Review of Paleontological Data on the Evolution of Aquatic Beetles (Coleoptera)

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Abstract—Paleontological data on the evolution of aquatic beetles are reviewed. A total of 37 beetle families are regarded as aquatic; five of them are extinct; three other extinct families could have had aquatic larvae; seven families are not known from the fossil record. The earliest records of fossil representatives of Recent families of aquatic beetles are given. The geological distribution of extinct families is reviewed, and the data on the modes of life of their representatives and on their evolution are provided. The new name Coleocatiniidae nom. nov. is proposed for Catiniidae Ponomarenko, 1968, a junior homonym of Catiniidae Embelton, 1901 (Crustacea, Copepoda).

Keywords: Coleoptera, fossils, paleontological data, evolution, extinct taxa, water beetles, Coleocatiniidae nom. nov.

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INTRODUCTION

Beetles (Coleoptera) are now the most diverse animal order on the planet; about 400 000 species have been described. Taking undescribed taxa into account, the actual species diversity of the order is estimated as at least a million. This order is one of the most diverse not only in the world, but also in Recent continental water bodies. About 12 600 species of the world fauna (3% of the total number of beetle species) are associated with the aquatic environment; together with all undescribed species, their number is estimated as about 18 000 (Jäch and Balke, 2008). If we accept the estimation of the total number of animal species living in continental water bodies as 125 530 (Balian et al., 2008), the proportion of aquatic beetles, including undescribed species, should be over 14% of this fauna.

A total of 3963 beetle species have been described from fossils (Kirejtshuk and Ponomarenko, 2014); 382 of them are in our opinion most probably associated with the aquatic environment; i.e., the described fossil species make up only 1% of their known Recent diversity, although the diversity of insects has remained essentially at the Recent level over tens of millions of years. We know only a minor part of the diversity of ancient insects. At the same time, the proportion of undoubtedly aquatic species among fossil beetles (about 10%) is greater than among Recent ones (3%), which is explained by taphonomic reasons—more

successful fossilization of remains of aquatic organisms, compared to terrestrial ones. However, the proportion of aquatic beetles in the ancient fauna is greater than today.

Although the earliest known beetles, tshekardocoleids, were most probably xylophagous, the very origin of beetles was associated with a semiaquatic environment, i.e., wood strongly decomposed by fungi, which was probably very moist or submerged underwater (Ponomarenko, 1991). It is likely that the origin of all Holometabola as early as the Carboniferous is also associated with substrates of this type, if the interpretation of *Metabolarva bella* Kirejtshuk et al., 2013 as a holometabolan insect larva is correct (Nel et al., 2013). Flatlands of the terminal Carboniferous and basal Permian periodically flooded and long remaining underwater contained peculiar ecosystems, now extinct: shallow lakes overgrown with giant arboreal lycopods and horsetails, which, although they were several dozen meters high, were essentially helophytes (plants rooted in the bottom of waterbodies). Their litter, which consisted of leaves and bark (bark of arborescent lycopods was deciduous), along with their fallen stems, which were fragile and often broken into pieces, formed in water bodies thick quagmires, in and on which many of inhabitants of these biomes lived. Beginning from the Middle Permian, such forests

became dominated by cordaites (Proctor and Jarzhembowski, 1999; Ponomarenko, 2010).

An important role in the colonization of aquatic environments was played by the fact that the wings of beetles are sheathed, thus, forming a subelytral cavity above the abdominal spiracles and preserving a supply of atmospheric air for breathing and providing for gas exchange with surrounding water (Ponomarenko and Prokin, 2013).

Aquatic environments were independently colonized by beetles in the course of their evolution at least ten times (Crowson, 1981), possibly even 20 times (Jäch and Balke, 2008). For instance, the superfamily Hydrophiloidea Latreille, 1802 came onto land at least three times and returned into water at least twice (Fikáček et al., 2012b). Hydrophilidae shifted to the life in border environments at least eight times, but these shifts never served as transitional stages for coming from water onto land (Bloom et al., 2014), which is true also of most semiaquatic groups of hydrophiloids and other families.

