subfamily groups of the family (Omaliine group for Pse-

laphidae, and Staphylinine group for Scydmaenidae)¹. After that, the analysis was limited to the framework of the corresponding informal subfamily group using a number of outgroups. An explanation of this can be found in Newton & Thayer [1995: 247–248]: “Ideally, consideration of ... the relationships of the family Pselaphidae should be done in the context of a comprehensive phylogenetic analysis of all staphylinoid beetles, since proposed sister taxa to pselaphids are scattered among members of this superfamily. The enormous size of this group ... makes such a comprehensive analysis impossible; restrictions of numbers of study taxa and compromises in analytical techniques are clearly needed. ... With the addition of *Protopselaphus*, which clearly belongs to the Omaliine Group and also shares more derived character states with pselaphids than any other taxon known to us [Newton and Thayer 1988a], we feel a *prima facie* case for restricting detailed analysis to the Omaliine Group of Lawrence and Newton [1982] is established”.

In the article of Grebennikov & Newton [2009: 277–278], the authors write: “We focus especially on two groups that have not been included in the more detailed recent studies within the Staphylinine Group mentioned in the second paragraph above: Solierinae, suggested but not yet demonstrated as a member of the group, and Scydmaenidae, whose placement has varied wildly in recent studies ...”. “The broader phylogenetic studies cited in the previous paragraph, and some recent phylogenetic studies of specific groups, have provided no suggestion of a relationship of scydmaenids to Leiodidae [Newton, 1998], Pselaphinae [Newton, Thayer, 1995], or Scaphidiinae [Leschen, Löbl, 1995], and the suggested possible relationship to the Staphylinine Group is addressed here”. “Both “families” [Silphidae and Scydmaenidae — S.K.], however, were suspected to be a part of the Staphylinine Group of subfamilies [Lawrence & Newton, 1982], which implies their origin within the rove beetle radiation and, therefore, not deserving their current “family” status”.

Thus, conclusion 1: In both articles [Newton, Thayer, 1995; Grebennikov, Newton, 2009] the inclusion of the Pselaphidae and Scydmaenidae into the Staphylinidae, or rather into one of the four informal subfamily groups of this family *is not the result of phylogenetic analysis* of staphylinomorphous beetles, but is carried out *a priori*, and moreover with little or no substantiation; the analysis is performed only to clarify the position of Pselaphidae and Scydmaenidae inside the corresponding informal subfamily group of Staphylinidae.

2. The next point author would like to draw attention to is the principles of character selection for use by these authors in their phylogenetic analysis. These approaches are declared particularly clearly in the first study. Newton and Thayer [1995, p. 277] write: “... our knowledge of additional conflicting characters not included in the present analysis and the fact that in compiling this data

¹ As suggested by Lawrence & Newton [1982: 273–274], all subfamilies of Staphylinidae are grouped into 4 informal groups (or lineages): Omaliine group, Tachyporine group, Oxyteline group and Staphylinine group.

set, we focused on characters whose patterns of variation made them potentially informative regarding the positions of *Protopselaphus* and Pselaphinae or the monophyly and composition of the Omaliine Group”.

In the author’s opinion, non-inclusion of “additional conflicting characters” when focusing on characters designed to confirm the authors’ hypothesis is methodologically incorrect and can greatly bias the results of phylogenetic analysis. Newton and Thayer themselves admit that “this bias in character selection is probably part of the reason for the less clear resolution outside the Pselaphine lineage”. At the same time, the preliminary selection of taxa for the analysis was limited in both cases to the framework of a single informal grouping of subfamilies within the Staphylinidae and several ingroups corresponding to this case. Note that in the chapter Historical review, three points of view on the relationship of Pselaphidae to different groups of Staphylinoidae are discussed. However, the analysis includes taxa according to only one of these points of view, and completely ignores other points of view; representatives of Euaesthetinae, Steninae, Leptotyphlinae, *Solierius* and Scydmaenidae are completely missing from the data matrix.

Conclusion 2. For the phylogenetic analysis, Newton & Thayer [1995] and Grebennikov & Newton [2009] used characters and taxa pre-selected according to unproved assumptions. With such an approach to the preliminary sample organization, the phylogeny estimation is doomed to be biased in advance, and the analysis performed cannot objectively resolve the question about the real relationships of the studied taxa.

3. The concept of Staphylinidae varies rather widely among different researchers. Some authors have divided the “classical” Staphylinidae into 3–6 separate families [Paulian, 1941; Jeannel, Jarrige, 1949; Coiffait, 1972; Naomi, 1985; et al.], but lately “unification” has dominated. Lawrence & Newton [1982], partly Hansen [1997], as well as Newton & Thayer [1995] and Grebennikov & Newton [2009] may be considered as representatives of this direction. They include into the Staphylinidae various groups previously considered as independent families or included in other families (e.g., Micropeplidae, Dasyceridae, etc.). Let us see what features are characterized by Staphylinidae *sensu lato*.

Newton & Thayer [1995] distinguished Staphylinidae on the basis of three apomorphies: a) wings are folded according to the “staphylinid” type, costal “gap” is present, b) intersegmental abdominal membranes in adults have “brick wall” structure and c) basal bulb (=phallobase) of aedeagus with internal musculature is present. In Grebennikov & Newton [2009], these characters were “forgotten” and instead the family was proposed to be distinguished by two other apomorphies: a) larval galea and lacinia are completely fused and b) most of the abdominal tergites (III through VII) in adults have a basal transverse keel. That is, in the two articles analyzed by us, family Staphylinidae is characterized by absolutely different characters.

In this connection, it may be pointed out that, for example, in Hansen [1997: 80] staphylinids are char-

acterized by “only one apparent apomorphy ... The abdominal tergite 3 (and subsequent tergites) lacks zones covered by bristles for wing folding”. Thus, the family searched is distinguished here by one more way, not coinciding with two previous ones. As a result, Hansen’s composition of Staphylinidae is somewhat different, as some groups are treated by this author as independent families, for example, Scaphidiidae, Empelidae, Apaticidae, and including Scydmaenidae.

It may also be noted that in one more paper Grebennikov & Newton [2012] staphylinids are also characterized by a feature (feature 105) such as the absence of antennal club in adults, which, by the way, is wholly inapplicable to very many Pselaphidae, as well as to Scydmaenidae, Euaesthetinae, Megalopinae and some others. A number of other articles on the phylogeny of Staphyliniformia or parts thereof, using both morphological and molecular data, can be pointed out. The results of these studies also varied and did not coincide with each other and with the above results, but Pselaphidae and Staphylinidae after the study of Newton & Thayer were treated in them as a single group and their relationships were no longer the subject of study here [Beutel, Leschen, 2005; Cai Ch.-Y. *et al.*, 2019; Caterino *et al.*, 2005; Korte *et al.*, 2004; McKenna *et al.*, 2015; Song *et al.*, 2021].

Conclusion 3. The family Staphylinidae *sensu lato*, into which Newton & Thayer [1995] and Grebennikov & Newton [2009] successively included Pselaphidae and Scydmaenidae, itself has no clear criteria as a taxonomic unit at present; these criteria differ drastically even in both analyzed articles.

4. However, such clear criteria do not exist not only for Staphylinidae *sensu lato*, but also for many subordinate taxa.

As already mentioned in point 1, the phylogenetic analysis in both articles is restricted to one of the four informal groups (or lineages) of Staphylinidae *sensu lato*. The monophyly of these large groups was given little or no justification for their delineation [Lawrence, Newton, 1982: 273–274]; the other major groupings within the Staphylinidae that existed at that time (e.g. Aleocharomorpha, Staphylinomorpha) were completely ignored. Further, for example, in Grebennikov & Newton [2009, fig. 14], phylogenetic analysis showed a bootstrap support of 29% for the Staphylininae group, which in fact means not only that there is no evidence of monophyly of this group, but rather the inappropriateness of separating the group to such an extent.

The characters supporting the monophyly of the Omaliine group [Newton, Thayer, 1995] will be discussed in more detail below when considering the substantive analysis. As for the lower rank taxa (mainly subfamilies and tribes) used for the analysis in this work, only 2 (!) groups (Empelinae and Pselaphinae) out of 31 were characterized by autapomorphies; all other taxa were characterized exclusively by homoplasy (see Newton & Thayer [1995], figs 56a, b). This is, however, also noted by the authors themselves [Newton, Thayer, 1995: 276]: “In contrast, among the Omaliine Group taxa outside the Pselaphine lineage, we found extensive

homoplasy and few uniquely derived characters". For the subfamily Omaliinae itself, the authors note: "The monophyly and composition of this subfamily are not entirely clear ..." and below "... even after these changes we have found only weak evidence for monophyly of Omaliinae based on the characters used" [p. 292]. As for Pselaphinae, of their six highest taxonomic groups Euplectitae, Goniaceritae and possibly Pselaphitae (as well as Batrisitae including Metopiasini, as it appears in the cited paper) are not monophyletic taxa [Chandler, 2001: 16; Kurbatov, Sabella, 2015; S.A. Kurbatov, unpublished data]; in general, the construction of the Pselaphinae taxonomic system is still very far from completion.

Conclusion 4. The analysis makes extensive use of informal groupings of staphylinid subfamilies and lower-level taxa that are not provably monophyletic and whose objective status is not recognized in phylogenetic systematics itself.

Now let's consider the analysis of Newton & Thayer [1995] in essence, and more precisely, conformity of its results to the initial hypothesis about relationships of Pselaphinae with *Protopselaphus* and in general with the Omaliine Group. The results are presented in a cladogram as a consensus tree with the characters plotted [Newton, Thayer, 1995, figs 56a, b].

A. According to the authors of the study, the Omaliine Group is characterized by the following five apomorphic characters (30, 61, 75, 92 and 11):

Character 30. *Mandibles: left mandibular apex not curled ventrad (state 0); curled ventrad forming channel for right apex (state 1)*. Having studied the data matrix of the authors themselves, we can state that the character is not an unconditional apomorphy. It has state 0 in Coryphiini, *Aphaenostemmus*, Micropeplinae, and among Pselaphinae only in Bythinoplectitae, and in other taxa it can take both states. Concerning Pselaphinae it absolutely does not agree with our data: we have studied mandibles of more than 100 genera of Pselaphinae, belonging to all their subordinate taxa of the highest level, and never met such state of this feature among them. The mandibular apex in both mandibles is always more or less in the same plane as the rest of the mandible.

Character 61. *Mesosternal-mesepisternal suture complete (membranous or solid (state 0); absent or represented at most by solid suture in posterior 1/3 (state 1)*. According to Newton & Thayer, this character is absent (state 1) in all representatives of Omaliine Group, and also in some outgroups (Figs 67–70). However, this suture is present in Faronitae (Fig. 71), and this fact is in direct contradiction with the concept of phylogeny of the group proposed by the authors, according to which Faronitae are at the base of the Pselaphinae lineage, but far from the base of the Omaliine Group. Repeated independent occurrence of this initial state of the character (peculiar according to data matrix and consensus tree to such distant groups as Trigonurinae, Oxyporinae and Tachyporini) seems to us extremely unlikely. As for all other Pselaphinae, this suture is really absent in them (Figs 72–78), but it is easily explained by its subsequent reduction, moreover, in Pselaphinae different sutures of

the mesometaventrite often disappear even in relatively closely related groups (Figs 75–76).

Character 75. *Wing: anal lobe large (>1/2 wing width), with small or no fringe (0); small (<1/2 wing width), with long fringe (1); absent (2) [ordered]*. According to the data matrix, state 0 is assigned to the outgroups, and states 1 and 2 to the Omaliine Group and Pselaphinae. However, it is obvious that the gradation of states 0 and 1 is highly subjective. In addition, in general, the decrease in the body size of beetles is accompanied by a decrease in the size of the anal wing margin with compensatory lengthening (or without it) of the fringe cilia of the posterior margin, which is a general pattern for Coleoptera (D. Fedorenko, pers. comm.). Thus, in our opinion, the phylogenetic non-obviousness of this character substantially limits its significance in the analysis performed.

Character 92. *Abdominal sternite 8 lacking anterior omaliine-type defensive gland and projection (0); with such gland, width of modified area of margin 0.2–0.5x sternite 8 width (1); with such gland, width of modified area ca. 0.1x sternite 8 width (2); with such gland, width of modified area of margin ≤ 0.06 sternite 8 width (3)*. Newton & Thayer give critical importance to this character in justifying the monophyly of the Omaliine Group. However, note that this gland is absent in Micropeplinae. As for Pselaphinae, the situation is as follows. The gland is completely absent in four of the seven highest ranking taxa of this group (Faronitae, Bythinoplectitae, Pselaphitae, Clavigeritae); it is present in Euplectitae, and in Goniaceritae; and for Batrisitae it is present only for some of the included taxa. It is important to note that the gland is absent in Faronitae, i.e. in the group occupying the very base of the phylum Pselaphinae on the consensus tree (which was previously considered the most "primitive" group of pselaphids). As Newton & Thayer [1995: 303] write "our analysis clearly shows that Faronitae is the sister group of all other Pselaphinae". In addition, according to author's data [Kurbatov, Sabella, 2008], in the tribe Tychini, the gland is present only in males and absent in females, which probably indicates the presence of another (non-protective) function of this gland. In any case, at present there are no data on the chemical composition of substances produced by this gland in Pselaphinae (see, for example, Dettner [1993]). The very structure of the gland in Pselaphinae does not quite correspond to that in representatives of Omaliine Group. Thus, we do not observe in them what Klinger [1980: 454] called "the large proximal projection" of sternite 8, and Newton & Thayer [1995: 264] — "the modified area of margin" of sternite 8. The membranous rounded reservoir in Pselaphinae (if present) is located on the even anterior margin of sternite 8, and only very rarely (e.g., in *Morana* group) may cuticular processes be located on its sides. In other words, an independent origin of the gland in some taxa of Pselaphinae is very probable. Besides, Lawrence & Newton [1982: 274] had already pointed to the presence of an "independently evolved abdominal defense gland" in each of the remaining three informal groupings

of subfamilies of Staphylinidae, which is confirmed by Newton & Thayer [1995: 283] by saying that the defensive gland of the Omaliine group "is independent of the development of defensive glands in other staphylinids, all of which appear to have occurred within individual subfamilies or in pairs of closely related subfamilies". All these facts lead to strong doubt unique origin of the abdominal gland on VIII sternite in pselaphines and in representatives of Omaliine Group. The division of this character by the authors into 4 states (depending on the width of the modified area) is extremely subjective. We believe that at present there is no reason to attach critical importance to this character when justifying the inclusion of the Pselaphinae in the Omaliine Group.

Character 11. *Ocelli on vertex present (0); absent (1)*. We do not analyze this character, as according to Newton & Thayer [1995: 254] it is "excluded from analysis, mapped onto cladogram".

Thus, of the 5 apomorphies characterizing the Omaliine Group according to the authors of the study, none of them can be correctly considered as such; at the same time, character 61 directly contradicts the assumption that the Pselaphinae belongs to this group.

B. According to the authors of the study, the Pselaphine lineage (Neophoninae, Dasycerinae, Protopselaphinae and Pselaphinae) is characterized by two apomorphies.

Character 53. *Pronotum: transverse antebasal impression absent (0); present (1)*. We prefer to call it antebasal sulcus as given by Chandler [2001]. The character matrix indicates that this sulcus is present in Euplectitae and Batrisitae, absent in Clavigeritae, and can assume that both states exist in the other four supertribes of Pselaphinae. In general, it is a very unstable character for Pselaphinae, which can take different states even in close taxa. Figs 3 and 4 illustrate pronotum of representatives of genera *Rybaxis* and *Reichenbachia* from the same subtribe Brachyglutina, which differ by presence/absence of this character. There are many such examples from different groups, for example (the first representa-

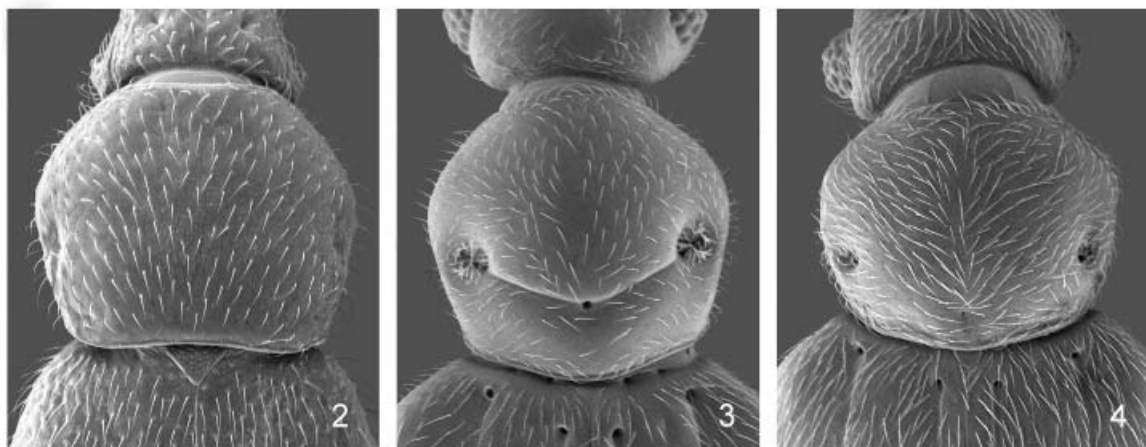
tive in a pair has this sulcus, the second one does not): *Piptoncus* / *Bibloporus*, *Saulcyella* / *Aphilia* (Euplectitae), *Atychodea* / *Tychus* (Goniaceritae), *Pselaphaulax* / *Pselaphus* (Pselaphitae), and a great many others. Among Batrisitae there are also many genera with this sulcus present (*Arthromelus* and others), completely absent (*Sathytes* and others) and a great number of genera with unclear condition of this character, especially among genera having conical tubercles or spines on the pronotal disc (e.g. *Batrisodes* and others). This sulcus in Pselaphinae, when present, can take a variety of shapes, and apparently there have been both multiple origins and multiple losses. On the other hand, it is rather difficult to agree with Newton & Thayer in their statement of presence of this sulcus in *Protopselaphus*. It is completely absent in this genus (see Fig. 2). In other words, there is no reason to be sure in the unity of origin of this character even within Pselaphinae proper, much less to consider it as providing evidence of the monophyly of the Pselaphine lineage.

Character 80. *Tarsi: number of segments 5 (0); 4 (1); 3 (2)*. The whole Pselaphine lineage is characterized by 3-segmented tarsi, including Pselaphinae proper, while one of the subgroups in the analysis, Bythinoplectitae, has the number of tarsi reduced to two. Since in this case it is a reduction, the phylogenetic significance of this character is weak.

Thus, of the two characters given by the authors of the study as apomorphies for Pselaphine lineage, only one can be considered as such, but its phylogenetic value is uncertain.

C. According to the authors of the study Pselaphinae + *Protopselaphus* (Protopselaphinae) are characterized by eight apomorphies.

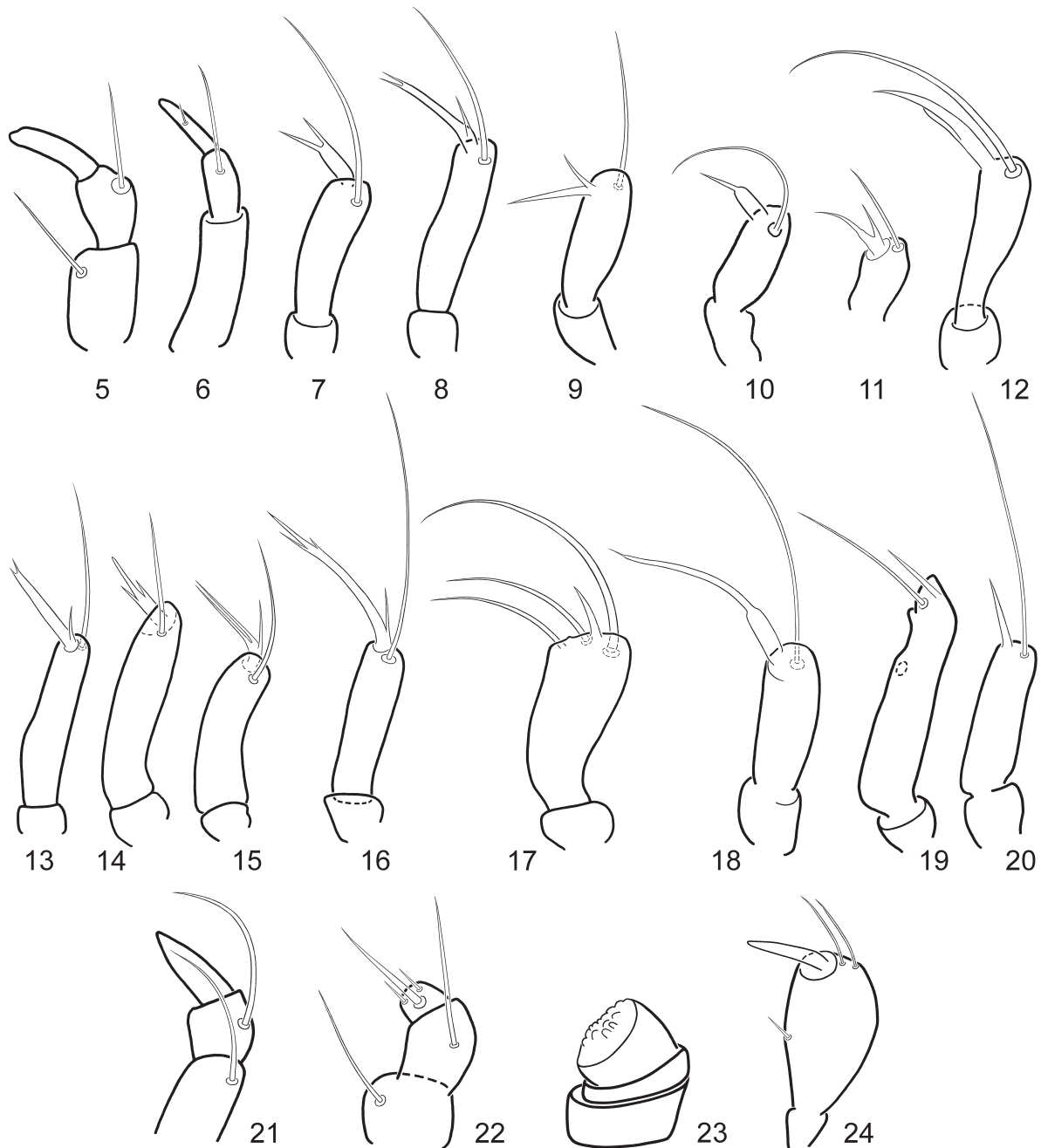
Character 21. *Connection between ends of tentorial bridge and anterior portion of tentorium present at least internally (0); absent (externally and internally) (1)*. Condition (1) is a reduction, so this character has weak phylogenetic significance.



Figs 2–4. Pronotum, dorsal view: 2 — *Protopselaphus* sp.; 3 — *Rybaxis nigrescens*; 4 — *Reichenbachia nigriventris*.
Рис. 2–4. Переднеспинка.

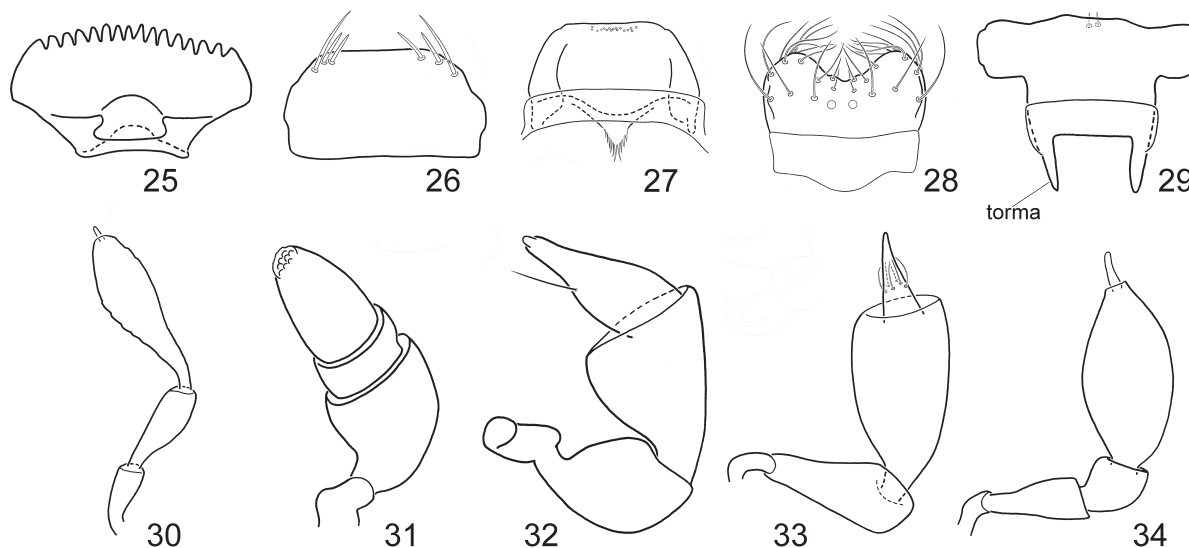
Character 46. *Labium: palp with segment 3 normal, similar to 1 and 2 (0); reduced, button like, with large apical hyaline process (1); represented only by elongate hyaline process (2) [ordered].* The character encoded in this way is completely misrepresented in the data matrix,

where state 1 is listed for Dasycerinae and state 2 is listed for Protopselaphinae and all higher taxa of Pselaphinae. In fact, Dasycerinae, Protopselaphinae, and Faronitae are characterized by state 0, Euplectitae and Batrisitae by state 1, Goniaceritae by states 1, 2 and Pselaphitae by



Figs 5–24. Labial palpi: 5 — *Faronidius africanus*; 6 — *Sagola laminata*; 7 — *Plectophloeus fischeri*; 8 — *Pteracmidius bicaudatus*; 9 — *Mirellus sulcicollis*; 10 — *Philoscotus rostratus*; 11 — *Zethopsus* sp.; 12 — *Thaumastocephalus* sp.; 13 — *Ambicocerus kaszabi*; 14 — *Hypochroeus humeralis*; 15 — *Proterus elenae*; 16 — *Brachygluta nodosa*; 17 — *Vadonites camerunensis*; 18 — *Circocerus batristoides*; 19 — *Holozodus raffrayi*; 20 — *Pselaphaulax dresdensis*; 21 — *Protopselaphus* sp.; 22 — *Dasycerus sulcatus*; 23 — *Micropeplus porcatus*; 24 — *Euaesthetus ruficapillus*.

Рис. 5–24. Нижнегубные щупики.



Figs 25–34. Labrum (25–29) and maxillary palpi (30–34): 25, 30 — *Euaesthetus ruficapillus*; 26, 31 — *Micropeplus porcatus*; 27, 32 — *Dasyce-
 rus sulcatus*; 28, 33 — *Protopselaphus* sp.; 29, 34 — *Faronus siculus*.
Рис. 25–34. Верхняя губа (25–29) и нижнечелюстные щупики (30–34).

state 2 (see Figs 5–24). For Clavigeritae this character has not been studied by us and its status is unknown.

Character 47. *Labium: palp with sensillum at or on base of segment 3 absent (0); present (1)*. It is absolutely unclear why on the consensus tree this character is indicated as an apomorphy for Pselaphinae + Protopselaphinae. In the data matrix of the authors, state 1 is indicated only for all higher taxa of Pselaphinae except Clavigeritae, whereas for Protopselaphinae (and for all other taxa used in the analysis) state 0 is indicated, which, incidentally, agrees with their own figure 5. In fact, state 0 is indeed characteristic for Protopselaphinae but also for Faronitae, whereas Euplectitae, Batrisitae, Goniaceritae, and Pselaphitae have state 1 (see Figs 5–24). For Clavigeritae the state of this character is unknown to us. It should be noted here that it is more correct to speak not about a sensillum, but about the process of the 3rd segment, which does not have the mode of attachment characteristic for sensillae, which is clearly seen on preparations.

Character 52. *Pronotum: without lateral subbasal impression backed by internal ridges (0); with two lateral subbasal impressions, each backed by internal vertical ridge (1)*. The state 1 of character thus formulated, which is characteristic of *Protopselaphus*, is not applicable to Pselaphinae (Figs 2–4 and all photos of general view of Pselaphinae), and thus it is not clear whether this absence is a reduction, or another character state, or whether these impressions (lateral antebasal foveae, according to nomenclature of Chandler [2001]) are independent structures in both taxa.

Character 56. *Procoxal fissure broad, trochantin clearly exposed in ventrolateral view (0); fissure very narrow, trochantin barely visible in ventrolateral view (1); fissure closed, trochantin completely concealed in ven-*

trotilateral view (2) [ordered]. There is no question about this character.

Character 63. *Mesopleural sulcus (and therefore epimeron) distinct at least adjacent to coxa, mesepimeron visibly reaching coxal cavity in ventrolateral view (0); sulcus distinct at least adjacent to coxa, contact between mesepimeron and coxal cavity not visible in ventrolateral view (1); sulcus absent (2) [ordered]*. The character is not quite clear to us.

Character 64. *Mesotrochantin exposed (0); concealed (1)*. There is no question about this character.

Character 72. *Elytron: internal surface latero-apically without parallel lamellae (though possibly with fine teeth) (0); latero-apically with patch of fine imbricate longitudinal lamellae (1)*. These “lamellae” are indeed present on the internal surface of elytra in *Protopselaphus*. In data matrix they are also indicated as present in almost all higher taxa of Pselaphinae (except Batrisitae and for some Clavigeritae), but after review of preparations of more than a hundred genera we did not find such a structure in any of the specimens examined.

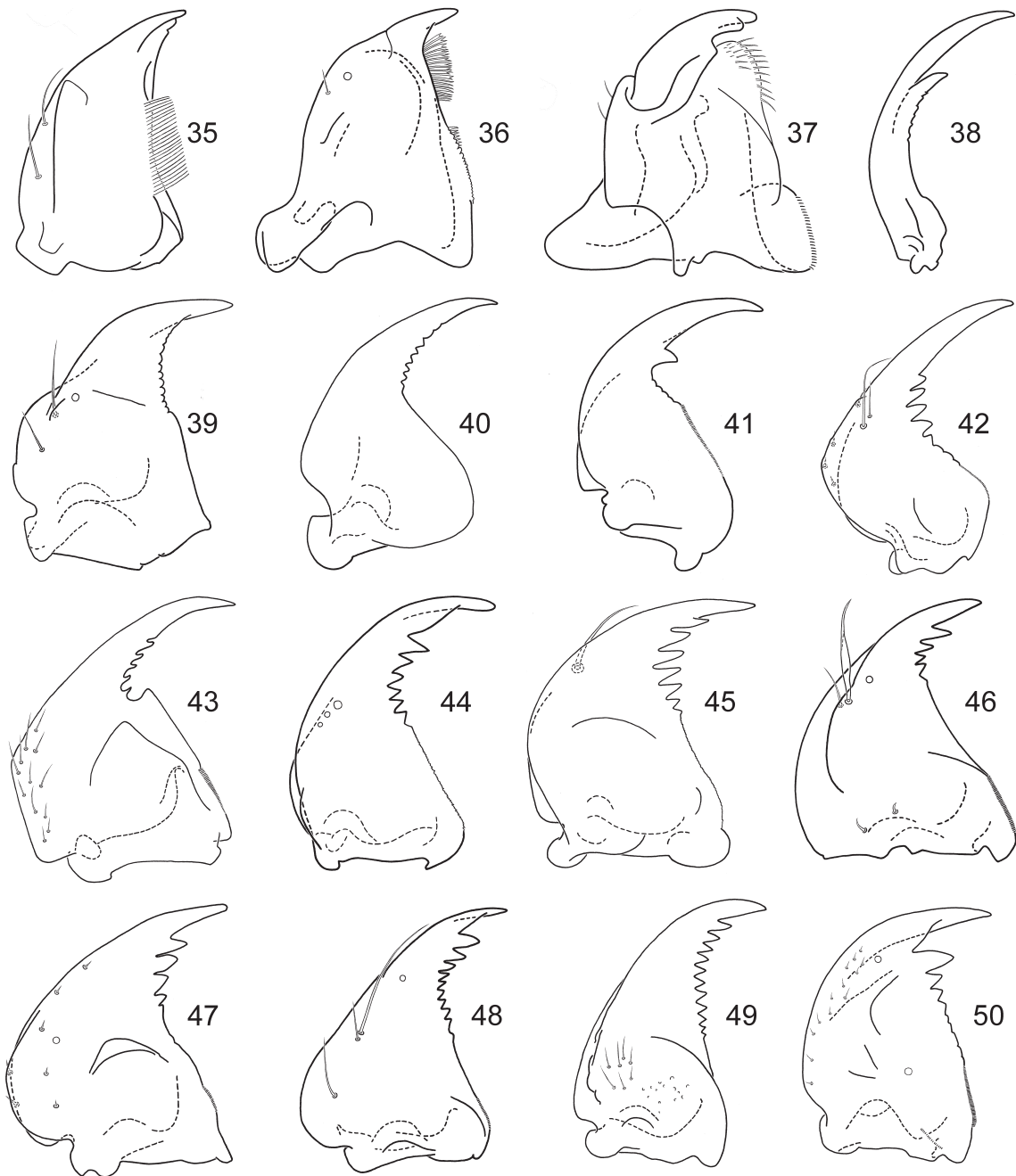
Thus, of the eight characters noted by the authors of the study as apomorphies for (Protopselaphinae + Pselaphinae), four are incorrectly coded and thus incorrectly used in the analysis, and one is a reduction and its phylogenetic significance is weak.

Among the array of other characters (both apomorphies and homoplasies) involved in the analysis, a substantial number of them also have incorrect or questionable interpretations, erroneous coding, unproven homologies, etc.

