

**ON ORIGIN AND EARLY EVOLUTION OF THE SUPERFAMILY CUCUJOIDEA
(COLEOPTERA, POLYPHAGA). COMMENTS ON THE FAMILY HELOTIDAE****Introduction**

Appearance in time, structure and systematic position of the superfamily Cucujoidea are rather important subjects for understanding phylogeny and composition of the order. Following the previous tradition Crowson (1955, 1981) regarded this superfamily together with Tenebrionoidea as one branch of the archaic cluster of the infraorder Cucujiformia. The superfamilies Chrysomeloidea and Curculionoidea were put by him as most advanced groups of this infraorder. This position looked like quite natural because the groups represented mostly by phyllophagous forms seemingly are more recent in comparison with the groups mostly mycetophagous bearing more simple structural characters. Although Sharp and Muir (1912) thought that connections of 'Phytophagoidea' with other coleopterous groups were only in 'procoleopterous phylogeny'. The more popular viewpoint concludes 'if we combine the primitive features found in Chrysomeloids with those found in Curculionoids but not in Chrysomeloids the resulting combination would be one found in primitive Cucujoids' (Crowson, 1955). At the same time the family Nitidulidae is usually regarded as a group slightly changed from the ancient common ancestor of Cucujoidea. Respectively Chrysomeloidea and Curculionoidea are thought to be derivated from the forms related to or at least similar to Nitidulidae (Mann, Crowson, 1981; Crowson, 1990 and so on). Lawrence and Newton (1982) divided Cucujoidea into two superfamilies corresponding to the former traditional sections Clavicornia and Heteromera, however Cucujoidea s. str. (or Clavicornia) remained in the same position in relation to the phytophagous groups as in most of the previous classifications.

Fifteen years of studies of the family Nitidulidae reveal that the traditional viewpoint mentioned above presents quite weak arguments. Most of these arguments are based on analyses of primitive and advanced states of structural characters of Nitidulidae and Cucujoidea as a whole (Kirejtshuk, 1994b, 1996 and others). In this paper I will try to show a way to study evolution and phylogeny which can be combined with analysis of structural characters or to give a key to understanding a pattern in distribution of characters. A further progress in phylogenetic reconstruction and systematics is proposed in a dialogue between formal analyses and ways of synthetic approach used in this paper for study of the order Coleoptera.

Some methodological problems

Uncertainty of phylogenetic reconstructions with usage of analysis of structural characters sends us in search for some additional ways to estimate adequacy of established phyletic links. Some obstacles to classifications reflecting phylogeny were traditionally discussed beginning with Simpson (1944) and particularly later in Hennig's publications. These obstacles include differing rates of evolution in different groups and at different time. The fact is that any recent family level taxon in the past was not more than a genus in composition of a family recognizable at that time and at present (Crowson, 1970; Mayr, 1974, 1988 and so on). The next traditional difficulty is laid at the time of appearance of apomorphy recognizable among other characters of any monophyletic group (Hennig, 1950, 1981; Løvtrup, 1975). Over the last decades many authors made repeated attempts to solve these and other problems of phylogenetic classification. Nevertheless basal cladistic difficulties connected with the impossibility to prove the 'holophyly' (= 'monophyly' in the Hennigian sense) and the artificial model of 'sister groups' give not only non-satisfaction in theory, but also instability and non-confidence in usage. Indivisibility of cladogenetic and anagenetic characters attributed to a group of relatives (supraspecific taxa) only complicates the situation. Although the stability of the group characters is higher than that of distinguishing characters between species. In some cases 'ideal history of morphotypes' (Hennig, 1981) seems to be more convenient as a temporal scheme than a cladogram and contains a more adequate image of phylogeny. The mentioned difficulties in usage of conclusions after cladistic procedures can be illustrated by the papers with analyses of characters of the polyphagan infraorder Elateriformia (Lawrence, 1988; Lawrence *et al.*, 1995). Finally, it should be

mentioned that the popular ignorance of data on extinct faunas in a cladistic analysis makes such systematic constructions scarcely phylogenetic in the true sense of the word (Crowson, 1991 etc.).

The main requirement to elaborate a natural system is a choice of any successive correspondence of elements in our theoretical construction to the facts. It is important to find an independent parameter to check such a correspondence (like to check correspondence of any other model to object). The most general independent parameter in biosystematics is, as a rule, time (i. e. geological time in phylogenetic reconstructions). Position and connections of a group depends upon the time of its appearance caused by some certain biotic circumstances. Its genealogic links with contemporaries are usually searched for in the characters which could be inherited from a common ancestor. If it is supposed that in the course of evolution most of the characters are maintained or can be revealed by means of special treatment, reconstruction of these links becomes quite regular due to some definite analyses of characters distribution. This viewpoint assumes that evolution is mostly monophyletic growth (structural increase in descendants). It is sometimes thought that some kinds of analyses of characters can give any projection from the genealogy (and correspondingly any projection of the phylogeny). In fact many cases of paedomorphous and many cases of gerontomorphous changes in structural transformations can be traced, but it is impossible to restore the complete dynamics of these processes in the real phylogeny. We can never be sure that the formation of any separate group (taxon) was conditioned mostly by divergent, but not convergent processes, although the divergent character of evolution seems to be in general more probable (though not in all cases), and this circumstance should be taken into consideration when we analyze the characters.

Both structural and embryological, bionomic and ecological peculiarities of any group have resulted from the influence and harmonic interactions of different inner and environmental factors. Stability of these interactions is connected with stability of both types of components, and changes of the latter give greater or lesser changes in interactions. There are frequent successions in both inner factors (heredity) and environmental conditions, both having some regular and apparently occasional reasons to be changed and causing fluctuations in the interactions. However, our knowledge is far from taking into consideration all or at least most kinds of these reasons and their results. Therefore we should seek different ways to study phylogeny and to check correctness of our constructions.

One of the main differences between micro- and macroevolution consists in different alignment of neutral and adaptive transformations. As macroevolutionary changes are usually combined with ecosystem changes, they act on a group of similar forms due to a similar selective regime causing a similar response to these changes among the relatives (Vavilov, 1987; Starobogatov, Levchenko, 1993; Markov, Naimark, 1998 and so on). A shortening of final structural differentiation as a usual reply to abnormal conditions of life is going as paedomorphosis in accordance with the Baer's ontogenetic law, i. e. less general and less dependent features disappear before more general and more dependent (Gould, 1977; Tikhomirova, 1992; DeSalle, Grimaldi, 1993 and others). The first reply to changes in ecological circumstances can be traced in the mode of life which find some reflection in structures only with some time (Crowson, 1970, 1981 and others). Kirejtshuk (1992/1991) tried to correct the previous interpretations of system and phylogenetic connections of the order Coleoptera according to the generalized mode of life and differences in ontogenesis and metamorphosis.

As an example the mastering of higher plants by some coleopterous groups was taken and considered in some details (Kirejtshuk, 1989, 1994a, 1996). The probable ways of trophic changes in beetles were shifting from mycetophagy to antho-, carpo- and phyllophagy (and so on). The complex of adaptive tendencies accompanying changes in mode of life as a necessary part of the anthophazation among the Nitidulidae includes acceleration of development and disembryonization in larvae, miniaturization and paedomorphous changes in imagines (as incomplete structural differentiation). Paedomorphosis has a particular significance and allows anthophagous forms to lose some features, characteristic of true nitidulid mycetophages with a comparatively high level of imaginal structural differentiation. By means of paedomorphous changes, organisms acquire more or less primitive appearance, making traces of relationship less clear. This is the reason why the Cucujoidea were formerly regarded as an archaic group in comparison with other Cucujiformia and Curculioniformia.

Gerontomorphosis allows to increase a definitive differentiation of structures (addition of characters) and to conserve some traits of relationship, whilst paedomorphosis decreases the level of differentiation (subtraction of characters) and eliminates traces of recent relationship. Gerontomorphosis conduces to canalization of possible pathways for structural changes but restricts possibilities for changes in general organization, whilst paedomorphosis takes away restrictions of structural differentiation and gets organisms free for changes in general organization. Keeping a certain mode of life in more or less optimal conditions is conducive to progressive specialization and thereby creates a certain fate in historical development and regularity in structural transformations partly overlapping 'underlying synapomorphies'. This fate makes a predisposition for appearance of a

taxonomic syndrome. Overcoming this fate by means of shortening structural differentiation and organizational generalization occur due to acceleration of development as a sequence of life in unusual conditions causing changes in the mode of life.

In this paper an attempt to use a way of study of phylogeny which can be combined with analysis of structural characters or give a key to understanding a pattern of characters is made. This attempt involves some non-structural peculiarities which are possible to use, despite difficulties with their formalization. The proposed method of grouping defines grades rather than clades, and scarcely can be regarded as an alternative to traditional analyses of characters and formalized peculiarities. This method allows us to reveal some contradictions and is considered only as one of ways to resolve them. It should add possible ways to bring our constructions in correspondence to somewhat independent parameters (external in relation to structural characters).

Disagreement between theoretical constructions and facts

Rather a strong impulse to revise a traditional interpretation came from palaeontology. The order Coleoptera is quite unique among the large insect orders in relation to a great number and great proportion of recent families which appeared during the Mesozoic era (about a third of recent families recorded from there) and a small number of palaeoendemic families regarding the total number of taxa with a family rank. Records of most recent families of different orders in deposits are mostly extended in fossils to the Palaeogene, although coleopterous families in contrast to those of other orders frequently reach the Cretaceous or even Jurassic and sometimes Triassic. In other words, the order Coleoptera presents the groups which were less dramatically changing during historical development of insects (among 67 families known from the Palaeozoic and Mesozoic eras only 19 became extinct: Ponomarenko, 1995; unpublished data). A somewhat similar situation can be traced only in the order Heteroptera, where 40 of about 50 recent families are recorded from deposits (9 from the Mesozoic deposits) and only 16 extinct families were described (Principles of palaeontology, 1962 / Rodendorf ed.).

The Mesozoic Cucujoidea are known exclusively from the Cretaceous and later deposits (table 2) (Schlee, Dietrich, 1970; Crowson, 1976, 1981; Zherikhin, 1978, 1980; Ponomarenko, 1983, 1995; Dmitriyev, Zherikhin, 1988; Kirejtshuk, Ponomarenko, 1990), showing an increase of representation to the end of this period. Relatively slight presence of Cucujoidea in fossils from the Cretaceous coincides with a greater representation of other superfamilies of the suborder Polyphaga (table 1). Ancient Cucujoidea with a long imaginal life and associated mostly with arboreal fungi had comparatively good chances to come into deposits among non-water inhabitants of terrestrial localities in the past. Thus, this fact should be explained in a way other than gaps in the palaeontologic chronicle. It is necessary to explain why rather advanced Curculionoidea (perhaps, primarily spore- or pollinophagous) appeared in this chronicle before 'archaic' cucujoid ancestors.

If the dynamics of appearance in time of different superfamilies is in any sense corresponding to fossil data, we can find some reasons for it in peculiarities of the recent representatives of these groups. It is easy to estimate some structural and bionomic features characteristic only or mostly of archaic cucujoid families. The most marked of them are: (1) comparatively simple structure of larval and imaginal instars; (2) adherence of most of them to wood infested by fungi; (3) larval life on the surface of wet food substrate (rarely on dry surface, almost never deeply inside substrate and very rarely feeding on fresh or live plant vegetative organs); (4) comparatively short duration of larval development; (5) quite usual larval leaving of food substrate to hide into soil for pupation.

One way of a probable explanation of these features is to link the origin of this group with the ancestors that lived in ephemeral localities infested by fungi in the types of forests which were more or less similar to the recent ones. These ancestors living in ephemeral localities should have a short larval development and leave these localities for pupation before they disappear. Taking into consideration that some archaic Cleroidea and Bostrichoidea partly or mostly share these peculiarities with archaic Cucujoidea, relationships between these superfamilies look like very highly probable. If we try to interpret available fossil records, we should suppose that appearance of Cleroidea, Tenebrionoidea and Chrysomeloidea in the Jurassic fossils and the appearance of Bostrichoidea and Cucujoidea in the Cretaceous fossils might not be occasional (Kirejtshuk, 1994b). The peculiarities listed above give evidence for a viewpoint that the formation of all these superfamilies seemed to be connected with arboreal localities. Most intimate interconnections with such localities, infested by fungi and frequently becoming rather ephemeral, show mostly archaic Cucujoidea. Therefore it allows us to suppose that the origin of this superfamily emerged more recently in comparison with other compared

**Appearance of superfamilies of suborder Polyphaga in fossil records
(after Ponomarenko, 1995 and database prepared by him;
T – Triassic, J – Jurassic, K – Cretaceous, Pg – Palaeogene)**

Infraordo STAPHYLINIFORMIA	
Staphylinoidea Latreille, 1802	J1
Hydrophiloidea Latreille, 1802	J1
Histeroidea Gyllenhal, 1808	Pg2
Infraordo ELATERIFORMIA (including Scarabaeiformia)	
Dascilloidea Guerin-Meneville, 1843	K2
Scarabaeoidea Latreille, 1802	J3
Scirtoidea Fleming, 1802	J3
Byrrhoidea Latreille, 1806	J1
Buprestoidea Leach, 1815	J2
Cebrionoidea Latreille, 1802 (= Elateroidea)	T2
Cantharoidea Latreille, 1802	Pg1
Infraordo CUCUJIFORMIA	
Derodontoidea LeConte, 1861	R
Bostrichoidea Latreille, 1802	K1
Lymexyloidea Fleming, 1921	N1
Cleroidea Latreille, 1802	J1
Cucujoidea Latreille, 1802	K1
Tenebrionoidea Latreille, 1802	J3
Chrysomeloidea Latreille, 1802	J3
Infraordo CURCULIONIFORMIA	
Curculionoidea Latreille, 1802	T2

Table 2

**Fossil records of families of Cucujoidea
(orig., after Ponomarenko, 1995 and database prepared by him;
T – Triassic, J – Jurassic, K – Cretaceous, Pg – Palaeogene, N – neogene, R – recent)**

Bothrideridae Erichson, 1845	Pg2–R
Byturidae Jacquelin du Val, 1858	K1–R
Cerylonidae Billberg, 1820	Pg2–R
Coccinellidae Latreille, 1807	K2–R
Corylophidae LeConte, 1852	Pg2–R
Cryptophagidae Kirby, 1837	K2–R
Cucujidae Latreille, 1802	Pg2–R
Endomychidae Leach, 1815	Pg2–R
Erotylidae Latreille, 1802	Pg2–R
Kateretidae Erichson, 1843	Pg3–R
Laemophloeinae Ganglbauer, 1899	Pg2–R
Languriidae Crotch, 1873	K1–R
Latridiidae Erichson, 1842	K2–R
Monotomidae Laporte, 1840	Pg2–R
Nitidulidae Latreille, 1802	K1–R
Passandridae Erichson, 1845/Blanchard, 1845	Pg2–R
Phalacridae Leach, 1815	Pg2–R
Propalticidae Crowson, 1952	N2–R
Silvanidae Kirby, 1837	Pg2–R
Sphindidae Jacquelin du Val, 1858	Pg2–R
Incertae Sedis:	
Parandrexidae Kirejtshuk, 1993	J2–J3

groups or, if their appearance occurred simultaneously, Cucujoidea were more successful in mastering such ephemeral localities. Perhaps more recent formation of Cucujoidea can be preferred, because it does not need an additional supposition and corresponds to the data from other fields of knowledge.

Appearance of Tenebrionoidea and Chrysomeloidea should be connected with evolution of other Cucujiformia. It was timed to the same period as the early records of Cleroidea, but all the earliest findings of Tenebrionoidea and Chrysomeloidea fall with deposits from the Upper Jurassic. In contrast to Cucujoidea the archaic groups of both the superfamilies are characterized by: (1) at least more complex structure of imaginal instars; (2) adherence to wide scope of localities both in forests and in other places (sometimes open and rather dry); (3) larval life more rarely on the surface of wet food substrate, but usual inhabitation deeply inside substrate or on fresh plant vegetative organs; (4) comparatively long duration of larval development (up to some years); (5) rare larval leaving of food substrate to hide into soil for pupation.

These peculiarities show that if the last mentioned superfamilies had their origin in the places similar to those which were characteristic of initial Cleroidea and Cucujoidea, the trace of this origin was lost in bionomic and structural peculiarities of most of Tenebrionoidea and Chrysomeloidea.