Aquatic beetles are a composite ecological group; it comprises members of all coleopteran suborders that display sets of various adaptations to aquatic environments. The suborder Myxophaga probably includes no truly terrestrial beetles; eight of 11 families of Adephaga and 20 of 150 families of Polyphaga are aquatic.

The earliest beetles belonged to the family Tshekardocoleidae, which represents the cupedoid lineage of Archostemata (Fig. 1). All cupedoids, from tshekardocoleids to extant cupedids, have lattice-like elytra with cells that contain the primary wing membrane. Their elytra consist of a plate, on which the former venation makes up a system of stiffening ribs. In the course of further evolution, the main veins became arranged along the elytron, making it rigid to bending. The resulting structure was light and strong and allowed cupedids to survive almost unchanged to this day. Since morphologically cupedoids have not changed much, it is very likely that all cupedoids were xylophagous, like extant Cupedidae; their larvae probably fed on fungi-infested dead wood.

Tshekardocoleids are the only beetles known from the Lower Permian, which, along with their morphological features, suggest that they are ancestral to all other beetles. Asiocoleidae evolved from tshekardocoleids at early stages of their evolution; the elytra of asiocoleids have only two or three longitudinal veins or ribs, with the spaces between them occupied by numerous rounded cells. They are known from the Middle Permian to Middle Jurassic and were probably also xylophagous, judging from the mode of life of *Micromalthus,* an extant relative of schizophoroids. Another change displayed by these beetles is their somewhat more organized venation. Their veins stretch along the longitudinal axis of the elytron, as in cupedoids; however, since the veins are fewer, the number of tangled rows of cells between them is three to six instead of two, as in cupedoids.

Certain early asiocoleids, or possibly tshekardocoleids gave rise to beetles with a smooth upper surface of the elytron (Fig. 2). As follows from the above-said, beetles with lattice-like elytra have successfully survived to this day; therefore, the shift to smooth elytra was a response to some new ecological requirements. It inevitably comes to mind that the new requirements could be linked to a switch to living in water or from living in submerged vegetation (Ponomarenko, 2003) to active moving in water or living in moving water. Under such conditions, lattice-like elytra create turbulent and laminar flows, which prevent movements of a beetle or detach it from substrate. This limitation is only important for larger beetles; for smaller , some millimeters long aquatic beetles, the effect of flows is unimportant; as a result, many of them have lattice-like elytra, mostly as a secondary reacquisition. However, in the basal Middle Permian, when the first beetles with smooth elytra emerged, beetles were large, some centimeters long. Smooth elytra evolved very rapidly, almost simultaneously with the appearance of Asiocoleidae. Elytra with a smooth upper surface are of two types: with tangled rows of depressed punctures or with longitudinal puncture grooves. The smooth elytral surface is formed as a result of dilating and fusing veins, with columellae, short tubules connecting the new upper surface with the former wing plate, forming in place of cells. The stages of this process are seen in both elytra with tangled punctures (Rhombocoleidae−Schizocoleidae) and those with puncture grooves (Taldycupedidae−Permosynidae) (Ponomarenko, 1969). To date, the elytron has become a strong and light two-layered structure with the layers connected by tubules (columellae). Assuming that beetles with smooth elytra appeared because of inhabiting water, it cannot be excluded that the history of all beetles, except cupedoids, includes adaptation to water habitats.