In general, the initial thesis of Newton & Thayer that *Protopselaphus* is “most similar to Pselaphidae in comparison with any other taxon known to us” is not

very understandable. Besides the already noted serious differences, unlike Pselaphinae, *Protopselaphus* completely lacks a foveal system of the ventral side of body, which is present, for example, in Dasycerinae (Figs 67–68, 71–78); the meso- and metaventrite of *Protopselaphus* has a different structure and does

not form closed mesocoxal cavities, as it exists in all Pselaphinae, as well as for example in Dasycerinae and Micropeplinae (cp. Fig. 67 with Figs 68–78). As for mouth parts (still understudied in systematics of this group), unlike Pselaphinae, *Protopselaphus* a) lacks tormae of the labrum (Figs 28–29, 84–85, 87–88),

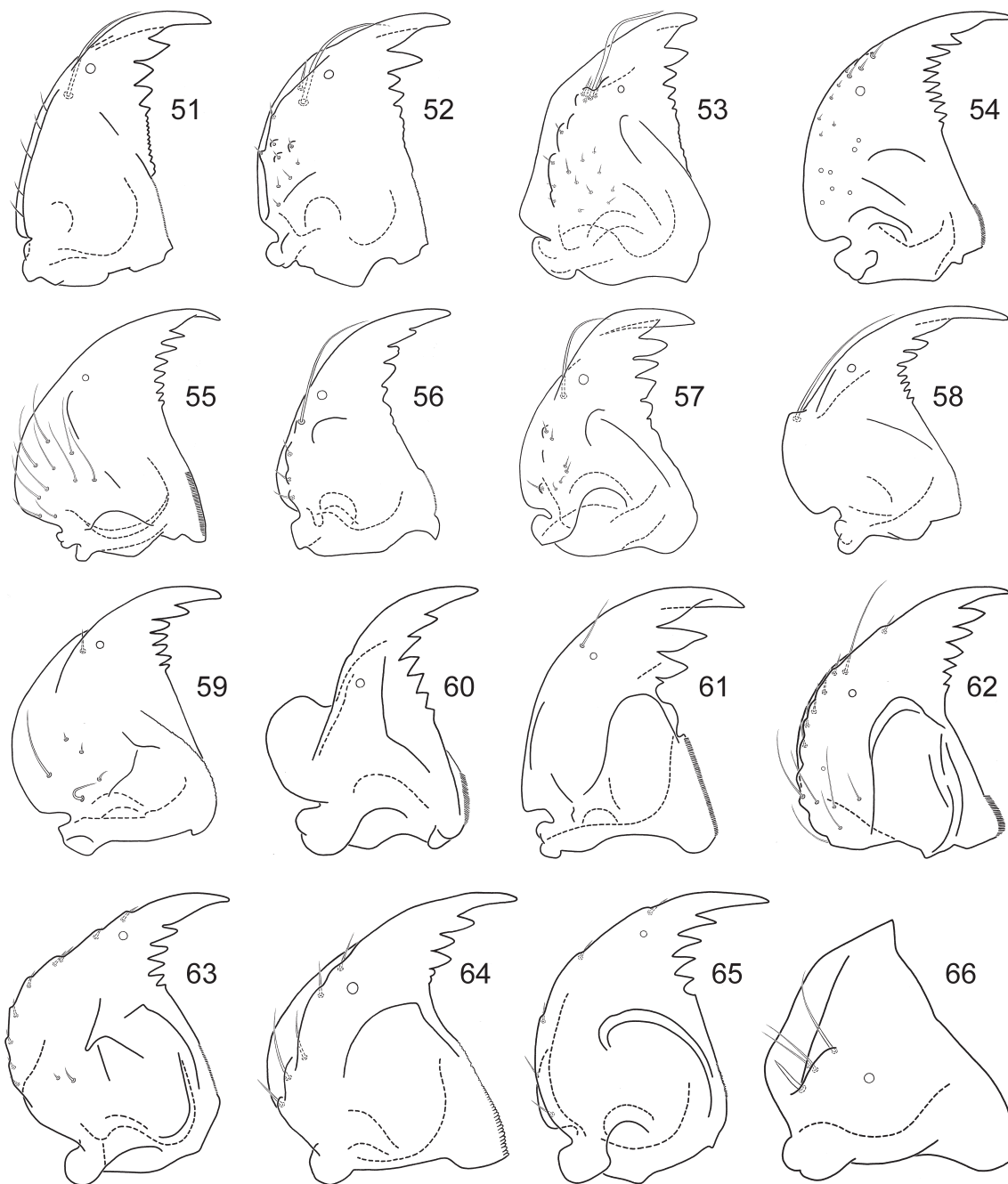


Figs 35–50. Mandibles: 35 — *Protopselaphus* sp.; 36 — *Dasycerus crenatus*; 37 — *Micropeplus porcatus*; 38 — *Euaesthetus ruficapillus*; 39 — *Faronus siculus*; 40 — *Sebaga notonoda*; 41 — *Octomicrus longulus*; 42 — *Leptoplectus perperus*; 43 — *Megalocarpus mirus*; 44 — *Philoscotus rostratus*; 45 — *Piptoncus duplex*; 46 — *Imirus lavagnei*; 47 — *Pygoxyon bythiniforme*; 48 — *Thaumastocephalus* sp.; 49 — *Metopiellus hirtus*; 50 — *Proterus elenae*.

Рис. 35–50. Мандибулы.

b) the configuration of the maxillary palpi is different (rather similar to Scydmaenidae), namely, their 3rd segment, or palpomere is the largest, while to the contrary the 4th one is very small, cone-shaped, and without an apical projection (palpal cone). Whereas in Pselaphinae the proportions of these segments are re-

versed, with very rare exceptions and typically the 4th segment is provided with a palpal cone (Figs 33–34, 101–103, 112–115), c) there is a well developed prosthema of the mandibles, which is lacking in Pselaphinae (Figs 35 and 39–66). In fact, the structure of the mouth parts determines the type of feeding behavior and, ac-



Figs 51–66. Mandibles: 51 — *Arthmius sabomba*; 52 — *Batrisoplilus raffrayi*; 53 — *Batrisus sibiricus*; 54 — *Barada mucronata*; 55 — *Harmophorus* sp.; 56 — *Natyleurus gibbicollis*; 57 — *Batraxis splendida*; 58 — *Bryaxis ussuriensis*; 59 — *Prespelea quirsfeldi*; 60 — *Barrosellus* sp.; 61 — *Mestogaster Barbieri*; 62 — *Phalepsus* sp.; 63 — *Holozodus raffrayi*; 64 — *Tmesiphorus carinatus*; 65 — *Pselaphaulax dresdensis*; 66 — *Claviger testaceus*.

Рис. 51–66. Мандибулы.

cordingly, the functioning of the most different systems of the organism, affecting its fundamental properties. As an analogy, the reader may refer to the vertebrates, whose maxillary structure forms one of the most important source of characters used in their systematics.

Taking into account all of the observations above, the hypothesis about placement of the Pselaphidae in the Omaliine Group within the family Staphylinidae, in our opinion, has not been supported by any convincing evidence. It equally refers to the position of *Protopselaphus* and, in general, to the monophyly of the Omaliine Group itself in the proposed composition. The analysis is carried out with significant methodological and factual errors. However, taking into account the enormous size of the group of staphylinoid beetles and poor knowledge of their morphology, it was difficult to expect more meaningful results. If we look at the situation, for example, in such a well-studied group as vertebrates, we see that phylogenetic analysis is carried out on a very solid base. Morphological (and not only) characters of almost every taxon have been studied in great detail; the discovery of a new character or even a different interpretation of the states of a known character is already an event; homologies are reliably justified by cross-sectional methods. Therefore, the results of analysis using this kind of data can be trusted. Another matter is such a group as Staphylinidae sensu lato. For example, among Pselaphinae Newton and Thayer studied representatives of only 4 genera of Batrisitae, and in fact 3 (one of these genera — *Metopiellus* — does not belong to this group), while for the world fauna they are known about 220, and the number of undescribed genera is at least many tens more. The situation with a study of the Euplectitae is much more catastrophic; in recent revision of Australian pselaphines [Chandler, 2001] among 65 genera of this group 44 were new for science, and the total number of undescribed genera of the world fauna (at present more than 400 are known) is even difficult to estimate. At the same time, the number of characters used by Newton & Thayer is very large (more than 100), and most of them are tested for the first time at least for Pselaphinae. Homologies, interpretation of states of these characters are justified very superficially or not justified at all, illustrations are extremely insufficient (comparative ones are absent at all), and often it is not even quite clear what this is about. Of course, the inadequate study of the group cannot prevent various phylogenetic hypotheses from being put forward, but what do nomenclatural changes have to do with it?

Thus, a critical analysis of the article by Newton & Thayer [1995] showed that the authors' change of placement for the Pselaphidae in the system of staphyliniform beetles and, accordingly, of their status is very far from being resolved. The inclusion of Pselaphidae and *Protopselaphus* in the Omaliine-group did not bring us to a better understanding about what the Omaliine-group is and what the Staphylinidae are in general (taking into account also the subsequent inclusion of Scydmaenidae in the Staphylinine-group). In our opinion, a phyloge-

netic analysis of Staphyliniformia at the present state of knowledge about this group will not lead to an acceptable result. The uncertainty of information constituting the data matrix is too high. It cannot, for example, even exclude that this entire group has no common origin at all, but is in the process of "staphylinization" (analogous to the well-known trends of ornithization or mammalization), carrying an evolutionary benefit in conducting an active lifestyle in a relatively loose, soft or borehole substrate and leading to the emergence of numerous parallelisms that mask the true relationships between taxa. In the given circumstances, in our opinion, it is more productive not to try to structure an existing large taxon with unobvious monophyly, but, on the contrary, to first identify the monophyly of relatively low-level taxa, and then successively unify them into higher-level taxa, so that the monophyly of these latter is no longer in doubt. As for the taxonomic position of Pselaphinae proposed by Newton & Thayer, we treat it rather philosophically, realizing that, given the status quo, any alternative would be equally doubtful. It is our profound conviction that in any research involving taxonomy, the principle of treating doubt in favor of maintaining the status quo is most justified. This is in a sense consonant with the principle in jurisprudence "doubts are interpreted in favor of the accused". Accordingly, in spite of the high degree of non-obviousness of the conclusions of the American authors, we are still inclined in favor of keeping the name Pselaphinae as subfamily Staphylinidae at this stage, especially since we do not have our own solution of the problem of the relationships of taxa among Staphyliniformia. Therefore, we propose to consider our criticism of this study as an appeal to taxonomists to observe reasonable caution in nomenclatural interpretation of ambiguous results.

Accepted classification

Among the Pselaphinae, 6 top-level taxa (supertribes) are currently distinguished: Faronitae, Euplectitae, Batrisitae, Goniaceritae, Pselaphitae and Clavigeritae. Of these, Faronitae and Clavigeritae are not represented in the Russian Far East, although the presence of the latter is not excluded on Sakhalin and the Southern Kurils, as at least one of its representatives, *Diantiger fossulatus* Sharp, is found on the Japanese island of Hokkaido. The division into these groups obviously does not reflect the real structure of Pselaphinae, since at least Euplectitae and Goniaceritae (and possibly Pselaphitae) are clearly not monophyletic groups, as we have already written in the previous section.

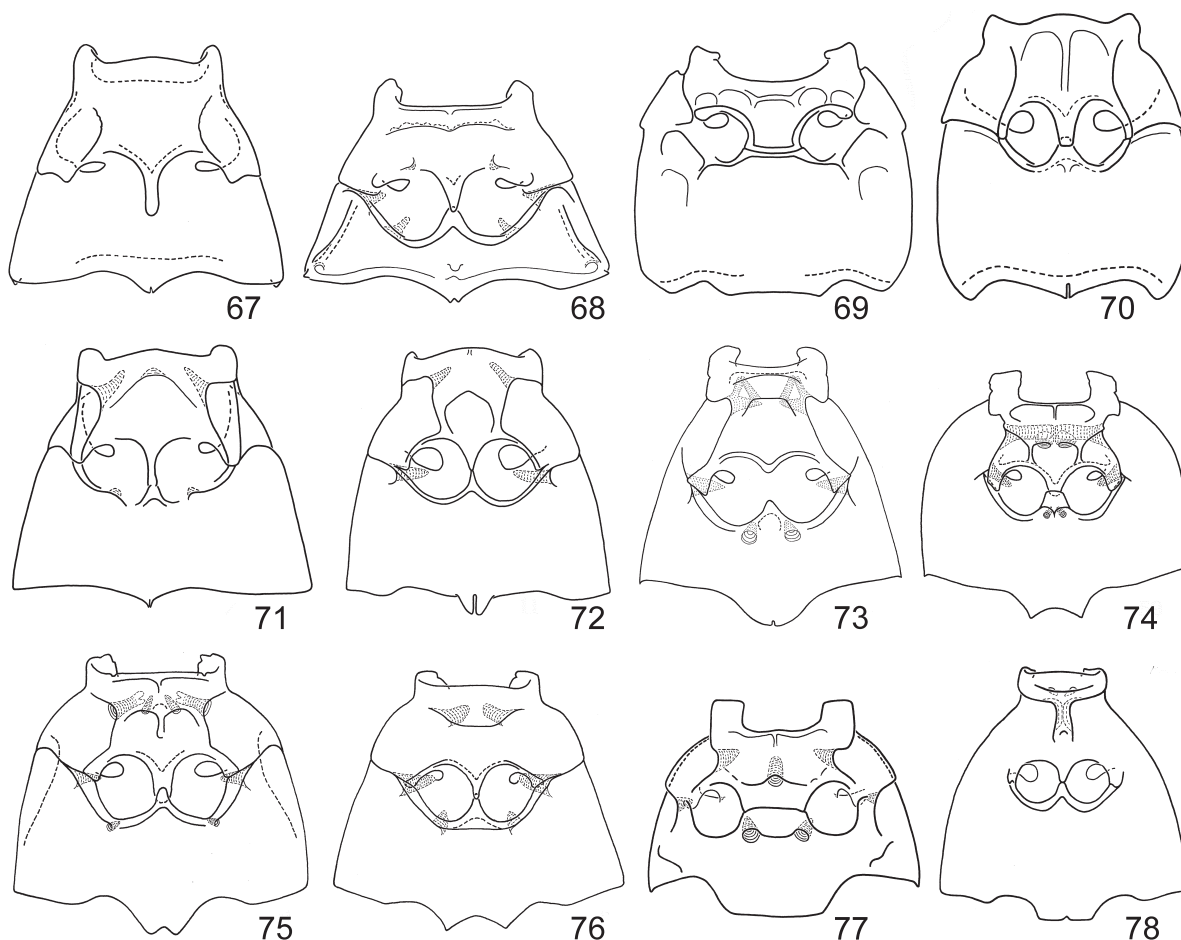
The internal structure of all 4 supertribes inhabiting in the Far East is also unsatisfactorily developed, therefore, in keys of the Pselaphinae, we prefer to operate only in categories not higher than genus. We consider that in general the system of Pselaphinae is still very far from adequate and will certainly undergo great changes in the future, starting from the number of higher taxa composing it.

Some aspects of morphology

Pselaphinae are insects of small size. Among their Far Eastern representatives, *Kuriporus creator* Kurbatov with a body length of 0.7 mm is the smallest, and the largest is *Tmesiphorus marani* Löbl, reaching 3.4 mm in length. The body shape varies from a narrow, strongly elongated, typically "staphylinoid" form, to hemispherical with all possible transitions between these two extremes. Coloration is usually more or less monochrome and ranges from light yellow-brown to black.

The basics of the general morphology of Pselaphinae were elaborated by Raffray [1908] and were developed in subsequent work by Park [1942], Jeanel [1950], and Chandler [2001]. External morphology of pselaphines with indication of taxonomically most important characters is given in Fig. 79. Perhaps the least studied features are the mouthparts, whose potential for taxonomic and phylogenetic studies is far from being realized. Some time ago, author

has already published figures of the labrum of more than 50 genera of pselaphines from many taxonomic groups [Kurbatov, 2007], and showed that its structure, for example, gives a reason to consider Batrissitae as a monophyletic group. Here there is a number of figures of mandibles (Figs 35–66) and labial palpi (Figs 5–24), which give preliminary support to the possibility of their use for taxonomic purposes and for establishment or confirmation of monophyly of separate taxa. In general, mandibles of pselaphines are slightly asymmetrical, but there are no principal differences in structure of left and right mandibles, therefore, we present the image of only one (left) mandible for each taxon. As Chandler [2001: 29] writes, mola is lacking in all pselaphines except some genera of Faronitae. In fact, it is present in representatives of very many groups studied by us, but it is often strongly reduced and visible only in the preparation under high magnification. In the figures provided it is present in almost group, but only distinct in *Megalocarpus*, *Imirus*, *Pro-*



Figs 67–78. Meso- and metaventrites: 67 — *Protopselaphus* sp.; 68 — *Dasycerus sulcatus*; 69 — *Micropeplus porcatus*; 70 — *Euaesthetus ruficapillus*; 71 — *Faronus siculus*; 72 — *Scotoplectus capellae*; 73 — *Intestinarius kuzmini*; 74 — *Batraxis splendida*; 75 — *Amorphodea lenticornis*; 76 — *Paratychnus mendax*; 77 — *Machadous teylori*; 78 — *Pselaphus heisei*.

Рис. 67–78. Мезо- и метавентриты.

terus, *Barada*, *Harmophorus*, *Barrosellus*, *Mestogaster*, *Phalepsus*, and *Tmesiphorus* (Figs 43, 46, 50, 54–55, 60–62, 64). As for the taxonomic and phylogenetic significance of the features of mandibles, which can be seen in the above figures, let us point out, for example, the following. The mandibles of the two studied representatives of Bythinoplectini, the Indian *Megalocarpus mirus* Coulon (Fig. 43) and *Zethopsus* sp. from Vietnam, have a peculiar form of the mesal margin: its flat basal half forms a distinct ledge in relation to the apical half bearing teeth. It is not excluded that a study of this character in other representatives of the tribe may well confirm monophyly of this group or some part of it. It is also interesting to note the presence of a large projection at the base of the outer margin of the mandibles in *Plagiophorus*, *Machadous*, and especially *Barrosellus* (Fig. 60), and it is apparent also in *Eichiella*, *Tetraglyptus*, and *Tetraglyptinus*, that suggests some reevaluation of the presence of the special polygonal structure of the elytral surface (sometimes partially reduced) in these genera. There are also other interesting structural features of the mandibles of other taxa.

The labial palpi seem morphologically less informative (Figs 5–24). Segment (palpomere) 1 is considerably shorter than 2, except in Faronitae; in *Zethopsus* it is completely reduced (Fig. 11). Palpomere 2 is always elongate, with long subapical bristles. Palpomere 3 is small, membranous (except Faronitae), often bristle-shaped, as pointed out by Newton & Thayer [1995]; often it is bipinnate or even tri-pinnate, and may have a small bristle-like projection at the base (see also above section Comments on the status of Pselaphinae, discussion of character 47).

The foveal system of dorsal and ventral sides of the body is described in detail by Chandler [2001]. It is shown in Fig. 79 with the nomenclature of its constituent foveae that takes into account recent changes [Lawrence *et al.*, 2011]. The variability of this foveal system (as well as the system of different sutures and keels) is partially reflected in the figures of meso- and metaventrites (Figs 71–78). Earlier this system of foveae was considered characteristic only for Pselaphinae, however, then it was found at least in *Dasycerus* (Fig. 68), some Scydmaeninae, some Endomychidae and Latridiidae, which rather testifies in favor of its independent origin in such different groups.

Abdomen of Pselaphinae (Figs 79, 188, 257–262, 314–318) usually consists of five visible tergites and five to six (females) or six to seven (males) visible sternites. However, in addition to these anteriorly there are also internally concealed more or less reduced membranous abdominal segments, and thus the first visible tergite is in fact the fourth, and the first visible sternite is the third or fourth depending on degree of advancement of the third sternite in different taxonomic groups. Numbering of morphologically true tergites and sternites following Chandler [2001] is given by Roman numerals, and visible tergites and sternites — by Arabic numerals, and thus 1st visible tergite is true IV, and 1st visible sternite is true III. This sternite III in many groups can only be seen between the hind coxae, and sometimes even there

it is poorly visible, especially if the boundary between it and sternite IV is indistinct. In the following identification keys, the morphologically true position of these abdominal segments is sometimes used, as it is shown on the figure of a pselaphine beetle (Fig. 79). In many groups, especially among “Euplectitae”, sternite IX of males can be split into 3 parts, from which median one is called penial plate (opercule in French-speaking literature), and lateral ones are more or less triangular and sometimes can be poorly visible (Figs 79, 98, 202, 315, 317–318, 344). Rarely (for example, in *Euplectus* and its close genera, and also in *Natypleurus*, *Nedarassus*, *Apoplectus* and some others) sternite IX is divided only into 2 triangular parts (Fig. 97). This sternite at the abdominal apex can also be entire, not divided (Fig. 259).

Jeannel attached great importance to the localization of the secondary sexual characters of males, having described many genera of Pselaphinae solely on this basis, especially among the Batrisitae. For most of such cases, if there are no other non-sex-related characters that are used to separate genera, then they can be no more than a group of species; otherwise, such an approach leads to many misunderstandings. For example, in the author's collection, among a large number of undescribed Batrisitae from East Asia, there are many of specimens, which, following Jeannel, should belong to two, or even to three genera at the same time according to the different position of their secondary sexual characters!

Geographical distribution

This paper adopts a relatively recently published scheme of zoogeographic division of the globe [Kryzhanovsky, 2002]. In favor of adopting this system is the fact that it is based on the study of insect distributions. According to the author of this scheme (p. 7), the distribution of insects “is noticeably more similar to the distribution of flowering plants than to such mobile groups of higher vertebrates as birds and many groups of mammals, which served as the main source material for the classical schemes of zoogeographic zoning”.

The majority of pselaphine species of the Far East (50 species) belong to endemics of the Stenopean sub-region of the East Asian region, i.e. a part of the land area, which includes territories adjacent to the middle reaches of the Amur River about as far as the city of Khabarovsk, Primorsky Krai (or Primorye), the Korean Peninsula except for its southern part, North-Eastern and Northern China, the south of Sakhalin and the Kuril Islands, Hokkaido Island and, probably, the northernmost part of Honshu Island. Other names used in the literature to refer to this area are Manchurian and Palaearctic sub-regions. Two of the three provinces that make up this sub-region, namely the Priamurye and Sakhalin-Hokkaido provinces, are also located in the Russian Far East. The Priamurye Province includes the continental part, and the Sakhalin-Hokkaido Province includes the island part of the Stenopean sub-region.

The following 30 species can be classified as endemics of the Priamurye province: *Euplectus epidemus*,

E. puncticollis, *E. gravis*, *E. domefactus*, *Leptoplectus pumilio*, *L. falcifer*, *Forinus macer*, *Bibloporus ferenarius*, *Piptoncus duplex duplex*, *Tiliactus properus*, *Ramussia parabile*, *Batrisodes tichomirovae*, *B. singularis*, *B. tornatilis*, *Dendrolasiophilus subitus*, *Batriscenellus admonitor*, *Bryaxis asciicornis*, *B. sichotensis*, *B. ussuriensis*, *B. validicornites*, *B. amurensis*, *B. testatus*, *Rybaxis pinguis*, *Rybaxis zelotypus*, *Reichenbachia commutabilis*, *Tainochus exiguus*, *Tmesiphorus marani*, *T. improvisus*, *Ctenisodes mroczkowskii*, *Pselaphus belovi*.

The species *Euplectus rubicundus*, *E. doryphorus*, *Leptoplectus solivagus*, *Leptoplectus perperus*, *Labroplectus occultus*, *L. depositor*, *Forinus secundus*, *Bibloporus pubens*, *B. neglectus*, *Ramussia captiosum*, *R. lovtsovae*, *R. svetlanae*, *Batrisodes vargus*, *B. cornutus* and *Batraxis kawaharai* should be considered endemic to the Sakhalin-Hokkaido province.

The distribution of the following five species covers the territory of both provinces: *Euplectus gibbipalpis*, *Leptoplectus similis*, *Bibloporus ponderosus*, *Batriscenellus vicarius*, *Tyrodes segrex*.

The species *Bryaxis koltzei*, *Rybaxis lamellifer*, *Stipesa rudis*, and *Tyrachus nitidus* have a similar distribution, which, however, also partially covers the east of the Orthrian, or Japanese-Chinese, subregion. The species *Batrisis sibiricus* has an even wider, East Asian, distribution, occurring in Priamurye, Primorye and the Korean Peninsula, and was also found by the author in southwestern China in Sichuan Province (see page 342).

A number of species occur in the Southern Kurils and the Japanese Archipelago, sometimes reaching Shikoku Island, namely: *Piptoncus duplex sobrinus*, *Kuriporus creator*, *Batrisis politus*, *Batrisodes harmandi*, *Basitrodes vestitus*, *Batriscenellus fallax*, *Tychobythinus aino*, *Bryaxis humilis*, *B. japonicus*, *B. extremalis*, *Trissemus alienus*, *Rybaxis nigrescens*, *R. princeps*, *Tainochus imperator*, *Tychus dichotomus*, *Lasinus micado*.

Two species are distributed both in the Primorye province and to the north, in the Angara-Okhotsk sector of the East Asia. These include *Euplectus rutilans* and *Pselaphaulax shaman*.

The following species can be considered as transpalearctic with a European-North Asian distribution: *Euplectus signatus*, *Euplectus mutator*, *Bibloporus bicolor*, *Tyrus mucronatus*, *Pselaphus heisei*. The only Holarctic species is *Euplectus karstenii*. *Euplectus piceus* (Europe, Caucasus, Primorye and Southern Kurils), *Euplectus punctatus* (Europe, Siberia and Southern Kurils), *Bibloporus minutus* (Middle Europe and Southern Primorye), and *Saulcyella schmidtii* (east of Middle Europe, Amur Region, Khabarovsk and Primorski Krai, Sakhalin and Southern Kurils) have differently disjunct areas. *Batrisodes pruinosus* is known from single specimens from Tibet (Amdo), Mongolia (Eastern Aimak), and Southern Primorye. Thus, it can be clearly seen that the fauna of Pselaphinae of the Russian Far East is mainly composed of East Asian elements (73 species), while the connections with Western Palearctic are much weaker (9 species). Only 1 species, *Ctenisodes*

mroczkowskii, belongs to the genus, 19 species of which inhabit the Nearctic and the Neotropics.

Biotope distribution

Far Eastern pselaphines are found in various habitat types, which we very conditionally subdivide into: near water, near thermals, in forest litter, in various plant remains, in moss on trunks of living trees, in dead wood, and in ant nests. Almost two dozen species are associated with water. These are the three species of the genus *Batriscenellus*, *Bryaxis asciicornis*, *B. extremalis*, *B. humilis*, *B. japonicus*, *B. sichotensis*, all species of *Rybaxis* (except *R. pinguis*), *Reichenbachia commutabilis*, *Trissemus alienus*, *Pselaphaulax shaman* and sometimes *Pselaphus heisei*. It is interesting to note that the species *Batriscenellus vicarius* and *Batriscenellus admonitor* have overlapping ranges in the southern Sikhote-Alin range, but are separated biotopically: the former occurs near flowing streams and small rivers, while the latter inhabits the banks of standing pools of water. No member of Pselaphinae from the Russian Far East has yet been found in plant remains (including marine macroalgae) on the oceanic coast.

Four species, *Tychobythinus aino*, *Tychus dichotomus*, *Tainochus imperator* and *Lasinus micado*, inhabiting Kunashir, are found only near thermals or along the shores of hot springs. Apparently, these species, which are also widespread in Japan, can survive only in thermal areas at the northern limit of their ranges. As for *Lasinus micado*, it is closely associated with the substrate formed by fallen decaying fronds around large ferns. According to the author's observations such connection with ferns is clearly traced almost in all representatives of genera belonging to the so-called *Pselaphodes* complex of genera (sensu Hlaváč [2002]) throughout their range from central China to Java and Kalimantan.

Nine species live in forest litter. These include *Leptoplectus solivagus*, *Ramussia svetlanae*, *Bryaxis amurensis*, *B. humilis*, *B. koltzei*, *B. testatus*, *B. ussuriensis*, *B. validicornites*, and *Tainochus exiguus*. The first two are known only from the holotype, so it cannot be precluded that they were collected in an uncharacteristic habitat.

Two species, *Ctenisodes mroczkowskii* and *Stipesa rudis*, inhabit the extreme south of Primorye, and are found in plant remains among stones in the more or less treeless areas in the relatively xerophilous conditions of the southern slopes.

One species, *Tyrodes segrex*, found both in the south of Primorsky Krai and on Kunashir recorded only among non-cushion mosses on trunks of living trees. It seems that, in general, representatives of this East Asian genus are associated with this habitat type. In any case, 4 undetermined species of this genus were collected by the author in similar conditions in the Chinese provinces of Hubei and Sichuan, Central Laos, and West Java.

Several species are associated with ants of the genus *Lasius*: these include *Batrisis sibiricus*, *Batrisis politus*, *Dendrolasiophilus subitus*, *Batraxis kawaharai*, and possibly *Batrisodes cornutus* and *Tmesiphorus marani*.

Table 1. Occurrence of xylobiont Pselaphinae in dead wood*.

Таблица 1. Встречаемость ксилобионтных Pselaphinae в мертвой древесине.

	In conifers, %	In deciduous, %	Picea	Pinus	Abies	Ulmus	Quercus	Betula	Alnus	Carpinus	Tilia	Salix	Populus	Acer	Phellodendron	Fraxinus
<i>Euplectus epidemus</i>	12	88			+	+			+		+					
<i>E. rubicundus</i>	25	75			+			+	+					+		
<i>E. piceus</i>	82	18	+	+	+		+	+		+	+					
<i>E. rutilans</i>	100	0	+		+											
<i>E. puncticollis</i>	88	12		+	+						+					
<i>E. punctatus</i>	36	64			+	+	+	+	+					+		
<i>E. gibbipalpis</i>	17	83			+		+	+	+		+		+	+		
<i>E. gravis</i>	100	0		+	+											
<i>E. karstenii</i>	17	83			+	+	+	+	+		+		+	+		
<i>E. domefactus</i>	24	76			+	+		+	+		+	+	+			+
<i>E. doryphorus</i>	46	54	+		+			+	+							
<i>Leptoplectus perperus</i>	49	51			+			+	+							
<i>L. similis</i>	15	85	+		+			+			+			+		+
<i>L. pumilio</i>	0	100									+					
<i>L. falcifer</i>	—	—			+						+					
<i>Labropectus occultus</i>	20	80			+			+	+							
<i>L. depositor</i>	100	0			+											
<i>Forinus macer</i>	—	—			+											
<i>F. secundus</i>	100	0			+											
<i>Bibloporus bicolor</i>	63	37		+	+		+	+	+		+	+				
<i>B. minutus</i>	0	100						+				+				
<i>B. ponderosus</i>	22	78			+		+	+	+		+	+		+	+	
<i>B. pubens</i>	42	58			+			+	+							
<i>B. neglectus</i>	44	56			+			+								
<i>Piptoncus duplex duplex</i>	9	91			+	+		+	+		+		+	+	+	
<i>P. duplex sobrinus</i>	17	83			+			+	+					+	+	
<i>Kuriporus creator</i>	72	28	+		+			+	+							
<i>Saulcyella schmidtii</i>	18	82		+	+	+	+	+	+		+		+	+	+	+
<i>Tiliactus properus</i>	2	98				+			+		+			+		
<i>Ramussia parabile</i>	58	42		+	+	+	+	+	+		+		+	+		+
<i>R. captiosum</i>	100	0	+		+											
<i>R. lovtsovae</i>	100	0	+													
<i>Batrisodes vargus</i>	—	—						+	+							
<i>B. singularis</i>	0	100									+					
<i>B. pruinus</i>	—	—									+					
<i>B. tichomirovae</i>	53	47		+	+	+	+	+	+		+		+	+		
<i>B. tornatilis</i>	7	93			+		+				+					
<i>B. harmandi</i>	29	71			+			+	+							
<i>B. cornutus</i>	25	75			+			+								+
<i>Rybaxis pinguis</i>	66	34			+				+		+					
<i>Tyrus mucronatus</i>	7	93						+		+	+		+	+		+
Total species			7	6	33	9	10	25	22	2	21	5	8	12	3	7

* The preference of different pselaphines species for coniferous or deciduous wood is presented in the first two columns of the table. It is expressed as a percentage of the number of specimens of a particular species collected in coniferous or deciduous wood alone to the total number of specimens of that species collected in wood, and is hereafter referred to as the "preference coefficient". This coefficient was not calculated for species known from fewer than four specimens; for such species, a "—" is shown in the appropriate places in the table.

Table 2. Some data on population density and biomass of xylobiont Pselaphinae of the Russian Far East.**Таблица 2.** Некоторые данные о плотности популяции и биомассе ксилобионтных Pselaphinae российского Дальнего Востока.

Tree species	Pselaphinae species	Number of specimens in the sample	Unit weight (mg)	Population density (in 1 dm ³)	Biomass (mg/dm ³)
Alder	<i>Euplectus domefactus</i>	14	0.035	2.5	0.09
	<i>Labroplectus occultus</i>	7	0.02	4.7	0.09
	<i>Ramussia parabile</i>	13	0.035	3.1	0.11
Lime	<i>Leptoplectus pumilio</i>	82	0.01	6.0	0.06
Birch	<i>Piptoncus duplex duplex</i>	41	0.015	7.5	0.11
		23	0.015	9.2	0.14
Maple	<i>Tiliactus properus</i>	16	0.02	8.0	0.16
Fir	<i>Leptoplectus similis</i>	13	0.015	8.7	0.13
	<i>Euplectus puncticollis</i>	3	0.035	0.8	0.03

The Japanese species *Basitrodes vestitus* on Kunashir Island occurs in *Myrmica* nests. The species *Saulcyella schmidtii* in the European part of its range (where it is rare) usually inhabits nests of *Formica* and *Lasius* ants according to Besuchet [1974], however, in the Far East this rather common species inhabits dead wood and occurs together with *Lasius* ants only rarely.

For the species *Bibloporus ferentarius* and *Tyraphus nitidus*, there is not any collection information on their biotopic habitat at this time.

Finally, almost half of all Far Eastern pselaphines (40 species) are associated with dead wood. Table 1 shows the occurrence of different species of pselaphines in wood of different tree species. When analyzing the data in this table, it should be taken into account that, since the vast majority of pselaphines are predators, their preference is most likely determined by the physical characteristics of the wood (density, humidity, etc.), degree of degradation, and the fauna of invertebrate organisms that are potential victims of these beetles, although the influence of other factors (e.g., composition of bacterial and fungal flora) cannot be excluded.

We conditionally divided xylobiont pselaphines into 3 groups according to the preference coefficient. The first group includes 9 species with no special preference for either coniferous or deciduous wood (preference coefficient fluctuates between 30 and 70%). It includes: *Euplectus punctatus*, *E. doryphorus*, *Leptoplectus perperus*, *Bibloporus bicolor*, *B. pubens*, *B. neglectus*, *Ramussia parabile*, *Batrisodes tichomirovae*, *Rybaxis pinguis*. The second group also includes 9 species that prefer conifers and are here named as “coniferophiles” (preference coefficient above 70% in favor of conifer wood). Here are: *Euplectus piceus*, *E. rutilans*, *E. puncticollis*, *E. gravis*, *Labroplectus depositor*, *Forinus secundus*, *Kuriporus creator*, *Ramussia captiosum*, *R. lovtsovae*. In the third group we included 18 species preferring deciduous species, names here as “foliiferophiles” (preference coefficient above 70% in favor of deciduous wood), namely: *Euplectus epidemus*, *E. rubicundus*, *E. gibbipalpis*, *E. karstenii*, *E. domefactus*, *Leptoplectus similis*, *L. pumilio*, *Labroplectus occultus*, *Bibloporus minutus*, *B. ponderosus*, *Piptoncus duplex duplex*,

P. duplex sobrinus, *Saulcyella schmidtii*, *Tiliactus properus*, *Batrisodes singularis*, *B. tornatilis*, *B. harmandi*, *B. cornutus*, *Tyrus mucronatus*. It follows from these data that Far Eastern xylobiont pselaphines are clearly more attracted to deciduous wood. Such species are twice as numerous as coniferophiles, and their taxonomic diversity at the genus level is also considerably higher.

Several species were found in wood of only one particular tree species (only species known from more than three specimens are considered): *Labroplectus depositor* and *Forinus secundus* were collected in wood of *Abies holophylla*; *Ramussia lovtsovae* — in wood of *Picea jezoensis*; and *Leptoplectus pumilio* and *Batrisodes singularis* are associated with wood of *Tilia*. *Leptoplectus pumilio* shows its preference very clearly: all 162 specimens of this species were caught exclusively in linden wood.

The most species were recorded in *Abies* wood — 33 species, followed by birch, alder and linden — 25, 22 and 21 species, respectively, with the other species following with a large gap in abundance. The table does not include *Larix*, *Sorbus*, and *Syringa amurensis*; only 1–2 specimens of *Kuriporus creator*, *Euplectus doryphorus*, and *Euplectus karstenii* were respectively collected in their woods.

Euplectus puncticollis has specific requirements for wood. It was always found in mossy recumbent trunks of large-diameter coniferous trees under permanent shade.

An understanding of the population density of Pselaphinae was obtained through comparison of several xylobiont species. By comparing the volume of wood and the number of beetles captured in it, the population density per 1 dm³ of substrate was calculated. Taking into account the weight of one beetle, the total biomass of the species in 1 dm³ of substrate was calculated. Since the weight of 1 specimen is very small, it was calculated based on weighing simultaneously several dozens of specimens, not necessarily collected in the same location. The results obtained are summarized in Table 2.