The difficulty in the traditional interpretation is connected with the position of Curculionoidea. It was impossible to explain the presence of rather advanced curculionid Oribionidae in the Middle Triassic before the appearance of all 'archaic' superfamilies. The problem is a considerable similarity of some organs of Chrysomeloidea and Curculionoidea which are traditionally and by many students up to now regarded as a sequence of a common ancestry. However, archaic curculionid wing venation as was pointed out by Crowson (1955) resembles the staphylinoid rather than chrysomeloid one (or cucujiformian venation in general). Therefore if Curculionoidea and Chrysomeloidea could be treated as relatives, we should be obliged to regard Curculionoidea as a group closer to the ancestor of Polyphaga than other superfamilies.

Quest for possible decisions

A key to clarify the mentioned conflict came from the analysis of peculiar distribution of types of ontogenesis and generalized mode of life of coleopterous groups of a high taxonomic rank. A certain regularity in structural differentiation through individual development and distribution of certain levels of differentiation among free (larva, imago) and concealed (egg, pupa) instars of life circle studied and formulated by Tikhomirova (1991 and so on) gives a possibility to explain some peculiarities of larval organization of different groups. In particular, difference in levels of silphoid differentiation of most cucujiformian groups, on the one hand, and bruchoid differentiation of Chrysomeloidea and Curculionoidea, on the other hand, are connected not with any progressive transformation of the joint ancestor group, but with some parallel shifts along the normal process of structural differentiation which was and is characteristic of the order as a whole. These shifts were conditioned rather by similar inactive mode of life and similar diet than by close relationship (Tikhomirova, 1977).

[Principal larval differentiation after Tikhomirova, 1991 (p. 35): Bruchoid level (II stage of late embryogenesis) – straightening of caudal curve (initially turned dorsally), fusion of paired maxillary and lacinial rudiments, elongation of moth parts and thoracic legs with simultaneous reduction of abdominal legs [in weevils – secondary simplification after reaching the mentioned level differentiation, a further reduction of antennae and legs begins]; silphoid level (III stage) – deflection of head and caudal part on ventral side, elongation and segmentation of antennae (up to 3 antennomeres), mouth parts (3-segmented maxillary and 2-segmented labial palpi), development of 2 lobes of maxillae not articulating from stipes, 5-segmented legs, articulation of urogomphae and development of gonopode; staphylinoid level (IV stage) – elongation of head with appearance of gular sutures (it becomes prognathous), 4-segmented antennae, fusion of labrum with frons (formation of nasale), lacinia reduces and galea elongates; Caraboid level (V stage) – 2-segmented galea, articulating tibia and tarsus.]

Some years ago an interpretation of the system of the order based not only on structural transformation but mostly on differences in type of ontogenesis and mode of life was proposed (Kirejtshuk, 1992/1991). Five suborders of Coleoptera were characterized by different trends (Fig. 1):

1. Mostly palaeozoic suborder Protocoleoptera or Archeocoleoptera were reconstructed as a group of the forms with xylomycetophagous larvae and adults living inside the substrate, mostly into subcortical spaces (Ponomarenko, 1969; Crowson, 1981 and so on). The initial type of coleopterous development can be characterized by desembryonization of larval development (larva coming out of an egg less differentiated than in the ancestor) and gerontomorphosis of the imago (i. e. long larval life enabling to reach a complete level of structural differentiation).

The rest of the four suborders appeared during the Triassic and reached the end of the recent epoch. They are as follows:

2. Archostemata mostly contains xylophagous borers in larval instars and frequently openly living imagines. Perhaps, this suborder inherited not only many characters of the palaeozoic ancestors, but also their characteristics of ontogenesis and mode of life. It is important to mention that this group gave some palaeoendemic relicts of the Triassic and Jurassic age almost of the generic rank (Ponomarenko, 1969; Kirejtshuk, 1999a, 1999b). This is a unique case among insects and terrestrial Arthropoda. This group has quite distinct structural peculiarities hardly changed over 200 million years.

Usually this suborder is thought to be opposed to the rest of the recent suborders (Beutel, 1997 and many others), although sometimes it is regarded as a sister group of the pair Adephaga+Myxophaga (Kukalova-Peck, Lawrence, 1993). The opinion grounded by Ponomarenko (1973) is here considered as more preferable not due to morphological argumentation alone, but also because of the palaeontological evidence used by him [this suborder is correspondent to Ponomarenko's 'Cupedoid lineage' with Micromalthidae].

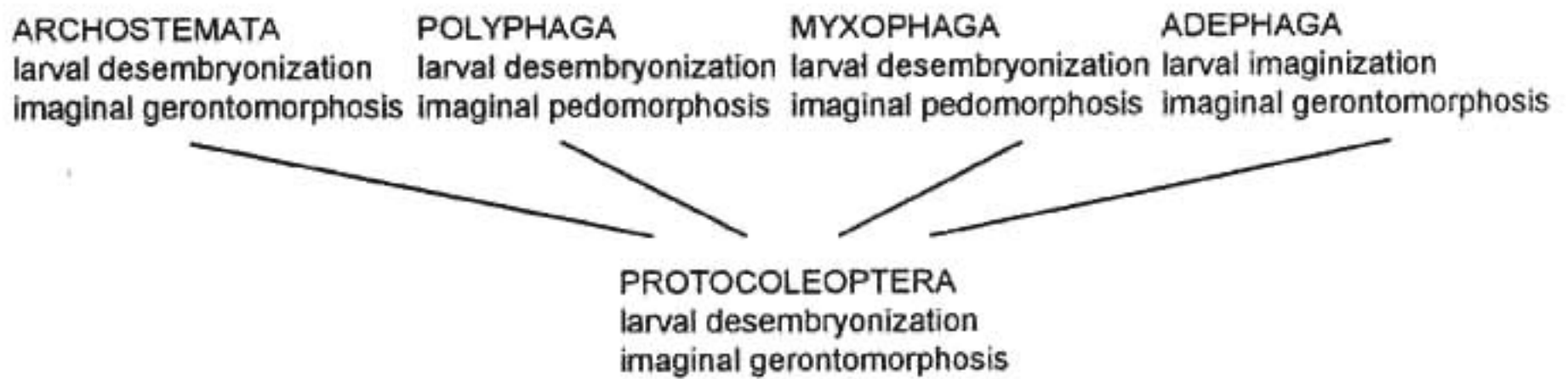


Fig. 1. Scheme of different trends of ontogenesis in the suborders of Coleoptera (orig., comments in the text).

3. Polyphaga is an extremely diverse suborder, but with a general trend to progressive disembryonization of larva and paedomorphous transformations of imago (both the active instars emerge with less advanced structures in comparison with their ancestors). These circumstances give a paradox connected with deficiency of any reliable synapomorphous character in this suborder. Appearance of Polyphaga with a progressive tendency to disembryonization of ontogenesis was mostly caused by intensification of the biotic processes on the whole-strengthening during the Mesozoic era and particularly during Caenozoic era.

'Schizophiroid lineage' formulated by Ponomarenko (1969 and so on) became the most successful group in the transition of beetles from under-bark habitats to continental basins or localities near them at the Rubicon between the Palaeozoic and Mesozoic eras. This lineage gave the recent Adephaga and Myxophaga or at least it was a group allied to their ancestors.

4. Myxophaga seemed to be almost a direct offshoot of the 'schizophiroid lineage', but probably with some paedomorphous transformations in imaginal organization (including a decreasing number of antennomeres and palpomeres). The studied larvae show a tendency to disembryonization of ontogenesis. Similarity of larvae of the recent myxophagan and polyphagan groups frequently referred to in publications (Crowson, 1955, 1981; Reichardt, 1973; Baehr, 1979 etc.) can be more easily explained by similar shifts in succession of structural differentiation distributed along free and concealed stages of normal ontogenesis than by close ancestral roots of both the suborders (see above).

5. Adephaga had an origin conditioned by adaptations in both the larva and imago to more active movement in water or near it with corresponding larval imaginization and imaginal gerontomorphosis (Ponomarenko, 1983 and so on). Archaic appearance of these groups is explained by their gerontomorphosis, which seemed to be connected with comparatively long individual life in both the active stages (larva and imago).

Diversification in suborder Polyphaga and its infraorders

Polyphaga show some differences in the generalized mode of life for each infraorder and they seem important to understand their peculiar historical fate and phylogeny. Perhaps the main diversification of the suborder occurred during the Triassic – at least Elateriformia, Staphyliniformia and Curculioniformia have been recorded from the middle of that period, but Cucujiformia appears in fossil records in the Early Jurassic (Ponomarenko, 1995). Formation of all infraorders (except Cucujiformia)

were connected with transitions of some ancient Polyphaga from initial localities: Staphyliniformia and Elateriformia in litter, soil and fresh water basins through intermediate localities in almost destructed wood and plant litter after a long period of decay, but Curculioniformia formed in generative organs of Gymnosperms. However, evolution and phylogeny of Cucujiformia took place mostly in sappy bark, subcortical and cortical places infested by fungi or in fungal fructifications (Fig. 2).

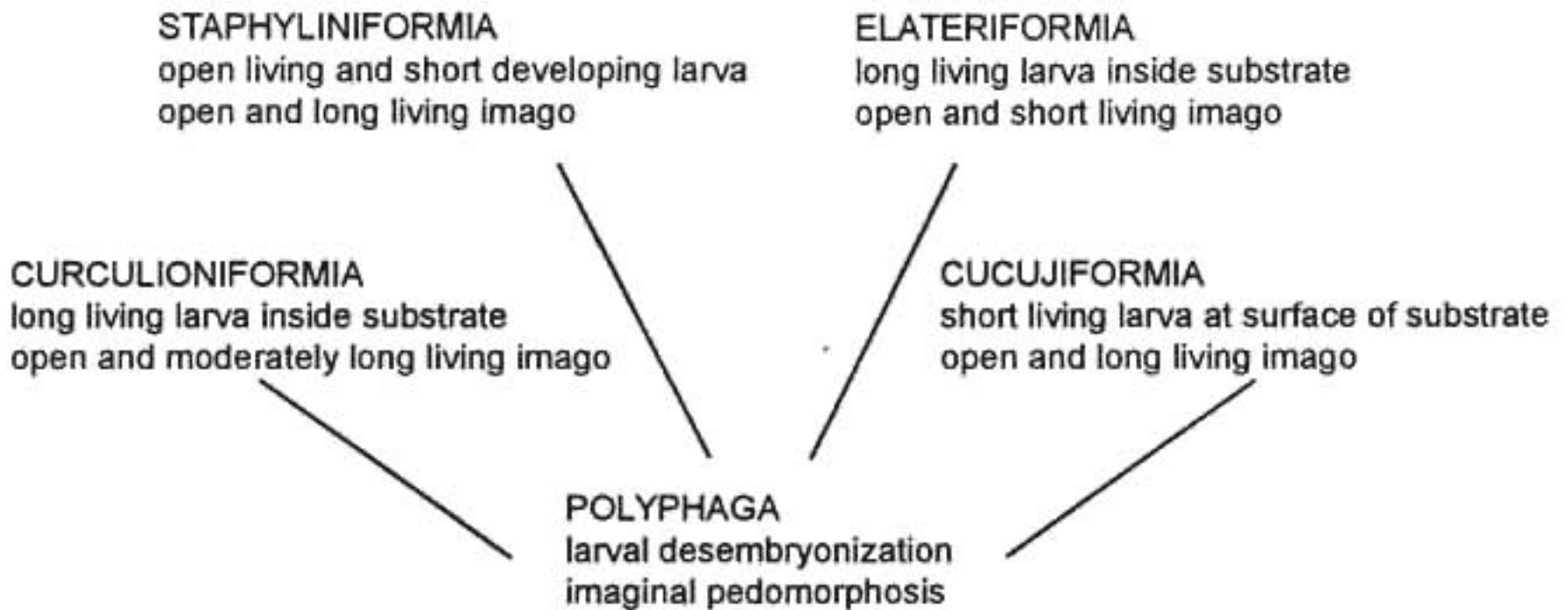


Fig. 2. Strategies in generalized mode of life of infraorders of Polyphaga (orig.).

Following the logic used for the taxonomic partition of higher groups we can try to study the level of the superfamily. Many archaic groups of Cucujiformia live in ephemeral consortii appearing in connection with fungal infection of trees or at least wet plant substrate. They are Derodontidae of Derodontoidea; Nosodendridae of Bostrichoidea; Phloiophilidae and Peltidae of Cleroidea; Sphindidae, Nitidulidae, Monotomidae, Boganiidae, Helotidae and most of other Cucujoidea (Crowson, 1984; Lawrence, Milner, 1996 and others). Probably Mycetophagidae, Tetratomidae, Archeocrypticidae, Pterogeniidae and Ciidae showing different archaic characters were initially adhered to the localities and mode of life closer to those of the ancestors of the infraorder. But keeping of the similar mode of life by some other Tenebrionoidea and cerambycid groups of Chrysomeloidea should be regarded as a secondary return to them. Fossil records at this level of knowledge become somewhat questionable to estimate time of appearance of the coleopterous groups with the family rank, likewise for groups of a lower taxonomic rank this kind of evidence in most cases is more or less ambiguous (i. e. presence and absence of any subfamilial or generic group in fossils frequently cannot be unequivocally interpreted). Nevertheless, some tendencies expressed in peculiarities of the mode of life of different superfamilies of the infraorder Cucujiformia can be traced (Fig. 3), and ancient changes in inhabitation and mode of life of ancestors can be shed light on. General tendency characteristic of the most groups was connected with a further mastering of dead wood at different stages of decay and, as a next stage, a further mastering of open spaces with larval development in soil. However, most Cleroidea demonstrate a strict tendency to development of predation in different substrates. Chrysomeloidea mastered life with feeding first on generative organs and later on vegetative organs of plants.

Origin of superfamily Cucujoidea and circumstances of its early evolution

Only among the superfamily Cucujoidea, a greater or lesser adherence to initial localities is expressed in all lineages of it. Some archaic Nitidulidae are extremely similar to Peltidae, including Jurassic Meligethiellinae. Except miniaturization in structure of many archaic groups, the only nonstructural difference between these superfamilies (Cleroidea and Cucujoidea) seems to be duration and intensity of individual development which can be estimated not only by absolute seasonal time, but also by a level of larval differentiation. Progressive simplification of advanced Nitidulidae, especially phytophagous forms is traced in detail (Kirejtshuk, 1994b, 1996). It is supposed that this tendency can be extrapolated to the superfamily as a whole. In this case we should explain the origin of this superfamily from a peltid-like ancestor due to intensification of individual development. However, it is necessary to find a reason for this event. If we recall that the appearance of the first Cucujoidea coincides in time with the Cretaceous crises and formation of the caenophytic groups of plants, intensification of development of this groups with respective maintaining of archaic bionomic features

becomes explicable in the context of general intensification of all the processes in the biosphere, which was reflected on the fate of many groups of plants and animals.