Representatives of the family Schizophoridae Ponomarenko, 1968 (Archostemata), isolated elytra of which are described in the formal family Schizocoleidae, were probably aquatic, if their characteristic schiza, the specific elytral structure (Fig. 3), is correctly interpreted as adaptation to tightly locking of the subelytral cavity under water (Ponomarenko, 2003). In addition, large aquatic holometabolan larvae known from the Permian and Triassic (Kargala, the Vosges, Coburger Sandstein, Garazhovka) and still difficult to assign with certainty to either Coleoptera or Megaloptera (Prokin et al., in prep.) could also belong to Schizophoridae and/or other families of Schizophomorpha Ponomarenko, 1968. In addition, adult Schizophoridae and Catiniidae Ponomarenko, 1968 (Fig. 4) are very close to the Recent family Torridincolidae Steffan, 1964 in the hind wing venation and presence of five abdominal ventrites (Ponomarenko, 1973; Lawrence and Newton, 1982). Some
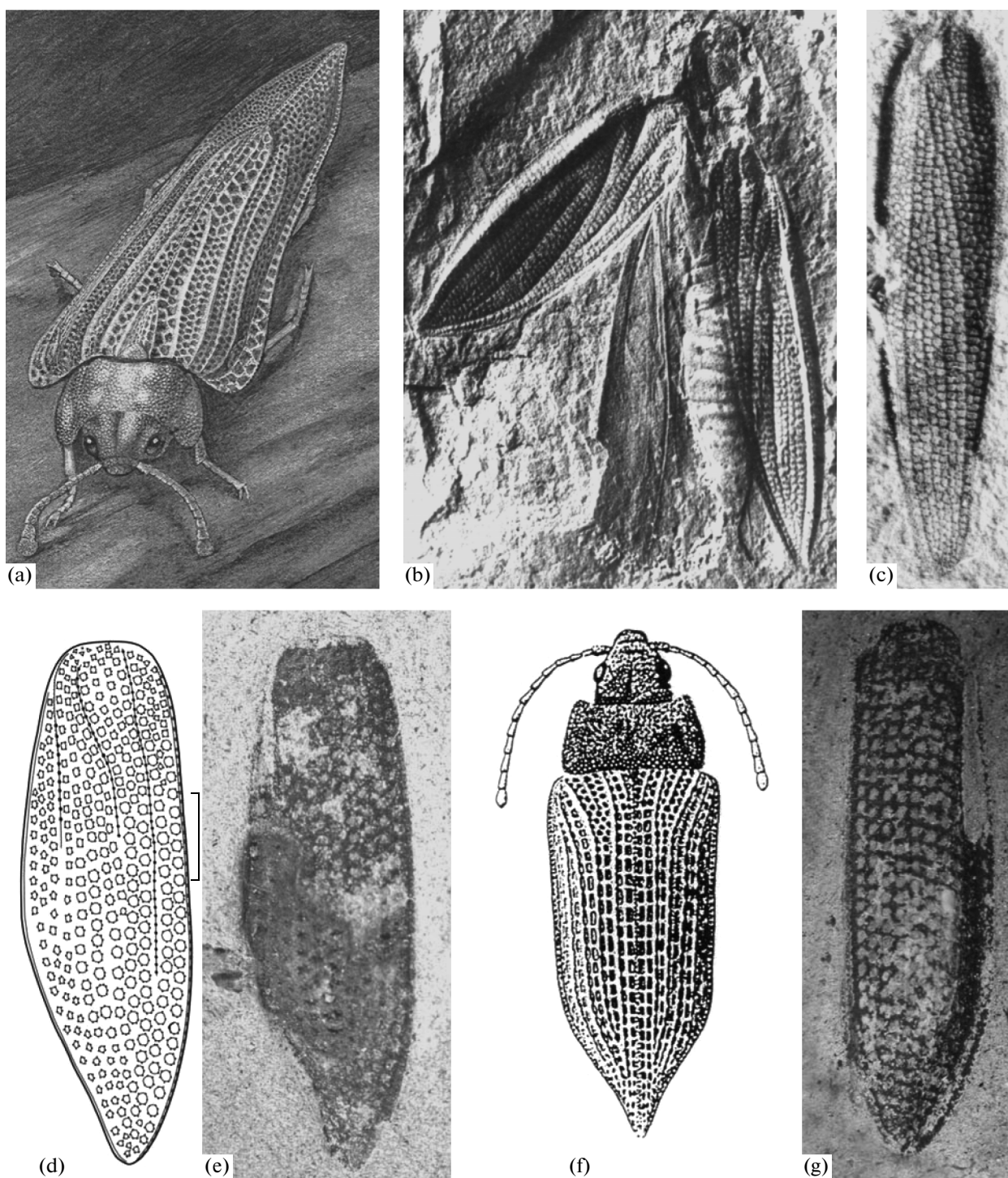
Fig. 1. Permian beetles with cellular elytra: (a–c) Tshekardocoleidae: (a) *Sylvacoleus* sp., reconstruction; European Russia; (b) *Moravocoleus permianus* Kukalova, 1969, Czech Republic, Obora; Lower Permian; (c) *Uralocoleus ultimus* Ponomarenko, holotype PIN, no. 3353/1055; European Russia, Soyana; Middle Permian, Kazanian Stage; (d–g) Asiocoleidae: (d, e) *Tetracoleus tricoleoides* Ponomarenko, holotype PIN, no. 3840/1212; European Russia, Isady; Middle Permian; Permocupedidae: (f) *Permocupes* sp., reconstruction; European Russia, Soyana; Middle Permian, Kazanian Stage; (g) *Protocupoides esini* Ponomarenko, 2013, holotype PIN, no. 3840/28; European Russia, Isady; Middle Permian.
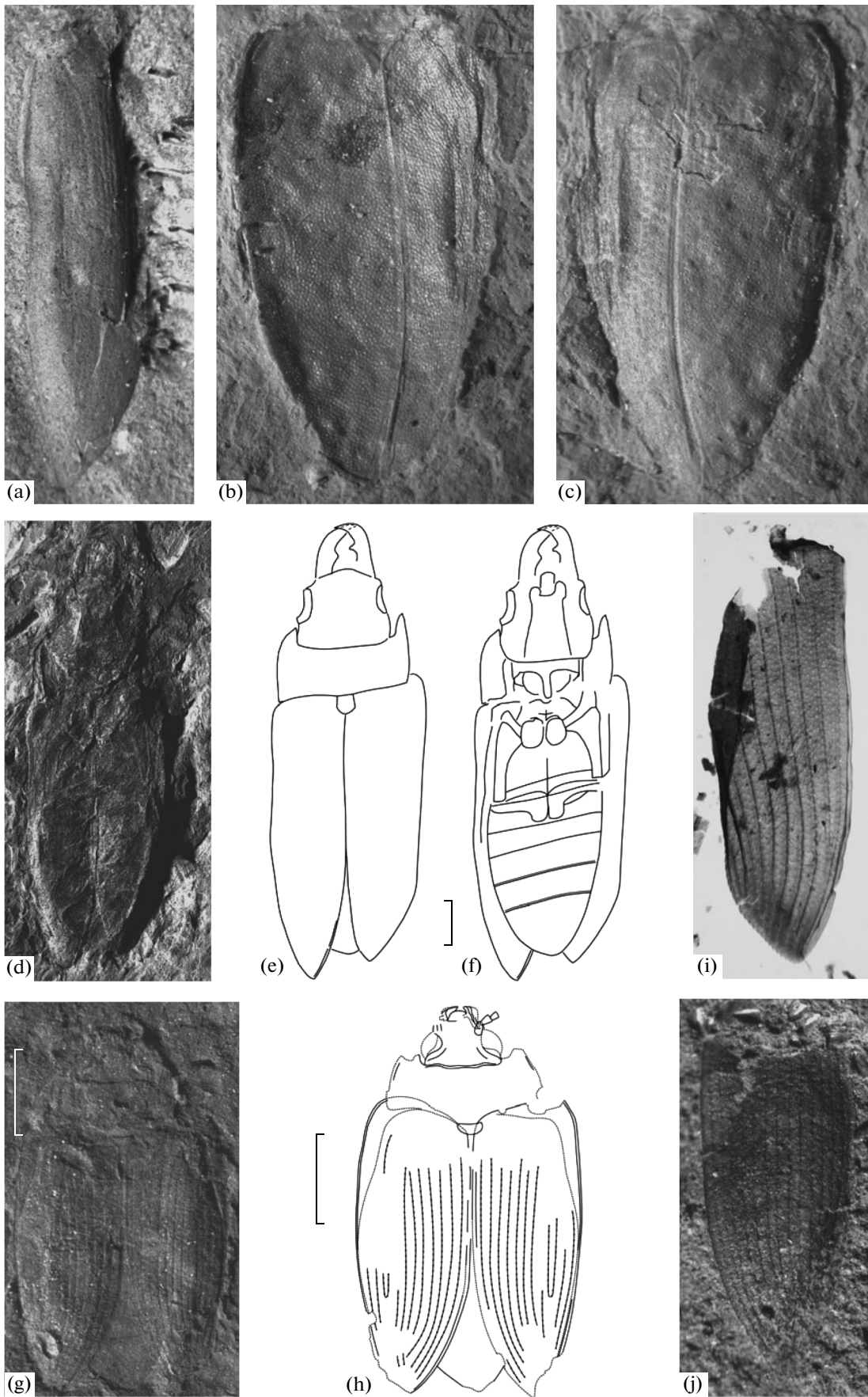
authors even place the infraorder Schizophoromorpha Ponomarenko, 1968 (Schizophoroidea Ponomarenko, 1968, Asiocoleoidea Rohdendorf, 1961, and Rhombocoleoidea Rohdendorf, 1961) in the suborder Myxophaga (Bouchard et al. 2011).