The table shows that population density correlates well with beetle mass. *Ramussia parabile*, *Euplectus domefactus*, and *E. puncticollis*, which have the highest body masses, have the lowest abundance (not more than 3.1 specimens per 1 dm³ of substrate). In contrast, the

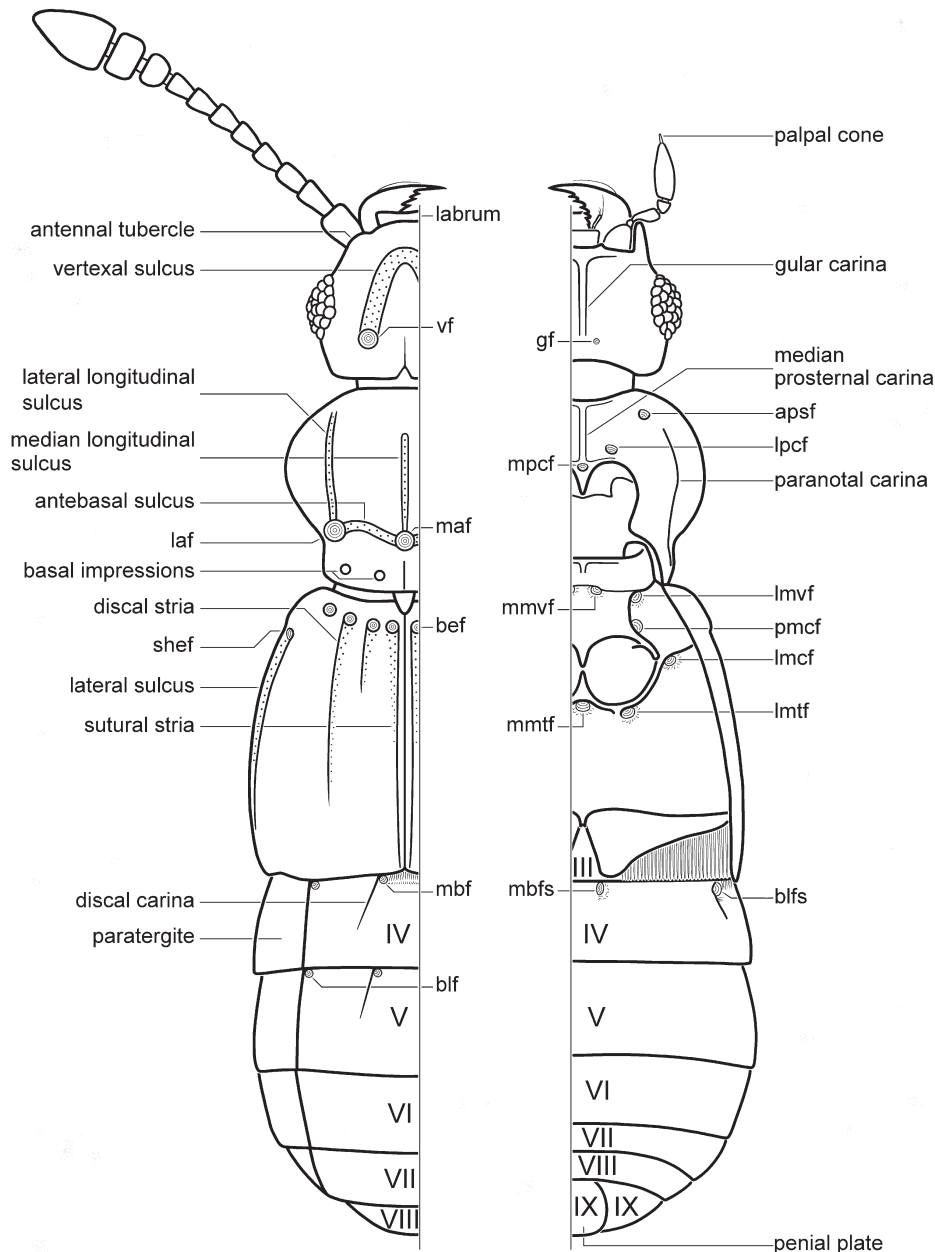


Fig. 79. Scheme of Pselaphinae with main characters used in taxonomy [based on idea of Chandler, 2001]. True morphological position of abdominal tergites and sternites indicated by Roman numerals (see Chapter "Some aspects of morphology"). Names of foveae abbreviated.

Dorsal foveae (from top to bottom): vf — vertexal foveae, or dorsal tentorial pits; maf — median antebasal fovea; laf — lateral antebasal fovea; bef — basal elytral foveae; shef — subhumeral elytral fovea; mbf — mediobasal foveae of abdominal tergites; blf — basolateral foveae of abdominal tergites. Ventral foveae (from top to bottom): gf — gular foveae, or ventral tentorial pits; apsf — anteroprostatic foveae, or notopleural foveae; lpcf — lateral procoxal foveae; mpcf — median procoxal fovea; lmvf — lateral mesoventral foveae; pmcf — promesocoxal foveae; lmcf — lateral mesocoxal fovea; lmtf — lateral metaventral foveae; mmtf — median metaventral fovea; mbfs — mediobasal foveae of abdominal sternites; blfs — basolateral foveae of abdominal sternites.

Рис. 79. Схема ошупника с основными таксономическими признаками (использована идея Чандлера, 2001). Истинное морфологическое положение тергитов и стернитов брюшка отмечено римскими цифрами (см. раздел "Some aspects of morphology"). Названия ямок сокращены.

Дорсальные ямки (сверху вниз): vf — теменные ямки, или дорсальные тенториальные ямки; maf — срединная антебазальная ямка; laf — боковая антебазальная ямка; bef — базальные ямки надкрыльев; shef — подплечевая ямка надкрылья; mbf — медиобазальные ямки тергитов брюшка; blf — базолатеральные ямки тергитов брюшка.

Вентральные ямки (сверху вниз): gf — гулярные ямки, или вентральные тенториальные ямки; apsf — передние ямки переднегруди, или нотоплевральные ямки; lpcf — боковые прококсальные ямки; mpcf — срединная прококсальная ямка; lmvf — боковые мезоventральные ямки; mmvf — срединные мезоventральные ямки; pmcf — передние мезококсальные ямки; lmcf — боковые мезококсальные ямки; lmtf — боковые метавентральные ямки; mmtf — срединная метавентральная ямка; mbfs — медиобазальные ямки стернитов брюшка; blfs — базолатеральные ямки стернитов брюшка.

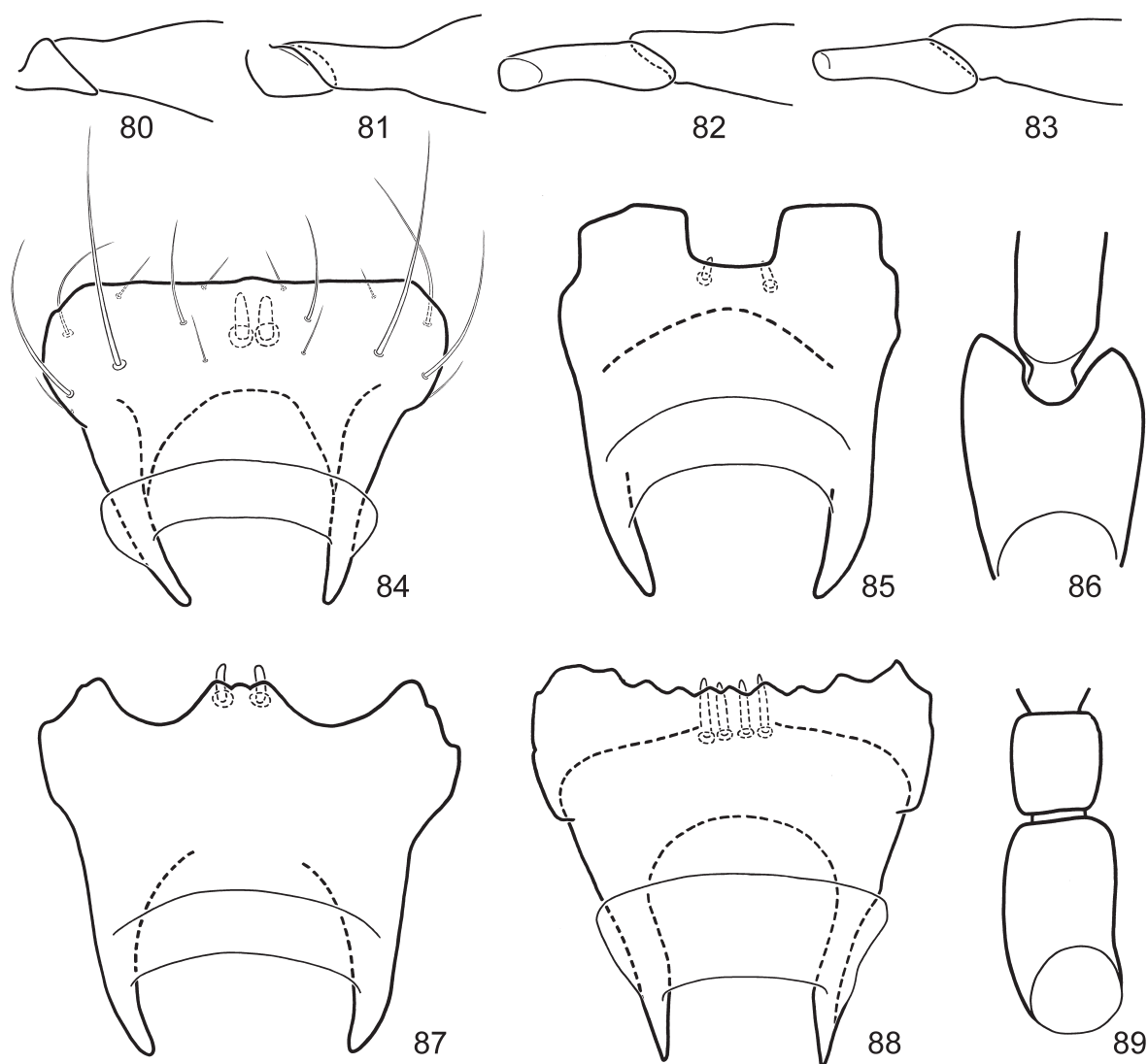
smaller species, *Leptoplectus pumilio*, *L. similis*, and *Piptoncus duplex*, reach densities of 6.0–9.2 specimens per 1 dm³ of substrate. The maximum biomass value (0.16 mg/dm³) was observed for the species *Tiliactus properus*.

Seasonality

The seasonal behavior of Far Eastern pselaphines has not been studied at all. On the basis of our own investigation, we can only generate two observations.

The species *Saulcyella schmidtii* is often found in the south of the Far East. We noticed that in the first half of

the warm period until about the middle of June males and females are found in an equal proportion. Then the males quickly disappear, and females continue to be found until at least the second half of August. From this it is possible to make an assumption that the females live much longer than the males. Such a major change in sex ratio was not observed for the other species of Pselaphinae. For *Euplectus puncticollis*, both sexes were equally present only in May–June; at later time it was never collected. This situation is similar to that of the European *E. decipiens*, which is very close related to it: in the conditions of the Moscow region it was also collected by us only in May–early June.

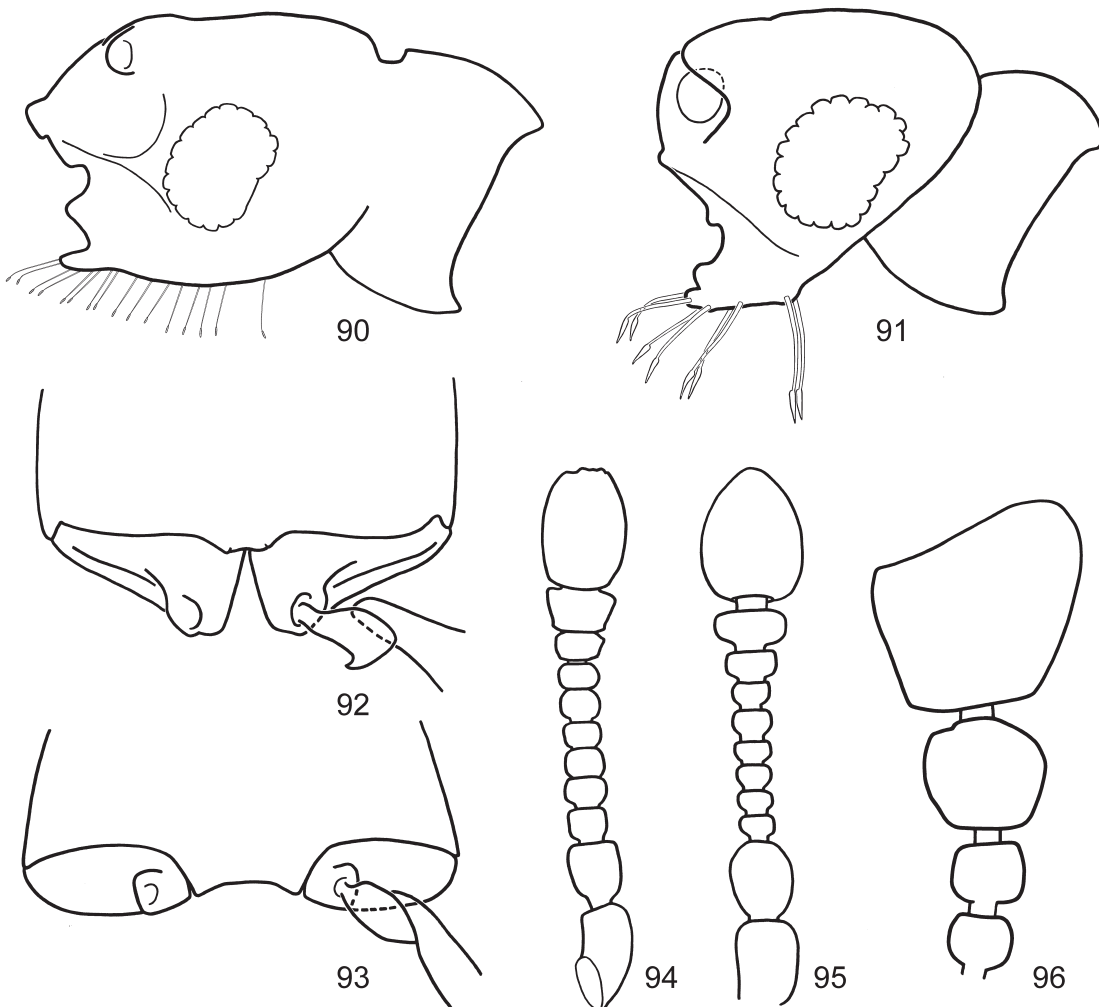


Figs 80–89. Details of Pselaphinae: 80 — *Forinus macer*; 81 — *Batraxis splendida*; 82 — *Ctenisodes mroczkowskii*; 83 — *Tyrodes segrex*; 84 — *Euplectus piceus*; 85 — *Leptoplectus perperus*; 86 — *Batriscenellus fallax*; 87 — *Labroplectus occultus*; 88 — *Batrisus sibiricus*; 89 — *Tainochus imperator*; 80–83 — protochanters; 84, 85, 87, 88 — labrum (84 — with complete chetotaxy); 86, 89 — antennal base.

Рис. 80–89. Детали строения щупиков; 80–83 — передние вертлуги; 84, 85, 87, 88 — верхняя губа (84 — с полной хетотаксией); 86, 89 — основание усика.

Key of genera of Pselaphinae of the Russian Far East

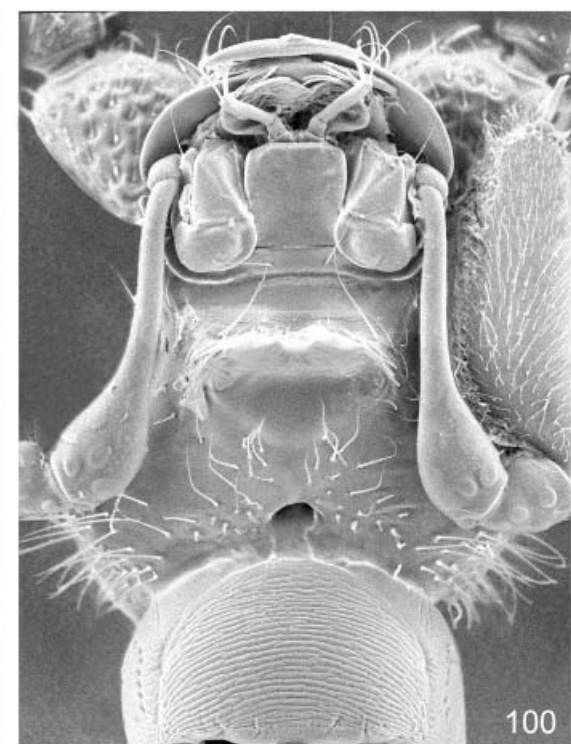
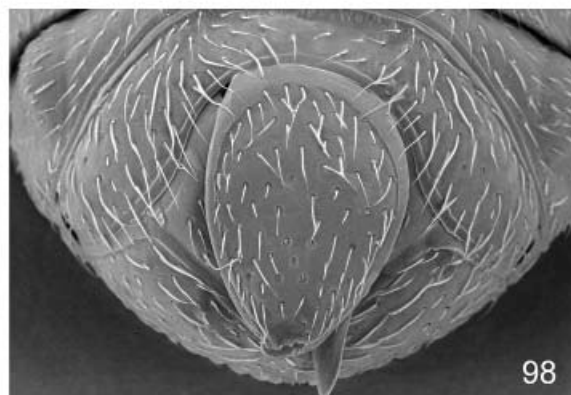
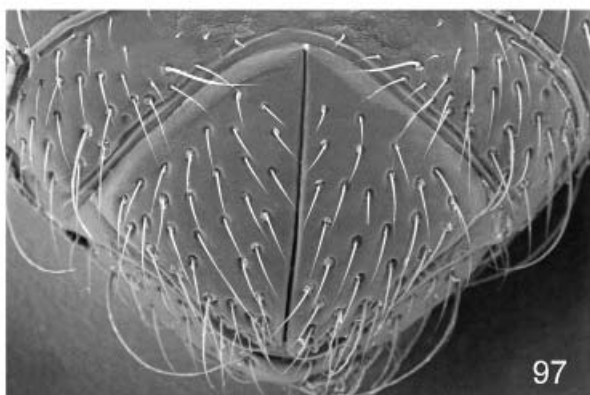
1. Trochanters 2 short, with their upper edge not longer than the line of articulation between trochanter and femur (Figs 80–81) ... **2**
 - Trochanters 2 distinctly elongate, with their upper edge significantly longer than the line of articulation between trochanter and femur and thus the base of middle femur is distant from the coxa 2 (Figs 82–83) **24**
2. Apex of antennomere 1 dorsally and ventrally distinctly notched and laterally toothed (Figs 86, 235, 252). Abdomen without paratergites. Anterior edge of labrum (epipharynx) at the middle with a row of 4 thick, specialized bristles close together (often only clearly visible in the preparation of the detached labrum) (Fig. 88) **3**
 - Apex of antennomere 1 unnotched, more or less straight (Figs 89, 95). At least abdominal tergites 1–3 laterally with paratergites. Anterior edge of labrum in the middle with at most two specialised bristles (clearly visible only in preparations) (Figs 29, 84–85, 87) **7**
3. Each elytron with one or three basal foveae. Eyes no longer than the temples when viewed laterally. Abdominal tergite 1 with pair of long outer lateral carinae, reaching the posterior margin of this segment near the posterior corners, obliquely positioned to the lateral margin of the tergite (Figs 228, 237), male abdominal tergites without secondary sexual characters **4**
 - Each elytron with two basal foveae. Eyes, at least in males, distinctly longer than the temples when viewed laterally. Abdominal tergite 1 without outer lateral carinae, male abdominal tergite 3 with secondary sexual characters (Figs 257, 259, 261) **Batriscenellus** Jeannel, 1958
4. Each elytron with one basal fovea. **Dendrolasiophilus** Nomura, 2010
 - Each elytron with three basal foveae. **5**
5. Pronotal disc with a pair of pointed conical tubercles in the basal third (Figs 229–230) **6**



Figs 90–96. Details of Pselaphinae: 90, 92 — *Ramussia parabile*; 91, 96 — *Saulcyella schmidtii*; 93 — *Trissemus alienus*; 94 — *Euplectus domefactus*; 95 — *Forinus macer*; 90, 91 — head lateral; 92, 93 — metacoxae; 94, 95 — antennae; 96 — antennal apex.

Рис. 90–96. Детали строения ошупников; 90, 91 — голова, вид сбоку; 92, 93 — задние тазики; 94, 95 — усики; 96 — вершина усика.

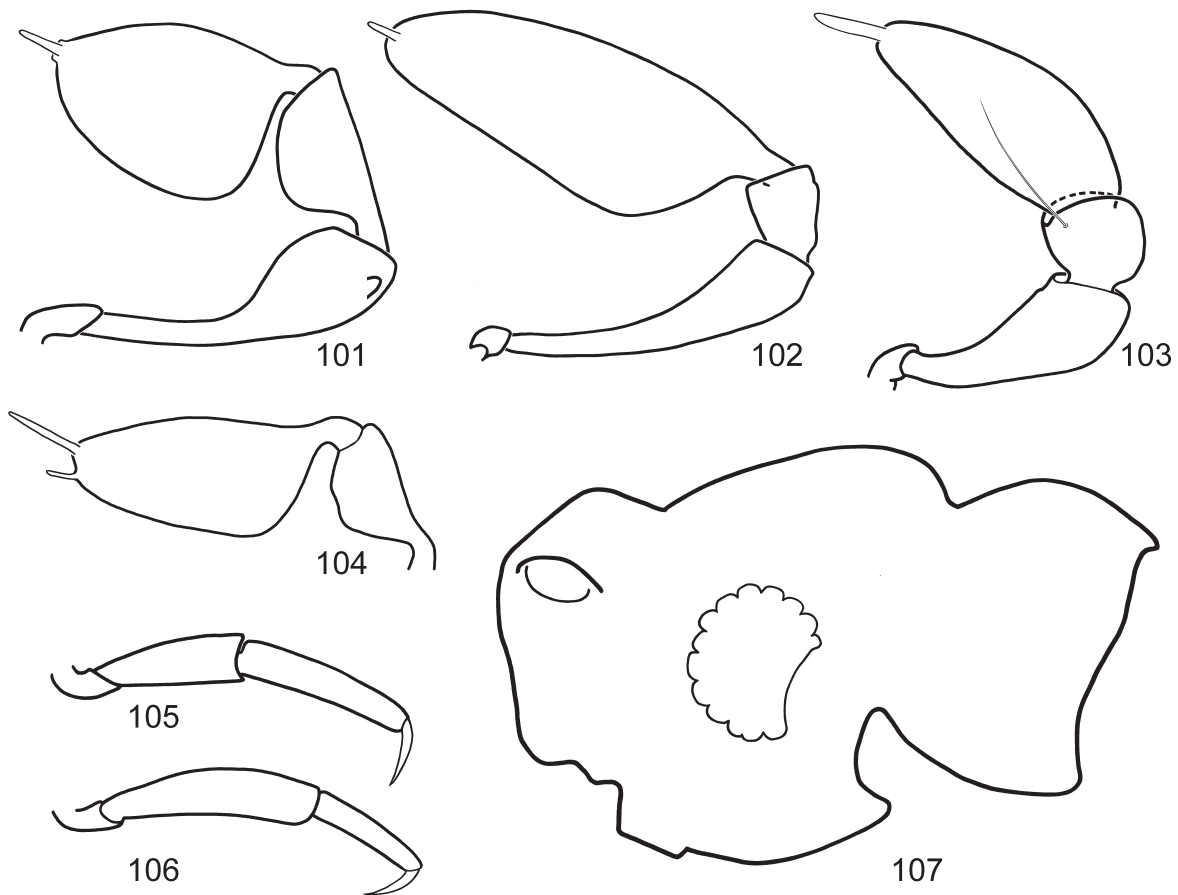
- Pronotal disc without conical tubercles *Batrisus* Aubé, 1833
- 6. Body length at most 2.6 mm. Femur 2 of male with a spine in the middle of the mesal margin (Fig. 231) (exception: *B. pruinosus* with only minute tubercle instead of spine) *Batrisodes* Reitter, 1882
- Body length at least 2.8 mm. Femur 2 of male without a spine in the middle of the mesal margin *Basitrodes* Jeannel, 1958
- 7. Coxae 3 contiguous (Fig. 92) 8
- Coxae 3 separated (Fig. 93) 17
- 8. Underside of head with more or less vertically arranged clavate setae (Figs 90–91). Abdominal tergite 4 no longer than any of the previous tergites 9
- Underside of head with normal, adjoining setae. Abdominal tergite 4 noticeably longer than any of the previous ones 14
- 9. Pronotum with lateral antebasal fovea continued forward to anterior margin as a long longitudinal sulcus; transverse antebasal sulcus entirely absent 10
- Lateral longitudinal sulcus of pronotum absent; transverse antebasal sulcus connecting median antebasal fovea of pronotum with lateral ones always present. 11
- 10. Prothorax with median prosternal carina. Two or three first visible abdominal tergites with pair of discal longitudinal carinae. Body not shorter than 1.1 mm *Bibloporus* Thomson, 1859
- Prothorax without median prosternal carina. Only first visible abdominal tergite with pair of discal longitudinal carinae. Body no longer than 0.8 mm *Kuriporus* Kurbatov, 1991
- 11. Each elytron with four longitudinal striae: one complete sutural and three shortened discal. Tergite 1 longer than 2 *Tiliactus* Kurbatov, 1992



Figs 97–100. Details of Pselaphinae: 97 — *Euplectus piceus*; 98 — *Forinus secundus*; 99 — *Rybaxis pinguis*; 100 — *Bryaxis koltzei*; 97, 98 — IX sternite male; 99, 100 — head ventral.

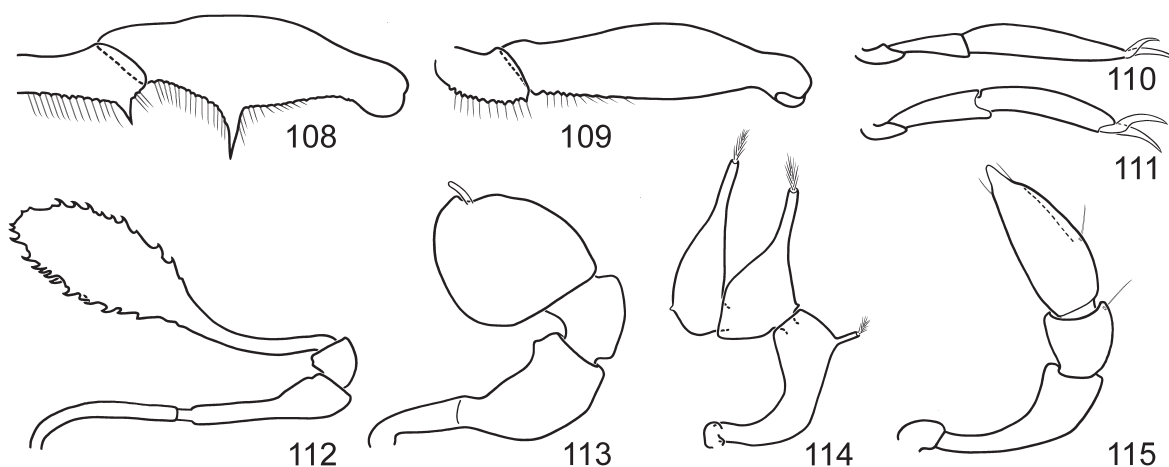
Рис. 97–100. Детали строения ощупников; 97, 98 — IX стернит самца; 99, 100 — голова, вид снизу.

- Each elytron with two longitudinal striae: one complete sutural and one shortened discal. Tergite 1 not longer than 2 **12**
- 12. Last (11th) antennomere asymmetrical, with large tubercle at the base (Fig. 96) *Saulcyella* Reitter, 1901
- Last antennomere without tubercle at the base **13**
- 13. Antennae short, at most reaching mid-length of pronotum, with rather 1-articulated club, as antennomeres 9 and 10 hardly wider than previous segments and about twice or more narrower than 11; antennomere 11 as long as the previous five, taken together. Antebasal pronotal sulcus of unequal depth and width, almost interrupted mid-length between median and lateral antebasal foveae. ♂: posterior corners of tergite 1 with a tuft of long bristles (Fig. 188) *Piptoncus* Kurbatov, 1991
- Antennae relatively long, almost reaching the posterior margin of pronotum, with rather 3-articulated club, as antennomeres 9 and especially 10 much wider than the previous ones; antennomere 11 as long as the 3 previous ones taken together (in *R. svetlanae* as long as the 4 previous ones). Antebasal pronotal sulcus of equal depth and width along its entire length between median and lateral antebasal foveae. ♂: posterior corners of tergite 1 without tuft of bristles ... *Ramussia* Kurbatov, 1991
- 14. Antennomeres 3–8 very small, each half as long as antennomere 2 and antennomeres 3–6 at least three times as short as 2 (Fig. 95). ♂: last (IX) abdominal sternite split longitudinally into three parts, of which the central one (penial plate) is large, more or less oval, and lateral are small, poorly visible triangular parts (Fig. 98) *Forinus* Kurbatov, 1991
- Antennomeres 3–8 each no more than 1.5 times narrower and twice as short as the antennomere 2 (Fig. 94). ♂: last (IX) abdominal sternite split longitudinally into two triangular parts, penial plate missing (Fig. 97). **15**
- 15. Labrum without modifications, its anterior margin more or less straight (Fig. 84) *Euplectus* Leach, 1817
- Labrum with anterior margin notched ones or twice (Figs 85, 87) **16**
- 16. Labrum deeply incised in middle of anterior margin (Fig. 85). Abdominal tergites 1 and 2 at mid-base with small transverse impression flanked by a pair of thin longitudinal discal carinae *Leptoplectus* Casey, 1908
- Labrum with two notches on anterior margin, so the middle of this margin protrudes forward (Fig. 87). Abdominal tergites 1 and 2 at mid-base with small transverse impression, but lack discal carinae on its sides *Labroplectus* Kurbatov, 1993
- 17. Maxillary palpi with 4th palpomere sharply and very strongly narrowed toward base, forming narrow “stalk” (Figs 101–102, 104), palpomere 3 and apex of palpomere 2 sometimes with small flat tubercles (Fig. 100). Underside of head without me-



Figs 101–107. Details of Pselaphinae: 101, 105 — *Tychus dichotomus*; 102, 106 — *Bryaxis japonicus*; 103 — *Batraxis splendida*; 104, 107 — *Tainochus imperator*; 101–103 — maxillary palpi; 104 — palpomeres 3 and 4 of maxillary palpus; 105–106 — protarsi; 107 — head lateral.
Рис. 101–107. Детали строения ощущников; 101–103 — нижнечелюстные щупики; 104 — 3-й и 4-й членики нижнечелюстных щупиков; 105–106 — передние лапки; 107 — голова, вид сбоку.

- dial longitudinal elevation, but in males may bear impressions or more complex structures (Figs 100, 313) 18
- 4th palpomere with broad base (Fig. 103), palpomeres 3 and 2 smooth. Underside of head in both sexes with long median longitudinal elevation (Fig. 99) 21
18. Maxillary palpi with palpomere 3 large, only slightly shorter than 4 (Figs 101, 104). Tarsal segment 2 no longer and only slightly wider than 3 (Fig. 105) 19
- Palpomere 3 small, more than three times shorter than 4 (Fig. 102). Tarsal segment 2 much longer and wider than 3 (Figs 106) 20
19. Each elytron with three basal foveae. Underside of head posteriorly with large tooth-like process directed backwards (Fig. 107). Palpomere 4 with small preapical projection in addition to the palpal cone (Fig. 104) *Tainochus* Kurbatov, 1992
- Each elytron with two basal foveae. Underside of head without process. Palpomere 4 without preapical projection, only with palpal cone (Fig. 101).....*Tychus* Leach, 1817
20. Body length at most 1.2 mm. Male: antennae without secondary sexual characters; underside of head with large compound projection (Fig. 313). *Tychobythinus* Ganglbauer, 1896
- Body length at least 1.35 mm (except *Bryaxis humilis*: 1.25–1.4 mm). Male: antennomere 2 (rarely 1 or 9) modified; underside of head without compound projections, usually with depression limited anteriorly by transverse elevation (Fig. 100) *Bryaxis* Kugelann, 1794
21. Eyes located far from posterior margin of head, eyes at least twice as short as the temples. Elytra without discal stria *Batraxis* Reitter, 1882
- Eyes not shorter than temples. Elytra with discal stria extending beyond the middle of their length 22
22. Pronotum with antebasal sulcus uniting median antebasal fovea with lateral ones (Fig. 3). Lateral elytral margin with subhumeral fovea and lateral sulcus extending backwards from it *Rybaxis* Saulcy, 1876
- Pronotum without transverse antebasal sulcus (Fig. 4). Lateral elytral margin without subhumeral fovea and lateral sulcus 23
23. Elytra with two basal foveae *Reichenbachia* Leach, 1826
- Elytra with 3 basal foveae *Trissemus* Jeannel, 1949
24. Abdominal tergite 1 at least three times as long as 2.....25
- Abdominal tergite 1 at most only slightly longer than 2, and often shorter than 28
25. Tarsomere 3 with two equal claws. Femora 1 and 2 with spine at middle of mesal margin, trochanters 1 with one and trochanters 2 with two spines along mesal margin (Fig. 108). Body length at least 3 mm *Lasinus* Sharp, 1874
- Tarsomere 3 with one claw. Trochanters 1 and 2 and femora 1 and 2 without spines (Fig. 109). Body no longer than 2 mm 26
26. Maxillary palpi very long and slender, palpomere 4 about as long as head and consists of very long and slender base and club-shaped apex (Fig. 112) 27
- Maxillary palpi rather short and thick, palpomere 4 wide, irregularly triangular, about three times shorter than head (Fig. 113) *Tyraphus* Sharp, 1874
27. Pronotum with transverse antebasal sulcus connecting median antebasal fovea with two lateral ones. Elytra with three basal foveae, with two inner ones adjacent to each other in common depression *Pselaphaulax* Reitter, 1909
- Pronotum without sulcus and foveae. Elytra without foveae *Pselaphus* Herbst, 1792
28. At least palpomeres 2 and 3 of maxillary palpi each with long and slender process on outer margin (Fig. 114). Trochanter 1 and at least base of femur 1 with many vertical setae along their mesal margin (Fig. 109) 29
- Palpomeres of maxillary palpi without processes on outer margin (Fig. 115). Trochanter 1 and femur 1 without vertical setae 30
29. Palpomere 3 and especially 4 of maxillary palpi strongly transverse, palpomeres 2–4 with long and slender process along their outer margin (Fig. 114). Tibia 1 gradually broadened from base to apex, very weakly curved. Only trochanter 1 and base of femur 1 with many vertical setae along their mesal margin. Tergite 2 barely longer than 1 *Ctenisodes* Raffray, 1897
- Palpomeres 3 and 4 of maxillary palpi not transverse, palpomere 4 without process on outer margin. Tibia 1 thickest



Figs 108–115. Details of Pselaphinae: 108 — *Lasinus micado*; 109, 114 — *Ctenisodes mroczkowskii*; 110, 115 — *Stipesa rudis*; 111 — *Tyrodex segrex*; 112 — *Pselaphus heisei*; 113 — *Tyraphus nitidus*; 108, 109 — protrochanter and profemur; 110, 111 — protarsi; 112–115 — maxillary palpi.
Рис. 108–115. Детали строения оцщупников; 108, 109 — передние вертлуги и бедра; 110, 111 — передние лапки; 112–115 — нижнечелюстные щупники.

- in middle part and then narrows to apex, strongly curved inwards. Trochanter 1, femur 1 and tibia 1 with numerous vertical setae along their mesal margin. Tergite 2 more than 1.5 times longer than 1 *Tmesiphorus* LeConte, 1849
30. Maxillary palpi comparable in length to head, their palpomeres 3 and 4 with stalked base. Tarsi with two equal claws, with segment 3 not or slightly longer and as wide as segment 2 (Fig. 111). Pronotum with antebasal sulcus **31**
- Maxillary palpi very small, several times shorter than head, their palpomeres 3 and 4 with wide base (Fig. 115). Tarsi with two unequal claws, with tarsomere 3 clearly wider and twice as long as tarsomere 2 (Fig. 110). Pronotum without transverse sulcus *Stipesa* Sharp, 1874
31. Femur 1 with tubercle at the middle of mesal margin. Trochanter 2 with long process. Male: antennomere 1 not modified *Tyrus* Aubé, 1833
- Femur 1 without tubercle. Trochanter 2 without process. Male: antennomere 1 with denticle on outer margin *Tyrodes* Raffray, 1908

Keys to species

Euplectus Leach, 1817 (Figs 116, 117). Labrum without notches along anterior margin (Fig. 84). Head with more or less distinct U- or V-shaped vertexal sulcus. Underside of head without clavate



Fig. 116. *Euplectus gibbipalpis* (photo K.V. Makarov).
Рис. 116. *Euplectus gibbipalpis* (фото К.В. Макарова).