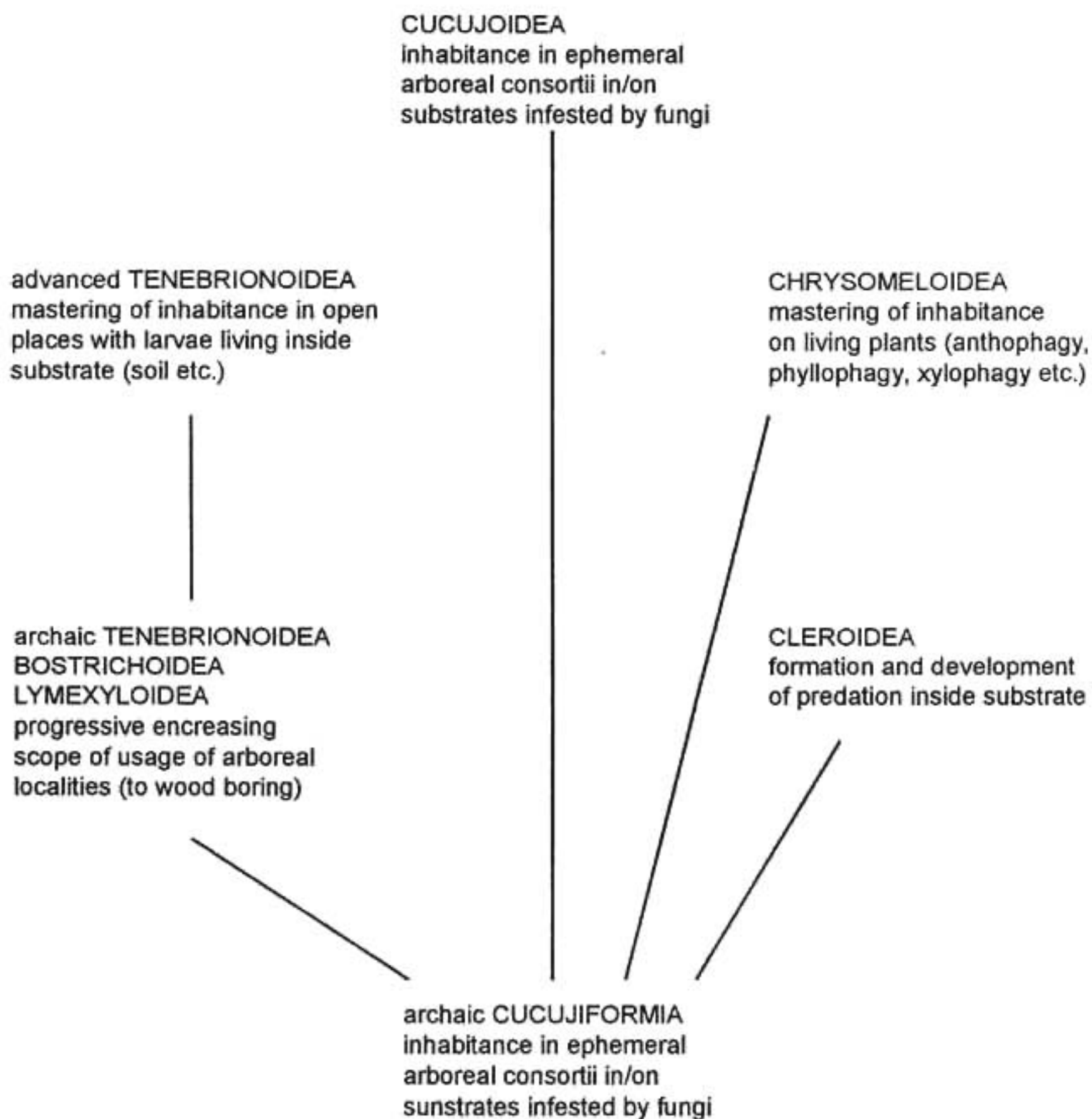


Fig. 3. Tendencies in change of mode of life in infraorder Cucujiformia (orig.).

Thus, if the mentioned reasoning is correct, we are obliged to make some essential correction in traditional understanding of phylogeny of the order, and in particular phylogeny of Cucujiformia. At least in the context of the proposed argumentation, the progressive evolution of Polyphaga in conditions of a more or less constant ecological niche that is in the exuded tree sap, is associated with subcortical and cortical arboreal habits infested by fungi and fungal fructifications proper.

Besides keeping the initial mode of life and probably the appearance of open-living predators (such as Cybocephalinae and Coccinellidae, the latter known from the Middle Cretaceous), in some cucujoid groups the transition from initial complete mycetophagy to some types of phytophagy could be traced. During the Mesozoic era the progressive expansion of the gymnosperm plants caused formation and development of interactions between beetles and fungi, including fungi habitating more open localities [even mildew fungi (like Erysiphales) on plant-leaf surfaces]. These localities frequently provided conditions for larval development only for a short period. A comparatively fast larval life perhaps was the basic factor for formation of Cucujiformia. Some recent Derodontidae, Peltidae, Nosodendridae, Nitidulidae, Helotidae and others bear extremely archaic character of both the

structure and bionomy. It is seen here that the most ancient group of this infraorder probably was the superfamily Cleroidea with Peltidae, but phytophagous forms are represented by Parandrexidae, some Nitidulidae, Katereridae, Smicripidae, some Boganiidae and Chrysomeloidea are certainly derivative. The Jurassic Chrysomeloidea with archaic appearance (Medvedev, 1968) and Parandrexidae were probably associated with cones of Bennettiales, Cheirolepiales or allied Gymnosperms (Kirejtshuk, 1994a). These Mesozoic groups of insects share some similarity with recent anthophagous groups from Smicripidae, Nitidulidae and Boganiidae. The first Chrysomeloidea seemed to have a comparatively short larval life, coinciding with the period of 'flowering' of host-plants, but then some of groups of this superfamily secondarily acquired rather a prolonged individual life (especially in Cerambycidae), although conservative groups retain some archaic traces making their relationship with Cucujoidea evident.

Thus, in addition to the Triassic Curculioniformia (Curculionoidea), at least 2 other groups became phytophagous during the Jurassic period. They are extinct Parandrexidae and now existing Chrysomelidea, the latter still being quite successful and abundant in the angiosperm associations despite their initial trophic connections with extinct groups of plants. By the time of the Cretaceous cataclisms in the biota, there were at least some phytophagous groups already living on Gymnosperms. It is difficult to speak about their particular fates during decreasing of life scale, however, when the next increase in flora made it possible for Angiosperms to dislodge the ancient groups of plants, the best chance for the ancient phytophagous groups to survive was connected with their transition to vegetative organs of plants, available for eating much longer than their 'flowers'. On the other hand, new chances to feed on generative organs of the newly appeared plants opened before the younger Cucujoidea. Therefore it is among the cucujoid families that we can find numerous transitions to true and complete anthophagy (Kirejtshuk, 1989, 1994, 1996).

The superfamily Cucujoidea is characterized by rather a short larval development and comparatively long-living imagines, but both the instars were and are quite shortly active in contrast to many coleopterous groups. Due to these peculiarities they could use many ecological gaps and narrow ecological niches, not accessible for the groups, less mobile in development and with less ecological plasticity. Therefore this group could master and be accustomed to extremely different types of substrate, including flowers of Angiosperms.

The Mesozoic Proangiosperms and early Angiosperms had small inflorescences and a rather short period of their flowering (Meyen, 1987; Gottsberger, 1991 and so on). Highly specialized forms, adapted to big cones of the Gymnosperms could not transit on new inflorescences, and therefore it is impossible to recognize the more traditional viewpoint on participation of beetles in the origin and formation of the flowering plants (Diels, 1916 and many of later publications). The main reason for appearance of Angiosperms seemed to be the same as for Cucujoidea. It was intensification of all biological processes in general. The young coleopterous group began a new epoch of mastering the higher plants according to the scheme proposed earlier (Kirejtshuk, 1989).

Only few of tenebrionoid groups shifted to feeding on living plants, because this superfamily had the time of its main diversification 50 million years before the Cretaceous crises occurred. It is in the Cretaceous that Cucujoidea were intensively diversifying in accordance with the formation of caenophytic flora, and therefore this group had more chances to be accustomed to new conditions. Anthophagization involved many groups of this young superfamily not connected by too close kinship. Anthophagous forms independently appeared in some nitidulid groups of the subfamilies Epuraeinae, Carpophilinae, Meligethinae, Nitidulinae, Cillaeinae. These changes in the trophics and mode of life conditioned an increase in convergent similarity, and therefore many anthophagous groups of the Nitidulidae were formerly regarded as the closest relatives.

In addition to continuity of initial ecological peculiarities, it is comparative recency and apparently unsteady modes of diversification that cause a gap which is not always clear between cucujoid families, numerous homoplastic transformations in organs, characters of which are usually important for diagnostics of families in other cucujiform superfamilies of an earlier origin. In accordance with the general trend in evolution of the superfamily, it is believed that characteristic cucujid peculiarities could be forming among some cleroid (and probably related) groups. As localities and substrate for inhabitation of most of the first Cucujoidea were rather similar (live trees and fresh wood infested by fungi), and their mode of life was slightly changing or not changing at all for a long time, divergences and specializations in many families frequently gave parallel development or homoplasy, partition of the superfamily into comparable groups or lineages of related families is rather problematic.

On 'superfamily Nitiduloidea'

The general structure and variations of groups of the family Nitidulidae are characterized in detail in some of the recent publications (Kirejtshuk, 1992, 1998b; Audisio, 1993 and so on). As it has

already been mentioned, the generalized appearance of Nitidulidae is quite archaic, resembling some of the recent and Mesozoic Peltidae (Kirejtshuk, Ponomarenko, 1990). Therefore there is a traditional viewpoint regarding Nitidulidae as the most plesiomorphous group among Cucujoidea or a group very close to the ancestor of Cucujiformia as a whole. The grouping together of the mentioned families makes sense since not only external characters, but even male genital structures in these groups demonstrate some rows of continued transitions. In order to show inseparable unity of Cucujoidea, we can consider connections of the families which were sometimes combined into a separate superfamily Nitiduloidea, including Nitidulidae, Kateretidae, and Smicripidae (Audisio, 1993; Crowson, 1995).

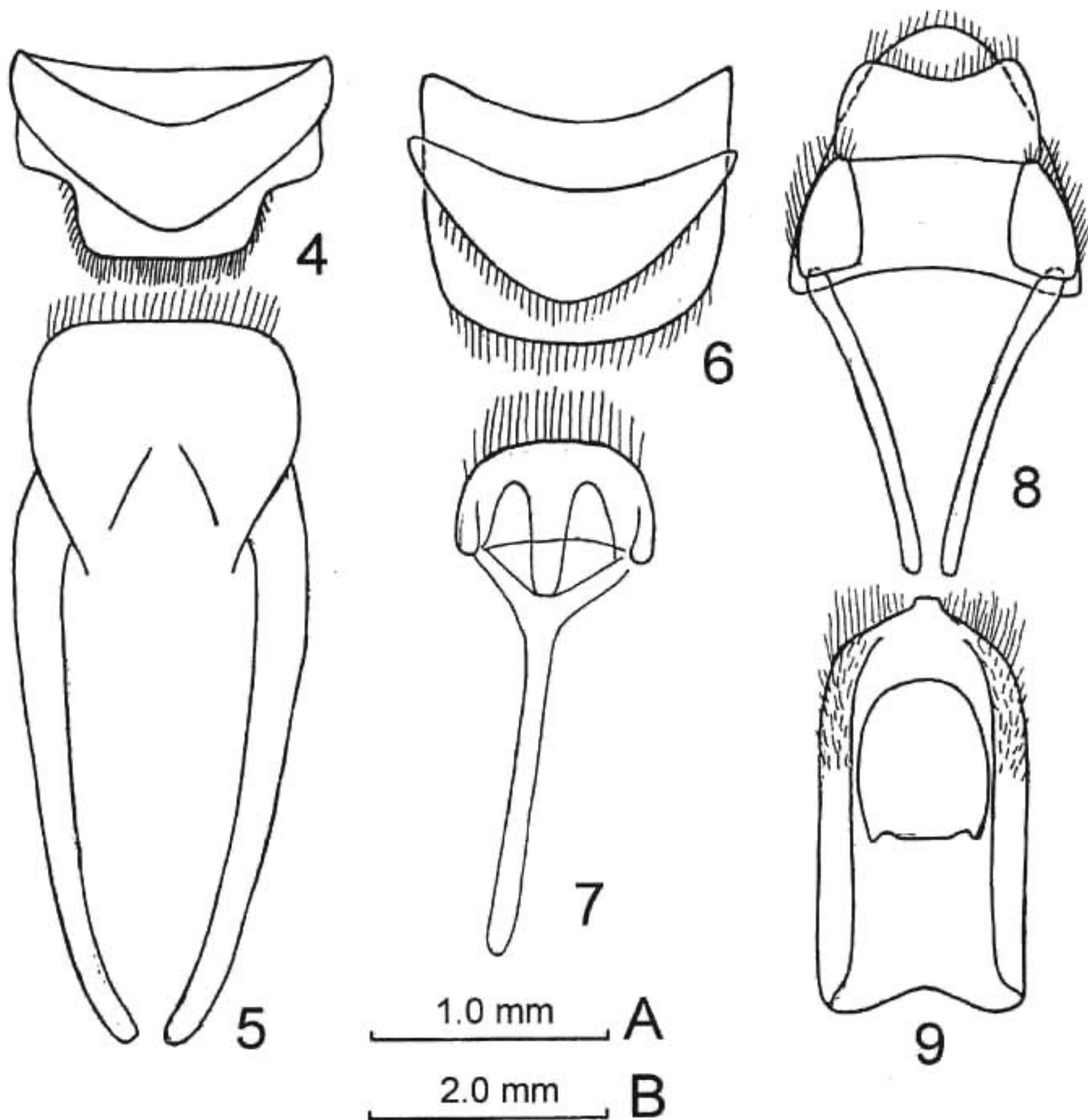
The ventral plate and articulated or fused *spiculum gastrale* form together with anal sclerite the so-called genital capsule, which apparently looked like characteristic of the families Nitidulidae, Kateretidae and Smicripidae. However, a similar organ surrounding aedeagus can be found in many groups. Particular similarity of this organ in the mentioned families can be traced among representatives of Helotidae, Monotomidae, Languriidae and many others, but the genital capsule of cleroid families is rather different. In many cucujoid, tenebrionoid and chrysomeloid families the abdominal segment preceding to male aedeagus (terminalia) forms an organ acting as a mechanical protection and as a device to direct movement of aedeagus when it is extracted outward. The *spiculum gastrale* usually lying on the first interconnecting membrane seems to provide an unfolding condition for this membrane and the inner sac of penis when aedeagus is retracted.

Morphogenetic coordination in structures of the genital capsule causes its similation in many groups. Comparison of this organ in representatives of different cucujiform families gives some arguments to doubt about the classical Verhoeff's homologization and his nomenclature of pregenital sclerites of the male. Probable remnants of the abdominal sternite 9 in the boganiid *Paracucujus rostratus* Sen Gupta et Crowson, 1966 look like certainly paired structures, while an appendage of sternite 8 looks like the unpaired *spiculum gastrale* in males of other families (Figs 25–26). Remnants of the abdominal tergite IX of the peltid *Zimioma grossum* (Linnaeus, 1758) are with paired long appendages of ? sternal origin (Fig. 5). The genital capsule of the trogossitid *Leperina squamulosa* Gebler, 1830 is also with paired spicules articulated to small sclerites at sides of the reduced abdominal sternite 8 (Fig. 8). At the same time the peltid *Thymalus limbatus* (Fabricius, 1797) resembling the species of the Jurassic Meligethiellinae has a male genital capsule very similar to that of many cucujoid groups (Fig. 6). But the male genital capsule of the protocucujid *Ericmodes fuscitarsis* Reitter, 1877/1878 has no distinct spicule proximally from probable remnants of sternite 8 (Fig. 9). Deuve (1988) concluded that the genital capsule is composed only by laterotergites, and sternites 8 and 9 are absent in adults of both sexes. It seems reasonable to presume that development of spicules of the genital capsule is to a certain extent coordinated with respective development of the inner sac of penis. The homology of sclerites in the genital capsule is questionable because embryological studies do not support the classical interpretation either. Blazejewski (1968) showed that the anal sclerite of the pollen-beetle *Meligethes aeneus* (Fabricius, 1775) developed from the imaginal discs of the 9th abdominal segment of larvae (not the 8th).

Besides similarity in the genital capsule, Nitidulidae, Kateretidae and Smicripidae show some other common tendencies towards structural transformations. One of them is the reduction of imaginal galea (as in Monotomidae), while a tendency to reduction of lacinia is more characteristic of many groups of Polyphaga (Boganiidae, some Chrysomeloidea and Curculionoidea). For example, maxilla of *Paracucujus rostratus* has an appendix which can be homologous with lacinia (Fig. 23). This peculiarity of maxilla is rather important and needs a special investigation, however, parallel or not completely parallel reduction (or more correctly paedomorphous underdevelopment) of one lobe can be hardly explained by close common ancestry (it appears in ontogenetic development between the silphoid and staphylinoid levels of larval differentiation – see above).

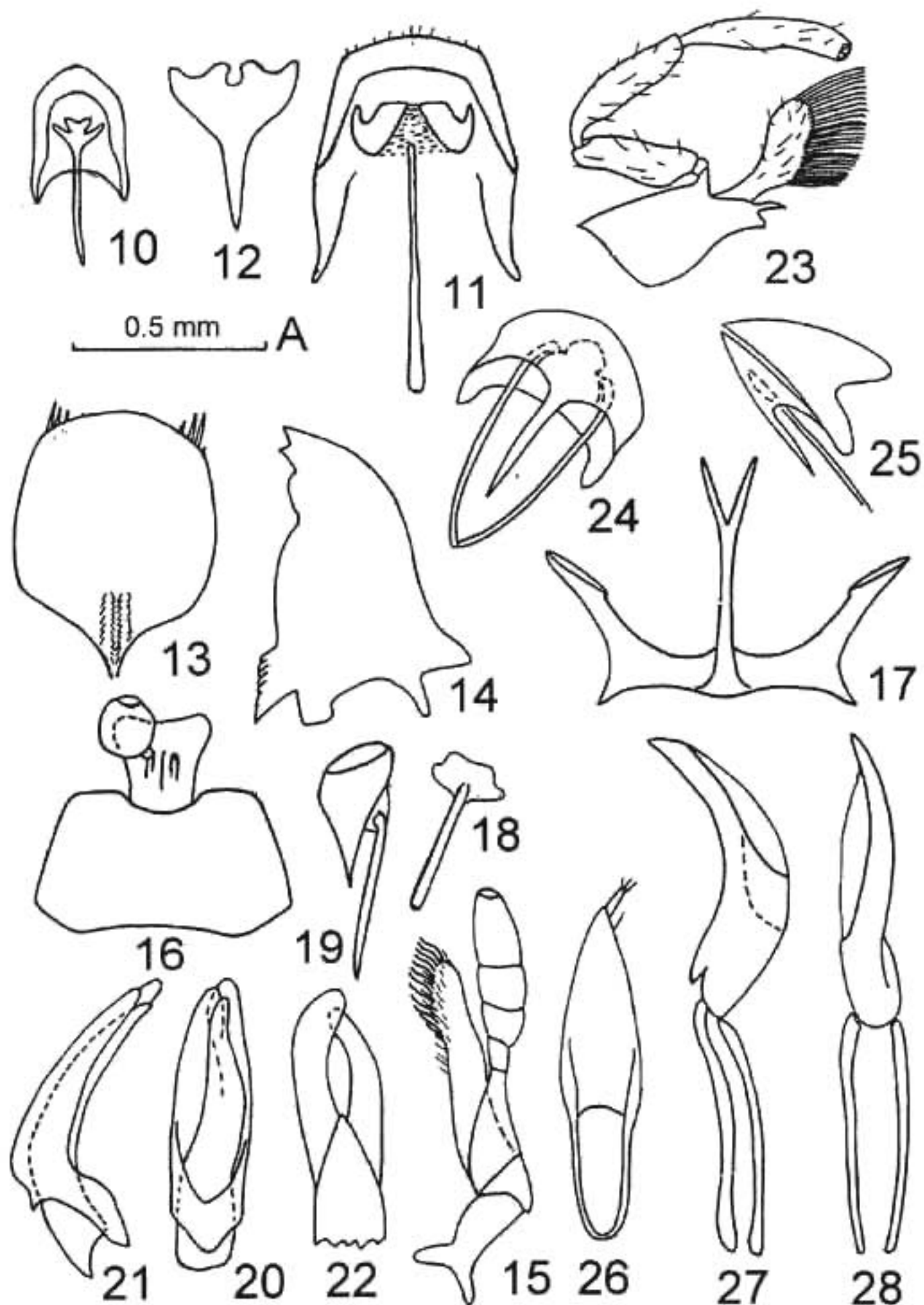
For these 3 families a reduction of functioning spiracles on abdominal segment 7 and absence of lateral expansions (plates or parts of ventral process) of metasternal furca in imagines are rather characteristic (both the features are usual for archaic Cucujoidea, and also Cleroidea, Lymexyloidea, Tenebrionoidea, Chrysomeloidea and Curculionoidea). It is evident that these similarities could be of an independent origin.

As diagnostic characters of Nitiduloidea, we also regard the articulating maxillary mala (? = galea) with sclerotized appendix (? = lacinia) in larvae (as in many cases among Boganiidae, some Cleroidea, Chrysomeloidea and Curculionoidea, but sometimes also in Lyctidae, Ptinidae, Peltidae, Lymexylidae, Endomychidae, but not in Kateretidae); 1-segmented labial palpi in larvae (also occurs among Lyctidae, Anobiidae and some Monotomidae); larval epicranium with not more than 4 (usually 2 or 4) stemmata on each side (although this feature is not unique among larvae of Polyphaga either).



Figs 4–9. Male pregenital sclerites of Cleroidea and Cucujoidea (genital capsule) (orig.): 4–5: *Zimioma grossum* (Linnaeus, 1758) (Peltidae) (ZIN – Vologda, Rimsky-Korsakov): 4 – abdominal segment 8, ventral; 5 – remnants of abdominal segment 9 of the same specimen, ventral; 6–7: *Thymalus limbatus* (Fabricius, 1797) (Peltidae) (ZIN – Krasnodarsky Kray: Lazorevka, A. G. Kirejtshuk): 6 – abdominal segment 8, ventral; 7 – remnants of 9th abdominal segment of the same species, ventral; 8 – *Leptina squamulosa* Gebler, 1830 (Trogossitidae) (ZIN – Primorsky Kray: Chernigovka, Emel'yanov): remnants of pregenital abdominal segments, ventral; 9 – *Ericmodes fuscitarsis* Reitter, 1877/1878 (Protocucujidae) (DEI – Chile, coll. Kraatz): remnants of pregenital abdominal segments of, ventral. Scale: A – to figs 4–9.

Similarity of hind wing venation of groups belonging to Nitidulidae, Kateretidae and Smicripidae appear to be connected with parallel adaptation of their ancestors to brachelytry accompanied by general miniaturization (particularly in the 2 last mentioned families). As a result of this adaptation wing venation lost many initial features and became somewhat similar to the Staphylinoid type because of the proximal displacement of venation.



Figs 10–28. Superfamily Cucujoidea (orig. and after Kirejtshuk, 1986; Kirejtshuk, Lawrence, 1992): 10 – *Propetes (Propetes) brittoni* (Kirejtshuk, 1986) (Nitidulidae, Epuraeinae) (ZIN – Australia, North Territory, Bessie Spring, E. D. Edwards): remnants of anal sclerite (? = tergite VIII) and ventral plate (? = sternite 8) with *spiculum gastrale* (? = sternite 9) of, ventral; 11 – *Rixerodes cunninghami* Kirejtshuk et Lawrence, 1992 (Nitidulidae, Nitidulinae) (ZIN – Australia, ACT, Canberra, Black Mountain, M. S. Upton): idem, ventral; 12 – *Jelinekiella* nom. n.¹ *aterrina* (Kirejtshuk, 1986), n. comb. (Kateretidae) (ANIC – Western Australia, Jadakot, F. H. Uther Baker): ventral plate and *spiculum gastrale*, ventral; 13–22: *Smicrips* sp. (Smicripidae) (ZIN – Panama, Barro Colorado I., A. Bulten): 13 – labrum, ventral; 14 – right mandible, dorsal; 15 – right maxilla, dorsal; 16 – mentum, ligula and labial palpus, ventral; 17 – metendosternite, dorsal; 18 – ventral plate and *spiculum gastrale*, ventral; 19 – genital capsule, lateral; 20 – aedeagus, ventral; 21 – idem, lateral; 22 – tegmen, dorsal; 23–28: *Paracucujus rostratus* Sen Gupta et Crowson, 1966 (Boganiidae) (ZIN – Western Australia, Margaret R., in *Macrozamia* cones): 23 – left maxilla, dorsal; 24 – genital capsule, ventral; 25 – idem, lateral; 26 – tegmen, ventral; 27 – penis trunk, dorsal; 28 – idem, lateral. Scales: A – to figs 10–28.

¹ The name *Jelinekiella* nom. n. is proposed for *Jelinekia* Kirejtshuk, 1986 (Kateretidae) (Entom. obozr., 65 (3): 559) because this name was preoccupied in 1980 for genus in subfam. Polycestinae (Buprestidae) (Cobos, 1980, Eos, 54: 88).

Aedeagi of Nitidulidae can be of either carpophiline or nitiduline types; they are always symmetrical, with fused tegmen (without 'parameres') and a dorsoventrally depressed penis trunk, while that of Kateretidae and Smicripidae is asymmetrical, laterally compressed and with 'phallobase' and articulating 'parameres'. It is rather a principal difference to reject the idea of close common ancestry of these groups.

Moreover, larvae of representatives of Kateretidae and Smicripidae are without distinct prostheca on their mandibles (although larval mandible of some *Cybocephalus* Erichson, 1844 is also without prostheca). In contrast to Nitidulidae, the family Kateretidae is additionally characterized by **i m a g i n e s** : by long narrow galea, reduced fold between elytral surface and epipleura (as only in the nitidulid *Calonecrus* J. Thomson, 1857, large 6th abdominal segment and the next segment partly retracted, spiracles on the 1–6 abdominal segments of usual oval configuration and a penis trunk well sclerotized and laterally depressed; in **l a r v a e** : by a head with developed endocarina; divergent hypostomal ridges; developed hypostomal rods and an oval pronotum without sclerotized areas. The Smicripidae – in **i m a g i n e s** : by a well-raised frontoclypeal suture, 2-segmented labial palpi, notosternal sutures rather distinct and the last abdominal segment very long; in **l a r v a e** : by parallel hypostomal rods (as in Laemophlaeidae) and without distinct cardines (as in Phalacridae and Cucujidae–Laemophlaeidae) (see Kirejtshuk, 1998b).

Thus, the characters used to separate the superfamily Nitiduloidea are, if not certainly convergent, more or less ambiguous for grounding common ancestry of this group. At the same time these families have some serious differences, most of which show aedeagal structure. Absence of distinct synapomorphy leaves this proposition without any sense.

Another question appears in connection with comparison of Nitidulidae with Helotidae. The last group is represented by many species formerly regarded as composing one genus. Imagines of this group according to their external characters, if non-oval and prominent procoxae or oval mesocoxae without exposed trochantin, could be regarded as a separate subfamily or a separate tribe of the subfamily Cryptarchinae (see below). The labrum of Helotidae fused with frons is also rather similar in the mentioned nitidulid group. However, mouth parts of *Helota* species are rather specialized, and their metendosternite has some peculiarities without definite analogies among cucujoid beetles (Crowson, 1955). Larvae of *Helota*, in contrast to Nitidulidae, have mandibles without prostheca, 2-lobed maxillae not articulating with gula and without a clear trace of a finger-shaped appendage, separated mentum and submentum, 2-segmented labial palpi and annular-biforous spiracles. Almost all the distinguishing characters of Helotidae could be regarded as ancestral for Nitidulidae, and therefore both the families can be grouped in one phyletic branch of the Cucujoidea (see below). Thus, it is thought that the families of Helotidae and Nitidulidae having close roots in the past were under different pressure-stimulated miniaturization and decrease of level of differentiation of both imagines and larvae. It was the main cause why Helotidae look like very archaic Cucujiform family with venation close to the Cleroid type, though Nitidulidae are characterized by considerable simplification with extremely reduced wing venation even in large specimens (Parsons, 1843). Nevertheless, the differences in structures of pro- and mesocoxae and their cavities between Helotidae and Nitidulidae give evidence that the roots of these families were not very close. The common tendencies connected with similarity in their past and recent habits and mode of life made them more similar in some structures.

At the same time the families Kateretidae and Smicripidae are similar to Boganiidae and Monotomidae not only by asymmetric uninverted aedeagus with more or less distinctly articulated 'parameres' (or one 'paramere'), but also common tendencies in transformations of imaginal and larval mouth parts, imaginal brachelytry, trophic and environmental preferences, miniaturization of structure, comparable level of structural differentiation and paedomorphosis. Therefore these families can be preliminarily approximated with one another as possible relatives (see below). The family Boganiidae is the most differentiated family among them in structures of both larvae and imagines, and aedeagus in this family has paired apodemes at the base of the penis trunk.

On composition of Cucujoidea

The main partition of the Cucujoidea was made by Crowson (1955, 1990) as well as by Sen Gupta and Crowson (1966, 1969a, 1969b, 1971), and further authors used their opinion as the base which needs to be developed. Taking into consideration all the information and sources, they preferred mostly some blocks of morphological argumentation, concerning general appearance, wing venation, larval and imaginal mouth parts, metendosternite, aedeagal structure. At the same time the family Ciidae is excluded from this superfamily, which in many later publications were put in the superfamily Tenebrionoidea (Lawrence, 1982, 1991 and others). Iablokoff-Khnzorian (1983) after studying male genitalia excluded the family Latridiidae from 'Clavicomia' and created a separate series 'Lathridimorphes' in which he put 2 families (Latridiidae and Prostomidae) demonstrating an aedeagal

structure intermediate between those of Cucujoidea s. str. (Cucujoidea sensu Lawrence et Newton, 1982) and Tenebrionoidea. He considered the trilobed type or tenebrionoid aedeagus as an alternative to the ring type or cucujoid aedeagus. However, even genitalia share some parallel transformations masking transformation rows. One good example of such evident homoplasy is aedeagus of dermestoid *Mariouta* Pic, 1898 (see Mroczkowski, Ślipiński, 1997) which is rather similar to those of tenebrinoid groups of the family Mycetophagidae.

The traditional understanding of the 'Clavicornia' (i. e. Cucujoidea sensu Lawrence et Newton, 1982), despite absence of distinct hiatus and apomorphy for taxonomic fixation, remains quite advisable, as the groups of this superfamily seem to have a coincidence in period of their appearance, similar general strategy in mode of life, habits and ecological adherence, common trends towards structural transformations (including the ring type or cucujoid aedeagus and its modifications). Thus, it is reasonable to conclude that their joint historical fate caused the features characterising the superfamiliar rank (immanent homology or 'underlying synapomorphy').

In this paper the scope and names of Cucujoid families given from the reference paper by Lawrence and Newton (1995). The only exception is connected with the name of Kateretidae (Erichson, 1843, Zeitschr. Ent., 4: 227), which should be preferable in comparison with Brachypteridae (Erichson, 1845, Naturgeschichte Ins. Deutschl., Berlin, 3: 125).

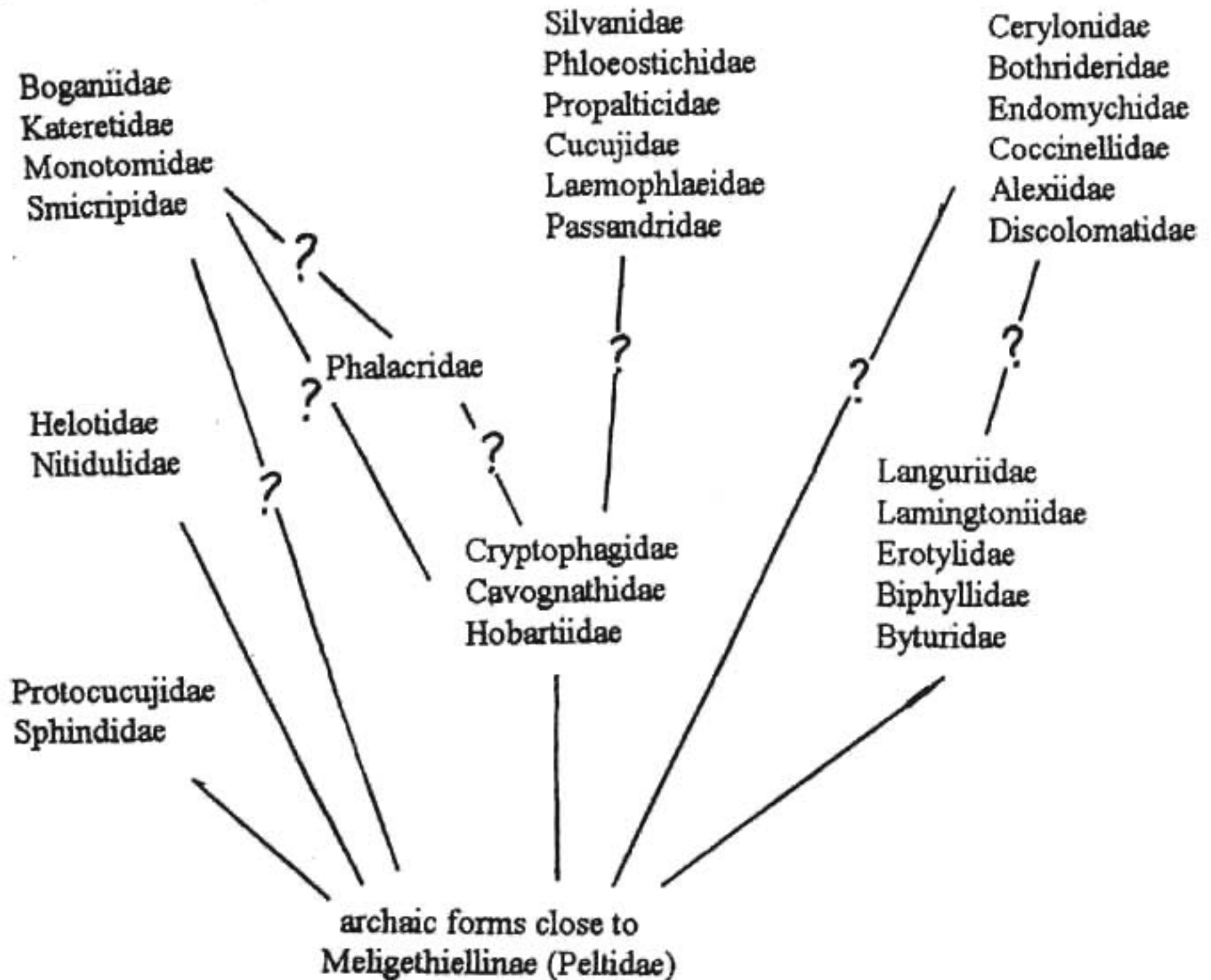


Fig. 29. Composition of superfamily Cucujoidea [explanations in the text] (orig.).