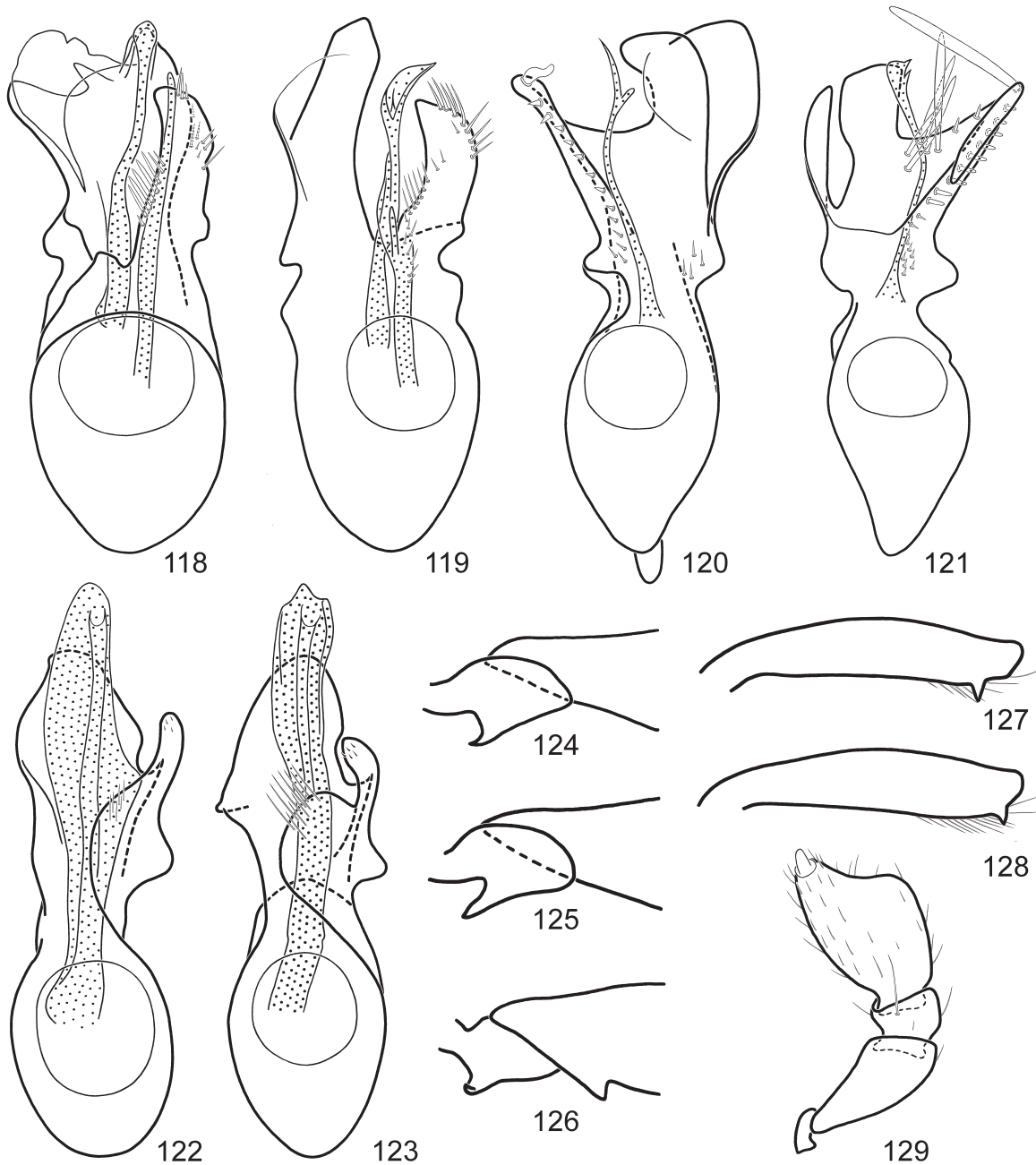


Fig. 117. *Euplectus piceus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 117. *Euplectus piceus* (фото С. Курбатова и Ю.А. Ловцовой).

setae. Pronotum with median antebasal and pair of lateral antebasal foveae united by antebasal sulcus and with median longitudinal sulcus. Pronotum with pair of lateral procoxal and pair of antero-prosternal foveae. Foveal system of meso- and metaventrite is insufficiently studied. Elytra together wider than length; each elytron usually with four basal foveae, sometimes reduced to two. Sternite IX of males is split longitudinally into two more or less equal triangular parts (Fig. 97). These beetles live in dead wood, rarely in compost, exceptionally may be associated with ants. Thirteen species (about 120 in the world, 60 in Palearctic).

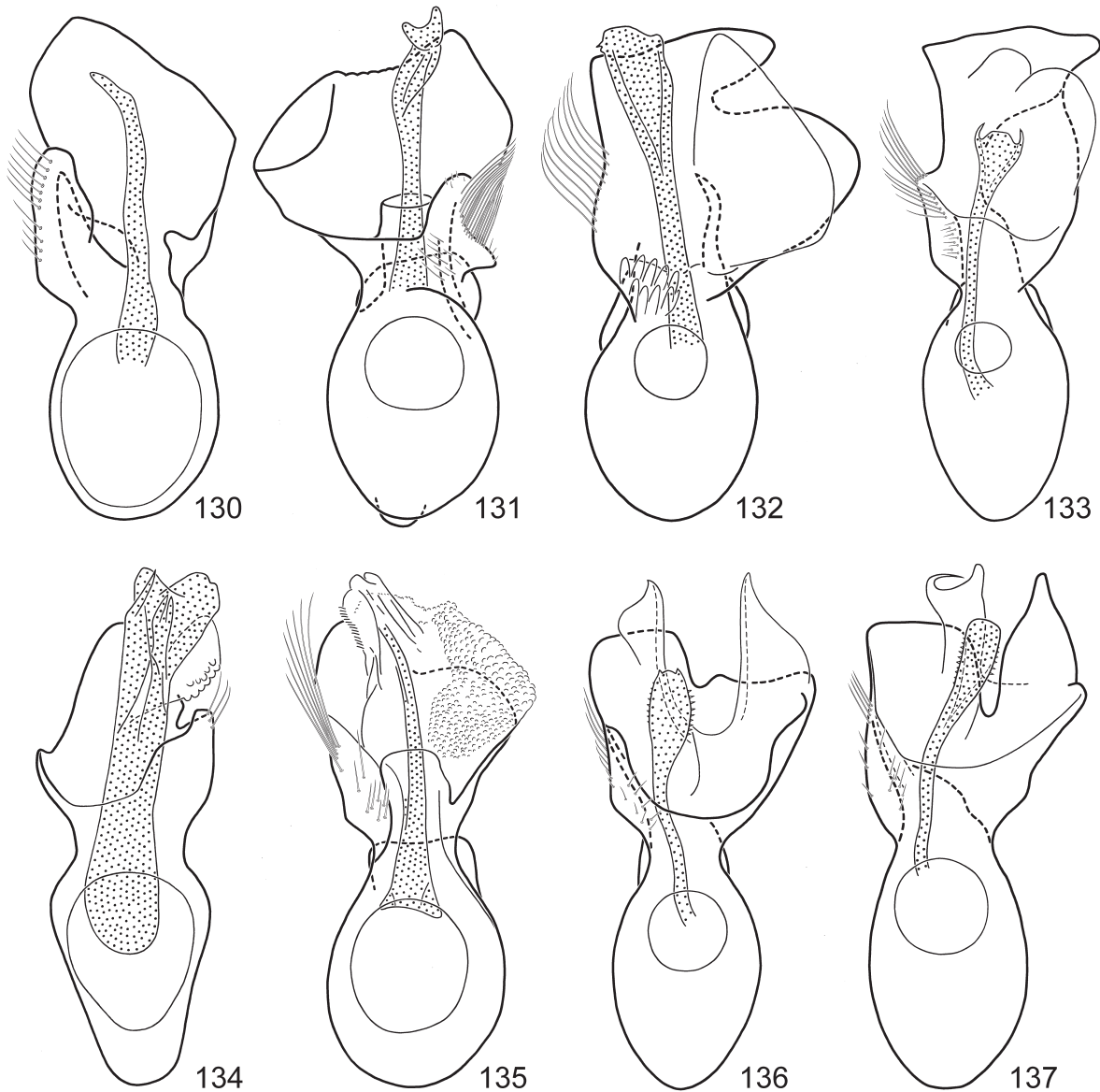
1. Each of three first visible tergites with pair of discal carinae 2
- Only two first visible tergites with pair of discal carinae 3
2. Male: basal half of 4th palpomere strongly thickened (Fig. 129); trochanters 3 simple; aedeagus as in Fig. 135. Body length 1.2–1.3 mm *gibbipalpis* Löbl, 1975
- Male: 4th palpomere simple; trochanters 3 with large blunt denticle; aedeagus as in Fig. 134. Body length 1.8–1.85 mm. *gravis* Kurbatov, 1988

3. Pronotum laterally with denticle at level of lateral antebasal foveae. Posterior margin of head with narrow longitudinal impression, anteriorly reaching level of posterior margin of eyes 4
- Pronotum laterally without denticle at lateral foveae, at most with a few granules. Posterior margin of head with very slight impression, distinctly not reaching level of posterior margin of eyes 7
5. Male: 6 sternite with transverse punctiform impression; trochanters 2 with denticle along mesal margin, trochanters 3 with flat denticle protruding downwards, apex bent forwards; aedeagus as in Fig. 119. Body length 1.6–1.8 mm *rubicundus* Kurbatov, 1988
- Male: 6 sternites with two adjacent weak impressions; trochanters 2 and 3 without denticles; aedeagus as in Fig. 118. Body length 1.9–2.0 mm. *epidemus* Kurbatov, 1991
6. Male: abdominal tergite 5 at middle with longitudinal denticle protruding backwards; abdominal sternite 4 with transverse impression, without row of long setae; femora 3 without denticle at base of mesal margin; aedeagus as in



Figs 118–129. Details of *Euplectus* spp.: 117 — *E. epidemus*; 118 — *E. rubicundus*; 119, 125 — *E. domefactus*; 120 — *E. doryphorus*; 121, 123, 126 — *E. puncticollis*; 122, 124, 127 — *E. decipiens*; 128 — *E. gibbipalpis*; 117–122 — aedeagi; 123–125 — metatrochanters; 126–127 — protibiae; 128 — maxillary palpus [after Löbl, 1975].

Рис. 118–129. Детали строения видов рода *Euplectus*; 117–122 — эдеагусы; 123–125 — задние вертлуги; 126–127 — передние голени; 128 — нижнечелюстной шупик [из Löbl, 1975].

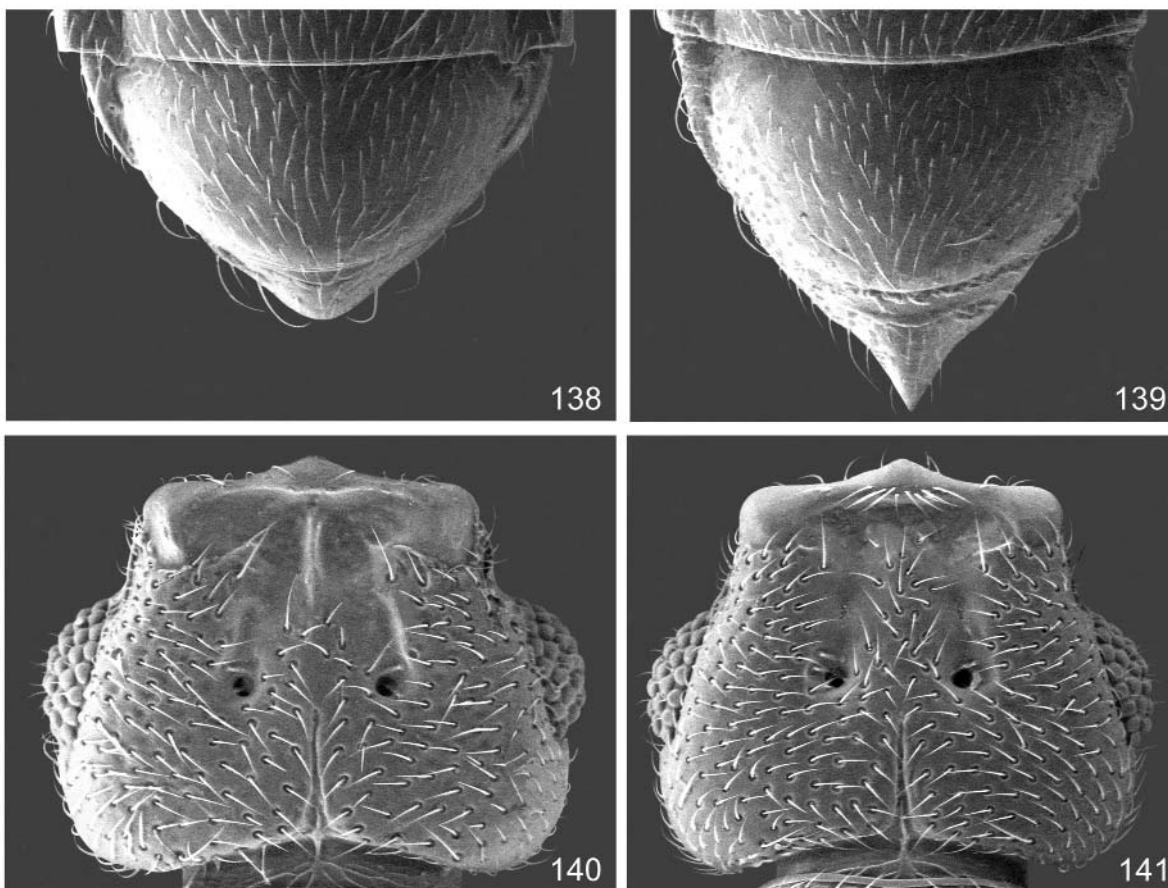


Figs 130–137. Aedeagi of *Euplectus* spp.: 130 — *E. rutilans*; 131 — *E. piceus*; 132 — *E. signatus*; 133 — *E. punctatus*; 134 — *E. gravis*; 135 — *E. gibbipalpis*; 136 — *E. mutator*; 137 — *E. karstenii*; 131–133, 136, 137 — after Besuchet, 1974; 135 — after Löbl, 1975.
Рис. 130–137. Эдеагусы видов рода *Euplectus*; 131–133, 136, 137 — из Besuchet, 1974; 135 — из Löbl, 1975.

Fig. 121. Female: apex of tergite 5 with long spine protruding backwards (Fig. 139). Body length 1.5–1.55 mm
 *doryphorus* (Kurbatov, 1991)
 – Male: abdominal tergite 5 rounded, without any denticles; abdominal sternite 4 without impression, but its posterior margin with row of long setae reaching posterior margin of sternite 5; femora 3 with denticle at base of mesal margin (Fig. 126); aedeagus as in Fig. 120. Female: tergite 5 uniformly rounded along its posterior margin (Fig. 138). Body length 1.3–1.5 mm *domefactus* (Kurbatov, 1991)
 7. Another pair of rather large additional foveae ahead of the vertexal foveae comparable to them in size 8
 – No other obvious foveae in front of the vertexal foveae 9
 8. Head between the eyes and the vertexal foveae are densely punctured; frons between the supplementary foveae are

also punctured, although less distinctly. Male: sternite 5 with pair of indistinct foveae united by transverse sulcus; sternite 6 at base not strongly impressed, at posterior margin on both sides from centre with row of long setae; aedeagus as in Fig. 131. Body length 1.5–1.7 mm .
 *piceus* Motschulsky, 1835
 – Sides of head and frons unpunctured. Male: sternite 5 without modification; sternite 6 at middle with very deep impression; aedeagus as in Fig. 130. Body length 1.55–1.6 mm *rutilans* Kurbatov, 1988
 9. Vertexal sulcus distinct, evenly deep throughout its length ... 10
 – Vertexal sulcus less distinct, superficial. Sides and posterior part of head distinctly punctured 11
 10. Discal carinae of abdominal tergites 1 and 2 small, not reaching middle of segment. Pronotum practically not

- punctured. Male: tibiae 1 without apicomeral denticle; aedeagus as in Fig. 132. Body length 1.3–1.4 mm *signatus* (Reichenbach, 1816)
- Discal carinae of tergites 1 and 2 not less than half length of corresponding segment. Pronotum densely punctured. Male: tibiae 1 with slightly curved apicomeral denticle (Fig. 127); aedeagus as in Fig. 122. Body length 1.7 mm. [This species is very close to the Central European *E. decipiens* Raffray, 1910, the male of which differs in the position of the denticle of the tibiae 1 (Figs 127–128), the shape of the denticle of the trochanters 3 (Figs 124–125), and details of the structure of the aedeagus (Figs 122–123)] *puncticollis* Kurbatov, 1988
11. Male: sternites 4 and 5 not modified; sternite 6 with a very deep, extending backwards impression, which is slightly wider than length; aedeagus as in Fig. 133. Body length 1.4–1.6 mm *punctatus* Mulsant et Rey, 1861
- Male: posterior margin of sternite 4 with two rather deep notches and a transverse plate between them; a fovea on the outer side of each notch, touching the posterior margin of the segment; base of sternite 5 with a deep transverse impression; sternite 6 with two rather deep foveae united by a distinct impression 12
12. More stout, elytra somewhat wider than their length along the suture. Discal carinae of abdominal tergites 1 and 2 distinctly longer than half length of corresponding segment. Male: Aedeagus as in Fig. 136. Body length 1.4–1.6 mm *mutator* Fauvel, 1895
- Narrower, elytra along suture approximately as long as their total width. Discal carinae of abdominal tergites 1 and 2 reach only middle of length of corresponding segment. Male: aedeagus as in Fig. 137. Body length 1.1–1.4 mm *karstenii* (Reichenbach, 1816)
- Leptoplectus* Casey, 1908 (Fig. 142). Underside of head without long, clavate setae. Labrum with deep notch at middle of outer margin (Fig. 85). Pronotum laterally with a small denticle at the level of the posterior margin of lateral foveae. Prosternum with pair of lateral procoxal foveae. Elytra together slightly longer than wide. Abdominal tergites 1 and 2 each with pair of discal carinae. Male: 7 (IX) sternite split longitudinally into two more or less equal triangular parts (as in Fig. 97). Beetles most often live in dead wood. 5 species in the Russian Far East.
1. Abdominal tergite 1 with discal carinae as long as half of segment length. Very small species, body length 0.9–1.0 mm. Aedeagus as in Fig. 148 *pumilio* Kurbatov, 1992
- Abdominal tergite 1 with discal carinae at least as long as 2/3 of segment length. Body length more than 1.1 mm 2



Figs 138–141. Details of *Euplectus* spp. (females) and *Leptoplectus* spp. (males): 138 — *E. domefactus*; 139 — *E. doryphorus*; 140 — *L. falcifer*; 141 — *L. perperus*; 138, 139 — abdominal apex, dorsally; 140, 141 — head.

Рис. 138–141. Детали строения видов рода *Euplectus* (самки) и *Leptoplectus* (самцы); 138, 139 — верхина брюшка, вид сверху; 140, 141 — голова.

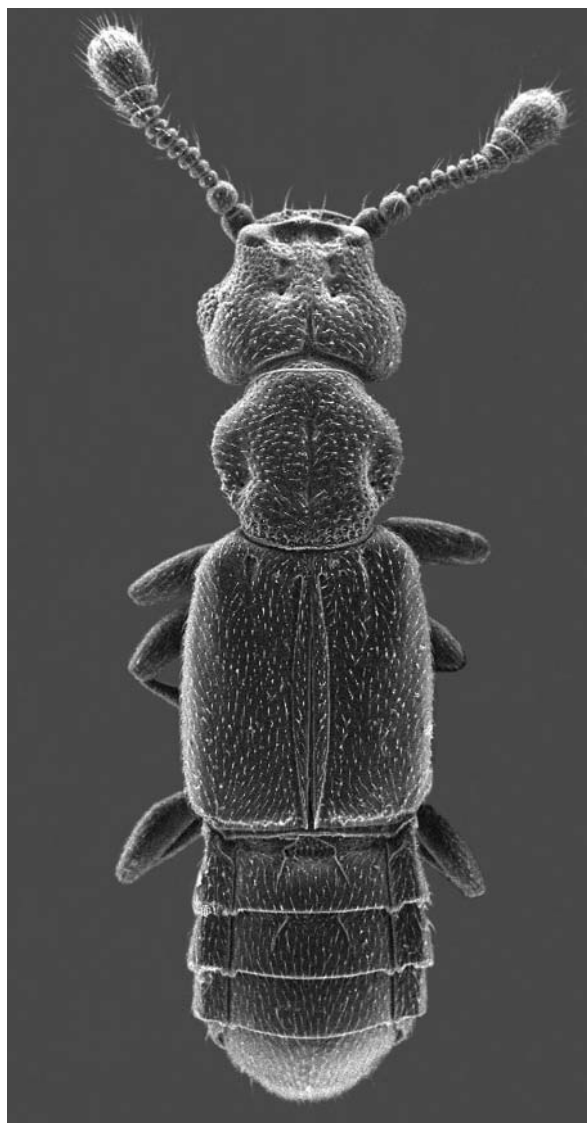


Fig. 142. *Leptoplectus perperus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 142. *Leptoplectus perperus* (фото С. Курбагова и Ю.А. Ловцовой).

2. Elytra relatively broad, 1.4 times wider than pronotum and 1.35 times wider than head. Body length 1.25 mm. Aedeagus as in Fig. 149 *solivagus* Kurbatov, 1991
- Elytra relatively narrow, 1.3 times wider than pronotum and 1.2 times wider than head 3
3. ♂: transverse branch of vertexal sulcus broadened, especially in median part and here divided by distinct longitudinal carina into two “cells” (Fig. 140). Body length 1.1 mm. Aedeagus as in Fig. 147 *falcifer* Kurbatov, 1992
- ♂: transverse branch of vertexal sulcus on middle without longitudinal carina 4
4. ♂: Aedeagus (Fig. 144) with several long setae on base of lateral margin of apical lobe below lateral spine; with long denticle on opposite side from lateral spine; shape of apical lobe rather stable; inversion of aedeagus not marked. Body length 1.15–1.3 mm.....*perperus* Kurbatov, 2022
- ♂: Aedeagus (Figs 145–146) with very fine, barely visible setae on base of lateral margin of apical lobe below lateral

spine; no denticle on opposite side of lateral spine; shape of apical lobe, including shape of spine, varies rather considerably (Figs 152–159); aedeagus may be inverted, with 'right' and 'left' variants occurring in populations with approximately equal frequency. Body length 1.15–1.3 mm .

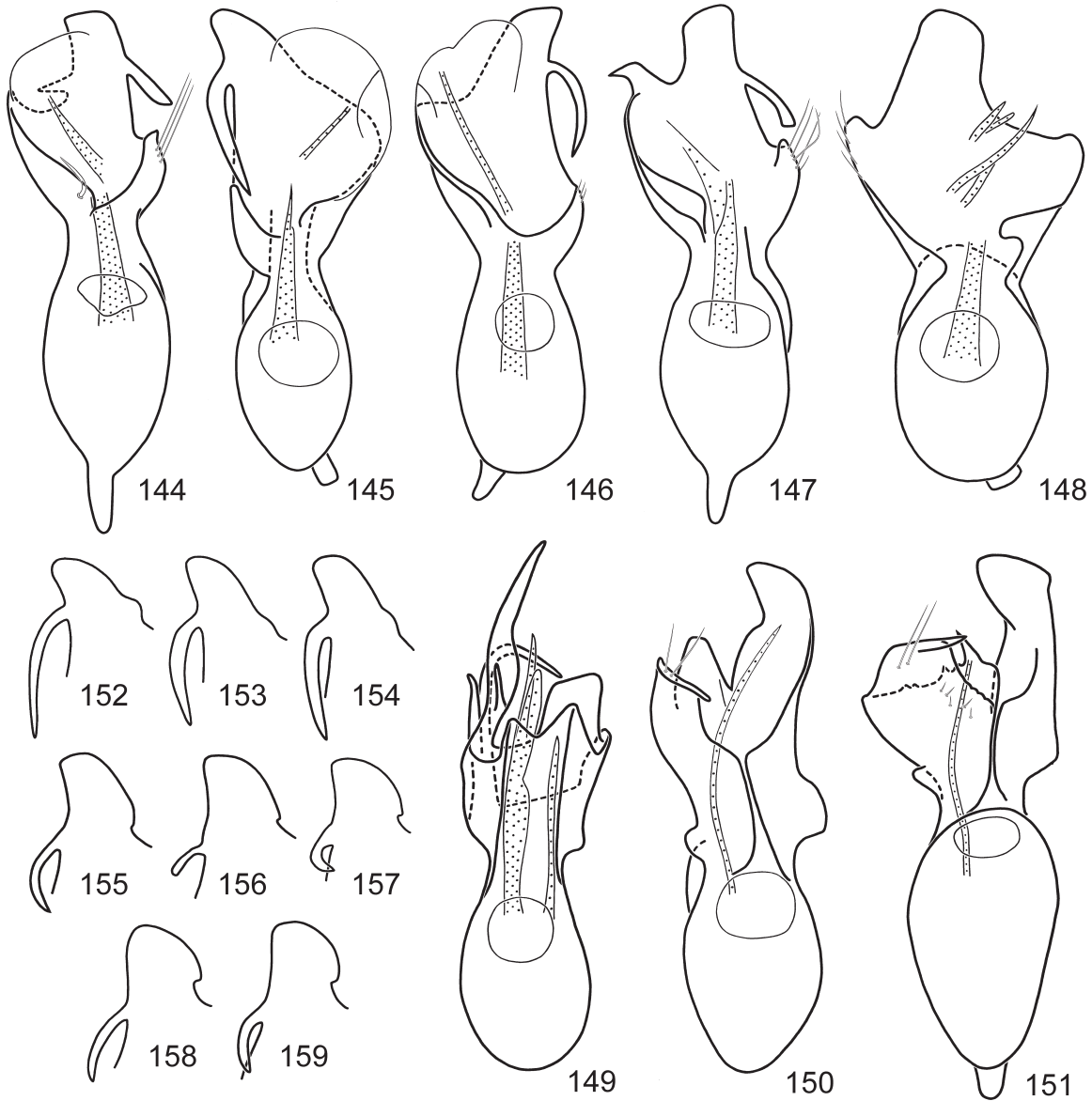
.....*similis* Kurbatov, 1991

Labroplectus Kurbatov, 1993 (Fig. 143). Close to genus *Leptoplectus*. Underside of head without long clavate setae. Labrum with two notches along anterior margin (Fig. 87). Pronotum with median antebasal and lateral antebasal foveae and median longitudinal sulcus, lacking antebasal sulcus, with lateral denticle at the level of lateral antebasal foveae. Prosternum with pair of lateral procoxal foveae, but without pair of anteroprosteral foveae. Mesoventrite with pair of lateral mesoventral foveae; metaventrite with pair of lateral mesocoxal and pair of lateral metaventral foveae. Abdominal tergites 1 and 2 without discal carinae. Abdominal sternite 2 with pair of mediobasal and pair of basolateral foveae. Male: sternite 7 (IX) split longitudinally into two more or less equal triangular parts (as in Fig. 97). Beetles associated with dead wood. 2 species in the Southern Kurils.

1. Longitudinal branches of vertexal sulcus long, two times longer than distance from their posterior margin to posterior margin of head. Male: middle of abdominal sternite 4 with point-like impression; sternite 5 simple; base of sternite 6 with large transverse impression. Aedeagus as in Fig. 150. Body length 1.2–1.25 mm
..... *occultus* (Kurbatov, 1991)



Fig. 143. *Labroplectus occultus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 143. *Labroplectus occultus* (фото С. Курбагова и Ю.А. Ловцовой).



Figs 144–159. Aedeagi (144–151) and their apical lobe (152–159) of *Leptoplectus* spp. and *Labroplectus* spp.: 144 — *Leptoplectus perperus*; 145, 146, 152–159 — *Leptoplectus similis*; 147 — *Leptoplectus falcifer*; 148 — *Leptoplectus pumilio*; 149 — *Leptoplectus solivagus*; 150 — *Labroplectus occultus*; 151 — *Labroplectus depositor*; 145 — morphologically ‘right’ version; 146 — morphologically ‘left’ version.

Рис. 144–159. Эдеагусы (144–151) и их апикальная часть (152–159) видов из родов *Leptoplectus* и *Labroplectus*; 145 — морфологически ‘правая’ версия; 146 — морфологически ‘левая’ версия.

– Longitudinal branches of vertexal sulcus short, barely longer than distance from their posterior margin to posterior margin of head. Male: middle of abdominal sternite 4 with two adjacent point-like impressions; sternite 5 with deep transverse impression; impression of sternite 6 smaller than impression of sternite 5. Aedeagus as in Fig. 151. Body length 1.3 mm *depositor* Kurbatov, 1993

Forinus Kurbatov, 1991 (Fig. 160). Underside of head without clavate setae. Pronotum with median antebasal and pair of lateral antebasal foveae united by biarcuate transverse antebasal sulcus. Each elytron with four basal foveae, full sutural and shortened discal sulcus, and also with subhumeral fovea and lateral sulcus. Abdominal tergites 1–3 with pair

of discal carinae each; tergite 4 longer than any of previous tergites. Prosternum with pair of lateral procoxal and pair of anteroprosteral foveae. Mesoventrite with one median mesoventral and two lateral mesoventral foveae. Mesocoxal cavities closed. Metaventrite only with a pair of lateral mesocoxal foveae. Abdominal sternite 2 with pair of basolateral foveae. Coxae 2 and 3 contiguous. Secondary sexual characters of male localised on middle legs; sternite 7 (IX) split longitudinally into three parts with penial plate large (Figs 98, 165–166). Aedeagus peculiarly shaped, with two long curved projections attached anteriorly and posteriorly to the basal capsule (Figs 161–164). Beetles are associated with dead wood. 2 species in Primorye and Southern Kurils, another species recently described from southern Japan.



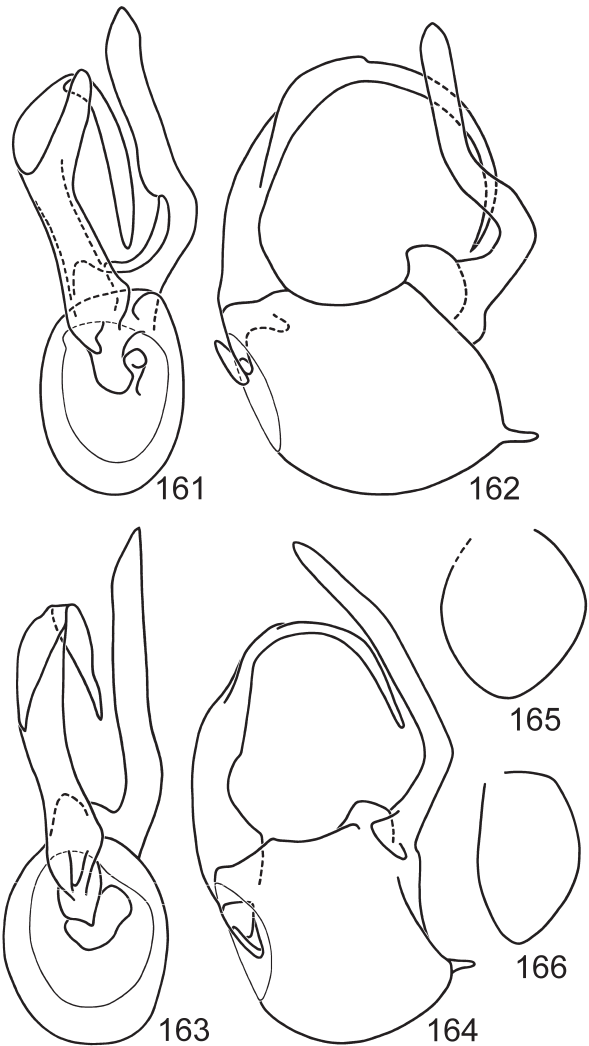
Fig. 160. *Forinus secundus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 160. *Forinus secundus* (фото С. Курбатова и Ю.А. Ловцовой).

- 1. Body length 1.05 mm. Male: eyes not strongly protruded, distance between their outer margins equal to width of head at level of temples; penial plate oval-rhomboid (Fig. 165). Aedeagus as in Figs 161–162 *macer* Kurbatov, 1991
- Body length 1.15–1.20 mm. Male: eyes more strongly protruded, distance between their outer margins bigger than width of head at level of temples; penial plate asymmetrical (one side more or less straight, other side arcuate) (Fig. 166). Aedeagus as in Figs 163–164 *secundus* Kurbatov, 1992

Bibloporus Thomson, 1859 (Fig. 167). Underside of head with multiple dense clavate hairs (as in Fig. 90). Pronotum with pair of lateral longitudinal sulci and with three foveae, one median antebasal and two lateral antebasal. Each elytron with four basal foveae and with subhumeral fovea and lateral sulcus. ♂: secondary sexual characters affect mainly the middle legs; in addition, last, or IX, sternite split longitudinally into three parts, of which the central one is a large, more or less oval penial plate, flanked by two small triangular parts (roughly as shown in Fig. 98).

The beetles are associated with decayed moist wood; both sexes fly well and are often caught in window traps. There are 6 species in the Far East, of which 2 (*bicolor* and *minutus*) also occur in the Western Palearctic. 14 species in total are described worldwide.

- 1. Abdominal tergites 1–3 each with pair of thin discal carinae 2
- Only abdominal tergites 1–2 each with pair of discal carinae 3
- 2. Head and pronotum with fine, dense punctation. ♂: femur 2 (Fig. 171) in basal third with row of 7–8 thick bristles; tibia 2 with small subapical denticle; penial plate rounded, as long as wide (Fig. 182); aedeagus as in Fig. 176. Body length 1.2 mm *ponderosus* Kurbatov, 1991
- Head and pronotum smooth, without punctation. ♂: femur 2 (Fig. 173) in basal third with high, narrow tubercle bearing 3–4 thick bristles at apex; tibia 2 with large subapical projection obliquely cut at apex; penial plate oval, longer



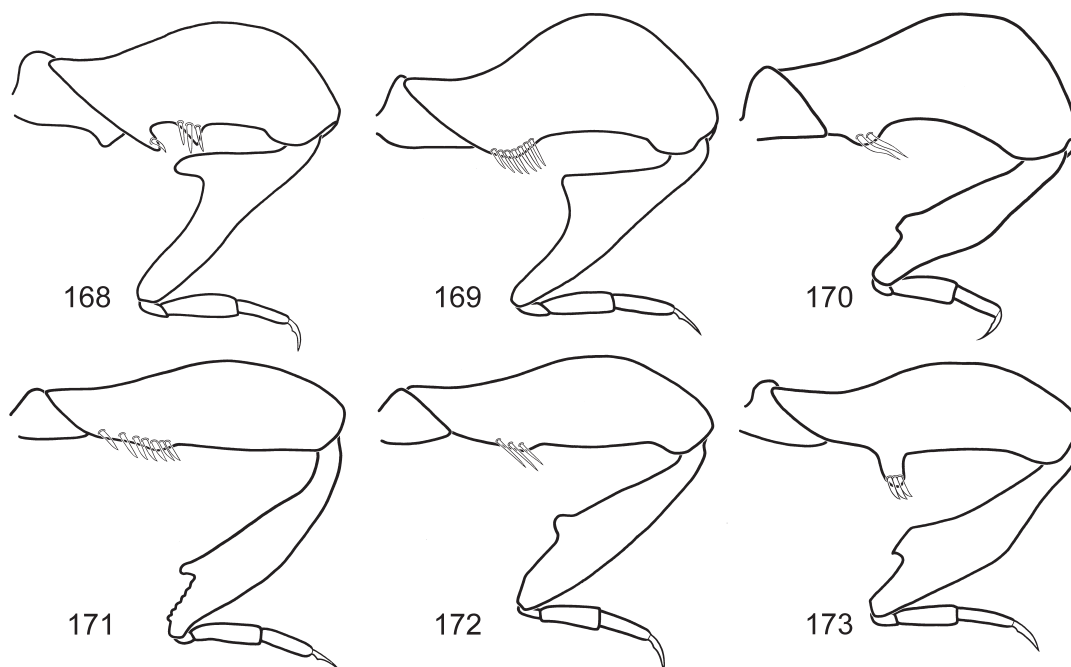
Figs 161–166. Details of *Forinus* spp.: 161, 162, 165 — *F. macer*; 163, 164, 166 — *Forinus secundus*; 161–164 — aedeagi; 165, 166 — penial plates; 161, 163 — dorsally, 162, 164 — laterally.
Рис. 161–166. Детали строения видов рода *Forinus*; 161–164 — эдеагусы; 165, 166 — penial plates; 161, 163 — дорсально, 162, 164 — латерально.

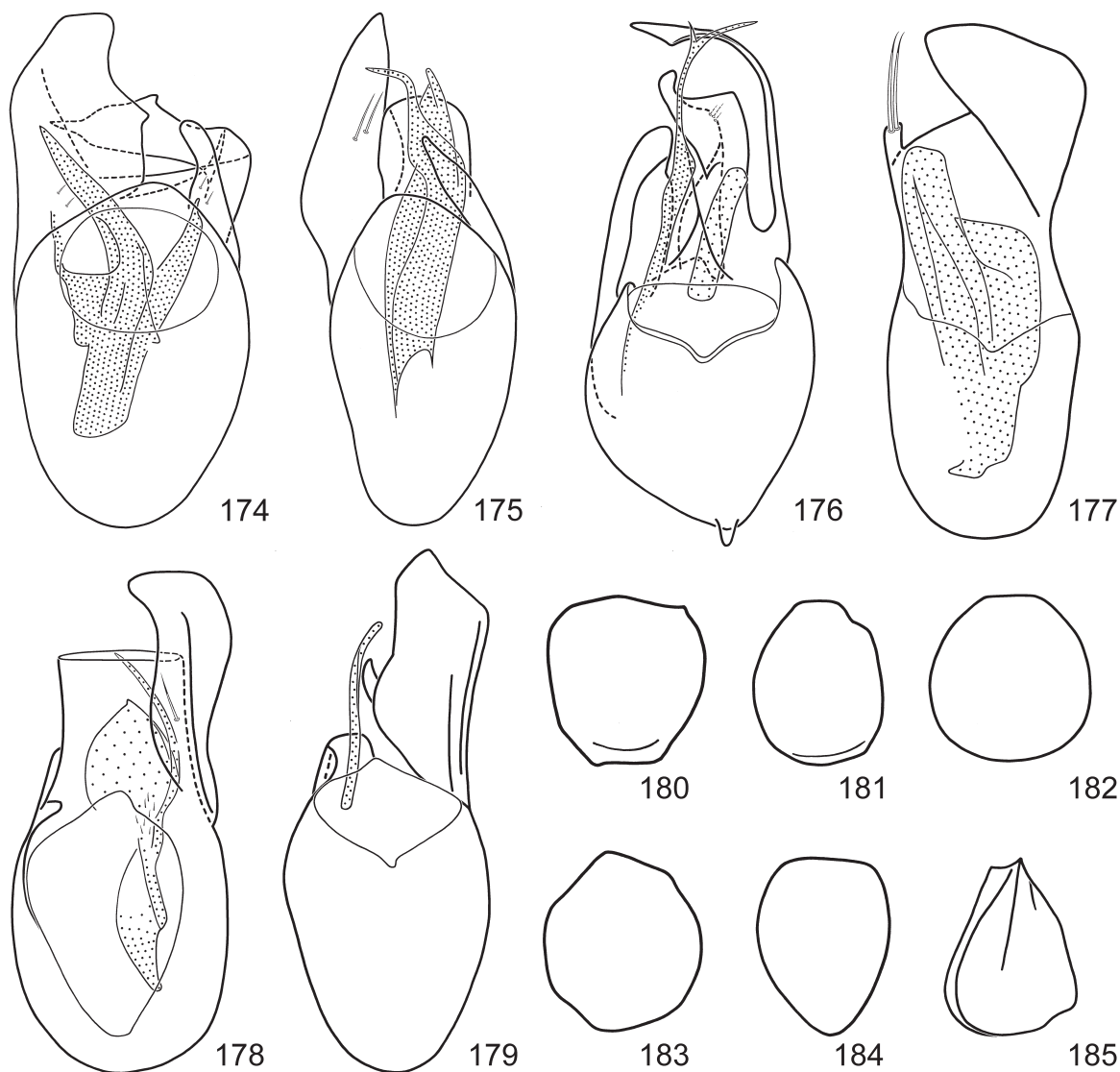


Fig. 167. *Bibloporus minutus* (photo S. Kurbatov & Yu.A. Lovtsova).
 Рис. 167. *Bibloporus minutus* (фото С. Курбатова и Ю.А. Ловцовой).

- than wide, with narrowed apex (Fig. 184); aedeagus as in Fig. 179. Body length 1.15–1.2 mm *ferentarius* Kurbatov, 1992
3. ♂: femur 2 strongly thickened and curved, distinctly thicker than femur 1, with at least one setiferous subbasal tubercle (Figs 168–170). 4
- ♂: femur 2 (Fig. 172) weakly thickened and not curved, distinctly thinner than femur 1, without distinct tubercle, with only three thick subbasal bristles; penial plate as in Fig. 183; aedeagus as in Fig. 178. Body length 1.25–1.3 mm *pubens* Kurbatov, 1991
4. Body blackish-brown, at least 1.2 mm long. ♂: tibia 2 (Figs 168–169) with large dent near the middle 5
- Body reddish-brown, 1.1 mm long. ♂: tibia 2 (Fig. 170) with small subapical denticle; penial plate as in Fig. 185; aedeagus as in Fig. 177. Body length 1.1 mm *neglectus* Kurbatov, 1993
5. ♂: trochanter 2 (Fig. 168) with tubercle on the mesal margin, femur 2 at base with two slender denticles; penial plate as in Fig. 181; aedeagus as in Fig. 175. Body length 1.1–1.2 mm *minutus* Raffray, 1914
- ♂: trochanter 2 (Fig. 169.) simple, femur 2 at base with broad rounded tubercle covered with row of thick bristles; penial plate as in Fig. 180; aedeagus as in Fig. 174. Body length 1.1–1.2 mm. *bicolor* (Denny, 1825)

Figs 168–173. Mesolegs of *Bibloporus* spp.: 168 — *B. minutus*; 169 — *B. bicolor*; 170 — *B. neglectus*; 171 — *B. ponderosus*; 172 — *B. pubens*; 173 — *B. ferentarius*; 168, 169 — after Besuchet, 1974.
 Рис. 168–173. Средние ноги видов рода *Bibloporus*; 168, 169 — из Besuchet, 1974.





Figs 174–185. Details of *Bibloporus* spp.: 174, 180 — *B. bicolor*; 175, 181 — *B. minutus*; 176, 182 — *B. ponderosus*; 177, 185 — *B. neglectus*; 178, 183 — *B. pubens*; 179, 184 — *B. ferentarius*; 174–179 — aedeagi; 180–185 — penial plates; 174, 175 — after Besuchet, 1974.

Рис. 174–185. Детали строения видов рода *Bibloporus*; 174–179 — эдеагусы; 180–185 — пеняльные пластинки; 174, 175 — из Besuchet, 1974.

Piptoncus Kurbatov, 1991 (Fig. 186). Externally resembles representatives of the genus *Bibloporus*. Underside of head with long clavate setae forming three longitudinal rows on both sides. Antennae short, rather with 1-segmented club, as antennomere 11 large, longer than previous five segments together, and antennomeres 9 and 10 much closer in width to the previous segments than to the 11. Pronotum without lateral longitudinal sulci, but with transverse antebasal sulcus, interrupted on both sides of median antebasal fovea. Median longitudinal prosternal carina missing. Each elytron with four basal foveae, full sutural and strongly shortened discal stria, and with subhumeral fovea and lateral sulcus. Median mesoventral foveae absent. Structure of abdominal tergite 1 (IV) differs in both sexes unusually within pselaphines: in male tergite 1 (Fig. 188) possesses broad transverse basal impression with pair of widely spaced mediobasal foveae and pair of discal carinae near the foveae, while in female (Fig. 189) basal impression very small,

rounded and the pair of mediobasal foveae inside it strongly close to each other and pair of discal carinae completely absent. Abdominal sternite 2 male on posterior corners provided with dense tuft of setae protruding from under the posterior corners of abdominal tergite 1 and clearly visible when viewed dorsally (Fig. 188). Male secondary sexual characters also localized on legs 1 and 2; abdominal sternite 7 (IX) split into three parts as in *Bibloporus*.

Beetles associated with decayed wood. 1 species with two subspecies.

1. ♂: trochanter 1 with spine shorter, at least 2 times shorter than distance from base of spine to base of femur 1 (Fig. 190); penial plate round (Fig. 193); aedeagus as in Fig. 200. Body length 1.0–1.15 mm. Southern Primorye .
..... *duplex duplex* Kurbatov, 1991
- ♂: trochanter 1 with spine longer, not more than 1.5 times shorter than distance from base of spine to base of femur 1



Fig. 186. *Piptoncus duplex*, male (photo S. Kurbatov & Yu.A. Lovtsova).

Рис. 186. *Piptoncus duplex*, самец (фото С. Курбатова и Ю.А. Ловцовой).

(Fig. 191); penial plate slightly oval (Fig. 194); aedeagus as in nominative subspecies but with different apical part (Fig. 201). Body length 1.0–1.15 mm. Southern Kurils, Sakhalin, Japan *duplex sobrinus* Kurbatov, 1991

Kuriporus Kurbatov, 1991 (Fig. 187). The smallest Russian pselaphine species with body length not exceeding 0.8 mm. Underside of head without longitudinal carina, provided with one and a half dozen erect clavate setae. Antennomere 11 slightly wider than 10 and longer than 8–10 taken together. Pronotum with median antebasal fovea connected with longitudinal median sulcus, with two lateral antebasal foveae and with two lateral longitudinal sulci beginning in them (as in *Bibloporus*). Transverse antebasal sulcus absent. Each elytron with four basal foveae and subhumeral fovea and lateral sulcus. Abdominal tergites 1–4 of approximately equal length; tergite 1 with basal impression, bordered laterally by a pair of longitudinal discal carinae. Prosternum without anteroprosteral and lateral procoxal foveae and median prosternal carina. Mesoventrite with pair of median mesoventral foveae and pair of undivided lateral mesoventral foveae. Metaventrite with pair of lateral metaventral and pair of lateral mesocoxal foveae. Mesocoxal cavities unclosed. Abdominal sternite 2 with two basolateral foveae. Coxae 2 and 3 contiguous. Male secondary sexual characters localized on metaventrite and tibia 2; abdominal sternite IX with penial plate.



Fig. 187. *Kuriporus creator* (photo S. Kurbatov & Yu.A. Lovtsova).

Рис. 187. *Kuriporus creator* (фото С. Курбатова и Ю.А. Ловцовой).

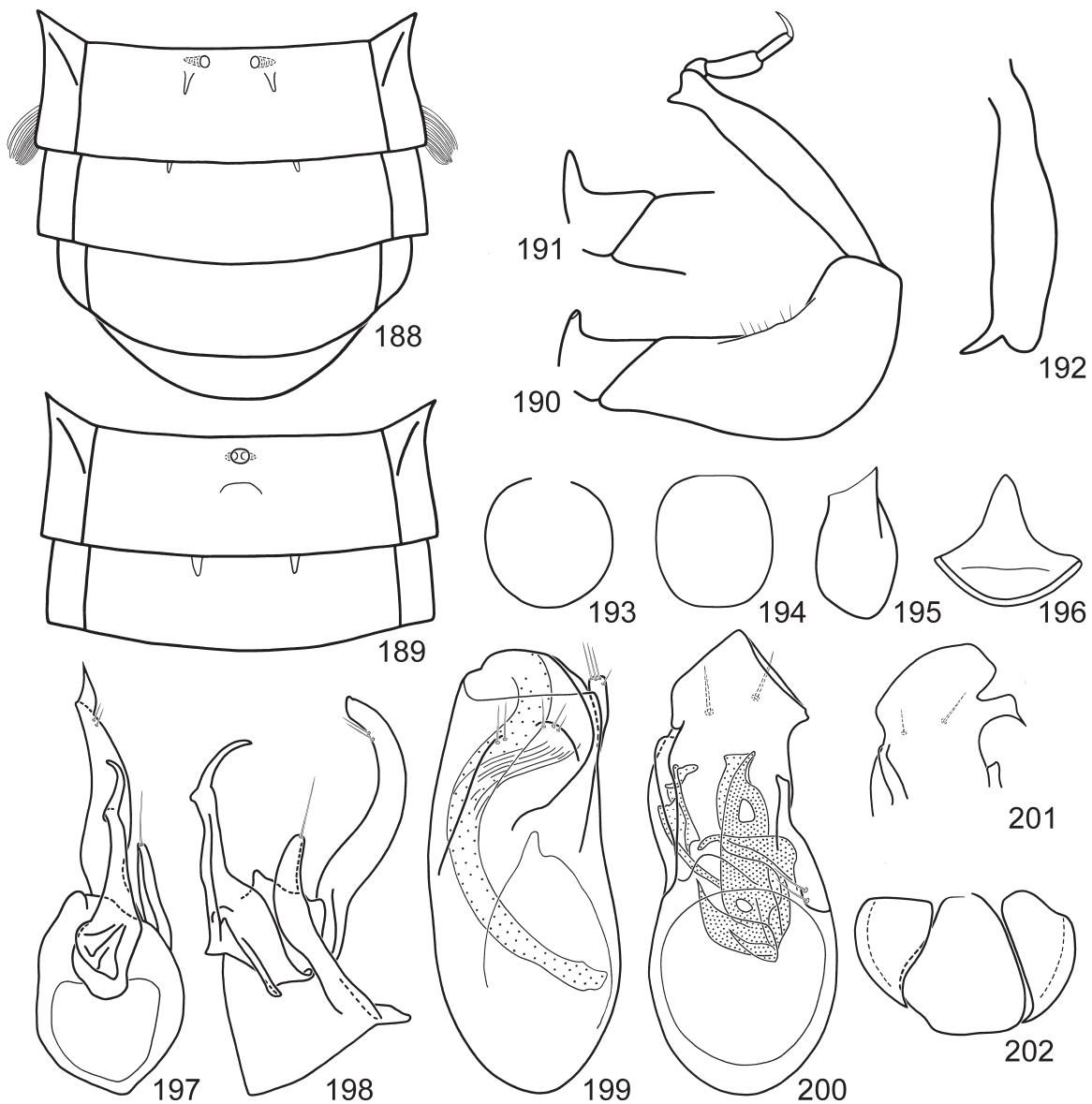
Beetles associated with decayed wood. Monotypic genus known from Sakhalin, Kunashir and Japan.

1. Elytral discal stria short, not reaching middle of elytral length. ♂: tibia 2 with long, slightly curved apical denticle (Fig. 192); penial plate oval, irregularly shaped (Fig. 195); aedeagus as in Figs 197–198. Light red-brown, 0.75–0.8 mm long *creator* Kurbatov, 1991

Saulcyella Reitter, 1901 (Fig. 203). Underside of head with several long club-like setae (Fig. 91). Antennomere 11 asymmetrical, with bulging inner margin (Fig. 96). Transverse antebasal pronotal sulcus V-shaped. Each elytron with two basal foveae, without subhumeral fovea and lateral sulcus. IX sternite of male with small penial plate (Fig. 202). One species with discontinuous European-Far Eastern range.

Beetles live in decayed wood, in Europe sometimes in association with ants.

1. Abdominal tergite 1 with two small discal carinae, spaced a quarter of the segment width. Male: abdominal sternite 6 with slight depression extending backwards, sternite 7 (IX) with penial plate as wide as length, widened toward apex (Fig. 202). Light red-brown, 1.1–1.3 mm *schmidtii* (Maerckel, 1844)



Figs 188–202. Details of Pselaphinae: 188–190, 193, 200 — *Piptoncus duplex duplex*; 191, 194, 201 — *Piptoncus duplex sobrinus*; 192, 195, 197, 198 — *Kuriporus creator*; 196, 199 — *Tiliactus properus*; 202 — *Saulcyella schmidtii*; 188 — male abdominal tergites IV–VII; 189 — female abdominal tergites IV–V; 190 — proleg; 191 — protrochanter; 192 — mesotibia; 193–196 — penial plates; 197–200 — aedeagi; 201 — apex of aedeagus; 202 — IX abdominal sternite male; 197, 198, 200 — dorsal; 198 — lateral.

Рис. 188–202. Детали строения Pselaphinae; 188 — IV–VII тергиты брюшка самца; 189 — IV–V тергиты брюшка самки; 190 — передняя нога; 191 — передний вертлуг; 192 — средняя голень; 193–196 — пеняльная пластинка; 197–200 — эдеагусы; 201 — верхушка эдеагуса; 202 — IX стернит брюшка самца; 197, 198, 200 — дорсально; 198 — латерально.

Tiliactus Kurbatov, 1992 (Fig. 205). Underside of head without longitudinal carina, with several long erect clavate setae. Antennomere 11 longer than 7–10 taken together. Pronotum with median antebasal and pair of lateral antebasal foveae connected by transverse antebasal sulcus; median longitudinal sulcus extending anteriorly from median antebasal fovea. Each elytron with four basal foveae, full sutural and three discal striae, as well as with lateral sulcus. Abdominal tergite 1 with pair of longitudinal discal carinae, surface between them slightly depressed. Prosternum with pair of lateral procoxal foveae, median prosternal carina absent. Mesoventrite with bifurcated median mesoventral fovea and pair of lateral meso-

ventral foveae. Mesocoxal cavities closed. Abdominal sternite 2 with two basolateral foveae. Coxae 2 and 3 non-contiguous. Male secondary sexual characters localized on frons and tibiae 2; abdominal sternite 7 (IX) with penial plate.

Beetles live in decayed wood. 1 species.

1. Median elytral discal stria extends beyond the middle of elytral length, other two discal striae shorter than half the elytral length. Male: anterior margin of frons angularly protruding forward, slightly overhanging clypeus; abdominal sternite IX with penial plate mushroom-shaped (Fig. 196). Aedeagus as in Fig. 199. Red-brown, 1.00–1.05 mm *properus* Kurbatov, 1992



Fig. 203. *Saulecyella schmidtii* (photo K.V. Makarov).
Рис. 203. *Saulecyella schmidtii* (фото К.В. Макарова).



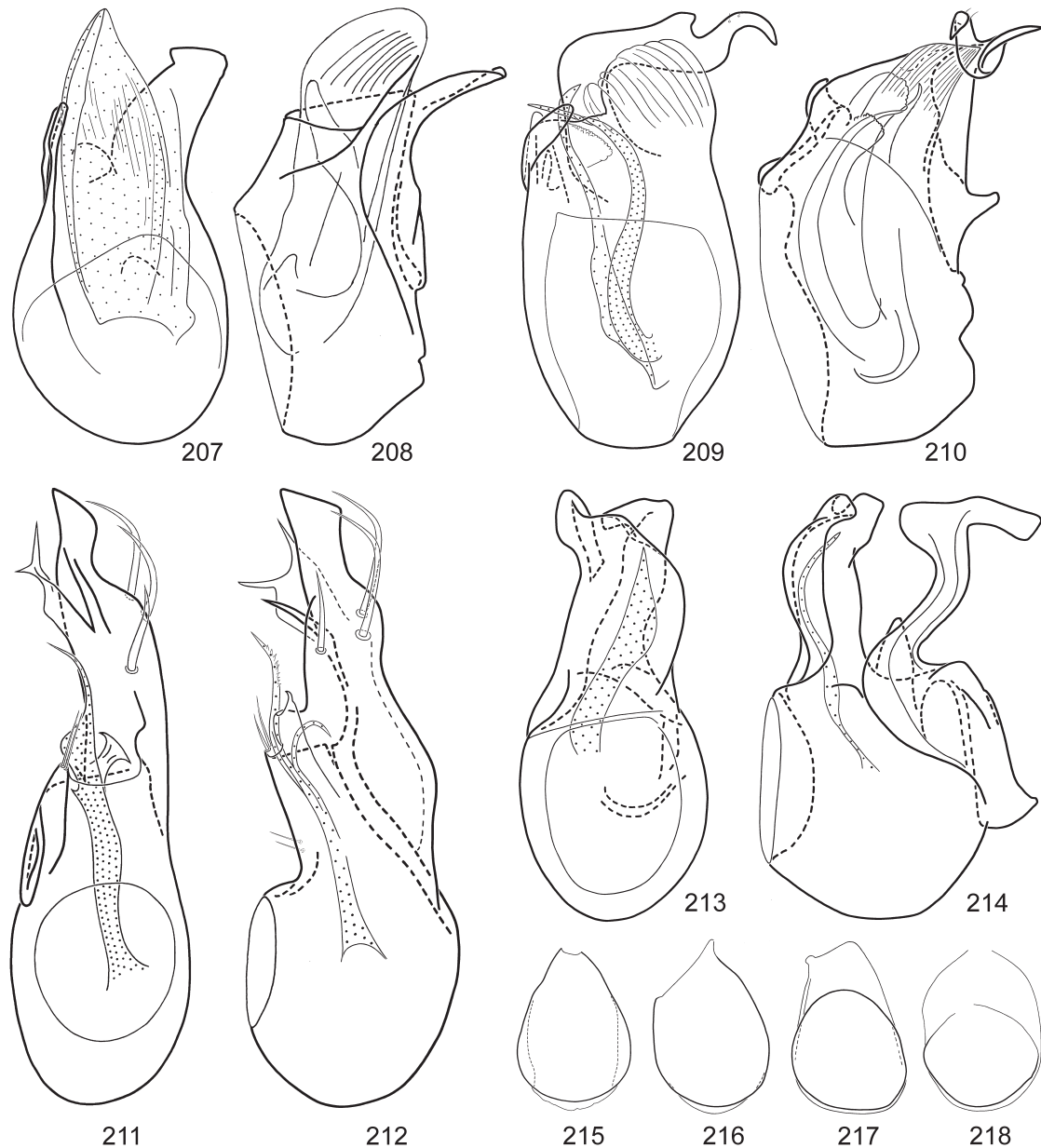
Fig. 204. *Ramussia lovtsovae* (photo K.V. Makarov).
Рис. 204. *Ramussia lovtsovae* (фото К.В. Макарова).



Fig. 205. *Tiliactus properus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 205. *Tiliactus properus* (фото С. Курбатова и Ю.А. Ловцовой).



Fig. 206. *Ramussia parabile* (photo K.V. Makarov).
Рис. 206. *Ramussia parabile* (фото К.В. Макарова).



Figs 207–218. Details of *Ramussia* spp.: 207, 208, 215 — *R. lovtsovae*; 209, 210, 216 — *R. svetlanae*; 211, 212, 217 — *Ramussia parabile*; 213, 214, 218 — *R. captiosum*; 207–214 — aedeagi, dorsally and laterally; 215–218 — penial plates.

Рис. 207–218. Детали строения видов рода *Ramussia*; 207–214 — эдеагусы, дорсально и латерально; 215–218 — пеняльные пластины.

Ramussia Kurbatov, 1991 (Figs 204, 206). Underside of head without longitudinal carina, with several long erect clavate setae (Fig. 90). Pronotum with median antebasal and pair of lateral antebasal foveae connected by biarcuate sulcus and with or without median longitudinal sulcus. Each elytron with two or three basal foveae and with subhumeral fovea and lateral sulcus. Abdominal tergites without discal carinae. Prosternum with pair of lateral procoxal foveae. Mesoventrite with two median mesoventral foveae and two lateral mesoventral foveae. Metaventrite with pair of lateral mesocoxal and pair of lateral metaventral foveae. Mesocoxal cavities may not be fully closed. Abdominal sternite 2 with pair of

basolateral foveae. Coxae 2 and 3 contiguous. Male: abdominal sternite 7 (IX) with penial plate. 4 species on Primorye, Sakhalin and Southern Kurils, another species, *R. camponoti* (Lea) known from Australia. Beetles live in decayed wood.

1. Each elytron with 3 basal foveae 2
- Each elytron with 2 basal foveae 3
2. Antennal club more elongate, antennomere 10 only 1.5 times wider than length, antennomere 11 more than 1.5 times longer than width. Male: anterior edge of frons with 5 long but poorly visible setae diverging from common centre; tibia 1 with denticle at middle of mesal margin; femur 2

with large rounded denticle at base; trochanter 3 with long denticle curved backward; penial plate as in Fig. 217; aedeagus as in Figs 211–212. Red-brown, 1.3–1.5 mm

- *parabile* Kurbatov, 1991
- Antennal club less elongate, antennomere 10 more than twice wider than length, antennomere 11 at most 1.2 times longer than width. Male: legs without pronounced secondary sexual characters; penial plate as in Fig. 218; aedeagus as in Figs 213–214. Light-brown, 1.35–1.4 mm
- *captiosum* Kurbatov, 2022
3. Antennomeres 4 and 5 as long as wide. Male: apical lobe of aedeagus (when viewed dorsally) strongly curved, with hook-shaped apex (Figs 209–210); penial plate as in Fig. 216. Yellowish-brown, 1.35 mm
- *svetlanae* Kurbatov, 2022
- Antennomere 5 and often 4 slightly wider than length. Male: apical lobe of aedeagus (when viewed dorsally) almost straight, only at apex with small denticle (Figs 207–208); penial plate as in Fig. 215. Light-brown, 1.25–1.35 mm .
- *lovtsovae* Kurbatov, 2022

Batrisus Aubé, 1833 (Figs 219–220). Maximal width of the 4th segment of the maxillary palpi is just after the middle (Fig. 226). Antennae and legs very robust. Pronotum with median antebasal and two lateral antebasal foveae connected by antebasal sulcus (another sulcus extends from lateral antebasal foveae anteriorly), and laterally with



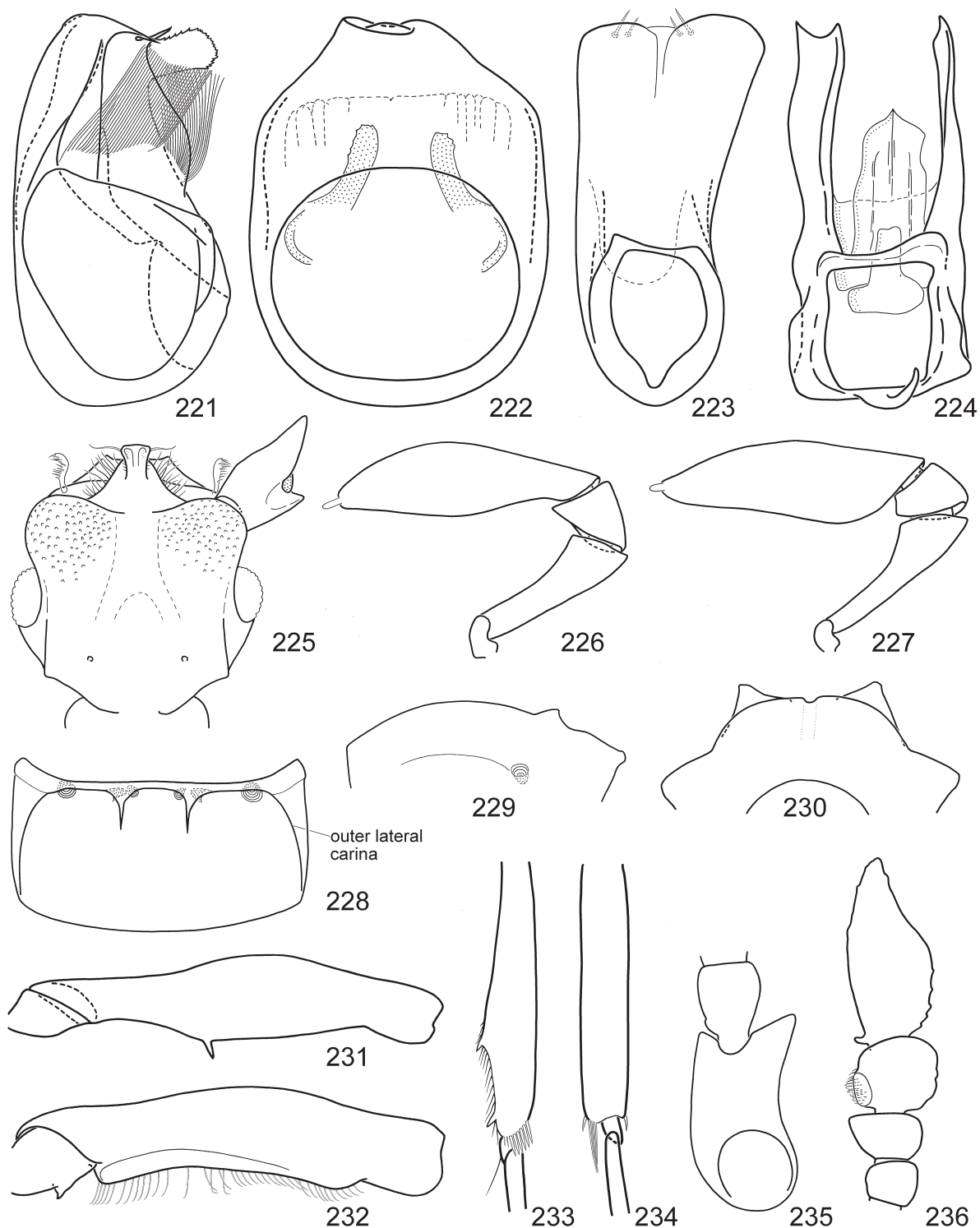
Fig. 219. *Batrisus sibiricus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 219. *Batrisus sibiricus* (фото С. Курбатова и Ю.А. Ловцовой).



Fig. 220. *Batrisus politus* (photo K.V. Makarov).
Рис. 220. *Batrisus politus* (фото К.В. Макарова).

4 basal impressions touching its posterior margin. Each elytron with 3 basal foveae and with more or less distinct lateral sulcus. Tibiae 3 with a long dense apicomeresal tuft of adherent setae (roughly as shown in Fig. 234). Males: 10th antennomere on underside with keel or fovea and lamina, 11th on underside at base with tubercle or spinule. 2 species (6 in Palaearctic). The generic systematics of *Batrisini*, which includes this and the following three genera, is poorly developed.

1. Body smooth, shining, not pubescent and not punctured; only frons at level of antennal tubercles punctured. Posterior margin of eyes without spine. Antennomeres 2–10 distinctly transverse. Aedeagus as in Fig. 223. Body length 2.9–3.0 mm
- *politus* Sharp, 1883
- Body more or less matt, with dense short adjacent pubescence, head and elytra entirely with dense punctation, pronotum densely punctured in posterior half, abdomen with very fine indistinct punctation. Posterior margin of eyes with projecting spine. 2–10 antennomeres generally more or less isodiametric, only 4–8 antennomeres slightly wider than length. Aedeagus as in Fig. 222. Body length 2.9–3.3 mm
- *sibiricus* Sharp, 1874



Figs 221–236. Details of Batrisitae: 221, 232 — *Dendrolasiophilus subitus*; 222, 226 — *Batrisis sibiricus*; 223 — *Batrisis politus*; 224, 225 — *Batrisodes vestitus*; 227–231, 233–236 — *Batrisodes tichomirovae*; 221–224 — aedeagi; 225 — head of male; 226, 227 — maxillary palpi; 228 — abdominal tergite 1 (IV); 229, 230 — pronotum laterally and frontally; 231 — mesofemur of male; 232 — metafemur of male; 233 — distal ¼ of male mesotibia laterally; 234 — distal half of metatibia dorsally; 235 — antennomeres 1 and 2 of male; 236 — apical part of male antenna; 222 — after Besuchet, 1979; 224, 225 — after Nomura, 2003, with modifications.

Рис. 221–236. Детали строения Batrisitae; 221–224 — эдеагусы; 225 — голова самца; 226, 227 — нижнечелюстные щупики; 228 — 1 (IV) тергит брюшка; 229, 230 — переднеспинка, вид сбоку и спереди; 231 — среднее бедро самца; 232 — заднее бедро самца; 233 — дистальные ¼ средней голени самца, вид сбоку; 234 — дистальная половина задней голени, вид сверху; 235 — 1-й и 2-й членики усика самца; 236 — верхняя часть усика самца; 222 — из Besuchet, 1979; 224, 225 — из Nomura, 2003, с изменениями.

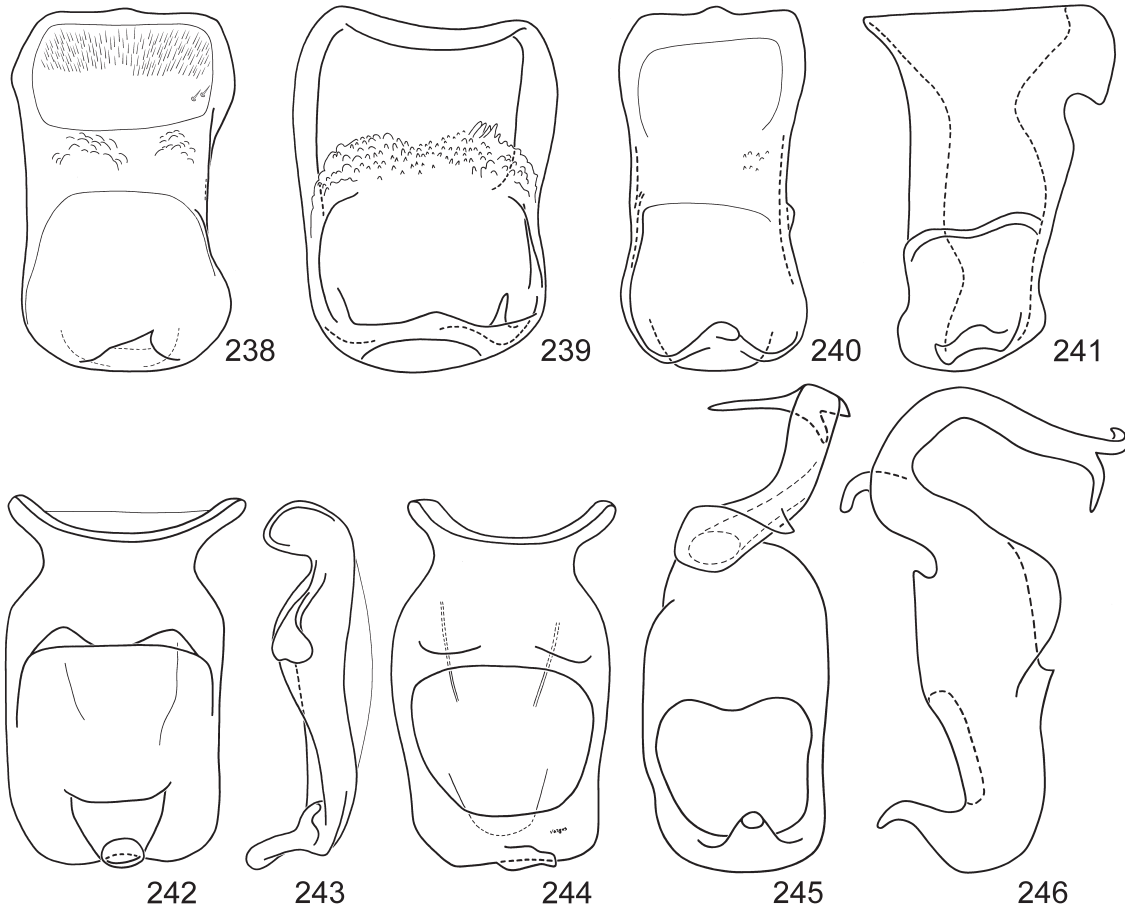
Fig. 237. *Batrisodes tichomirovae* (photo M.E. Smirnov).
Рис. 237. *Batrisodes tichomirovae* (фото М.Э. Смирнова).