As a result the main groups of the related families among the superfamily Cucujoidea can be presumably listed as follows:

1. Protocucujidae–Sphindidae have symmetric and uninverted aedeagus with unilobed tegmen bearing fork-like sclerite and with penis trunk bearing or not short paired apodemes (struts); formulated by Crowson (1955) and supported by Ślipiński (1998);

2. Helotidae–Nitidulidae have symmetric uninverted aedeagus with uni- or bilobed tegmen with fork-sclerite and penis with single or paired apodemes (struts); here proposed (see above and below);

3. Boganiidae–Kateretidae–Monotomidae–Smicripidae are united based on the common tendency in transformation of imaginal mouth parts as well as on the tendency towards asymmetry of uninverted aedeagus with articulated 'parameres'; proposed here (see above) [Kirejtshuk (1986a) admitted connections between Kateretidae and Cryptophagidae];

4. Cryptophagidae–Cavognathidae–Hobartiidae are linked mostly due to external characters of imago and plesiotypic similarity; reviewed by Sen Gupta and Crowson (1966, 1969a, 1969b, 1971 and so on) and later their interconnections supported by Leschen (1996), who attributed them to the Cucujid lineage of Cucujoidea (aedeagal structures of Cryptophagidae are much more diverse than in Nitidulidae, but in all cases aedeagus is uninverted);

5. Silvanidae–Phloeostichidae–Propalticidae–Cucujidae–Laemophlaeidae–Passandridae have imaginal body more or less flattened, symmetric aedeagus (inverted or sometimes uninverted), tegmen basically with articulate parameres (Propalticidae without) and fork sclerite, penis usually with single apodeme (strut); initially regarded as members of the Cucujidae s. l.; supported with a special emphasis by Wilson (1930), although Crowson (1955) and further researchers regarded affinities of the mentioned families as uncertain;

6. Languriidae–Lamingtoniidae–Erotylidae–Biphyllidae–Byturidae have adults with elongate body shape and tarsi 5–5–5; divided into 2 groups: the first 3 families with a tendency towards asymmetric aedeagus lying at side with articulating 'parameres' and one apodeme (strut) at the base of penis trunk; and the last 2 families with symmetric aedeagus without 'parameres' and with paired apodemes at the base of penis trunk; were elaborated by Crowson (1955), Sen Gupta and Crowson (1966, 1969a, 1969b, 1971), Iablokoff-Khnzorian (1983) and others;

7. Cerylonidae–Bothrideridae–Endomychidae–Coccinellidae–Alexiidae–Discolomatidae–Corylophidae–Latridiidae are characterized by adults bearing equally reduced tarsomeres of all pairs of legs, aedeagus resting on its side and with reduced tegmen; grounded by Crowson (1955) and supported by Ślipiński (1990) as well as by Ślipiński and Pakaluk (1992/1991).

8. Phalacridae have uninverted aedeagus, somewhat similar to Nitidulidae and Helotidae, but larva rather similar to the lineage Silvanidae–Passandridae, although some resemblance with Cryptophagidae also has been recorded (Crowson, 1955, Sen Gupta, Crowson, 1966), and Lawrence (1991) pointed out similarity of larvae to those in Laemophloeidae and Smicripidae.

Summary

The paper demonstrates possibilities and effectiveness of some reasoning with the usage of palaeontological, developmental, ecological and bionomic information to solve problems of phylogenetics and systematics. These sources of information are particularly important to reconstruct a scenario of historical development (circumstances of 'ideal history of morphotypes'). This ideal model can give us advisable arguments to analyze structural characters, transformational rows and incongruence between them. Searching of developmental and bionomic reasoning for partition of all groups with high taxonomic rank (above genus) should be important to clarify phylogenetic interconnections and to ground systematic position of the studied groups. Hiatus in developmental and bionomic characteristics between groups with a higher taxonomic rank usually is greater than that between groups with a lower taxonomic rank. Traditional computer-aided cladistic analysis is useful to estimate structural differences, establish a pattern of characters distribution and find some contradictions. It becomes reasonable mostly in cases when it is impossible to use other type of argumentation, though in other cases it is better to find some ways to create a scenario before the cladistic analysis.

The mentioned approach is applied to analyze different interpretations of phylogenetic connections and the system proposed for the infraorder Cucujiformia and superfamily Cucujoidea. It was shown that this superfamily should not be regarded as quite an old group, close to the root of the infraorder, but rather as one of the youngest which seemingly appeared in connection with intensification of biotic processes during and after the Cretaceous crises and especially during Caenozoic era. Parallel pedomorphous transformations were promoting similarization of some groups that appeared under a similar selective regime ('superfamily Nitiduloidea'), although the ancestors of these groups could hardly be close relatives. At the same time, a difference in the level of structural differentiation of both larva and imago can mask probable close phyletic relations. These relations are supposed for the families Nitidulidae and Helotidae, on the one hand, as well as for families Kateretidae, Smicripidae, Monotomidae and Boganiidae, on the other. Resemblance in aedeagal structures gives a basis for putting forward the hypotheses of close relationship between the mentioned families of both the groups, and these hypotheses are supported by some other data.

Notes on family Helotidae

Type-genus: *Helota* Macleay, 1825 [Annul. Javan., p. 42]

Helotidae Reitter, 1876 [Verh. Naturf. Ver. Brünn, 14: 5] / Chapuis, 1876 [Librairie Encyclopedique de Foret, Paris, p. 15]; Gorham, 1874 (Trans. R. Ent. Soc. London: 447-449) mentioned the family status but not family-group name (Lawrence, Newton, 1995). Figs 31–65.

Redescription of imago (partly after Lawrence and Kirejtshuk, 1999): Length 6–16 mm and breadth 2–3 times less than length; subflattened to moderately convex; usually dark brown with an expressed metallic lustre and not infrequently greater or lesser part of body and appendages much lighter (yellow). Integument distinctly and differently punctured with longitudinal rows of punctures on elytra; mostly glabrous, only sparse hairs on antennomeres, sometimes brushes at tibial apices and tarsi, and separate bunches on male metasternum and ventrite 1. **H e a d** usually elongate, anteriorly or ventrally oriented, with temples not closely adpressed to prothorax or absent, with more or less reduced frontoclypeal suture and convex fore edge of frons, without transverse occipital ridge or carina and without ocelli. Eyes elongate. Mouth cavity anteriorly or anteroventrally oriented. 11-segmented antennae with a distinct, dorsoventrally compressed and compact 3-segmented club with sensory elements mostly concentrated on ultimate antennomere. Antennal insertions concealed from above. Labrum concealed beneath clypeus, partly or completely fused to clypeus or frontoclypeus. Mandibles moderately well developed, gradually curved mesally, with bidentate apex, well-developed mola, well-developed protheca. Pronotum somewhat shorter than wide, widest posteriorly, with sides more or less straight, not or slightly explanate and crenulate or denticulate lateral carina; its base not or slightly narrower than elytral bases and with mesal lobe, fore corners produced and broadly rounded or obtusely angulate, hind corners moderately to strongly acute and projecting posteriorly. Elytra 1.6–2.3 times as long as combined width and 2.2–3.1 times as long as pronotum, with 10 puncture rows, interstices between them sometimes elevated, subcostate or costate; their apices rounded or subacute (to rather acuminate in some females); their epipleura nearly complete. Rather often each elytron with 2 oval isolated and smooth yellow places without or with very reduced punctation (fluorescent in live beetles) and rather different from general elytral coloration (these isolated places subequal and disposed before and behind the middle of elytra) or only with a medial isolated smooth place oblique and concoloured with the surrounding surface. Scutellum somewhat narrowed at base and with broadly rounded or obtusely angulate apex. Pygidium not long and well clerotized, with subtruncate apex, from under which apex of anal sclerite is exposed in males. **A n t e n n a l g r o o v e s** well-developed and extending mentum. Submental furrows well raised along antennal grooves. Gular sutures widely separated. Corporotentorium narrow and with or without median process. Maxillae with distinct galea and lacinia. Apical maxillary and labial palpomeres cylindrical to fusiform. Prothorax with rather wide, long and flat or concave prosternal process, deeply emarginate at apex; deepened places laterally from procoxal cavity for reception of femoral base. Procoxae externally globular, not or slightly projecting below prosternum and moderately to widely separated. Mesosternum with anterior edge at midline on same plane as metasternum, mesosternal cavity rather shallow and circular to slightly transverse. Mesocoxae moderately to widely separated. Metasternum flattened, with raised paracoxal lines and submesoxal lines arched and strongly recurved at its fore corners, its hind edge between coxae subtruncate or shallowly emarginate. Metacoxae widely separated, with weakly developed metacoxal plates. Submetacoxal lines follow closely edge of metacoxal cavity. Hypopygidium subtruncate in both sexes, in males frequently widely depressed. **M e t e n d o s t e r n i t e** with lateral arms moderately to very long and absent laminae, its ventrolateral processes absent or weakly developed, its anterior process short or absent and anterior tendons on lateral arms or not apparent. Hind wing with normal transverse folds, well-developed elongate radial cell, right or obtuse inner posterior angle formed at base of radial cell, medial bar not crossed by fold. Abdominal spiracles raised on segments 1–7, 1st pairs of them largest. **L e g s** narrow and rather long. Protrochanter nearly of elongate type, but meso- and metatrochantera of tenebrionoid type. Femora narrow and not dorsoventrally depressed, with a weak groove for reception of tibiae. Tibiae simple, with very small spurs, but without crenelation or longitudinal rows of setae or hairs along outer edge. Tarsi with 4 short and simple tarsomeres and tarsomere 5 very long bearing 2 long and simple claws and bisetose empodium. **V e n t r a l p l a t e** weakly or moderately sclerotized and anal sclerite with fork sclerite (as that in tegmen and homologous with *spiculum gastrale*). Aedeagus of symmetrical and bilobed, consisting of dorsoventrally flattened penis trunk and tegmen. Tegmen with fork sclerite (ring type). Penis trunk with dorsal subapical orifice and usually its anterior edge with paired apodemes (struts), sometimes medially fused. Ovipositor mostly membraneous and only with heavily sclerotized apical parts of gonocoxites and large styli.

Larvae were described for the only (or ? two) species of the genus *Helota* (Fukuda, 1943; Lawrence, 1991; Hayashi, 1986 and so on).

Diagnosis: Imagines of most species of this family are easily recognizable due to the combination of the following characters: elongate and more or less subflattened body with characteristic shape of pronotum, narrowed base of scutellum, metallic shine and frequently strong and coarse punctation of integument, isolated spots on elytra (fluorescent in live specimens) and labrum fused with elongate fore part of frons. Especially peculiar feature of this group is development of submental furrows, subparallel to antennal grooves. Larvae of this family have rather a primitive appearance somewhat similar to that of Phloeostichidae (Lawrence, 1991) and Erotylidae (Roberts, 1958). At the same time the latter rather resemble some of the Nitidulid forms living in exuded tree sap, such as larvae of *Amphicrosus* Erichson, 1843; *Cryptarcha* Shuckard, 1839; and *Glischrochilus* (*Librodor*) Reitter, 1884, but very distinct in mouth parts (see below). Besides, one of unusual features of Helotidae is a weak development of tibial spurs (sometimes scarcely raised on protibiae).

This family is very similar to Nitidulidae differing from the latter in the following characters: **i m a g o** : elongate eyes, bilobed maxillae, raised submental furrows along antennal grooves; procoxal cavities closed posteriorly by a wide stripe of hypomera; oval pro- and mesocoxae; well-developed elongate radial cell; more complete remnants of radial, medial, cubital, and anal veins, without proximal displacement; raised and functioning spiracles on abdominal segment 7; unsclerotized *spiculum gastrale* in males, paired spur of base of penis trunk and distinct structure of ovipositor; **l a r v a** : not arcuately convergent outer outline of maxillary base, short cardines, 2-segmented labial palpi, separated mentum and submentum, very long urogomphi oriented posteriorly.

In contrast to many nitidulid groups, imagines of Helotidae are also characterized by very large and coarse punctation of integument, dentate or crenelate pronotal carinae, complete elytra, raised or subcostate elytral interstices, 4 fluorescent spots on elytra, depression on hypomera for reception of profemora, not excavate mesosternum, narrow legs with almost or completely simple tarsomeres 1–4; and their larvae with transverse cardo and maxillary mala longitudinally divided. However, R. A. Crowson studied larvae of ? *Lioschema* Fairmaire, 1861 (Cryptarchinae) collected by the Royal Society Expedition of 1958–1959 in Chile and informed the author through the e-mail that they have 2-segmented labial palpi and maxillae very similar to those in larvae of *Helota*. It is important to mention that appearance of imagines and male genitalia of species of Helotidae and large representatives of subfamily Cryptarchinae are rather similar. Epipharyngeal surface in imago of *Helota* fused with inner surface of frons is also very similar to that in Cryptarchinae. Finally, not homogenous spiracles on abdominal segments of imago give also some reminiscence with diversity of these organs among Nitidulidae (Kirejtshuk, 1998a).

Referring to imaginal characters Crowson (1955) separated Smicripidae and Nitidulidae (with Kateretidae) from all other Cucujoid families (including Helotidae) by transverse pro- and mesocoxae with exposed trochantin, smallest tarsomere 4, unfunctional 7th pair of abdominal spiracles and unilobed maxillae, rather reduced wing venation with proximal displacement of all veins and lack of all cells and some other characters mentioned above. Probably only pro- and mesocoxae could be regarded as apomorphies, but other distinguishing characters are plesiomorphous rather than apomorphous in comparison with such characters of different groups of Nitidulidae. Wing venation of even the largest sap-beetles of the subfamily Cryptarchinae are characterized by almost the same level of reduction of veins and their similar proximal displacement, as those in medium-sized representatives of different subfamilies. It can be supposed that the large representatives of Nitidulidae originated from small- and medium-sized forms, and therefore their ancestors overcame the period of greater or longer pressure of factors causing progressive paedomorphosis than those which affected the ancestors of Helotidae. The family under consideration, except for more differentiated mouth appendages, is distinguished from Kateretidae and Smicripidae in many characters common to diagnostic features of Nitidulidae (Kirejtshuk, 1998b).

N o t e s : During the last century and not infrequently in the first half of this one the considered group was often treated as a genus or a subfamily within the families Erotylidae or Cucujidae. Nevertheless, Sharp and Muir (1912) regarded aedeagus of this group as certainly similar to that in Nitidulidae. Crowson (1955) recognized this group with a family rank and tried to trace its connections with Cucujidae, Languriidae–Erotylidae or Cryptophagidae.

Olliff (1882) showed a way to divide the genus *Helota* into groups for the Indo-Malayan species and his division is in general correspondent to the genera here recognized for the fauna of this region. Later Ritsema made a similar work for the African fauna (Ritsema, 1905). Ritsema (1915c) also elaborated the key to all species which were known by the moment of preparation of his manuscript. In this key the author made the characteristics of the groups, which are erected in separate genera. Therefore the division of the family here proposed is in any sense a summary of these 3 papers and the characters used in the key here proposed are partly borrowed from the keys published in them. Although *Scrophohelota* gen. n. is understood as a separate group only here.

Composition: *Helota*, *Neohelota* stat. n., *Metahelotella* gen. n., *Afrohelotina* gen. n. and *Strophohelota* gen. n. The species of this family considered as members of the genus *Helota* were catalogued by Ritsema (1911, 1915b).

Bionomy: Imagines of all genera and larvae of *Helota* live at sap flows and under fermenting bark.

Age: At least 2 species are described as representatives of the genus *Helota* among Miocene insects from East China: *H. chinensis* Zhang Junfeng, Sun Bo et Zhang Xiyu, 1994 (Beijing, Sci. Press: 98) and *H. senilis* Zhang Junfeng, Sun Bo et Zhang Xiyu, 1994 (Beijing, Sci. Press: 99).

Distribution: This family is mostly represented in the Palaearctic (East-Chinese) province of Palaearctic region and continental part of Indo-Malayan region (Indian and Indochinese provinces), to a lesser extent it is represented on the Greater Sunda Islands and in the Afrotropical region coming to the south not far than Angola.