Batrisodes Reitter, 1882 (Fig. 237). Maximal width of 4th palpal segment is usually in the basal half (Fig. 227). Two conical tubercles between lateral and median antebasal foveae of pronotum (Figs 229–230). Antennae and legs thinner than in *Batrisus*. Tibiae 3 with long and thin dense apicomeseal tuft of adherent setae (Fig. 234). Male: secondary sexual characters more often localised on anterior part of head and antennae; trochanters 2 usually with spine; femora 2 near middle of mesal margin usually with small curved spine (Fig. 231). A species-rich Holarctic genus. 7 species in the Russian Far East. The boundaries of the genus are not sufficiently delimited.

1. Small species, body length not more than 1.75 mm 2
 – Large species, body length not less than 2.0 mm 3

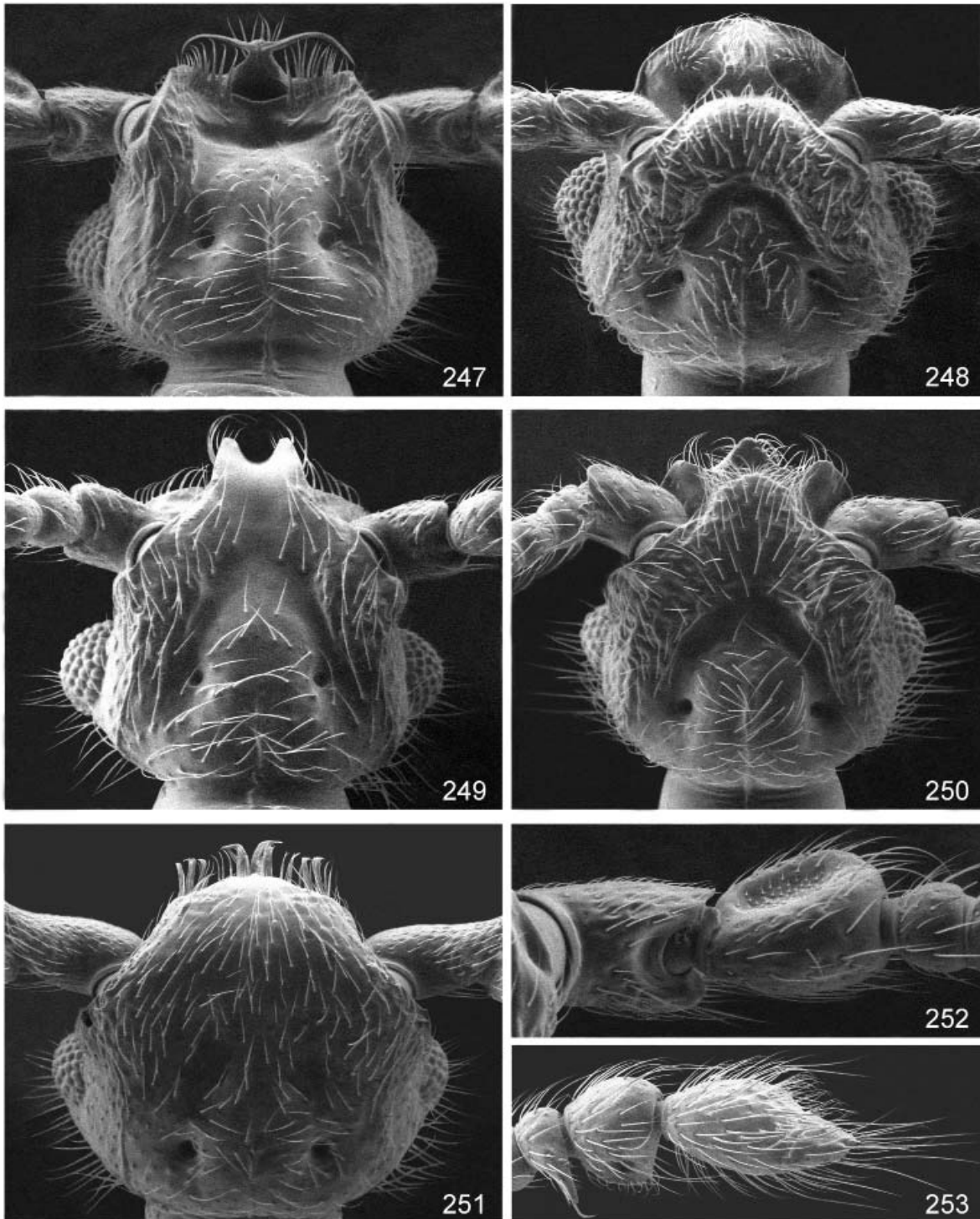
2. Pronotum practically not punctate. Discal carinae of abdominal tergite 1 completely absent. Male: anterior margin of frons semicircularly protruding forward, its inferior part with fringe of hairs; slightly in front protrudes small pubescent horn with rounded apex (Fig. 248); underside of 10th antennomere with small fovea; underside of 11th antennomere on base with thin, long denticle; femora 1 without notch on base of mesal margin. Aedeagus as in Figs 242–243. Body length 1.7 mm *tornatilis* Kurbatov, 1990



Figs 238–246. Aedeagi of *Batrisodes* spp.: 238 — *B. pruinosus*; 239 — *B. harmandi*; 240 — *B. tichomirovae*; 241 — *B. singularis*; 242–243 — *B. tornatilis*; 244 — *B. vargus*; 245–246 — *B. cornutus*; 238–242, 244, 245 — dorsally; 243, 246 — laterally
Рис. 238–246. Эдеагусы видов рода *Batrisodes*; 238–242, 244, 245 — вид сверху; 243, 246 — вид сбоку.

– Pronotum with dense, fine punctation. Discal carinae of abdominal tergite 1 short, less than 1/5 of segment length. Male: anterior margin of frons without modifications; antennomere 10 without fovea, underside

of antennomere 11 at base with thin and long tooth; femora 1 at base of mesal margin distinctly semicircularly notched. Aedeagus as in Fig. 244. Body length 1.75 mm *vargus* Kurbatov, 1992



Figs 247–253. Details of males of *Batrisodes* spp.: 247, 252 — *B. singularis*; 248 — *B. tornatilis*; 249 — *B. cornutus*; 250, 253 — *B. harmandi*; 251 — *B. tichomirovae*; 247–251 — head without mouthparts; 252 — antennomeres 1–3; 253 — antennomeres 9–11.

Рис. 247–253. Детали строения самцов видов рода *Batrisodes*; 247–251 — голова без ротовых органов; 252 — 1–3-й членики усиков; 253 — 9–11-й членики усиков.

3. Lateral longitudinal sulci of pronotum superficial, very slightly expressed. Article 4 of maxillary palpi widest just after the middle. Male: frons straightly passing to clypeus, forming frontoclypeus, which is provided with flattened tubercle, smooth and glabrous; antennomeres 10 and 11 simple; femora 2 with tiny tubercle at middle of mesal margin. Aedeagus as in Fig. 238. Body length 2.4–2.6 mm *pruinus* Reitter, 1889
- Lateral longitudinal sulci of pronotum well expressed. Article 4 of maxillary palpi widest in basal half. Male: femora 2 with a sharp spine near the middle of the mesal margin 4
4. Mesal (if antennae directed forwards) apical angle of antennomere 1 (especially in males) protruding much more strongly than outer apical one (Fig. 235). Male: anterior margin of frons broad, truncated or rounded when viewed from above, overhanging above clypeus (Fig. 251); antennomere 9 angularly projecting downwards; antennomere 10 large, with fovea at base of underside, antennomere 11 with small pointed projection at base of underside (Fig. 236). Aedeagus as in Fig. 240. Body length 2.2–2.5 mm *tichomirovae* Löbl, 1973
- Apical angles of antennomere 1 equally protrude 5
5. Elytra with relatively coarse and dense punctation, distances between punctures on average approximately equal to diameter of individual puncture; discal stria

short, reaching only 1/3 of elytral length. Male: anterior margin of frons with two “horns” bent downwards (Fig. 249); antennomere 10 with small fovea at base of underside, antennomere 11 with denticle at base of underside. Aedeagus as in Figs 245–246. Body length 2.1 mm *cornutus* (Kurbatov, 1984)

- Elytra in fine superficial punctation, distances between punctures averaging twice the diameter of an individual puncture; discal stria extending to mid-length of elytra 6
6. Antennomere 2 about half as long as 1 in both sexes, without modification. Male: underside of antennomere 9 with long acute projection, 10th segment broadened, with large fovea on underside (Fig. 253). Aedeagus as in Fig. 239. Body length 2.1–2.2 mm *harmandi* Raffray, 1904
- Antennomere 2 in ♀ slightly shorter than 1, simple, in ♂ approximately as long as 1 and strongly widened, with large rounded impression on upper side (Fig. 252); male antennomeres 9–10 unmodified. Aedeagus as in Fig. 241. Body length 2.0 mm *singularis* Kurbatov, 1985

Basitrodes Jeannel, 1958 (Fig. 254). Very close to *Batrisus* and *Batrisodes*. Characterised by the structure of the aedeagus, which consists of a closed basal capsule with 2 long apophyses. Tibiae 3 with long apicomeral spine. 1 species; several more species in Japan and South Korea.

1. Large species, body length about 3 mm. Male: frons straightly passing to clypeus, which is provided with apophysis sticking forward (Fig. 225); antennomere 1 strongly enlarged, its inner apical angle protruding much more strongly than outer one; antennomeres 10 and 11 simple; tibiae 1 with sharp tooth on middle of mesal margin, and then, in distal half, distinctly incised; underside of trochanters 2 with tooth; aedeagus as in Fig. 224. Body length 2.8–3.2 mm *vestitus* (Sharp, 1883)



Fig. 254. *Basitrodes vestitus* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 254. *Basitrodes vestitus* (фото С. Курбатова и Ю.А. Ловцовой).



Fig. 255. *Dendrolasiophilus subitus* (photo by A.V. Kovalev after Kurbatov & Kovalev, 2022).
Рис. 255. *Dendrolasiophilus subitus* (фото А.В. Ковалёва из Kurbatov & Kovalev, 2022).

Dendrolasiophilus Nomura, 2010 (Fig. 255) (for the corrected year of description see Kurbatov et Kovalev, 2022). Maximal width of 4th segment of maxillary palpi is just after the middle. Pronotum with mediobasal and two lateral foveae. Each elytron with only one basal fovea, without lateral sulcus. Tibiae 3 without long dense apicomeral tuft of adherent setae. 1 species in Primorye, 4 more species in Japan and China.

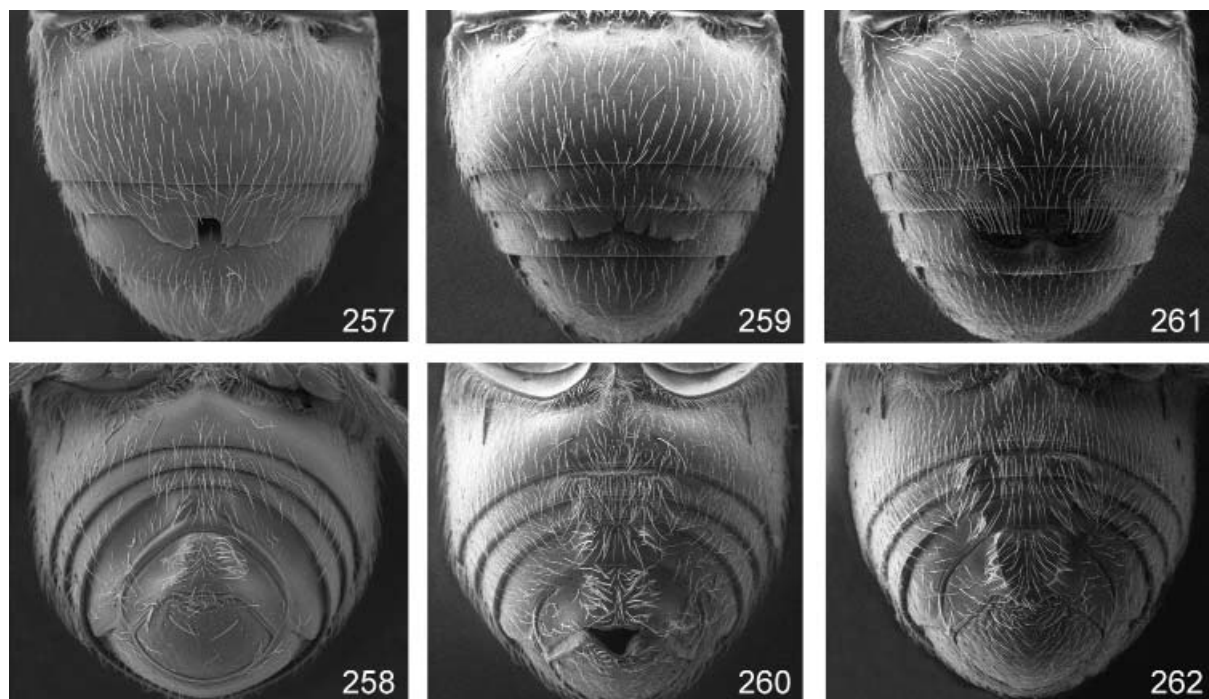
1. Body smooth, shining, only anterior margin of frons and to a lesser degree antennal tubercles with fine wrinkling and tangled punctation. Antennomeres 2–6 with strong punctation, which gradually weaken to apex of antennae. Male: Tibiae 2 with bent apicomeral spur; trochanters 3 with denticle, femora 3 modified as in Fig. 232; tibiae 3 without obvious modification. Aedeagus as in Fig. 221. Body length 2.8 mm *subitus* Kurbatov et Kovalev, 2022

Batriscenellus Jeannel, 1958 (Fig. 256). Eyes large, at lateral view distinctly longer than temples. Abdominal tergite 1 many times longer than tergites 2 or 3; outer oblique lateral carinae of tergite 1 practically not expressed (Figs 257, 259, 261), compare, for example, with Fig. 228; abdominal tergite 3 of males with deep excavation, sometimes covered by row of setae of posterior margin of tergite 2. Oriental genus, there are 3 species in the Russian Far East.

1. Discal stria of elytra uniformly and very slightly curved toward suture. Discal carinae of abdominal tergite 1 short, not reach 1/5 length of segment. Male: posterior margin of abdominal tergite 2 with fringe of simple setae, not hiding excavation of tergite 3 (Fig. 261). Median elevated part of male abdominal sternites 3–6 distinctly keeled on sides (Fig. 262). Aedeagus as in Figs 267–268. Body length 2 mm *fallax* (Sharp, 1883)

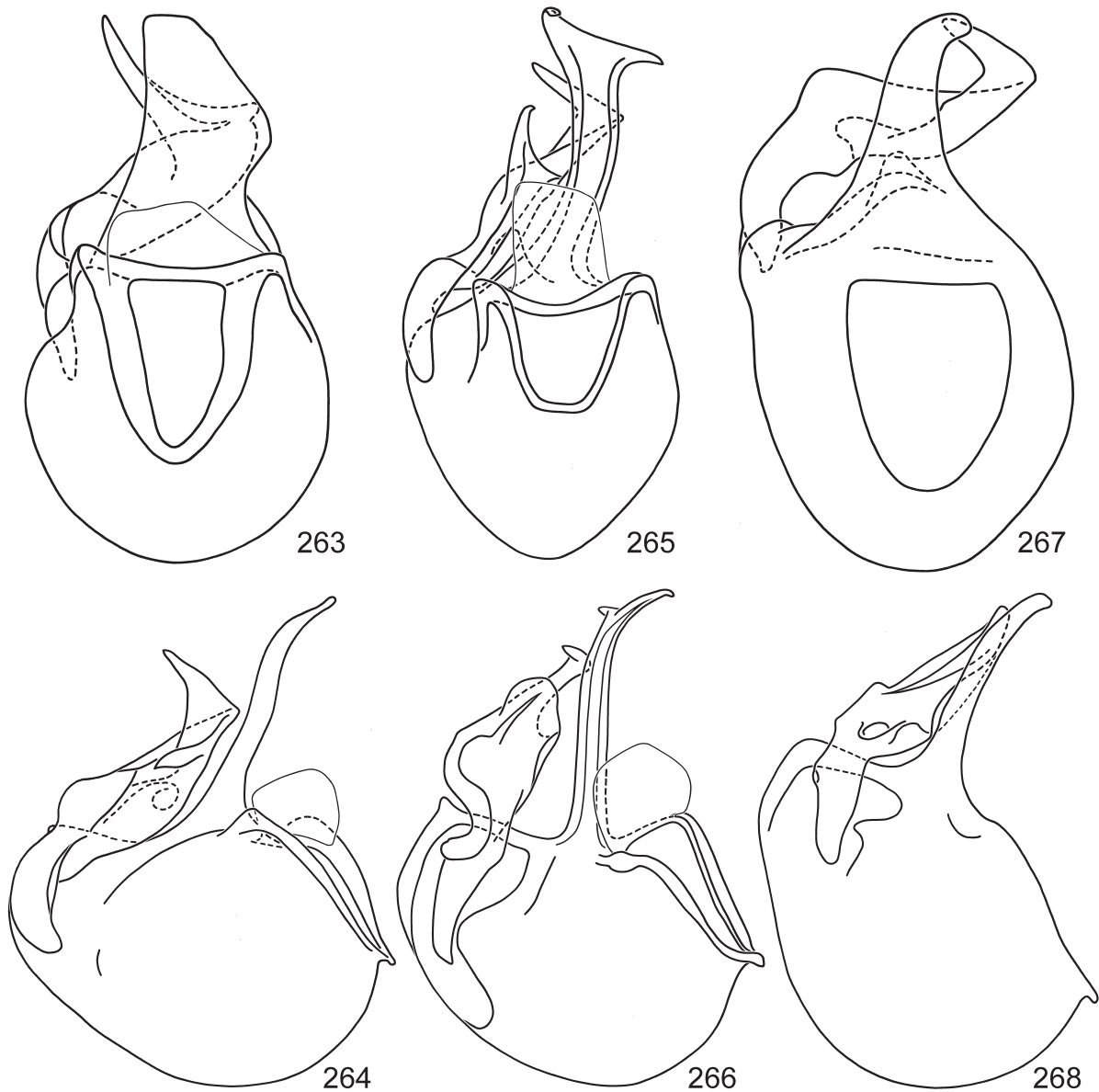


Fig. 256. *Batriscenellus vicarius* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 256. *Batriscenellus vicarius* (фото С. Курбатова и Ю.А. Ловтцовой).



Figs 257–262. Abdomen of *Batriscenellus* spp.: 257–258 — *B. admonitor*; 259–260 — *B. vicarius*; 261–262 — *B. fallax*; 257, 259, 261 — dorsally; 258, 260, 262 — ventrally.

Рис. 257–262. Брюшко видов рода *Batriscenellus*; 257, 259, 261 — вид сверху; 258, 260, 262 — вид снизу.



Figs 263–268. Aedeagi of *Batriscenellus* spp.: 263–264 — *B. vicarius*; 265–266 — *B. admonitor*; 267–268 — *B. fallax*; 263, 265, 267 — dorsally; 264, 266, 268 — laterally; 263–264 — after Löbl, 1973;

Рис. 263–268. Эдеагусы видов рода *Batriscenellus*; 263, 265, 267 — вид сверху; 264, 266, 268 — вид сбоку; 263–264 — из Löbl, 1973;

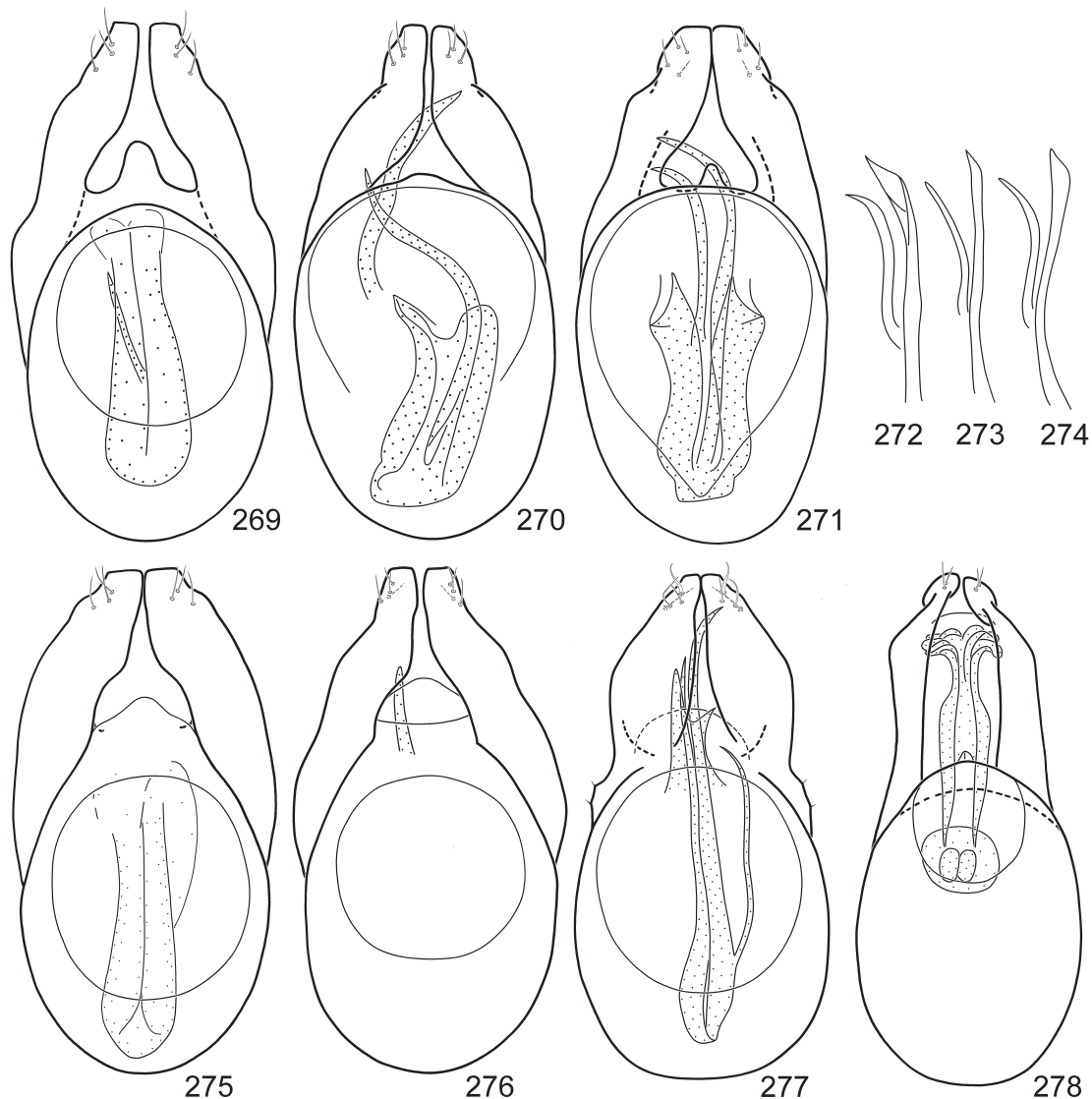
– Discal stria of elytra not bent toward suture. Discal carinae of tergite 1 longer, slightly longer than $\frac{1}{4}$ length of segment. Male: posterior margin of abdominal tergite 2 with very dense fringe of vitreous setae, wholly or almost wholly covering excavation of tergite 3 (Figs 257, 259). Male abdominal sternites 3–6 without clear lateral borders of their middle part (Figs 258, 260) 2
 2. Occipital carina distinct, passing forward between vertexal foveae and reaching posterior margin of transverse branch of frontal sulcus. Discal stria of elytra at apex rather distinctly curved to outer margin of elytra. Male: abdominal tergite 2 before apex impressed, its posterior margin on sides from this impression slightly elevated and not strongly (sometimes very slightly) semicircularly protrude; apex

of tergite 3 with small median tubercle, but tergal posterior margin straight (Fig. 259); tibiae 2 with very small sharp apicomeral tooth. Female: tergite 3 at apex uniformly rounded. Aedeagus as in Figs 263–264. Body length 2.1–2.3 mm *vicarius* Löbl, 1973
 – Occipital carina indistinct, not passing forward beyond level of midline of vertexal foveae. Male: abdominal tergite 2 without impressions; apex of tergite 3 at middle more or less extended backwards and pubescent (Fig. 257); tibiae 2 with rather thick, bluntly rounded apicomeral tooth. Female: apex of tergite 3 at middle not strongly angularly elongated. Aedeagus as in Figs 265–266. Body length 2.1–2.2 mm *admonitor* Kurbatov, 1990

Bryaxis Kugelann, 1794 (Fig. 310). Maxillary palpi large, underside of palpomeres 2 and 3 sometimes with small tubercles, palpomere 4 as long as head or somewhat shorter, without tubercle or impression on upper side (Fig. 102). Pronotum with two lateral antebasal foveae united by antebasal sulcus. In males, mesal margin of anterior tibiae more often excised apically; antennomeres 1 and 2 modified (in our Far Eastern species antennomere 1 more often simple, and 2nd modified; *Bryaxis extremalis* has a modified antennomere 9 as an exception); underside of head often with depression (Fig. 100). In males it is often possible to observe intraspecific forms, called *gracilipes* and *inflatipes*, occurring together, characterized by degree of thickening of legs, and sometimes also thickening of the pronotum and parameres of aedeagus. In addition, there are forms *macropterus*, *micropterus* and *apterus* according

to the degree of development of wings, as well as forms *ornaticornis* and *simplicicornis*. In the Far Eastern species *B. asciicornis* there are several forms of males differing in the degree of development of the 2nd antennomere. The genus is very species-rich, numbering about 370 species. Almost all of them occur within the Palearctic, but 1 species is described from tropical China (Hainan Island) [Yin, 2023] and two not yet described species were found by the author in Burma and Laos (only females). In the Far East, 10 species have been recorded.

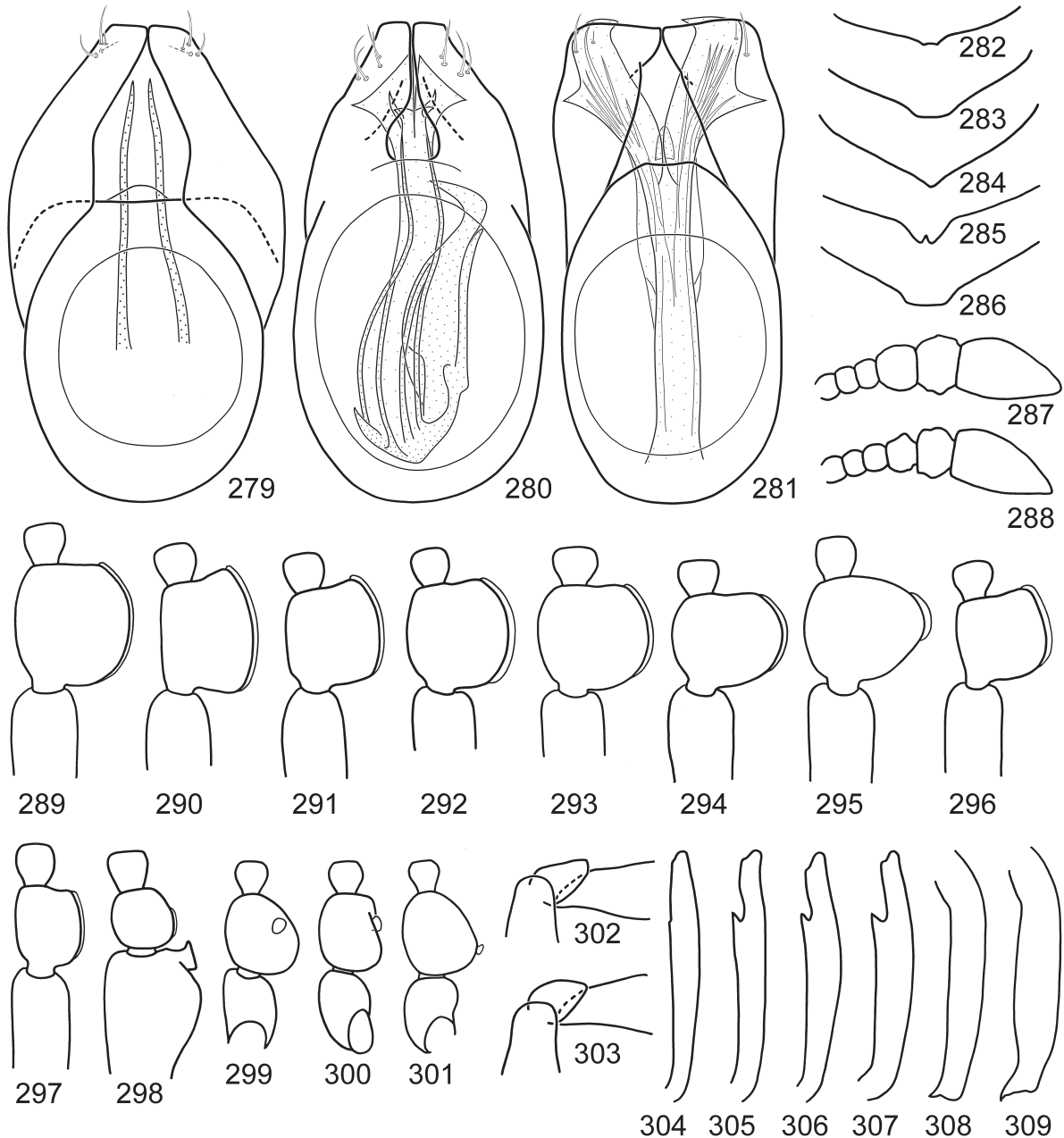
1. Apex of anterior margin of trochanters 1 angularly protrude (Fig. 302). Male: antennomere 1 subcylindrical, antennomere 2 strongly thickened, with keel along mesal margin, and with long setae on upper side (Figs 289–297) (species group *ussuriensis*); last abdominal sternite of males with pointed apex (Fig. 284) 2



Figs 269–278. Aedeagi (269–271, 275–278) and elements of their internal sac (272–274) of *Bryaxis* spp.: 269 — *B. ussuriensis*; 270 — *B. asciicornis*; 271–274 — *B. sichotensis*; 275 — *B. amurensis*; 276 — *B. validicornides*; 277 — *B. testatus*; 278 — *B. humilis*.

Рис. 271–280. Эдеагусы (269–271, 275–278) и элементы их внутреннего мешка (272–274) видов рода *Bryaxis*.

- Anterior margin of trochanters 1 uniformly rounded (Fig. 303). Male: antennomeres 1 and 2 (Figs 298–301) and last abdominal sternites (Figs 282–283, 285–286) differently arranged 7
- 2. Male: antennomere 2 with short keel, occupying only median part of its mesal margin and not longer than antennomere 3 (Fig. 295). Aedeagus as in Fig. 276. Body length 1.45–1.5 mm *validicornides* Newton, 2015
- Male: antennomere 2 with long keel, occupying most of mesal margin of segment and at least twice as long as antennomere 3 3
- 3. Aedeagus small, 0.29–0.30 mm long, armature of inner sac very indistinct 4
- Aedeagus rather large, 0.31–0.36 mm long, armature of inner sac well expressed, with two or more long thin spines 5



Figs 279–309. Details of *Bryaxis* spp.: 279, 282, 301, 303 — *B. japonicus*; 280, 286, 298, 306, 307, 309 — *B. koltzei*; 281, 285, 287, 288, 304, 305, 308 — *B. extremalis*; 283, 299, 300 — *B. humilis*; 284, 293, 294, 302 — *B. ussuriensis*; 289–291 — *B. ascicornis*; 292 — *B. sichotensis*; 295 — *B. validicornides*; 296 — *B. testatus*; 297 — *B. amurensis*; 279–281 — aedeagi; 282–286 — apical abdominal sternite of males; 287 — male antennal apex; 288 — female antennal apex; 289–301 — male antennal base; 302–303 — protibiae of male, *f. gracilipes*; 305, 307 — protibiae of male, *f. inflatipes*; 308–309 — metatibiae of male, *f. inflatipes*.
Рис. 279–309. Детали строения видов рода *Bryaxis*: 279–281 — эдеагусы; 282–286 — верхний стернит брюшка самца; 287 — верхняя часть усика самца; 288 — верхняя часть усика самки; 289–301 — основание усика самцов; 302–303 — передние вертлуги; 304, 306 — передние голени самца, *f. gracilipes*; 305, 307 — передние голени самца, *f. inflatipes*; 308–309 — задние голени самца, *f. inflatipes*.



Fig. 310. *Bryaxis extremalis* (photo K.V. Makarov).
 Рис. 310. *Bryaxis extremalis* (фото К.В. Макарова).

4. Male: antennomere 2 large, 0.10–0.115 mm long, at least 2.5 times longer and wider than antennomere 3 (Figs 293–294). Aedeagus as in Fig. 269. Body length 1.45–1.5 mm *ussuriensis* Löbl, 1964
 – Male: antennomere 2 relatively small, 0.07–0.08 mm long, 2 times longer and wider than antennomere 3 (Fig. 297). Aedeagus as in Fig. 275. Body length 1.4–1.5 mm *amurensis* Kurbatov, 1985
5. Male: outer basal margin of paramere straightly cut and there bearing two very small bristles (Fig. 277); antennal base as in Fig. 296. Body length 1.5 mm *testatus* Kurbatov, 1994
 – Male: outer basal margin of paramere weakly evenly rounded, devoid of bristles 6
6. Male: mesal margin of tibia 1 with sharp denticle in distal third and then distinctly excised; antennomere 2 not variable (Fig. 292) Aedeagus as in Figs 271–274. Body length 1.45–1.5 mm *sichotensis* Kurbatov, 1994
 – Male: mesal margin of tibia 1 slightly flattened in distal third, without denticle; several forms of males, differing in the degree of development of the antennomere 2 (Figs 289–291). Aedeagus as in Fig. 270. Body length 1.45–1.5 mm *asciicornis* Kurbatov, 1985
7. Small species, not longer than 1.4 mm. Male: antennomere 1 simple, subcylindrical, antennomere 2 strongly thickened and inside provided with small tubercle 8
 – Larger species, not shorter than 1.5 mm. Male: antennae differently arranged 9
8. Male: antennomere 2 (Figs 299–300) on upper side with rather large and shallow impression, with small flattened tubercle in its centre, last abdominal sternite (Fig. 283) with broad apical projection. Aedeagus as in Fig. 278. Body length 1.25–1.4 mm *humilis* Raffray, 1909
 – Male: antennomere 2 (Fig. 301) without impression, but with very small tubercle on mesal margin, last abdominal sternite (Fig. 282) with weak apical projection. Aedeagus as in Fig. 279. Body length 1.35–1.4 mm *japonicus* (Sharp, 1874)
9. Frons between antennae distinctly angular. Punctuation of pronotum extremely dense, distance between punctures much less than diameter of individual puncture; elytra less densely punctured. Antennomeres 9 and 10 much wider than length. Male: antennomere 1 thickened, with rather large and flat apical tubercle on mesal margin; antennomere 2 with very indistinct keel on mesal margin (Fig. 298), last abdominal sternite (Fig. 286) with broad apical projection; males *f. gracilipes*: tibiae 1 (Fig. 306) with distinct apicomeseal notch; males *f. inflatipes*: tibiae 1 (Fig. 307) slightly thickened, with apicomeseal notch deeper, tibiae 3 (Fig. 309) strongly thickened, distinctly narrowed near apex, with large sharp apicomeseal tooth. Aedeagus as in Fig. 280. Body length 1.5–1.65 mm *koltzei* (Reitter, 1887)
 – Frons between antennae convex. Punctuation of pronotum less dense, punctures small; elytra punctured somewhat weaker. Antennomere 9 as long as wide, antennomere 10 slightly wider than long. Male: antennomeres 1 and 2 simple, antennomere 9 thickened compared to those of female (Figs 287–288), much larger than 8th, almost as wide as 10 or 11, last abdominal sternite (Fig. 285) with bidentate apical projection; males *f. gracilipes*: tibiae 1 (Fig. 304) not thickened, lacking apicomeseal notch; males *f. inflatipes*: tibiae 1 (Fig. 305) slightly thickened, with distinct apicomeseal notch, tibiae 3 (Fig. 308) thickened, with small apicomeseal tooth. Aedeagus as in Fig. 281. Body length 1.55–1.65 mm *extremalis* Kurbatov, 1990
- Tychobythinus* Ganglbauer, 1896 (Fig. 311). It is not clearly distinguished well from the genus *Bryaxis*. Characterized by longer and more slender antennomere 1, localization of secondary sexual characters (more often on underside of head, but not on antennomeres 1 and 2) and form of the aedeagus. Predominantly West Palaearctic genus with one species in the Russian Far East (more than 60 in total). One more species is known only from 1 female taken in the Jewish Autonomous Region; it is probably undescribed and is not included in the key.
1. Head, pronotum and elytra densely punctured. palpomeres 2 and 3 of maxillary palpi with numerous tubercles on underside. Male: antennomere 1 only two times longer than width; underside of head (Fig. 313) with large complex outgrowth at middle and with two large lanceolate bristles at base; tarsomeres 2 and 3 of tarsus 1 (Fig. 346) on underside with tubercle bearing pair of thick bristles. Aedeagus as in Fig. 319. Body length 1.05–1.2 mm *aino* Kurbatov, 1992



Fig. 311. *Tychobythinus aino* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 311. *Tychobythinus aino* (фото С. Курбатова и Ю.А. Ловцовой).

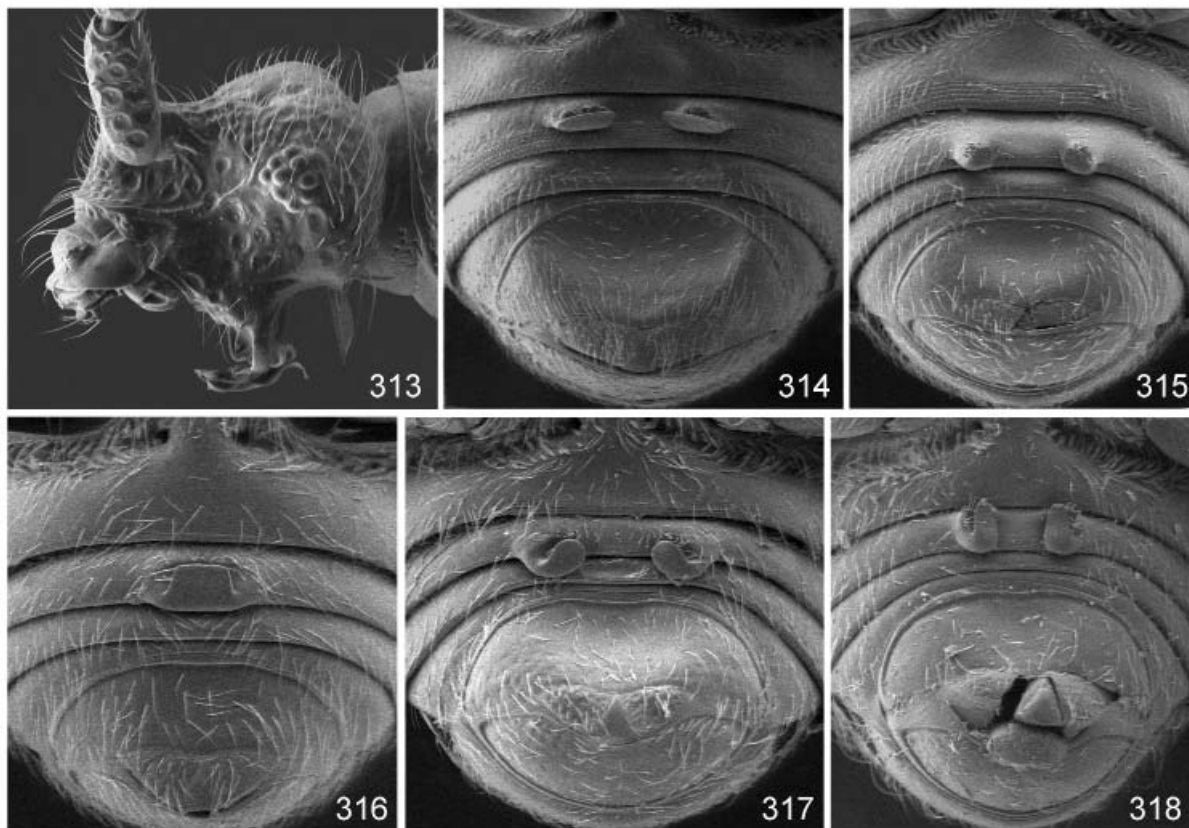
Rybaxis Saulcy, 1876 (Fig. 312). Body strongly convex. Head with two well expressed vertexal foveae and with rather deep impression between antennae. Pronotum (Fig. 3) with large lateral antebasal and very small median antebasal foveae united by antebasal sulcus. Each elytron with two basal foveae and with subhumeral fovea and lateral sulcus. Antennae, tibia 1, metaventricle, and abdominal sternites usually bear secondary sexual characters; IX abdominal sternite often poorly visible, split into 3 sclerites (Figs 314–318). The genus is distributed all over the world with the exception of South America.

1. Upperside of body more or less solid brown 2
– Elytra, and sometimes pronotum reddish, abdomen brown 3
2. Discal carinae of abdominal tergite 1 divergent, long, almost reach middle of tergite length. Male: antennomere 11 not modified; tibiae 1 (Fig. 335) with very small apicomesal tooth and with another tooth in the middle of mesal margin, trochanters 2 with tooth along inferior margin,

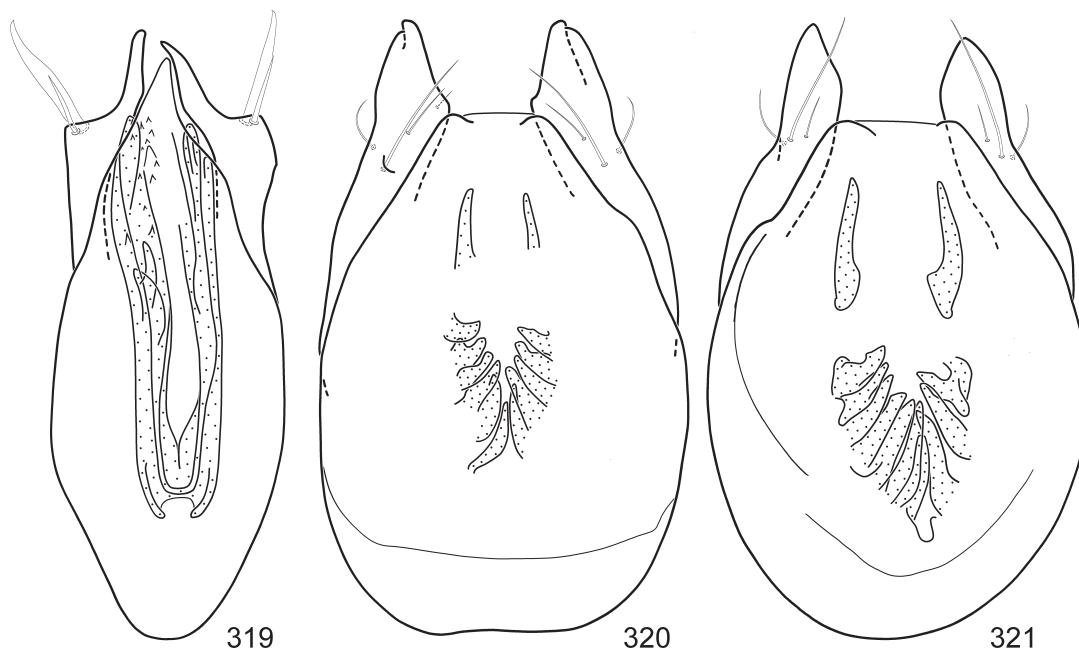
- tibiae 2 (Fig. 340) with apicomesal tooth slightly moved from apex; abdominal sternite 3 with two adjacent projections (Fig. 318). Aedeagus as in Fig. 323. Body length 1.9–2.1 mm *zelotypus* Kurbatov, 1992
- Discal carinae of abdominal tergite 1 more or less parallel, short, sometimes only barely visible from under posterior margin of elytra. Male: antennomere 11 not far from base of mesal margin with thin oblique tooth; tibiae 1 (Fig. 336) with relatively big apicomesal tooth and with another tooth in the middle of mesal margin; trochanters 2 without tooth; abdominal sternite 3 with slightly expressed median lamina (Fig. 316). Aedeagus as in Fig. 324. Body length 1.9–2.1 mm *lamellifer* Löbl, 1973
3. Male: trochanters 1 and 2 with denticle or spine on underside, femora 2 with denticle at base of mesal margin, tibiae 2 clearly narrowed near apex, with large curved notched apicomesal denticle 4
- Male: trochanters 1 and 2 without denticles or spines on underside, femora 2 without denticle at base of mesal margin, tibiae 2 (Fig. 339) in distal half with more or less parallel sides, with small simple apicomesal denticle; paired projections of abdominal sternite 3 as in Fig. 317. Aedeagus as in Fig. 322. Body length 2.0–2.3 mm
..... *pinguis* Kurbatov, 1990
4. Male: antennomeres 9 and 10 slightly wider than long, antennomere 11 as long as 8–10 combined (Fig. 331); trochanters 1 with rather long spine on underside; tibiae 1



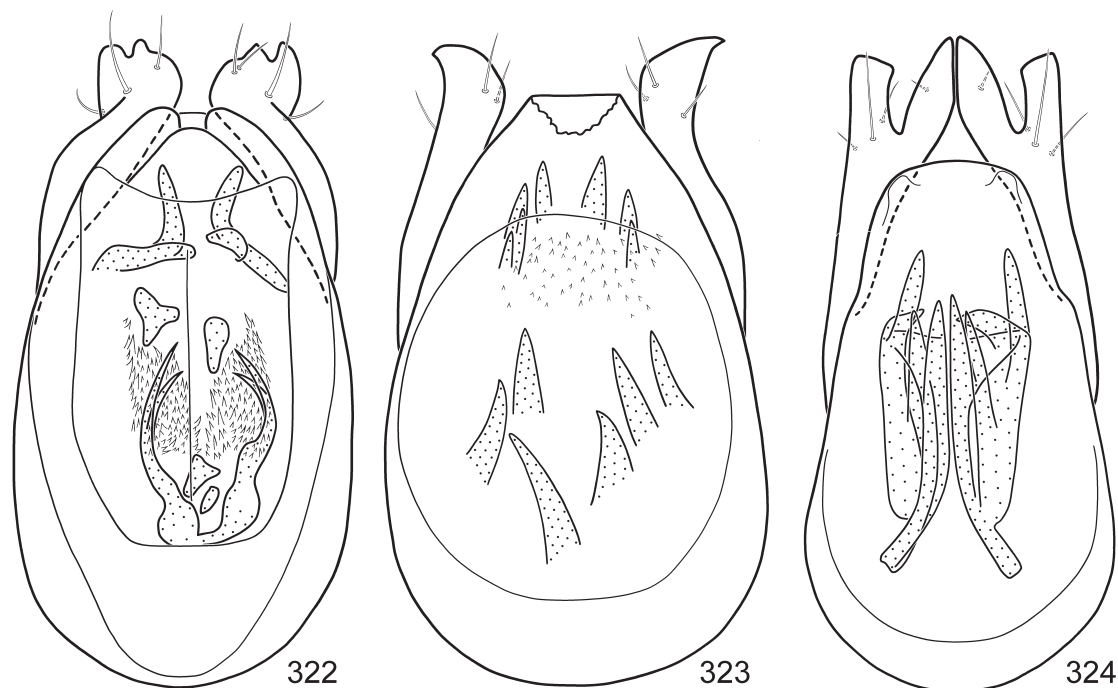
Fig. 312. *Rybaxis princeps* (photo K.V. Makarov).
Рис. 312. *Rybaxis princeps* (фото К.В. Макарова).



Figs 313–318. Details of males of Pselaphinae: 313 — *Tychobythinus aino*; 314 — *Rybaxis princeps*; 315 — *Rybaxis nigrescens*; 316 — *Rybaxis lamellifer*; 317 — *Rybaxis pinguis*; 318 — *Rybaxis zelotypus*; 313 — head laterally without maxillary palpi; 314–318 — abdomen ventrally.
Рис. 313–318. Детали строения самцов Pselaphinae; 313 — голова без нижнечелюстных щупиков, вид сбоку; 314–318 — брюшко, вид снизу.



Figs 319–321. Aedeagi of Pselaphinae: 319 — *Tychobythinus aino*; 320 — *Rybaxis princeps*; 321 — *Rybaxis nigrescens*.
Рис. 319–321. Эдеагусы Pselaphinae.



Figs 322–324. Aedeagi of Pselaphinae: 322 — *Rybaxis pinguis*; 323 — *Rybaxis zelotypus*; 324 — *Rybaxis lamellifer*.
Рис. 322–324. Эдеагусы Pselaphinae.

- in apical part strongly curved, tooth of their mesal margin located almost at the level of basal third of tibiae length (Fig. 338), tibia 2 as in Fig. 342; paired projections of abdominal sternite 3 (Fig. 314) directed strictly downward when viewed laterally; parameres of aedeagus mesally concave, with apicomesal notch (Fig. 320). Body length 2.3–2.6 mm *princeps* (Sharp, 1874)
- Male: antennomeres 9 and 10 as long as large, article 11 as long as 9–10 combined (Fig. 332); trochanters 1 with small denticle on underside; tibiae 1 weakly curved in apical part, tooth of their mesal margin close to the middle of tibia length (Fig. 337), tibia 2 as in Fig. 341; paired projections of abdominal sternite 3 (Fig. 315) hooked forward; parameres of aedeagus mesally not concaves, without apicomesal notch (Fig. 321). Body length 1.9–2.3 mm
 *nigrescens* Jeannel, 1958

Reichenbachia Leach, 1826 (Fig. 325). Body strongly convex. Pronotum without antebasal sulcus (Fig. 4). Each elytron with two basal foveae, lacking subhumeral fovea and lateral sulcus. Male: antennae without secondary sexual characters, tibia 2 with small apical spurs. The genus is distributed all over the world except Australia and New Zealand. In Palearctic only 6 species.

1. Head unpunctured, pronotum and elytra densely punctured, but punctures small, superficial. Antennomere 2 oval, as long as 3, but wider. Male: trochanter 2 simple, tibia 2 with rather long apicomesal spur. Aedeagus as in Fig. 328. Body length 1.35 mm *commutabilis* Kurbatov, 2015



Fig. 325. *Reichenbachia commutabilis* (photo S. Kurbatov & Yu.A. Lovtsova).

Рис. 325. *Reichenbachia commutabilis* (фото С. Курбатова и Ю.А. Ловцовой).

Trissemus Jeannel, 1949 (Fig. 326). Pronotum without antebasal sulcus. Each elytron with three basal foveae, without subhumeral fovea and lateral sulcus. In males antennae very often with modified segments. The genus is very rich in species, distributed all over the world, except Australia and New Zealand. There is 1 species in the Russian Far East. American authors do not support this genus and place its representatives within the genus *Reichenbachia*, which is probably true, because there are *Trissemus* species with reduced number of basal elytral foveae. For example, *T. brittoni* Jeannel from Saudi Arabia has specimens with atrophy of the middle basal elytral fovea, sometimes even on only one elytron (Besuchet, 1981a).

1. Male: antennae (Fig. 333) with antennomeres 1–6 longer than width, antennomere 6 rather strongly enlarged, wider and much longer than 5, antennomere 11 at base with flat tubercle, which when viewed from under side is long and narrow with well-defined margins, and when viewed laterally sharply protrude forward; tibiae 2 (Fig. 343) with long flat apicomeral apophysis bearing a small spine at apex; tarsomere 2 of posterior tarsi distally widened (Fig. 345). Aedeagus as in Fig. 330. Body length 2.0 mm
..... *alienus* (Sharp, 1874)



Fig. 326. *Trissemus alienus* (photo K.V. Makarov).
Рис. 326. *Trissemus alienus* (фото К.В. Макарова).

Batraxis Reitter, 1882 (Fig. 327). Antennal club consists of 2 antennomeres. Elytra without discal striae. Number of foveae on dorsal side is affected by reduction: pair of vertexal foveae of head sometimes may be absent; median antebasal fovea of pronotum tends to be reduced; pair of basal elytral foveae also may disappear. Meso- and metaventrite as in Fig. 74. Secondary sexual characters of the male usually located on the trochanters 1 and tibiae 1. The structure of the sternite 7 (IX) of the male has been studied in preparation in *B. kawaharai* (Fig. 344) and two unidentified East Asian species; this sternite is distinctly split into 3 parts approximately as in representatives of the genus *Rybaxis* (see above). About 50 species from East Asia and Australia, 1 species known from Greece.

1. Head widest at level of antennal articulation, vertexal foveae almost completely lacking; antennomeres 8 and 9 short,

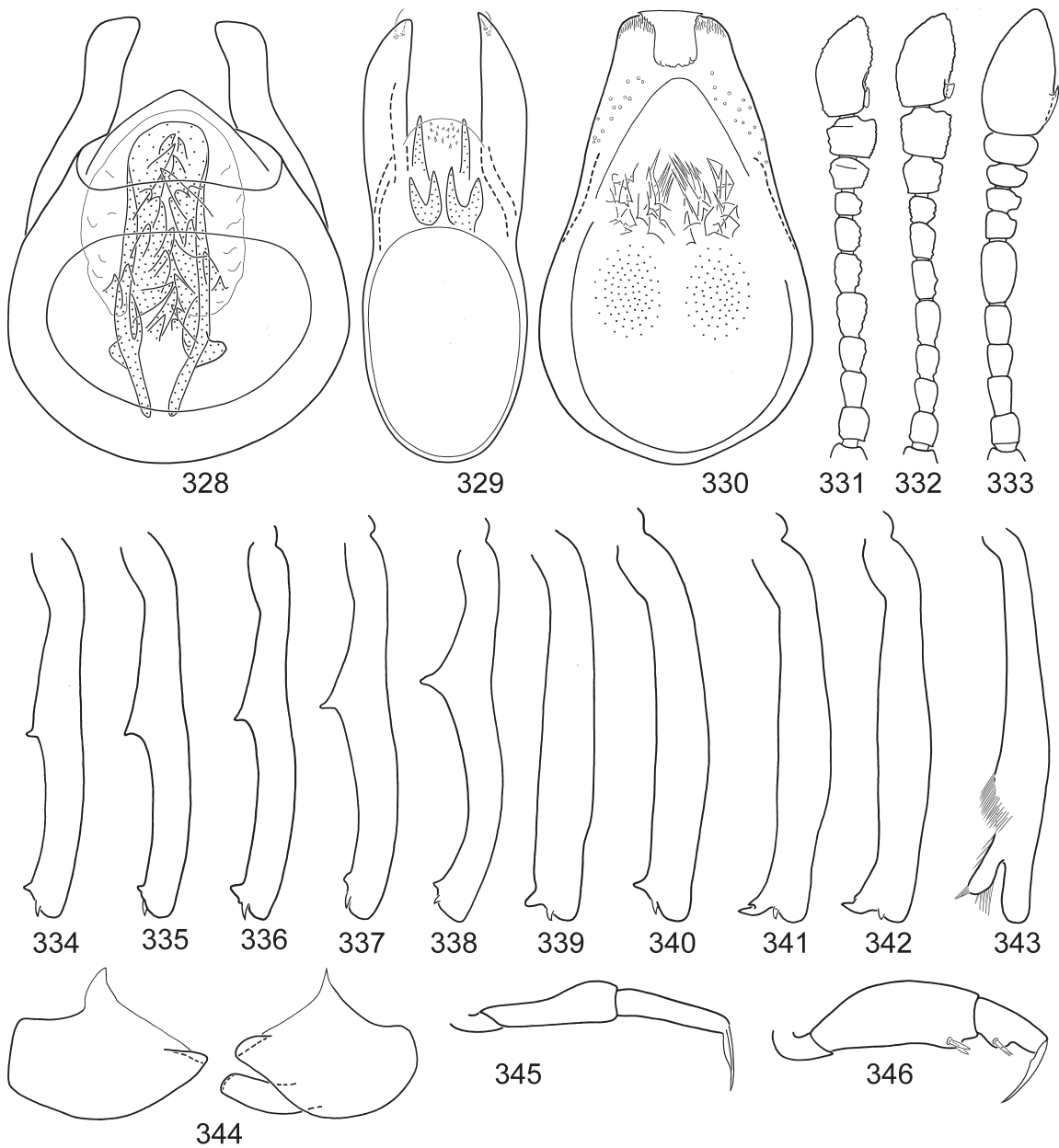


Fig. 327. *Batraxis kawaharai* (photo K.V. Makarov).
Рис. 327. *Batraxis kawaharai* (фото К.В. Макарова).

about as long as wide, much shorter than previous segments. Median antebasal and lateral foveae of pronotum very small; basal elytral foveae reduced. Discal carinae of abdominal tergite 1 reach $\frac{3}{4}$ of segment length, they are more or less parallel to each other and only distally slightly curved laterally. Male: trochanters 1 with large bilobed flattened apophysis sticking forward, with lower tooth bilobed; tibiae 1 with large and flat apicomese lamina. Aedeagus as in Fig. 329. Body length 2.7 mm
 *kawaharai* Maruyama et Sugaya, 2004

Tainochus Kurbatov, 1992 (Fig. 347). Underside of head at base with large tooth-like outgrowth (Fig. 107). Maxillary palpi with palpomere 3 much longer than wide, palpomere 4 with thin apical projection in addition to palpal cone (Fig. 104). Each elytron with three basal foveae. Aedeagus with well-developed long parameres, bearing at apex several bristles. Seven species in Japan, Korea and southern Russian Far East.

1. Antennae with antennomere 9 long as wide or slightly wider than long, considerably narrower than 10. Prono-



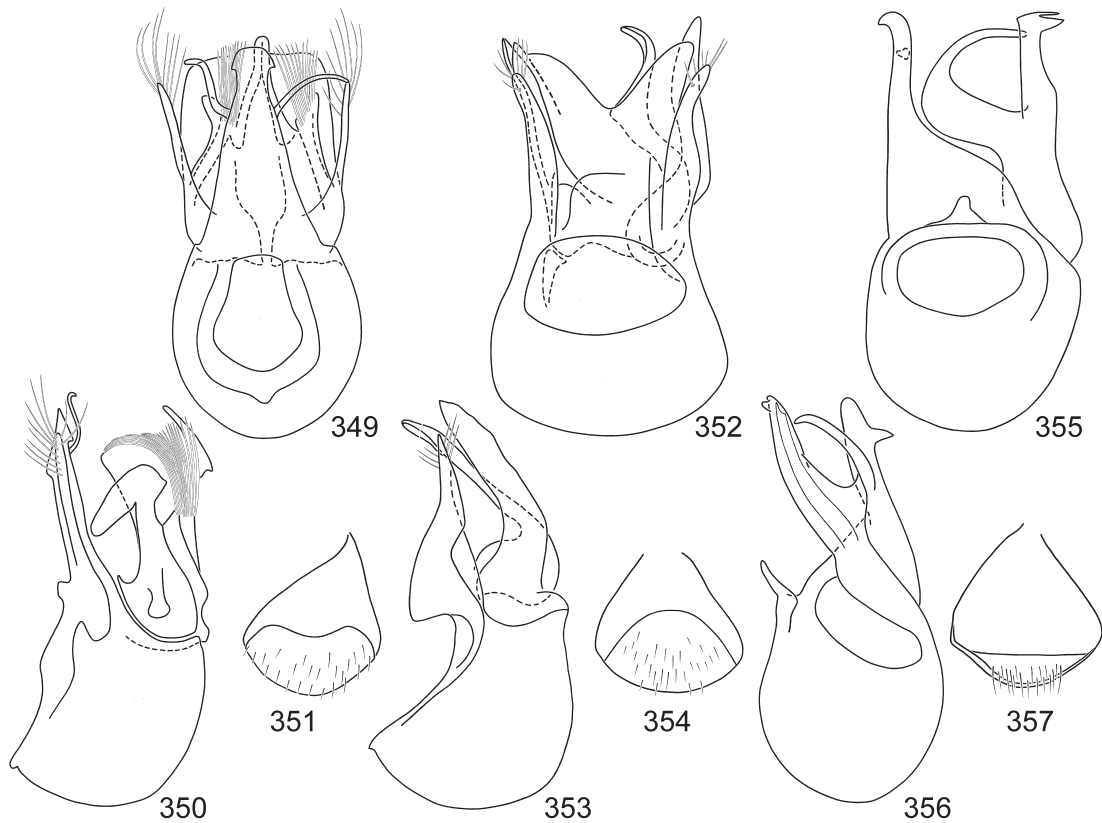
Figs 328–346. Details of Pselaphinae males: 328 — *Reichenbachia commutabilis*; 329, 344 — *Batraxis kawaharai*; 330, 333, 343, 345 — *Trissemus alienus*; 331, 338, 342 — *Rybaxis princeps*; 332, 337, 341 — *Rybaxis nigrescens*; 334, 339 — *Rybaxis pinguis*; 335, 340 — *Rybaxis zelotypus*; 336 — *Rybaxis lamellifer*; 346 — *Tychobythinus aino*; 328–330 — aedeagi; 331–333 — antennae; 334–338 — protibiae; 339–343 — mesotibiae; 344 — abdominal sternite IX; 345 — metatarsus; 346 — protarsus.

Рис. 328–346. Детали строения самцов Pselaphinae; 328–330 — эдеагусы; 331–333 — усики; 334–338 — передние голени; 339–343 — средние голени; 344 — IX брюшной стернит; 345 — задняя лапка; 346 — передняя лапка.



Fig. 347. *Tainochus imperator* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 347. *Tainochus imperator* (фото С. Курбатова и Ю.А. Ловцовой).

Fig. 348. *Tychus dichotomus* (photo K.V. Makarov).
Рис. 348. *Tychus dichotomus* (фото К.В. Макарова).



Figs 349–357. Details of Tychini: 349–351 — *Tainochus imperator*; 352–354 — *Tainochus exiguus*; 355–357 — *Tychus dichotomus*; 349–350, 352–353, 355–356 — aedeagi; 351, 354, 357 — abdominal sternite IX.
Рис. 349–357. Детали строения Tychini; 349–350, 352–353, 355–356 — эдеагусы; 351, 354, 357 — IX тергит брюшка.

tum very densely and roughly punctured. Male: median impression of metaventricle limited anteriorly by long outgrowth; abdominal sternite 7 (IX) with pubescent part bounded by broadly concave line (Fig. 351). Aedeagus as in Figs 349–350. Body length 1.6–1.7 mm

- *imperator* Kurbatov, 1992
- Antennae with antennomere 9 noticeably wider than long, barely narrower than 10. Pronotum practically not punctured. Male: median impression of metaventricle anteriorly without outgrowth; last abdominal sternite (Fig. 354) with pubescent part bounded by uniformly rounded line. Aedeagus as in Figs 352–353. Body length 1.5 mm
- *exiguus* Kurbatov, 1992

Tychus Leach, 1817 (Fig. 348). Underside of head without tooth-like outgrowth. Maxillary palpi (Fig. 101) with palpomere 3 much longer than wide, 4 segment without apical projection. Elytra with two basal foveae. Aedeagus with almost completely reduced parameres (see Kurbatov & Sabella [2008]). More than 150 species in the Holarctic.

- 1. Head and pronotum unpunctate. Frontal lobe rather narrow, with maximal width 0.15 mm. Male: trochanters 2 with denticle on underside; 2–5 abdominal sternites at middle with very superficial common impression; abdominal sternite 7 (IX) with pubescent part bounded by straight line (Fig. 357). Aedeagus as in Figs 355–356. Body length 1.4–1.5 mm
- *dichotomus* Nomura et Lee, 1992

Tyrus Aubé, 1833 (Fig. 358). Pubescence of the upper side of the body consists of short adjoining setae. Maxillary palpi with palpomeres 3 and 4 with short stalk-like base, palpomere 4 spindle-shaped. Abdominal tergites 1 and 2 approximately



Fig. 358. *Tyrus mucronatus* (photo K.V. Makarov).
Puc. 358. *Tyrus mucronatus* (фото К.В. Макарова).



Fig. 359. *Tyrodes segrex* (photo K.V. Makarov).
Puc. 359. *Tyrodes segrex* (фото К.В. Макарова).

of equal length, two following ones slightly shorter; tergite 1 with median carina. Male antennomere 1 without secondary sexual characters. About two dozen Holarctic and East Asian species.

- 1. Vertex and pronotum shining, finely punctured. Basal third of femora 1 mesally with rounded tubercle. Trochanters 2 with large flat projection, thicker and more convex in males. Black-brown, elytra reddish-brown. Aedeagus as in Fig. 363. Body length 2.2–2.4 mm
- *mucronatus* (Panzer, 1805)

Tyrodes Raffray, 1908 (Fig. 359). Pubescence of upper side of the body consists of rather long oblique setae. Pronotum with antebasal sulcus. Abdominal tergite 1 longer than 2. Femora 1 without tubercle on mesal margin. Trochanters 2 without projection. Male: antennomere 1 of antennae (Fig. 366) with big tooth at middle of outer margin. Dozen species in eastern and southern Asia.

- 1. Head in anterior half moderately and in posterior half weakly punctate, strongly convex in most posterior part. Male: lateral margin of frontoclypeus in front of eyes with rounded denticle; middle of metaventricle flattened with large tubercle in posterior half of this flattening; tibiae 2 with thin apicomeral spur; outer margin of femora 3 in basal third distinctly emarginate, covered with long dense setae; mesal margin of femora 3 in basal third also with long setae. Aedeagus as in Fig. 364. Body length 1.9–2.0 mm
- *segrex* Kurbatov, 1990

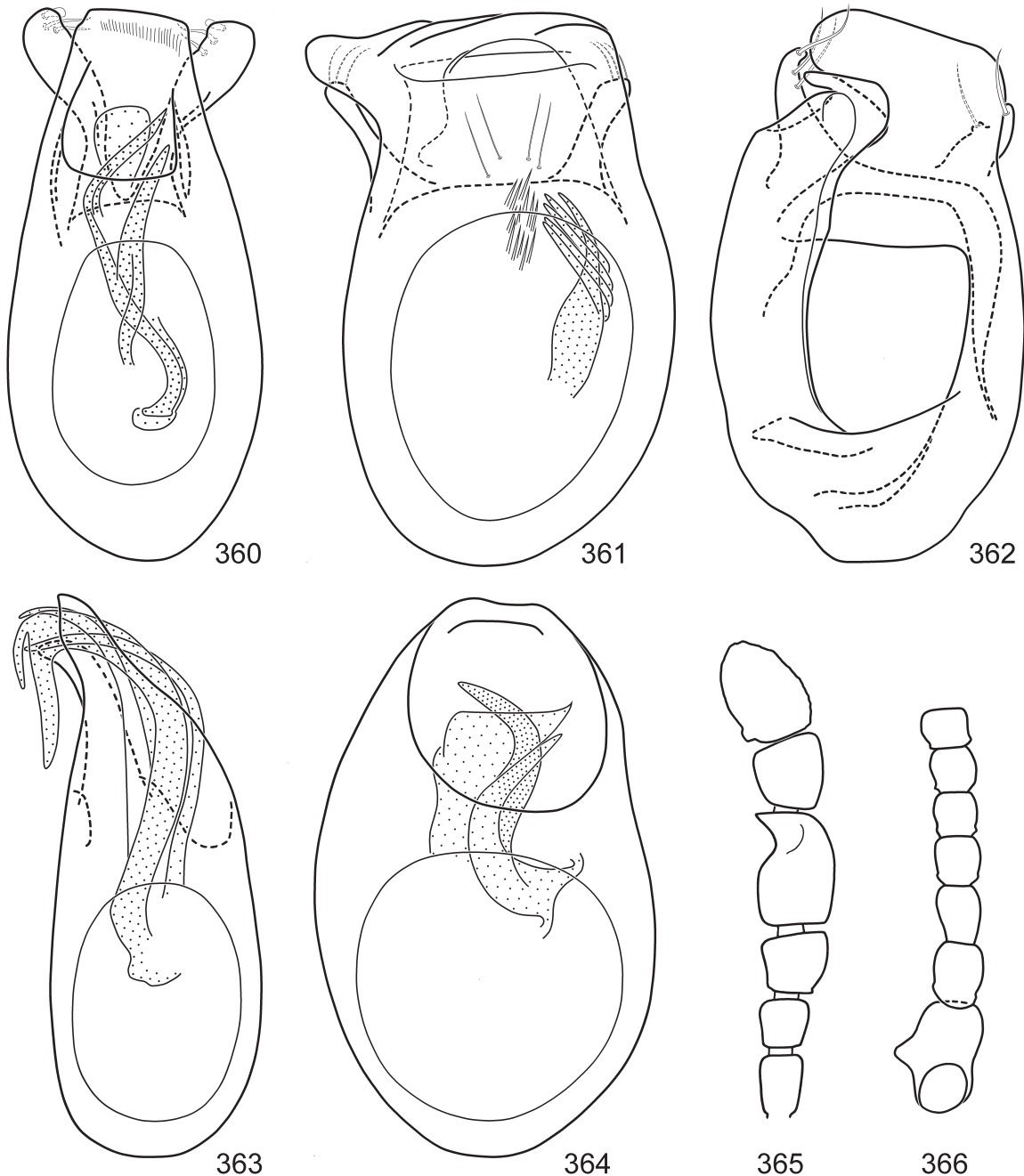
Lasinus Sharp, 1874 (Fig. 367). Maxillary palpi small, their articles without any outgrowths, palpomere 3 and 4 with stalked base. Pronotum with median antebasal and pair of lateral antebasal foveae, lacking antebasal sulcus. Abdominal

tergite 1 at least two times longer than 2, with pair of short discal carinae. Trochanters and femora 1 and 2 (Fig. 108) with spines in both sexes. Front and especially middle tibiae strongly curved. Male: antennal club usually modified. Large beetles, 2.5 to 3.8 mm. 11 East Asian species.

1. Head and pronotum with dense fine punctation. Trochanters 2 with one (male) or two (female) spines. Male: antennae (Fig. 365) with antennomere 9 slightly shorter than 10 and

11 together, not narrower than them, its apicomeral angle protruding as flat transverse plate; tibiae 1 with strong apicomeral tooth. Female: antennae with antennomere 9 simple, slightly longer and considerably narrower than 10; tibiae without apical tooth. Aedeagus as in Fig. 360. Body length 3.0–3.1 mm

..... *micado* Bekchiev, Hlavač et Nomura, 2013



Figs 360–366. Details of Pselaphinae: 360, 365 — *Lasinus micado*; 361 — *Ctenisodes mroczkowskii*; 362 — *Stipesa rudis*; 363 — *Tyrus mucronatus*; 364, 366 — *Tyrodes segrex*; 360–364 — aedeagi; 365 — apical part of antenna; 366 — basal part of antenna.

Рис. 360–366. Детали строения Pselaphinae; 360–364 — эдеагусы; 365 — апикальная часть усика; 366 — базальная часть усика.



Fig. 367. *Lasinus micado* (photo K.V. Makarov).
Рис. 367. *Lasinus micado* (фото К.В. Макарова).



Fig. 368. *Ctenisodes mroczkowskii* (photo K.V. Makarov).
Рис. 368. *Ctenisodes mroczkowskii* (фото К.В. Макарова).



Fig. 369. *Tmesiphorus marani* (photo K.V. Makarov).
Рис. 368. *Tmesiphorus marani* (фото К.В. Макарова).



Fig. 370. *Stipesa rudis* (photo K.V. Makarov).
Рис. 370. *Stipesa rudis* (фото К.В. Макарова).

Tmesiphorus LeConte, 1849 (Fig. 369). Head with frontal and two vertexal foveae. Palpomeres 2 and 3 with needle-shaped outgrowths, palpomere 4 roundly broadened on outer margin, sharp at apex. Abdominal tergite 2 usually longer than I. The genus is distributed in Africa south of Sahara, South and East Asia and Australia; 2 species known from the USA.