Key to genera of Helotidae

- 1a Elytra with 4 oval isolated and smooth yellow places without or with very reduced punctation (fluorescent in alive beetles) and rather different from general elytral coloration; these isolated places disposed before and behind the middle of elytra 2
- 1b Elytra without oval smooth places different from general elytral coloration or at most only with 2 isolated smooth places oblique and concoloured with surrounding surface; these isolated places (if traced) disposed at the middle of elytra..... 3
- 2(1)a Pronotum rugous, irregularly and coarsely punctured, and with raised patches; elytra tuberculate or frequently subcostate; head more elongate and with convex fore edge; antennal club not more than 1.5 times as long as wide; males with slightly more curved protibiae or without expressed sexual dimorphism in tibiae, except frequently more raised brushes of long hairs at tibial apices *Helota*
- 2(1)b Pronotum more finely and evenly punctured, without raised patches; elytra never tuberculate nor subcostate; head usually as long as wide and with subtruncate fore edge; antennal club usually about twice as long as wide; males of many species with rather curved protibiae *Neohelota* stat. n.
- 3(1)a Elytra smoothly costate or with more or less elevated interstices; elytral apices subacute to narrowly acute and forming deep sutural corner; elytra more projecting in females; male protibiae more curved at apices and with somewhat raised longitudinal subapical ridges along inner side; males usually with bunches of long hairs on the middle of metasternum and ventrite 1, and also at tibial apices; antennal club not more than 1.5 times as long as wide *Afrohelotina* gen. n.
- 3(1)b Elytra gently vaulted and without trace of costae, convexities or tubercles; elytral apices jointly or separately rounded, forming at most only a shallow sutural corner; elytra without sexual dimorphisms..... 4
- 4(3)a Head distinctly transverse; pronotum with deeply bisinuate base; antennal club usually about twice as long as wide; male fore tibiae usually more curved than female ones *Metahelotella* gen. n.
- 4(3)b. Head more elongate; pronotum with subtruncate base (with 4 rather weak sinuations); antennal club not more than 1.5 times as long as wide; sexual dimorphism not expressed in fore tibiae .. *Strophohelota* gen. n.

Genus *Helota* Macleay, 1825, Annul. Javan. 42. Figs 31–43, 61–63.

Type-species: *H. vigorsi* Macleay, 1825 [Annul. Javan. 43], by monotypy.

Diagnosis: It is well characterized with very coarse punctation and sculpture of dorsum, and therefore imagines of it in contrast to other genera not infrequently are with slight lustre (sometimes leaden) or almost dull, although in other cases pronotal and elytral surface with convex tubercles and interstices nearly smooth and unpunctured. Pronotal base in species of this genus is deeply bisinuate. Very commonly elytral apices in females are much more acuminate and sometimes explanate. Males very rarely have a little more curved protibiae than those in females, but their hypopygidium is not infrequently with medial subapical depression densely covered with small sensilla and their tibial apices with dense brush of rather long hairs.

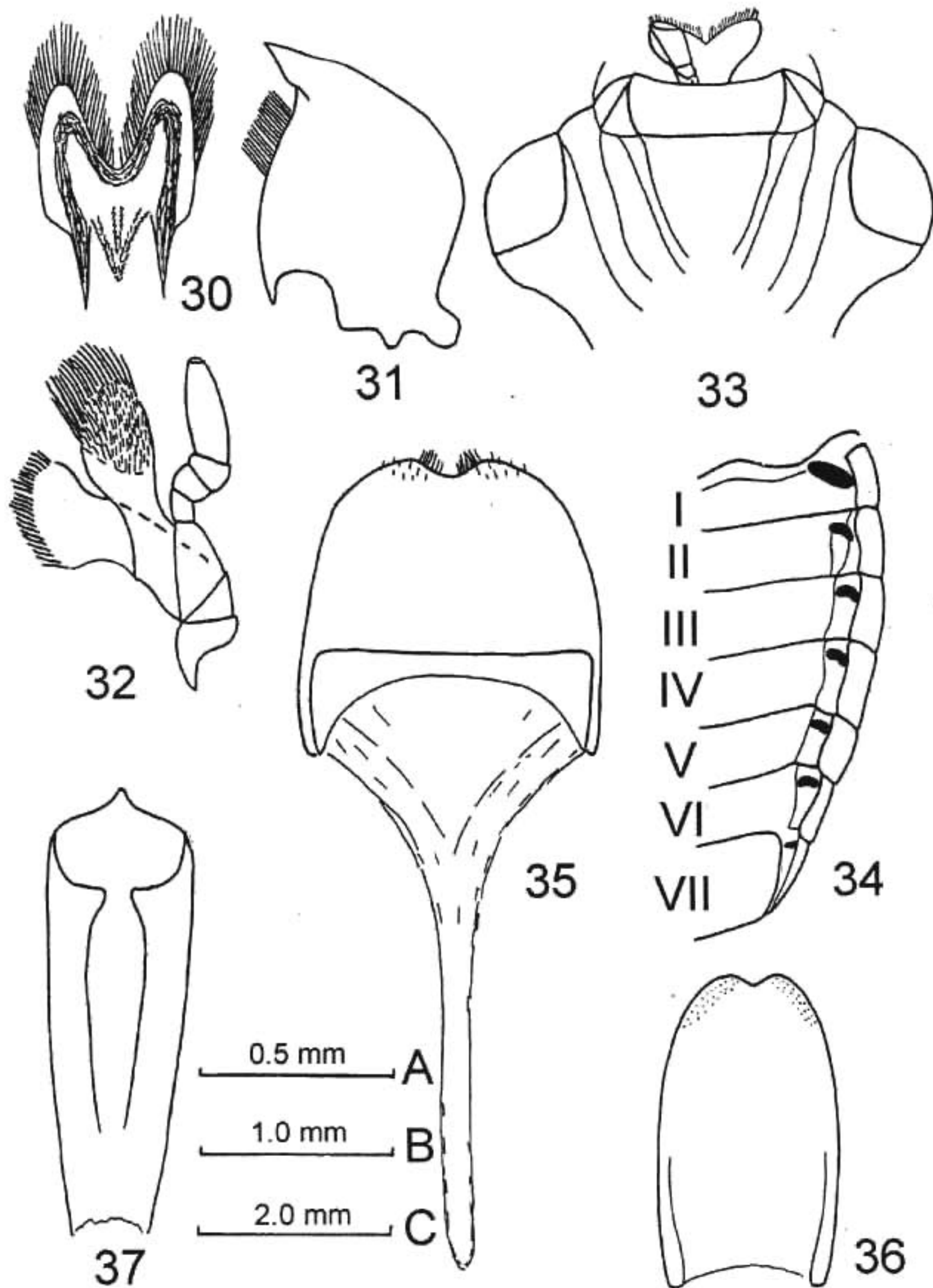


Fig. 30 – *Paracucujus rostratus* Sen Gupta et Crowson, 1966 (Boganiidae) (ZIN – Western Australia, Margaret R., in *Macrozamia cones*): labrum, ventral.

Figs. 31–34: *Helota fulviventris* Kolbe, 1886 (Helotidae, Cucujoidea) (Primorsky Kray: Yakovlevka, D'yakonov-Filipp'yev) (orig.): 31 – right mandible, dorsal; 32 – right maxillae, dorsal; 33 – ventral surface of head with antennal grooves, submental furrows, ligula and labial palpus, ventral; 34 – abdominal spiracles (Latin figures indicate segments), dorsal.

Figs 35–37 – *H. fulviventris* (ZIN – Primorsky Kray: Suchan, Palshikov): 35 – male genital capsule (8th abdominal segment), ventral; 36 – tegmen, ventral; 37 – penis trunk, dorsal.

Scales: A – to fig. 30; B – to figs 31, 32, 35–37; C – to figs 33, 34.

The male genital capsule and tegmen of the *Helota* species have weakly sclerotized or sometimes nearly membraneous fork sclerites, tegmenal one with unpaired appendage (sometimes tegmenal one without unpaired appendage and membraneous connection between almost separated sclerites beginning with the base of tegmen). Their penis trunk is with separated paired apodemes (struts), and its inner sac is with weakly sclerotized and frequently unclearly outlined armature.

This genus with *Afrohelotina* gen. n. forms a pair of similar groups very different in their ranges. Except the characters given in the above key, the *Helota* species have more or less dark and metallic dorsum with unicoloured elytra (each of them bears 2 isolated oval yellow spots – before and behind the middle), while those of *Afrohelotina* gen. n. are with bicolorous dorsum: elytra with reddish and black and with one medial oblique place isolated by punctures but as coloured as surrounding surface.

Composition (species studied by the author are marked by asterisk after name and reference to description):

- H. acutipennis* Ritsema, 1914b, Notes Leyd. Mus. 36: 166.
- H. caudata* Ritsema, 1889, Notes Leyd. Mus. 11: 102.
- H. distincta* Ritsema, 1914a, Notes Leyd. Mus. 36: 59.
- H. donkieri* Ritsema, 1891, Notes Leyd. Mus. 28: 213.
- H. fairmairei* Ritsema, 1889, Notes Leyd. Mus. 11: 101 (*).
- H. feae* Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 886.
- H. feae mushana* Ohta, 1928, Ins. Mats. 3 (2–3): 109.
- H. fruhstorferi* Ritsema, 1905, Notes Leyd. Mus. 25: 107.
- H. fulviventris* Kolbe, 1886, Arch. Naturgesch. 52. 1: 182 (*).
- H. fulviventris awana* Ohta, 1928, Ins. Mats. 3 (2–3): 110.
- H. gemmata* Gorham, 1874, Trans. R. Ent. Soc. London. 448 (*).
- H. gorhami* Olliff, 1882, Cistula Ent. 3: 53 (*).
- H. japonica* Ohta, 1928, Ins. Mats. 3 (2–3): 110.
- H. jentkini* Ritsema, 1906, Notes Leyd. Mus. 26: 223.
- H. kolbei* Ritsema, 1889, Notes Leyd. Mus. 11: 103 (*).
- H. lesnei* Ritsema, 1906, Bull. Mus. Paris. 12: 196 (*).
- H. longipes* Ritsema, 1889, Notes Leyd. Mus. 11: 101.
- H. lugubris* Ritsema, 1914b, Notes Leyd. Mus. 36: 57, 165.
- H. oberthuri* Ritsema, 1889, Notes Leyd. Mus. 11: 100 (*).
- H. pasteuri* Ritsema, 1893, Notes Leyd. Mus. 15: 111 (*).
- H. ritsemana* Heller, 1923, Ent. Bl. 19 (2): 68.
- H. rouyeri* Ritsema, 1906, Notes Leyd. Mus. 28: 131.
- H. scintillans* Olliff, 1884, Cistula Ent. 3: 99 (*).
- H. servillei* Hope, 1840, Col. Man. 3: 187 (*).
- H. sinensis* Olliff, 1882, Cistula. Ent. 3: 54.
- H. thibetana* Westwood, 1841, Ann. Mag. Nat. Hist. 8: 123
= *mellyi* Westwood, 1848, Cabin. Orient. Ent. 86.
- H. thoracica* Ritsema, 1896, Notes Leyd. Mus. 17: 49 (*).
- H. tonkinensis* Ritsema, 1905, Notes Leyd. Mus. 25: 119 (*).
- H. vandepolli* Ritsema, 1891, Notes Leyd. Mus. 13: 197, 223.
- H. ventralis* Ritsema, 1891, Notes Leyd. Mus. 13: 257 (*).
- H. verrucosa* Ritsema, 1895, Notes Leyd. Mus. 16: 98.
- H. vigorsi* Macleay, 1825, Annul. Javan. 43 (*).
- H. vigorsi borneensis* Ritsema, 1909, Notes Leyd. Mus. 31: 183 (*).
- H. vigorsi sumatrensis* Ritsema, 1909, Notes Leyd. Mus. 31: 183 (*).
- H. westwoodi* Ritsema, 1907, Notes Leyd. Mus. 28: 216 (*).

Distribution: Most of diversity of this genus tends to the south of the Palaearctic (East-Chinese) province of the Palaearctic region and to the mountains of the Himalayas and Northern Indochina. Only a few species reach the northern part of the mentioned palaearctic province (Jacobson, 1915). Besides, *H. vigorsi* spreads through Malaysian and Indonesian islands (Java, Kalimantan, Sumatra), *H. pasteuri* and *H. scintillans* – on Java, *H. jentkini*, *H. rouyeri* and *H. verrucosa* – on Sumatra, and *H. vandepolli* – on Kalimantan.

Genus *Neohelota* Ohta, 1929, Ins. Mats., 4 (2–3): 67, stat. n. (as subgenus of *Helota*). Figs 44–51, 64.

Type-species: *Helota (Neohelota) tumaaka* Ohta, 1929 [Ins. Mats., 4 (2–3): 67], by monotypy.

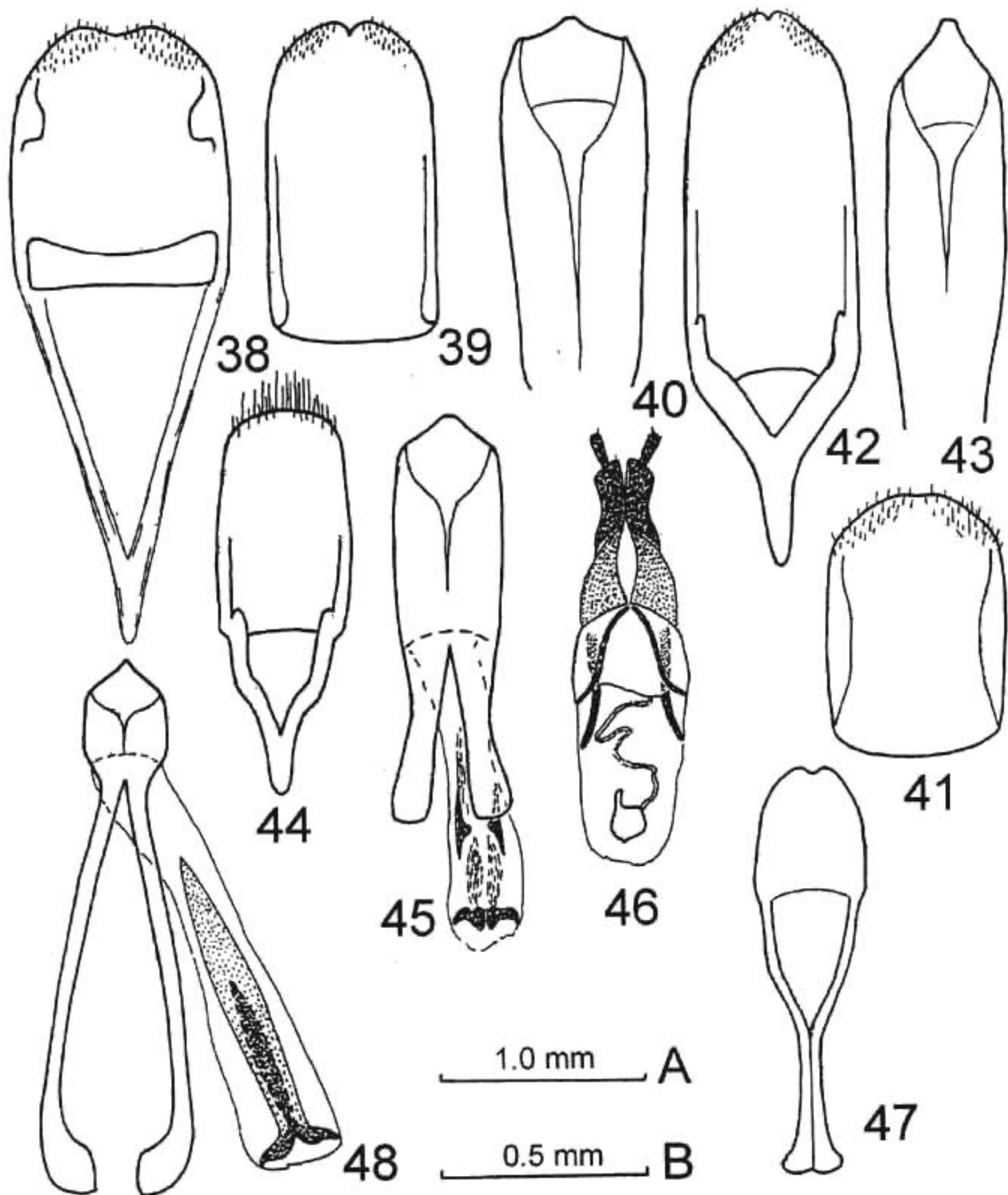
Diagnosis: This genus is rather distinct from other genera of the family due to fine and almost regular punctation of even surface of pronotum and completely regular longitudinal rows of punctures on elytra, which also bear 4 oval spots: a pair before the middle and a pair – behind (as those in species of *Helota*). Coloration of dorsum is always dark to blackish with a metallic lustre, but ventral surface is usually yellowish or reddish, although there are some species with brown spots on elytra and brownish underside (f. e., *N. culta* comb. n.). Head of members of this genus is nearly or clearly transverse with truncate fore edge. Pronotal base of them is deeply bisinuate. Males of most species have rather curved protibiae, not infrequently dilated along inner edge before apex. Male hypopygidium, as in species of the preceding genus, not infrequently has a medial subapical depression densely covered with small sensilla and sometimes metasternum and base of ventrite 1 in males is rather depressed. Sexual dimorphism in elytral apices of some species of this genus is as expressed as in many *Helota* species, but many of its species have elytral apices quite similar in both the sexes.

The male genital capsule and tegmen of the *Neohelota* species have moderately or weakly sclerotized fork sclerites, tegmenal one with an unpaired appendage. The penis trunk of them is with separated paired apodemes (struts), and its inner sac is usually with heavily sclerotized, enlarged and well outlined armature.

Notes: This taxon first was proposed as a subgenus to separate some of species of *Helota* with strongly expressed sexual dimorphism in tibial shape. However, this feature is expressed only among many but not all species of the group outlined in the above key and diagnosis.

Composition (species studied by the author are marked by asterisk after name and reference to description):

- N. affinis* (Ritsema, 1891, Notes Leyd. Mus. 13: 253), comb. n.
- N. attenuata* (Ritsema, 1895, Notes Leyd. Mus. 16: 112), comb. n.
- N. boulei* (Ritsema, 1915a, Tijdschr. Ent. 58: 247), comb. n.
- N. boysi* (Ritsema, 1889, Notes Leyd. Mus. 11: 189), comb. n. (*).
- N. bretaudeaui* (Ritsema, 1895, Notes Leyd. Mus. 16: 116), comb. n. (*).
- N. brevis* (Ritsema, 1891, Notes Leyd. Mus. 13: 199), comb. n. (*).
- N. bhutanensis* (Chûjô, 1975, Ent. Basil. 1: 287), comb. n. (*).
- N. candecei* (Ritsema, 1899, Notes Leyd. Mus. 20: 199), comb. n.
- N. cereopunctata* (Lewis, 1881, Ent. Mon. Mag. 17: 255), comb. n. (*).
- N. chinensis* (Mader, 1955, Koleopt. Rundsch. 33: 63), comb. n.
- N. claudiae* (Nguyen-Phung, 1985, Rev. fr. Ent. (N. S.), 7 (1): 15), comb. n.
- N. consanguinea* (Ritsema, 1915a, Tijdschr. Ent. 58: 248), comb. n. (*).
- N. culta* (Olliff, 1882, Cistula Ent. 3: 55), comb. n. (*).
- N. curvipes* (Oberthür, 1883, Col. Novitatis. 1: 60), comb. n. (*).
- N. desgodinsi* (Ritsema, 1893, Notes Leyd. Mus. 15: 131), comb. n.
- N. dohertyi* (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 896), comb. n.
- N. dubia* (Ritsema, 1891, Notes Leyd. Mus. 30: 901), comb. n.
- N. durrell* (Ritsema, 1905, Notes Leyd. Mus. 25: 127), comb. n. (*).
- N. elongata* (Ritsema, 1905, Notes Leyd. Mus. 25: 121), comb. n.
- N. epipleuralis* (Ritsema, 1914b, Notes Leyd. Mus. 36: 167), comb. n.
- N. fryi* (Ritsema, 1895, Notes Leyd. Mus. 16: 101), comb. n.
- N. gestroi* (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 893), comb. n.
- N. grouvellei* (Ritsema, 1910/1911, Notes Leyd. Mus. 33: 76), comb. n.
- N. guerini* (Hope, 1840, Coleopt. Manual. 3: 188), comb. n.
- N. guttata* (Ritsema, 1893, Notes Leyd. Mus. 15: 134), comb. n. (*).
- N. hopei* (Ritsema, 1915a, Tijdschr. Ent. 58: 245), comb. n.
- N. indicator* (Ritsema, 1905, Notes Leyd. Mus. 25: 130), comb. n. (*).
- N. intermedia* (Ritsema, 1905, Notes Leyd. Mus. 25: 125), comb. n. (*).
- N. jocelinae* (Nguyen-Phung, 1985, Rev. fr. Ent. (N.S.), 7 (1): 16), comb. n.
- H. jordani* (Ritsema, 1899, Notes Leyd. Mus. 20: 252), comb. n.
- N. klapperichi* (Mader, 1955, Koleopt. Rundsch. 33: 63), comb. n.
- N. krugeri* (Ritsema, 1900, Notes Leyd. Mus. 22: 29, 32), comb. n. (*).
- N. laevigata* (Oberthür, 1883, Coleopt. Novit. 1: 59), comb. n. (*).



Figs 38–48. Genus *Helota* Macleay, 1825 and *Neohelota* Ohta, 1929, stat. n. (Helotidae, Cucujoidea) (orig.): 38–40: *H. gorhami* Olliff, 1882 (ZIN – Korea, Herz): 38 – male anal sclerite, ventral; 39 – tegmen, ventral; 40 – penis trunk, dorsal; 41–43: *H. vigorsi* Macleay, 1825 (ZIN – Java, Mts Kavie, J. B. Ledru): 41 – male genital capsule (abdominal segment 8), ventral; 42 – tegmen, ventral; 43 – penis trunk, dorsal; 44–46: *N. consanguinea* (Ritsema, 1915a), comb. n. (NMB – Eastern Nepal, Arun Valley, M. Brancucci and Habagayri, B. H. Bhakta): 44 – tegmen, ventral; 45 – penis trunk with armature of inner sac, dorsal; 46 – ovipositor, ventral; 47–48: *N. culta* (Olliff, 1882), comb. n. (NMB – Nepal, Cathmandu Valley, M. Brancucci): 47 – tegmen, ventral; 48 – penis trunk with armature of inner sac, dorsal. Scale: A – to figs 38–43, B – to figs 44–48.

- N. lewisi* (Ritsema, 1915a, Tijdschr. Ent. 58: 244), comb. n.
N. magdalenae (Ritsema, 1910/1911, Notes Leyd. Mus. 33: 75), comb. n.
N. margaretae (Ritsema, 1900, Notes Leyd. Mus. 22: 27, 31), comb. n. (*).
N. mariae (Ritsema, 1899, Notes Leyd. Mus. 20: 239), comb. n. (*).
N. miwai Ohta, 1931, Ins. Mats. 5 (3): 136.
N. montana (Ohta, 1929, Ins. Mats. 4 (2-3): 67), comb. n.
N. moutoni (Ritsema, 1905, Notes Leyd. Mus. 25: 129), comb. n.
N. neglecta (Ritsema, 1915c, Zool. Med. 1: 235, 238), comb. n.
N. notata (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 900), comb. n.
N. ocellata (Ritsema, 1881, Notes Leyd. Mus. 3: 79), comb. n. (*).
N. olliffi (Ritsema, 1899, Notes Leyd. Mus. 20: 251), comb. n.
N. pusilla (Oberthür, 1883, Coleopt. Novit. 1: 60), comb. n. (*).
N. pustulata (Ritsema, 1893, Notes Leyd. Mus. 15: 133), comb. n. (*).
N. renati (Ritsema, 1905, Notes Leyd. Mus. 25: 123), comb. n. (*).
N. rotundata (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 891), comb. n. (*).
H. serratipennis (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 890), comb. n.
N. severini (Ritsema, 1893, Notes Leyd. Mus. 15: 138), comb. n.
N. sharpi (Ritsema, 1915a, Tijdschr. Ent. 58: 249), comb. n. (*).
N. sonani (Ohta, 1929, Ins. Mats. 4 (2-3): 67), comb. n.
N. sumbawensis (Ritsema, 1909, Notes Leyd. Mus. 31: 183), comb. n.
N. taiwana (Ohta, 1929, Ins. Mats. 4 (2-3): 66), comb. n.
N. tibialis (Ritsema, 1893, Notes Leyd. Mus. 15: 136), comb. n. (*).
N. tumaaka Ohta, 1929, Ins. Mats. 4 (2-3): 68.
N. yezoana Kôno, 1939, Ins. Mats. 4 (2-3): 68.

Distribution: Range of this genus mostly coincides with that of *Helota*, although *N. cereopunctata* comb. n. goes to the north not farther than Hokaido (Sasaji, 1985). Some species of this genus are recorded from Taiwan (Ohta, 1931); *N. grouvellei* comb. n. and *N. ocellata* comb. n. – from Java; *N. brevis* comb. n. – from Kalimantan; *N. magdalenae* comb. n., *N. jordani* Ritsema comb. n. and *N. neglecta* comb. n. – from Sumatra; *N. sumbawensis* comb. n. – from Sumbawa.

Genus *Metahelotella* gen. n. Figs 52–54.

Type-species: *Helota semifulva* Ritsema, 1881 [Notes Leyd. Mus., 3: 80].

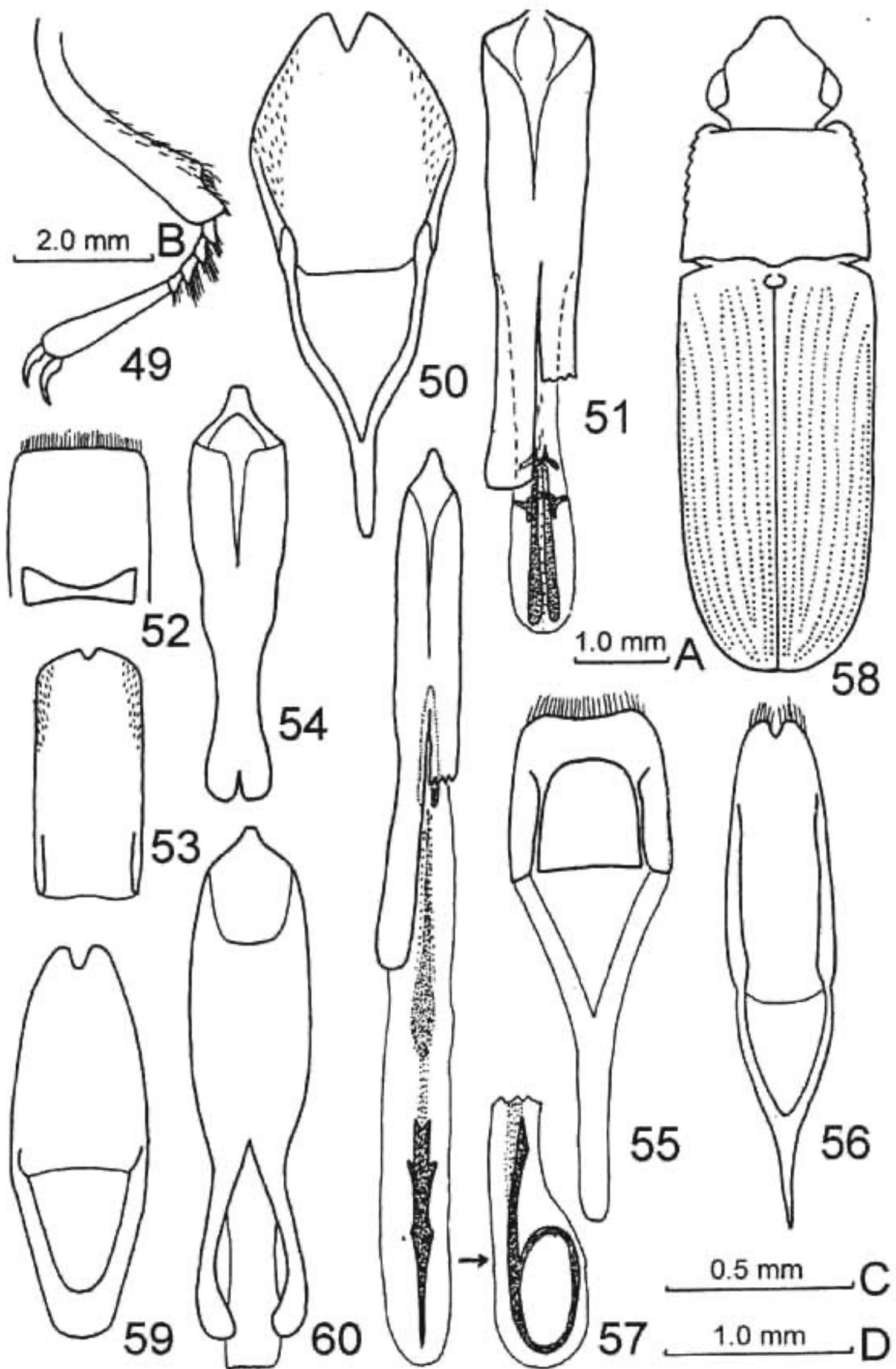
Diagnosis: Besides the characters listed in the above key, this new genus is particularly distinct by bicolorous dorsum (although pronotum in most cases unicoloured reddish or unicoloured reddish with a green metallic lustre); smooth dorsal surface without tubercles, patches, costae and so on; pronotum with comparatively sparse and regular fine punctures; elytra with regular longitudinal rows of rather small and not dense punctures. In contrast to species of other genera of the family, pronotum of some species of *Metahelotella* gen. n. is narrowed both anteriorly and posteriorly, but the pronotal base is rather deeply bisinuated. Sexual dimorphism in this new genus is slightly expressed in shape of protibiae, but not traced in metasternum, hypopygidium and elytral apices.

The male genital capsule and tegmen of the *Metahelotella* gen. n. species have weakly sclerotized or sometimes nearly membranous fork sclerites, tegmenal one with an unpaired appendage. Their penis trunk is with fused (unpaired) apodemes (struts), and its inner sac is with weakly sclerotized and frequently unclearly outlined armature.