1. Head and pronotum densely punctured and pubescent (Fig. 373). Temples behind eyes simple. Abdominal tergite 2 with discal carinae reaching to middle of segment length. Male: antennomere 9 with big longitudinal impression on outer margin, antennomere 10 much shorter than 9 (Fig. 371). Aedeagus as in Fig. 383. Body length 3.15–3.40 mm
..... *marani* Löbl, 1963

– Posterior half of head and pronotum almost not punctured at all and glabrous (Fig. 374). Temples behind eyes with rounded projection. Abdominal tergite 2 with discal carinae reaching only one third of segment length. Male: antennomere 9 as long as 10, with weak longitudinal groove along outer margin (Fig. 372). Aedeagus as in Fig. 384. Body length 2.85 mm
..... *improvisus* Kurbatov, 1992

Ctenisodes Raffray, 1897 (Fig. 368). Palpomeres 2–4 of maxillary palpi (Fig. 114) with needle-shaped outgrowths, bearing at apex a small tuft of setae. Antennae without distinct club, gradually thickening towards apex. 15 species in North America, one each in Mexico and Cuba, and 2 more species in Japan, Korea and South Primorye.

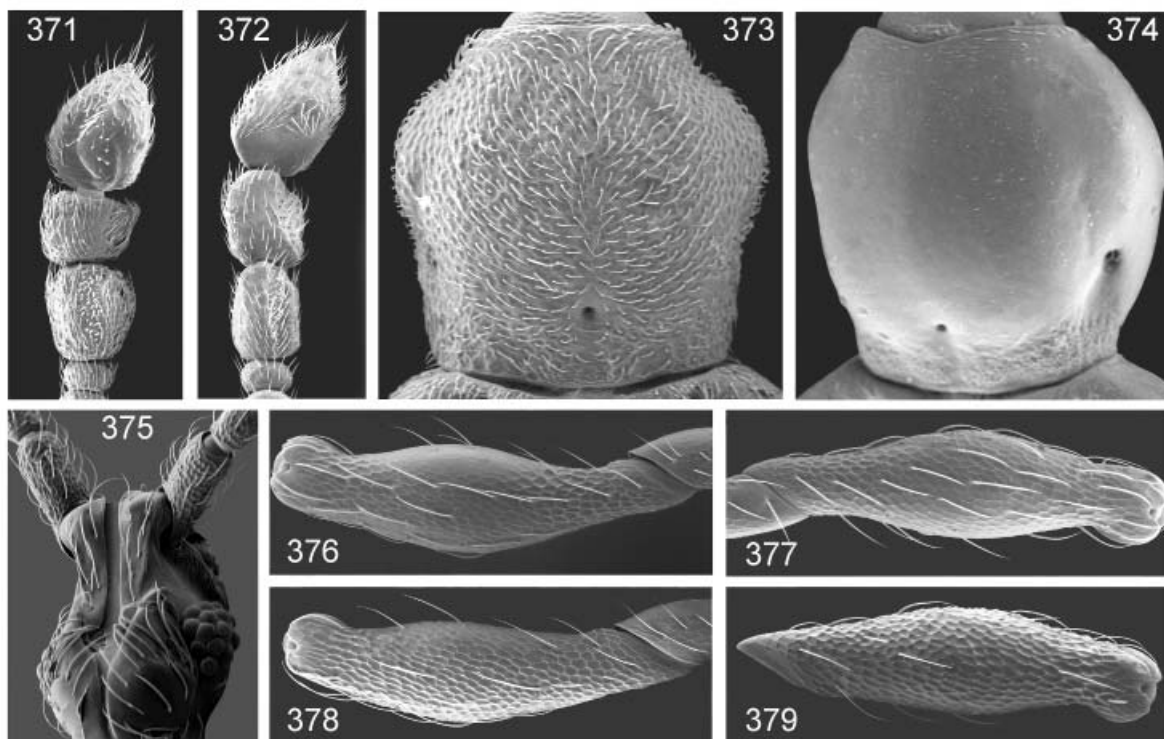
1. Frontal and vertexal foveae large, diameter of the latter larger than the distance between them. Antennomeres long, anten-

nomere 3 twice as long as wide, antennomeres 4–8 gradually shortened. Aedeagus as in Fig. 361. Light brown. Body length 2.0 mm
..... *mroczkowskii* (Löbl, 1968)

Stipesa Sharp, 1874 (Fig. 370). Body covered with scale-like setae. Maxillary palpi (Fig. 115) very small, much shorter than head. Antennae with 3-segmented club. When disturbed, the beetles tuck their head with antennae downwards, fold their legs and may stay in this position for several minutes. More than 20 species in Tropical Africa, East Asia and Australia. One Japanese species reaches the extreme south of Primorye.

1. Antennae with antennomeres 9 and 10 wider than long. Tibiae 1 thickened throughout except at the base, much thicker than tibiae 2 and 3. Tarsomere 3 widest near the base, distinctly narrowed towards apex (Fig. 110). Aedeagus as in Fig. 362. Body length 1.25–1.35 mm . *rudis* Sharp, 1874

Pselaphus Herbst, 1792 (Fig. 380). Head in anterior half with evenly deepened median longitudinal sulcus (Fig. 375). Maxillary palpi (Fig. 112) very long and slender, with palpomere 1 as long as 2, palpomere 4 usually not shorter than head. Underside of head at base with area of very dense white bristles that almost reaches ventral margin of eyes. Pronotum without foveae and sulci. Elytra without basal foveae, only with sutural and discal striae. Male: abdominal sternite 7 (IX) divided into two triangular parts. Holarctic and Indo-Malayan genus, also known from East Africa. There are 19 species in the Palearctic.



Figs 371–379. Details of Pselaphinae. 371, 373 — *Tmesiphorus marani*; 372, 374 — *Tmesiphorus improvisus*; 375–377 — *Pselaphus heisei*; 378–379 — *Pselaphus belovi*; 371–372 — apical part of antennae; 373–374 — pronotum; 375 — head; 376, 378 — profemora; 377, 379 — mesofemora.

Рис. 371–379. Детали строения Pselaphinae; 371–372 — верхняя часть усиков; 373–374 — переднеспинка; 375 — голова; 376, 378 — передние бёдра; 377, 379 — средние бёдра.



Fig. 380. *Pselaphus heisei* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 380. *Pselaphus heisei* (фото С. Курбагова и Ю.А. Ловцовой).



Fig. 381. *Pselaphaulax shaman* (photo S. Kurbatov & Yu.A. Lovtsova).
Рис. 381. *Pselaphaulax shaman* (фото С. Курбагова и Ю.А. Ловцовой).

1. All tibiae and femora solidly shagreened with finely cellular sculpture, rather matt (Figs 378–379). Male: abdominal sternite 2 in basal half with small smooth and flat area; aedeagus as in Fig. 387. Body length 1.75–1.85 mm
..... *belovi* Kurbatov, 1985
- All tibiae and femora less strongly shagreened, more shiny, especially in middle third (Figs 376–377). Male: abdominal sternite 2 in basal half with larger, smooth and slightly concave area; aedeagus as in Fig. 386. Body length 1.7–1.95 mm
..... *heisei* Herbst, 1792

Pselaphaulax Reitter, 1909 (Fig. 381). Head in anterior half with evenly deepened median longitudinal sulcus. Maxillary palpi and underside of head as for the previous genus. Pronotum with median and lateral antebasal foveae united by antebasal sulcus. Elytra with three basal foveae and sutural and discal striae. Male: abdominal sternite 7 (IX) divided into two triangular parts. Widespread in Old World and Australia, 7 species in Palaearctic.

1. Maxillary palpi with palpomere 4 provided with groove at the thickened apex. Male: antennomere 8 slightly thickened, distinctly wider than 7th. Female: antennomere 8 not thickened, as wide as previous articles. Aedeagus as in Fig. 388. Body length 1.7–1.8 mm
..... *shaman* Kurbatov, 1990

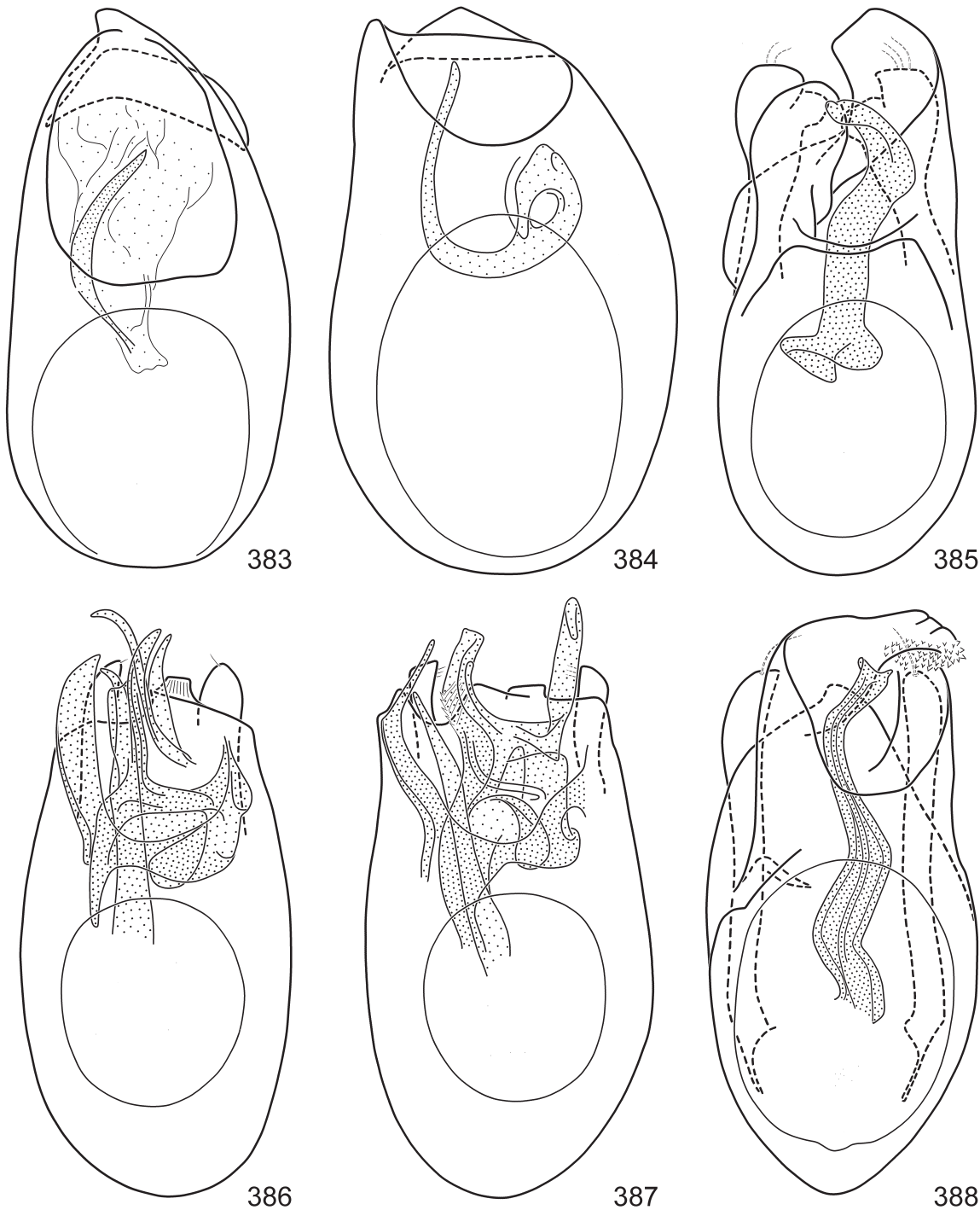


Fig. 382. *Tyraphus nitidus* (photo Giulio Cuccodoro).
Рис. 382. *Tyraphus nitidus* (фото Giulio Cuccodoro).

Tyraphus Sharp, 1874 (Fig. 382). Close to two previous genera, sharing with them a broad longitudinal frontal sulcus with a flat smooth nude bottom, and also strongly elongate palpomere 1. However, the general shape of the maxillary palpi differs greatly (Fig. 113); they are rather short and thick, with an especially thickened palpomere 4, which is irregularly tri-

angular, without stalked base, much shorter than head. Nineteen species in eastern, southeastern Asia and Australia.

1. Antennae short and rather thick, not longer than the head and pronotum taken together. Pronotum smooth, with indistinct antebasal sulcus. Aedeagus as in Fig. 385. Body length 1.7 mm *nitidus* Raffray, 1909



Figs 383–388. Aedeagi of Pselaphinae: 383 — *Tmesiphorus marani*; 384 — *Tmesiphorus improvisus*; 385 — *Tyraphus nitidus*; 386 — *Pselaphus heisei*; 387 — *Pselaphus belovi*; 388 — *Pselaphaulax shaman*.
Рис. 383–388. Эдеагусы Pselaphinae.

Annotated list of species of Pselaphinae of the Russian Far East

Supertribe Euplectitae

1. *Euplectus domefactus* (Kurbatov, 1991). Known from the Jewish Autonomous Region and Primorsky Krai. Recently found also in South Korea [Byeon *et al.*, 2021]. Lives in dead wood of various tree species. Common.

2. *Euplectus doryphorus* (Kurbatov, 1991). Occurs in southern Sakhalin and Kunashir Island, where it inhabits dead wood of fir, alder, and birch. Also found in Japan (Shikoku Island) [Nomura, 2007b] Common.

3. *Euplectus epidemus* Kurbatov, 1991. The species is known only from a dozen specimens from the Khasansky and Ussuriyskiy districts of Primorsky Krai. It occurs in dead wood of predominantly deciduous species. Rare.

4. *Euplectus gibbipalpis* Löbl, 1975. This species was described from North Korea. Found in the Russian Far East, where it occurs from the Jewish Autonomous Region to the south of Primorsky Krai, as well as on Kunashir Island. Recently it has been recorded in South Korea [Byeon *et al.*, 2021]. It lives in dead wood of various species (fir, linden, birch, elm, oak, poplar, alder). Infrequent.

5. *Euplectus gravis* Kurbatov, 1988. The species is known only from the Amur Region (Zeya Reserve) and from the vicinity of Ternei settlement (Primorsky Krai). Occurs in dead wood of conifers. Very rare.

6. *Euplectus karstenii* (Reichenbach, 1816). Holarctic species. In the Far East it is found from the Amur Region (Zeya Reserve) to Southern Primorye; it is also recorded on Sakhalin and Kunashir Islands. Lives in dead wood of various species. Common.

7. *Euplectus mutator* Fauvel, 1895. European-Siberian species. Found in the western part of the Jewish Autonomous Region, in Norsk and Lazovsky Reserve and Sakhalin Island. We have no information on the biotopic habitat of the species in the Far East, as of the few specimens known from this area, almost all of them were collected in flight intercept traps or without indication of the biotope. Very rare in the Far East.

8. *Euplectus piceus piceus* Motschulsky, 1835. Western Palaearctic species, also found in Primorsky Krai and on the islands Sakhalin and Kunashir. Inhabits mainly dead wood of coniferous species. Frequent.

9. *Euplectus punctatus* Mulsant et Rey, 1861. European-Siberian species. In the Far East it is recorded only on the island of Kunashir, where it is found in dead wood of various tree species. Rare.

10. *Euplectus puncticollis* Kurbatov, 1988. Found in the Jewish Autonomous Region and Primorsky Krai. Inhabits strongly moistened dead wood almost exclusively of coniferous species (prefers large mossy logs in conditions of strong shading). Occurs as solitary specimens Not common.

11. *Euplectus rubicundus* Kurbatov, 1988. This species occurs on Kunashir and Sakhalin Islands, where it inhabits dead wood of various tree species. Found also in Japan (Honshu Island) [Nomura, 2007b]. Not common.

12. *Euplectus rutilans* Kurbatov, 1988. In the Far East it is known from the Amur Region and Primorsky Krai. It is also found on the right bank of the Lena River in the vicinity of Yakutsk. It gravitates to dark coniferous forests, where it is found in dead wood of spruce and fir. Rare.

13. *Euplectus signatus* (Reichenbach, 1816). European-Caucasian-Siberian species, facultatively associated with *Formica* ants. In the Far East it is known only from three specimens from the Jewish Autonomous Region (found in a nest of *Formica* group *rufa*).

14. *Leptoplectus falcifer* Kurbatov, 1992. Known from two specimens from Ussuriyskiy District, Primorsky Krai (vicinity of Kamenushka village), where it was collected in dead wood of *Abies holophylla* and linden.

15. *Leptoplectus perperus* Kurbatov, 2022. Occurs on the islands of Sakhalin and Kunashir, where it inhabits dead wood of mainly alder and fir. Earlier we identified specimens as being the European species *L. spinolae* (Aubé) (Kurbatov, 1991c), however, later it was found out that they are different species [Kurbatov, 2022]. Frequent.

16. *Leptoplectus pumilio* Kurbatov, 1992. This species was found only in Ussuriyskiy District, Primorsky Krai (vicinity of Kamenushka village), where it occurs exclusively in moist dead wood of linden.

17. *Leptoplectus similis* Kurbatov, 1991 = *Leptoplectus illex* Kurbatov, 1992 [Kurbatov, 2022]. The species is known from Amur Region (Zeya Reserve), from Primorsky Krai, and from Sakhalin and Kunashir Islands. It was also found in North-Eastern China, Liaoning Province [Coulon, Li, 1995]. Occurs in dead wood of predominantly coniferous species. It is more common on the islands of Sakhalin Region than in the mainland Far East.

18. *Leptoplectus solivagus* Kurbatov, 1991. Known from the holotype from Kunashir Island (vicinity of Cape Ivanovsky), where it was caught in forest litter.

19. *Labropectus depositor* Kurbatov, 1993. Known from the south-western part of Kunashir Island. Until now it has been found only in dead wood of fir. Rare.

20. *Labropectus occultus* (Kurbatov, 1991). Initially the species was described on the basis of a single specimen as being in the genus *Leptoplectus*, but study of additional material showed the necessity of description of a new genus. The species is known only from Kunashir Island. Occurs in dead wood mainly of alder. Rare.

21. *Forinus macer* Kurbatov, 1991. Known from two specimens from the middle reaches of the Malaya Elduga River (Nadezhdinskiy District, Primorsky Krai). Caught at the top of a hill in a rotten log of *Abies holophylla*.

22. *Forinus secundus* Kurbatov, 1992. The species is known only from Kunashir Island. Occurs in dead wood of fir. Rare.

23. *Bibloporus bicolor* (Denny, 1825). European-Siberian species found in Amur Region (Norsk Reserve), Jewish Autonomous Region, and Primorsky Krai (from Khasansky District to the vicinity of Ternei settlement). The beetle lives in dead wood of both coniferous and deciduous tree species. One male was collected in an anthill of *Formica* sp. Rare in Far East.

24. *Bibloporus ferentarius* Kurbatov, 1992. Known from the southern part of Primorsky Krai. Collected only in flight intercept traps and thus the biotope of the species is unknown. Presumably occurs in heavily moistened rotten wood, which may make it very difficult to sift such a small object from this substrate.

25. *Bibloporus minutus* Raffray, 1914. European species found in South Primorsky Krai (Ussuriyskiy District and Vladivostok neighbourhood) and in South Sakhalin. The species is most commonly occurs in dead birch. Rare.

26. *Bibloporus neglectus* Kurbatov, 1993. Occurs on the islands of Sakhalin and Kunashir, where it was collected in the rotten wood of fir and birch trees. Known only from a few specimens.

27. *Bibloporus ponderosus* Kurbatov, 1991. The species is known from the islands of Sakhalin, Kunashir, and Iturup and from Primorye (Ussuriyskiy District and the vicinity of Ternei settlement). It has also been found on the islands of Hokkaido and Honshu (Japan) [Nomura, 2005, 2007c]. The beetles live in rotten wood of various species, both coniferous and deciduous. It is rarer in the continental part of its range.

28. *Bibloporus pubens* Kurbatov, 1991. Known only from the island of Kunashir. Found in rotten wood of various species. Rare.

29. *Piptoncus duplex duplex* Kurbatov, 1991. The species inhabits the Southern Primorye. It is found mainly in rotten wood of linden and alder, less frequently in wood of other tree species. Often occurs in clusters of dozens of specimens. Common.

29a. *Piptoncus duplex sobrinus* Kurbatov, 1991. Known from the islands of Sakhalin and Kunashir. Also found in Japan on Shikoku Island [Nomura, 2007a]. Occurs in dead wood of various species. Not common.

30. *Kuriporus creator* Kurbatov, 1991. The species inhabits the islands of Sakhalin and Kunashir, where it is found in rotten wood of various tree species (mainly fir, but also spruce, alder, and birch). It has been recorded in Japan (Shikoku Island) [Nomura, 2007c]. Occasionally frequent.

31. *Saulcyella schmidtii* (Maerkel, 1844). Considered a very rare Eastern European species. However, it was found in the south of the Far East, where it is widely distributed from the Amur Region (Norsky Reserve) to the extreme south of Primorye (Khasansky District); it was also found on the islands of Sakhalin and Kunashir. In the European part of its range it is recorded as a facultative myrmecophile of *Lasius brunneus*, *Lasius fuliginosus* and *Formica* group *rufa*. In the Far East region it is rarely associated with *Formica* ants. It is found in relatively dry rotten wood of both coniferous and deciduous species. Starting at the end of June there is a significant predominance of females over males (approximately 7:1). Common.

32. *Tiliactus properus* Kurbatov, 1992. The species is known from several localities in Primorsky Krai, where it was collected in rotten wood mainly of linden and maple. It is rarely encountered, but usually many specimens are found together.

33. *Ramussia captiosum* Kurbatov, 2022. The species is known only from the south-west of Sakhalin Island. Several specimens were collected on a hilltop in a rotten downed *Picea* trunk in direct solar exposure; another specimen was caught nearby in a rotten *Abies*.

34. *Ramussia lovtsovae* Kurbatov, 2022. Known from south-western Sakhalin, where it was collected cohabiting with the previous species in the same *Picea* trunk.

35. *Ramussia parabile* Kurbatov, 1991. Occurs in Southern Primorye, where it inhabits rotten wood of coniferous and deciduous tree species. One of the most common pselaphine beetles in the south of the Far East.

36. *Ramussia svetlanae* Kurbatov, 2022. Known only from a single male collected on the south-eastern coast of Kunashir Island in the vicinity of the Alyokhino in the litter near thermal springs.

Supertribe Batrisitae

37. *Batrisus politus* Sharp, 1883. Japanese species. One female was collected on Kunashir Island in the vicinity of Ozerny cordon, in a *Lasius* nest in a dead birch stump in an deforested patch.

38. *Batrisus sibiricus* Sharp, 1874. A species with probably an East Asian pattern of distribution. In the Russian Far East it is known from the Jewish Autonomous Region to the extreme south of Primorye (Khasan District). It was also collected in Sichuan Province of China (Wolong natural reserve, ca 1000 m, with *Lasius* sp., 15.V.1994, S. Kurbatov leg.) and on the Korean Peninsula (Nomura and Lee, 1993). Myrmecophile, associated with ants of the genus *Lasius*. Relatively frequent in our Far East.

39. *Batrisodes cornutus* (Kurbatov, 1984). The species is known only from Kunashir Island. Occurred both under moss

on trunks of living trees of birch and ash, and in dead wood of fir and birch. Rare.

40. *Batrisodes harmandi* Raffray, 1904. Japanese species, also found on Sakhalin and Kunashir Islands. Occuring in dead wood of both coniferous and deciduous tree species, in litter mixed with wood mould at the base of old stumps, and also together with *Lasius* ants. It is less common on Sakhalin than on Kunashir.

41. *Batrisodes pruinosus* Reitter, 1889. The species is known from single specimens from Tibet and Mongolia. In the Far East it inhabits Southern Primorye (Kavalerovsky and Partizansky districts, where it was caught in rotten wood, and Khasansky district, where it was collected in plant remains near a stone on the forestless slope of Golubiny Hill). [4 specimens are also known from Chita Region (WSW from Nizhny Tsasuchey village, vicinity of Butevken Lake, 3 and 4.VI.1995, R.Yu. Dudko leg.)]. Very rare.

42. *Batrisodes singularis* Kurbatov, 1985. This species is known from the Jewish Autonomous Region (vicinity of Dichun) and from Ussuriysky District, Primorsky Krai (vicinity of Kamenushka village). It is found under bark and in the rotten wood of dead linden trees. Probably associated with ants of the genus *Lasius*. Very rare.

43. *Batrisodes tichomirovae* Löbl, 1973. This species is widely distributed from the Amur Region (Zeya Reserve) to the extreme south of Primorsky Krai; it is also known from the Korean Peninsula. Associated with dead wood of both coniferous and deciduous species. Common.

44. *Batrisodes tornatilis* Kurbatov, 1990. Known only from Primorsky Krai. Inhabits mainly rotten wood of linden, although it is also found in wood of other tree species. Rare, but dozens of specimens may occur at the same place at the same time.

45. *Batrisodes vargus* Kurbatov, 1992. This species is known from two specimens taken in the vicinity of Mendelevo, Kunashir Island; found in rotten wood of alder and birch.

46. *Basitrodes vestitus* (Sharp, 1883). Japanese species found on Kunashir Island. Three males of this species were collected together in the vicinity of Ivanovsky cordon in a *Myrmica* nest in a dead alder stump.

47. *Dendrolasiophilus subitius* Kurbatov et Kovalev, 2022. Known only from the vicinity of the village Chernyatino (Oktyabrsky District, Primorsky Krai). A single male was taken at night using light from a lantern to observe a trail of *Lasius* (*Dendrolasius*) *capitatus* (Kuznetsov-Ugamsky, 1928) ants on a living oak tree trunk.

48. *Batriscenellus admonitor* Kurbatov, 1990. This species is known from Kirovsky and Ussuriysky districts of Primorsky Krai, where it was caught along the banks of small reservoirs with standing water. Males may fly to the light. Rare.

49. *Batriscenellus fallax* (Sharp, 1883) (= *insularis* Kurbatov, 1990). A Japanese species, also found on Kunashir Island, where it inhabits wet litter along stream banks. Common in some areas.

50. *Batriscenellus vicarius* Löbl, 1973. A species known from Japan, North and South Korea, and north-east China (Liaoning Province). In the Russian Far East it is widespread in Southern Primorye (especially in the Khasansky District), where it inhabits wet litter along stream banks or in marshy areas both under the forest canopy and in open spaces. Males fly to light. Common in some areas.

Supertribe Goniaceritae

51. *Bryaxis amurensis* Kurbatov, 1985. This species is known from the Amur Region (Zeya Reserve) and the Jewish Autonomous Region. Inhabits litter, also recorded in rot-

ten wood of *Pinus coreanus* and birch. Common in the Jewish Autonomous Region.

52. *Bryaxis ascicornis* Kurbatov, 1985. This species is widespread from the Amur Region (Zeya Reserve) to the extreme south of Primorye (Khasansky District). Inhabits in moss in marshy areas or in forest litter and plant remains along the banks of streams and rivers. Males may fly at sunset. There are several forms of males living together, differing in the degree of development of the 2nd segment of the antennae. Occasionally frequent.

53. *Bryaxis extremalis* Kurbatov, 1990. This species is known from Kunashir and Iturup islands, also found in the Japanese archipelago [Nomura, Kamezawa, 2016; Nomura, Ozaki, 2017; Nomura, Yoshida, 2019; Taru, Nomura, 2021, etc.]. Occurs in litter along stream banks. Occasionally frequent.

54. *Bryaxis humilis* Raffray, 1909. Japanese species discovered on Kunashir Island, where it was found in the litter near the stream in the vicinity of Tretyakovo (only in one locality, but dozens of specimens).

55. *Bryaxis japonicus* (Sharp, 1874) (= *brevipalpis* Jeannel). Japanese species, also found on Kunashir Island. Inhabits litter along the banks of streams. Less localised, but also less abundant than the previous species.

56. *Bryaxis koltzei* (Reitter, 1887) (= *coreanus* Nomura & Lee, 1992; = *kintaro* Nomura, 1995). In the Russian Far East, the species inhabits the Southern Primorye, where it often occurs in extra-zonal or disturbed localities, occurring in plant remains, litter and rotten wood. Common in some areas. This species is also known from Northeast China (Liaoning Province), the Korean Peninsula, and Japan.

57. *Bryaxis sichotensis* Kurbatov, 1994. The species is known from the Amur Region (Norsky Reserve), from the south of Khabarovsk Krai (east of Bikin settlement) and from the south of Primorsky Krai (western slope of Olkhovaya Mountain). Occurs in similar conditions to the previous species; in the south of its range it is found in rotten wood of Korean pine and maple. Occasionally frequent.

58. *Bryaxis testatus* Kurbatov, 1994. Known from one male in the middle reaches of the Malaya Elduga River (Nadezhdinsky District, Primorsky Krai). Caught in dry litter.

59. *Bryaxis ussuriensis* Löbl, 1964. The species is widespread in Southern Primorye; also known from North Korea. Found mainly in forest litter, much less frequently taken in dead wood. Common.

60. *Bryaxis validicornides* Newton, 2015 (nom.n. for *B. validicornis* Löbl, 1974). The species is described from North Korea. Found in Southern Primorye (Nadezhdinsky and Ussuriysky districts), where it occurs in forest litter. Occasionally frequent.

61. *Tychobythinus aino* Kurbatov, 1992. This species was described from Kunashir Island; later it was found in Japan [Nomura, 1996c]. On Kunashir it is known from the vicinity of Cape Stolbchatiy, where it occurs in litter in low-growing bamboo thickets around hot springs outside the forest canopy. A significant predominance of females over males (ratio 3:1) was noted.

[1 female of *Tychobythinus* was found in a boggy area in the Jewish Autonomous Region. It very likely belongs to a new species, but the absence of the male does not allow the opportunity to adequately describe this species]

62. *Rybaxis lamellifer* Löbl, 1973. This species is known from the Korean Peninsula and Japan (including Kyushu Island). In our country it is found in the Amur Region (Norsky Reserve) in moss and in plant remains in bogs. Rare.

63. *Rybaxis nigrescens* Jeannel, 1958 (= *korolevi* Kurbatov, 1984). A Japanese species, also found on South Sakhalin and the islands of Iturup, Kunashir and Shikotan. It lives along the

banks of marshes and streams, and on Kunashir it is sometimes caught in dry ferns hanging over streams. In the Russian Far East it is more common on Kunashir.

64. *Rybaxis pinguis* Kurbatov, 1990. The species is known from Southern Primorye. Lives in dead wood of various species, both coniferous and deciduous. Occasionally frequent.

65. *Rybaxis princeps* (Sharp, 1874). Japanese species. Found on Kunashir Island in litter and dry last year's ferns. One specimen was collected on a lake shore.

66. *Rybaxis zelotypus* Kurbatov, 1992. Known from a few specimens from the Norsky Reserve (Amur Region) and Kirovsky and Ternei Districts of Primorye, where it was caught in plant remains in a swamp and along the banks of rivers and near the seashore. Rare.

67. *Reichenbachia commutabilis* Kurbatov, 2015 (nom.n. for *R. ignobilis* Kurbatov, 1992). Known from the Amur Region (Norsky Reserve and vicinity of the Khingansky Reserve). Occurs in moss and in plant remains in wetlands. Rare.

68. *Trissemus alienus* (Sharp, 1874) (= *pseudalienus* Kurbatov, 1990). Japanese species, known from South Sakhalin, Kunashir Island, and the Partizansky and Lazovsky districts of Primorsky Krai. Most often found in fallen leaves and other plant remains on stony riverbanks. Relatively rare in the Russian Far East.

69. *Batraxis kawaharai* Maruyama et Sugaya, 2004. The only specimen (a male) of this species known from the Russian territory was collected by author in South Sakhalin Island in the vicinity of Khomutovo Airport in a swampy sparse larch forest at the base of a rotten larch stump together with *Lasius* ants.

70. *Tainochus exiguus* Kurbatov, 1992 (= *abdominalis* (Nomura et Lee, 1993)). The species has been described from the extreme south of Primorsky Krai (Khasansky District, Golubiny Hill); later it was found in South Korea. On Golubiny Hill it was found in plant debris in treeless areas.

71. *Tainochus imperator* Kurbatov, 1992. The species was described from Kunashir Island; later it was found in Japan (Honshu and Hokkaido) [Nomura, 1996a]. In Kunashir it is found in litter along the banks of streams. Rare.

72. *Tychus dichotomus* Nomura et Lee, 1992 (= *kurilensis* Kurbatov, 1992). The species is known from South Korea and Japan. In the Russian Far East it was found on Kunashir Island in the vicinity of Tretyakovo and Alyokhino in plant debris near hot springs, where it has been abundant at some localities.

Supertribe Pselaphitae

73. *Tyrus mucronatus* (Panzer, 1805). European-Siberian species, also inhabiting Southern Primorye. Occurs under bark and in rotten trees. Rare. One female, found on Kunashir Island, probably belongs to a possibly undescribed species; it is close to *T. mucronatus*, but lack of a male does not allow a decisive statement.

74. *Tyrodex segrex* Kurbatov, 1990. Known from Ussuriysky and Khasansky districts of Primorye and from Kunashir Island. Most often occurs in valley forests where it lives under moss on trunks of living hardwoods (elm, maple, linden; on Kunashir — *Calopanax* and maple). Known also from Japan (Hokkaido, Honshu, Kyushu) [Inoue, Nomura, 2023]. Infrequent in the Russian Far East.

75. *Lasinus mikado* Bekchiev, Hlavač et Nomura, 2013. Occurs on Kunashir Island in the vicinity of Tretyakovo and Alyokhino, where it lives in litter and dry last-year's ferns near hot springs, where it is sometimes frequent. Widespread in Japan (Hokkaido, Honshu, Shikoku). In an earlier paper [Kurbatov, 1992a] this species was erroneously reported from Kunashir as *L. spinosus*.

76. *Tmesiphorus marani* Löbl, 1963. The species is known from the south of Khabarovsk Krai (vicinity of Bikin) and from Primorsky Krai (Ussuriysky District). Found also in North Korea. Occurs under bark and under stones; associated with ants of genus *Lasius*. Very rare.

77. *Tmesiphorus improvisus* Kurbatov, 1992. Known only from the holotype from the vicinity of Kamenushka village (Ussuriysky District, Primorsky Krai) without indication of biotopic habitat. Probably associated with *Lasius* ants.

78. *Ctenisodes mroczkowskii* (Löbl, 1968). The species was described from the Korean Peninsula. In the Russian Far East it was found in the extreme south of Primorye (Khasansky District, Golubiny Hill), where it occurs in relatively dry plant debris between stones in treeless areas.

79. *Stipesa rudis* Sharp, 1874. Japanese species. Found in the extreme south of Primorye (Khasansky District, Golubiny Hill). It lives in plant debris among stones in the unforested areas of the middle part of slopes with a southern exposure together with *Ctenisodes mroczkowskii*. Significant predominance of females over males is observed (ratio 5:1). Not abundant in its habitat on Golubiny Hill.

80. *Pselaphus heisei* Herbst, 1792. European-Siberian species. In the Far East it has been found in the Amur Region (Norsk Reserve), Khabarovsk Krai (Bureinsky Reserve), Kamchatka (Valley of Geysers), southern Sakhalin, and southwestern Kunashir. The species is found in moss and fallen leaves in swampy places (on Kunashir it was caught only in the vicinity of Alyokhino, in plant remains between stones near hot springs). Rare in the Far East.

81. *Pselaphus belovi* Kurbatov, 1985. The species is known from a few specimens taken in the Ussuriysky and Khasansky districts of Primorsky Krai, as well as from Dublikansky Reserve of Khabarovsk Krai. Found in moss and various plant debris. Very rare.

82. *Pselaphaulax shaman* Kurbatov, 1990. Described from two specimens taken in Central Yakutia (vicinity of Khara-Aldan settlement). Subsequently found also in the Amur Region (Norsk Reserve), where it is found in boggy areas in moss and in various kinds of plant debris. Occasionally frequent in the Norsk Reserve. It is interesting to note that in the eastern margin of its range the European-Siberian *Pselaphaulax dresdensis* (Herbst, 1792) reaches the left bank of the Lena River (the author knows of 1 male from the vicinity of Yakutsk (Sergelakh settlement), and thus, probably, the natural boundary between these two species is the Lena River.

83. *Tyraphus nitidus* Raffray, 1909. The species inhabits Japan and South Korea. In the Russian Far East it was collected in the Khankaisky and Khasansky districts of Primorsky Krai by sweeping grasses and trapping in a meadow on sandy soil near the sea; thus, the exact biotopic occurrence of the species is still unclear. The species is very rare in Primorsky Krai.

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