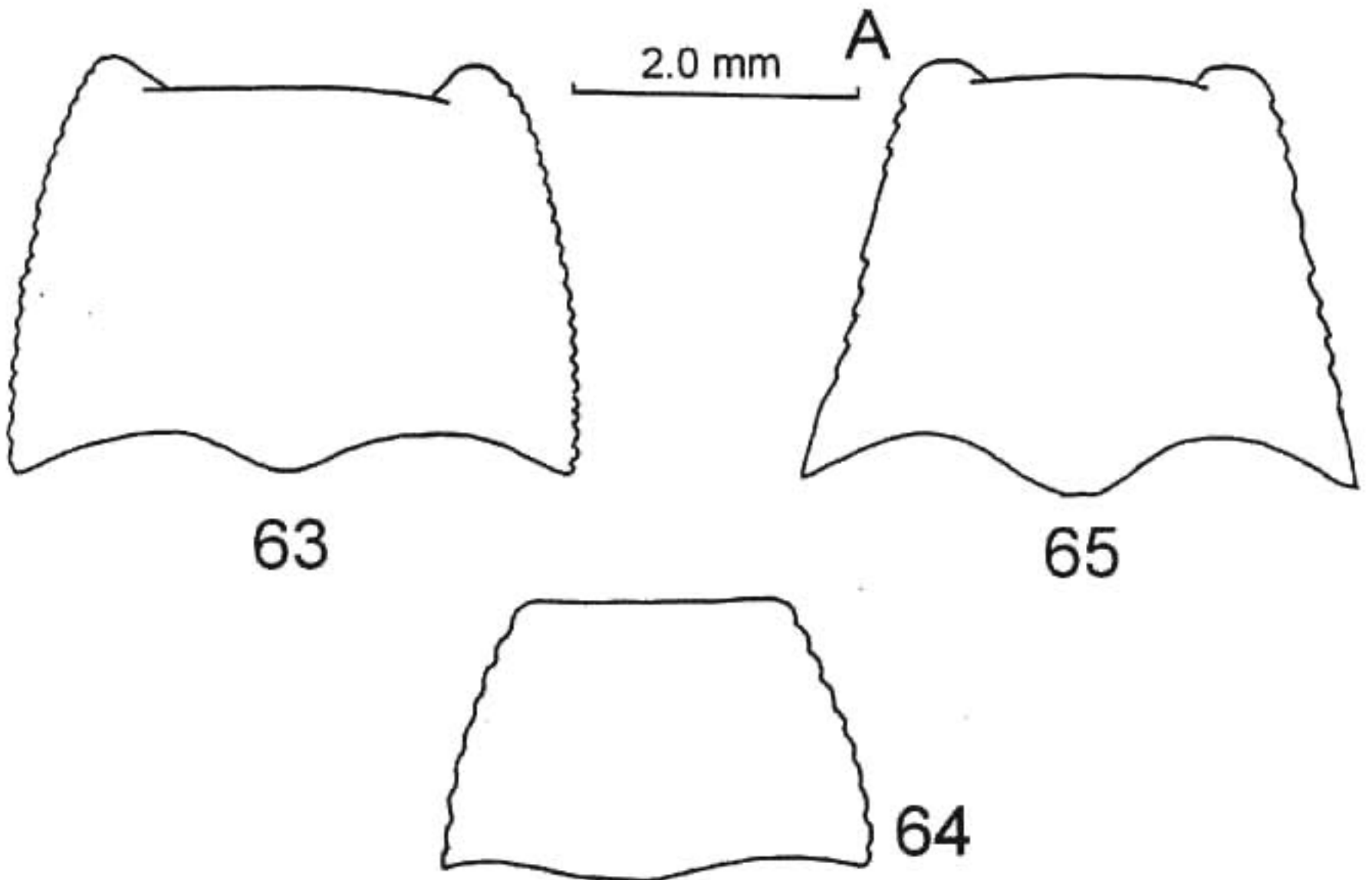
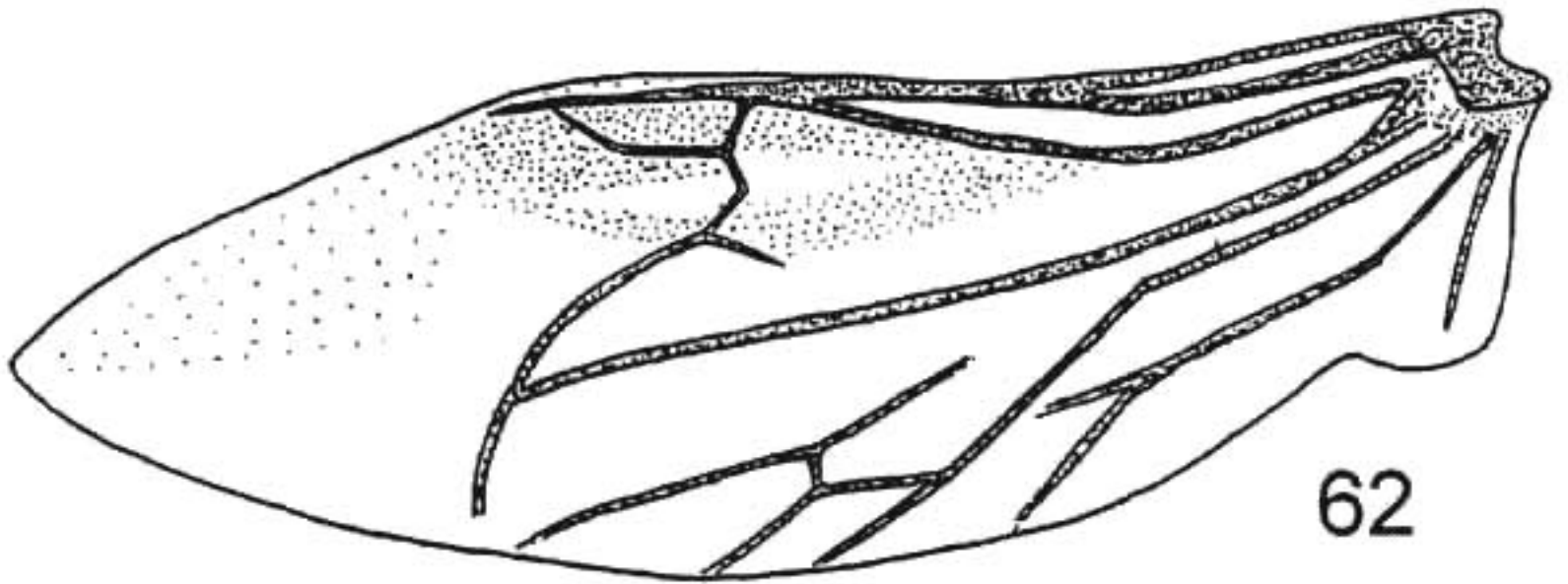
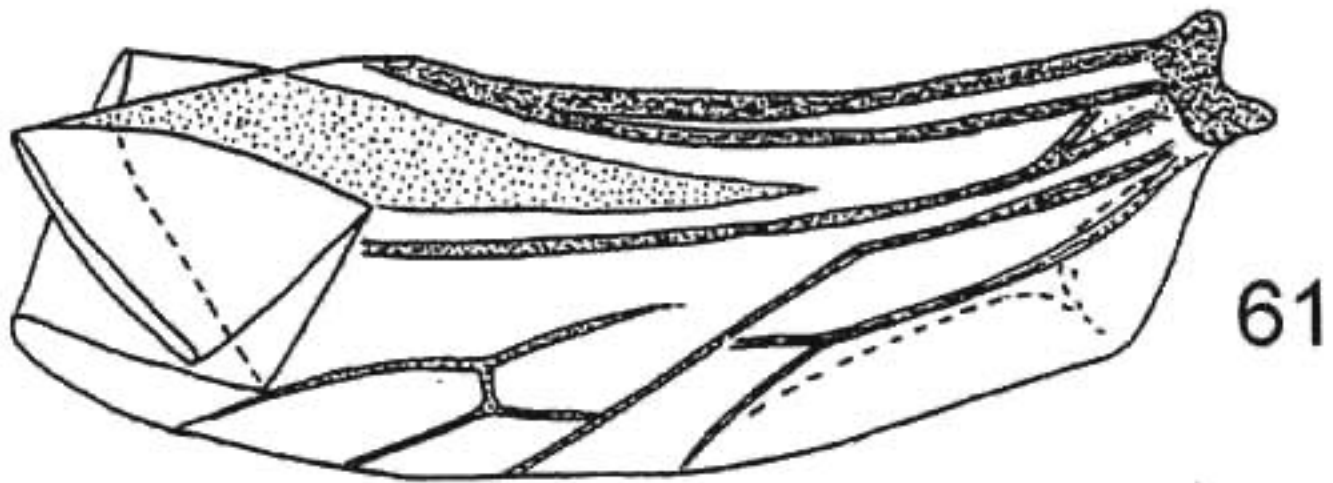
Composition (species studied by the author are marked by asterisk after name and reference to description):

- M. bouchardi* (Ritsema, 1897, Notes Leyd. Mus. 27: 131), comb. n. (*).
M. difficilis (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 896), comb. n. (*).
M. fulvitaris (Ritsema, 1889, Notes Leyd. Mus. 11: 107), comb. n. (*).
M. immaculata (Ritsema, 1891, Ann. Mus. Civ. Genova. 30: 895), comb. n. (*).
M. martae (Ritsema, 1910/1911, Notes Leyd. Mus. 33: 78), comb. n.
M. semifulva (Ritsema, 1881, Notes Leyd. Mus. 3: 80), comb. n. (*).

Distribution: This genus is sporadically distributed in the Himalayas, Indochinese and Malayan provinces of the Indo-Malayan region.



Figs 49–60. Genera *Neohelota* Ohta, 1929, *Metahelotella* n. gen., *Afrohelotina* n. gen. and *Strophohelota* n. gen. (Helotidae, Cucujoidea) (orig.): 49–51: *N. tibialis* (Ritsema, 1893), comb. n. (NMB – Eastern Nepal, Arun Valley, M. Brancucci): 49 – male protibia, dorsal; 50 – tegmen, ventral; 51 – penis trunk with armature of inner sac, dorsal; 51–54: *M. fulvitaris* (Ritsema, 1889), comb. n. (ZIN – Bhutan, 'Maria Basti', Oberthür): 52 – male genital capsule, ventral; 53 – tegmen, ventral; 54 – penis trunk, dorsal; 55–57: *A. costata* (Ritsema, 1889), comb. n. (ZIN – Tanzania, 'Pareh', Chr. Schröder): 55 – male genital capsule, ventral; 56 – tegmen, ventral; 57 – penis trunk with armature of inner sac, dorsal; 58–60: *S. tripatria* (Ritsema, 1905), comb. n. (ZMB – holotype – 'N. Kamerun, Joh Albrechthöhe, L. Conradt'): 58 – body, ventral; 59 – tegmen, ventral; 60 – penis trunk, dorsal. Scales: A – scale to fig. 58; B – to fig. 49; C – to figs 50–53, 59, 60; D – to figs 55–57.



Figs 61–65. Genera *Helota* Macleay, 1825; *Neohelota* Ohta, 1929, n. stat. and *Afrohelotina*, n. gen. (Helotidae, Cucujoidea) (orig.): 61–63: *H. fulviventris* Kolbe, 1886 (the same specimen as on figs 31–34): 61 – folded hind wing, ventral; 62 – unfolded hind wing; 63 – pronotal outline of the same species, dorsal; 64 – *N. tibialis* (Ritsema), 1893, comb. n. (same specimen as on figs 49–51): idem, dorsal; 65 – *A. sjoestedti* (Ritsema, 1905), comb. n. (ZIN – Guinea, 'Nkolentagan', G. Tessmann): idem, dorsal. Scale: A – to figs 61–65.

Genus *Afrohelotina* gen. n. Figs 55–57, 65.

Type-species: *Helota costata* Ritsema, 1889 [Notes Leyd. Mus. 11: 108].

Diagnosis: This new genus is well characterized by bicolorous (black and reddish) pronotum with black medial stripe, very sparse and coarse punctation on even surface; bicolorous (black and reddish) elytra with almost regular longitudinal rows of moderate punctures, more or less elevated interstices (up to distinct costae) and oblique medial spot on each elytron isolated by small punctures. Sexual dimorphism is expressed – in females: in more projecting and more acuminate elytral apices; and in males: in more curved and bordered protibiae, frequently raised bunches of long hairs on the middle of metasternum and ventrite 1, and also on tibial apices, wide medial depression on hypopygidium (but without small sensilla).

The male genital capsule and tegmen of the *Afrohelotina* gen. n. species have weakly sclerotized fork sclerites, tegmenal one without unpaired appendage. The penis trunk of them is with separated paired apodemes (struts), and its inner sac is with well sclerotized and clearly outlined armature.

Afrohelotina gen. n. has a certain similarity to *Helota* but quite different in the characters mentioned in the diagnosis to the latter and in the above key.

Composition (species studied by the author are marked by asterisk after name and reference to description):

A. africana (Olliff, 1884, Ann. Mag. Nat. Hist. (5) 13: 253), comb. n.

A. congoana (Achard, 1920, Rev. Zool. Afr. 8 (2): 270), comb. n. (*)

A. costata (Ritsema, 1889, Notes Leyd. Mus. 11: 108), comb. n. (*)

A. costata stigma (Ritsema, 1905, Notes Leyd. Mus. 25: 209), comb. n. (*)

A. ferranti (Ritsema, 1913, Notes Leyd. Mus. 35: 156), comb. n.

A. guineensis (Ritsema, 1889, Notes Leyd. Mus. 11: 108), comb. n.

A. lujae (Ritsema, 1910, Notes Leyd. Mus. 32: 219), comb. n.

A. pauli (Weise, 1903, Deutsch. Ent. Zeitschr. 1: 171), comb. n. (*)

A. semipurpurea (Ritsema, 1905, Notes Leyd. Mus. 25: 210), comb. n.

A. sjostedti (Ritsema, 1905, Notes Leyd. Mus. 25: 163), comb. n. (*)

Distribution: This genus spreads along the equatorial zone of the Afrotropical region reaching Angola (*A. africana* comb. n.).

Genus *Scrophohelota* gen. n. Figs 58–60.

Type-species: *Helota tripartita* Ritsema, 1905, Notes Leyd. Mus., 25: 212, 215 (examined).

Diagnosis: This new genus has much structural similarity with *Metahelotella* gen. n., but its coloration is more similar to *Afrohelotina* gen. n. At the same time *Scrophohelota* gen. n. differs from both of them in almost straight base of pronotum and lack of characters of sexual dimorphism in tibiae, elytral apices as well as in structure of metasternum, ventrite 1 and hypopygidium. Taking into consideration distribution of both the compared taxa and distinct peculiarities of *Scrophohelota* gen. n. it seems to be quite reasonable to regard this group (of one species) as a separate genus.

The genital capsule and tegmen of the *Scrophohelota* species have weakly sclerotized or sometimes nearly membraneous fork sclerites, tegmenal one without unpaired appendage. The penis trunk is with separated paired apodemes (struts), and its inner sac is without definite armature.

Notes: Contrary to the mention in the original description, the holotype is male.

Composition: For now this genus is known after one species.

Distribution: The range of this new genus is known only after type-locality of its type-species: Cameroon.

Depositories

ANIC – Australian National Insect Collection, C.S.I.R.O., Division of Entomology, Canberra

DEI – Deutsches Entomologische Institut, Eberswalde-Finow

NMB – Naturhistorisches Museum, Basel

SMS – Staatliches Museum für Naturkunde, Stuttgart

ZIN – Zoological Institute of the Russian Academy of Sciences, St-Petersburg

ZMB – Museum für Naturkunde an der Humboldt-Universität, Berlin

Acknowledgements

For this publication the author used specimens from different collections thanks to the kind assistance of many colleagues and, in particular M. Brancucci (NMB), L. Dieckmann (DEI), F. Hieke (ZMB), B. Jager (ZMB), J. F. Lawrence (ANIC), W. Schawaller (SMS), E. Spercher (NMB), M. Uhlig (ZMB), L. Zerche (DEI) and H. Wendt (ZMB). Special thanks should be expressed to R. A. Crowson, W. Schawaller and J. F. Lawrence for their friendly encouragement during the many-year course of the author's study and for help in various aspects including very useful advice and rather critical comments on different questions. The author had also an essential assistance from R. A. B. Leschen (Landcare Research, Auckland) in improving the English of this paper and very useful critique. The study was supported by the grants of the Deutscher Akademischer Austauschdienst (1998) and Deutsche Forschungsgemeinschaft (1992, 1994, 1996).

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О ПРОИСХОЖДЕНИИ И НАЧАЛЬНОЙ ЭВОЛЮЦИИ НАДСЕМЕЙСТВА CUSUJOIDEA
(COLEOPTERA, POLYPHAGA). ЗАМЕЧАНИЯ ПО СЕМЕЙСТВУ HELITIDAE

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Анализ различий в строении, типе онтогенеза, образе жизни и экологических предпочтений позволил установить, что надсемейство Cusujoidea не одна из наиболее древних, а сравнительно молодая группа жуков инфраотряда Cusujiformia. Архаичный облик многих кукуйюидных обусловлен структурным упрощением, явившимся как следствие особенностей развития и образа жизни. Короткое личиночное развитие в условиях эфемерных консорций, по-видимому, явилось одним из главных обстоятельств, вызвавших появление этого надсемейства и определявших начальные этапы его эволюции. Примитивные группы надсемейства обитают в субстратах вблизи поверхности стволов и веток деревьев, зараженных грибами. Уровень структурной обособленности кукуйюидных семейств обычно ниже, чем в других надсемействах жесткокрылых. Появление и ранняя эволюция этого надсемейства существенно стимулировалась общими биотическими изменениями, вызванными сменой мезозойской биоты кайнозойской. Формирование надсемейства Cusujoidea и появление лесов с кайнофитным характером, по-видимому, в общем совпадают (по крайней мере в палеонтологической летописи), в то время как основные диверсификации других надсемейств в подотряде Polyphaga скорее всего протекали до мелового периода.

Разобрана аргументация различных интерпретаций системы инфраотряда Cusujiformia в контексте соответствия с данными по индивидуальному развитию, палеонтологической летописи, а также с данными по экологии и биологии. Показаны принципиальные различия в стратегии онтогенеза и генерализованного образа жизни различных групп кукуйюидных, объединенных в таксоны с рангом выше семейства. Проанализированы некоторые филетические связи между семействами надсем. Cusujoidea. Сделано переписание сем. Helotidae, а также определено его положение в системе. Обосновано разделение рода *Helota* Macleay, 1825 на несколько родов, обособленных как по структурным признакам, так и по распространению: *Helota* Macleay, 1825; *Neohelota* Ohta, 1929, stat. n.; *Metahelotella* gen. n.; *Afrohelotina* gen. n. и *Strophohelota* gen. n. и предложена определительная таблица для этих родов. Родовое название *Jelinekiella* nom. n. предложено для *Jelinekia* Kirejtshuk, 1986 (Kateretidae), поскольку это название было преокупировано в 1980 г. для обозначения рода златок подсем. Polycestinae (Cobos, 1980).