The family name Catiniidae Ponomarenko, 1968 is a junior homonym of Catiniidae Embelton, 1901 (Crustacea, Copepoda); therefore, we propose here the replacement name Coleocatiniidae nom. nov., from Coleoptera and the generic name *Catinius* Ponomarenko, 1968.

Aquatic beetles in the broad sense are represented by several ecological groups, which are distinguished based on the following features: (1) time spent in contact with water; (2) degree of submergence; (3) degree of dependence on water; and (4) motivation of contact with water (search for food, shelter, etc.) (Jäch, 1998; Jäch and Balke, 2008).

The following groups are recognized based on these criteria: true aquatic beetles, amphibiotic beetles (true amphibionts and phytophilous beetles), semiaquatic beetles (shore beetles and commensals of aquatic mammals), and facultative aquatic beetles (Jäch, 1998; Jäch and Balke, 2008; Prokin, 2008). We do not consider the group of facultative aquatic beetles in this study, for lack of information on the modes of life of fossil taxa. For the same reason, we included all Hydrophiloidea Latreille, 1802, Dryopidae Billberg, 1820, Elmidae Curtis, 1830, and Hydraenidae Mulsant, 1844 in the group of true aquatic beetles and all Donaciinae Kirby, 1837, Tanysphyrini Seidlitz, 1887, and Bagoini C.G. Thomson, 1859 in the phytophilous group.

According to this approach to the composition of aquatic beetles, some 37 coleopteran families belong to this group or have aquatic representatives; five of these families are extinct: ?Triaplidae Ponomarenko, 1977, Colymbothetidae Ponomarenko, 1993, Coptoclavidae Ponomarenko, 1961, Parahygrobiidae Ponomarenko, 1977, and Liadytidae Ponomarenko, 1977. In addition to Schizophoridae, it can be suggested that Mesocinetidae Kirejtshuk et Ponomarenko, 2010 and Lasiosynidae Kirejtshuk et al., 2010, described from adults could also be associated with the aquatic environment at the larval stage, by analogy with related recent groups.

MATERIAL AND METHODS

This study is an enlarged and corrected version of the study published earlier in Russian in the Materials of the Fifth All-Russia Symposium on Amphibiotic and Aquatic Insects (Ponomarenko and Prokin, 2013). It is based on our work with accessible paleontological materials and with publications on the subject.

The illustrations to this study were prepared using a Tescan Vega XMU scanning electron microscope and a Leica M165c light stereomicroscope with a Leica DFC420 digital camera (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow), and a Nikon Eclipse 50i light stereomicroscope with a digital camera (Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok). Most of the materials illustrated are stored in the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN); the others are stored in the Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences (IBIW), Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (NIGP), and Capital Normal University, Beijing (CNU).

RESULTS

The taxonomic position of some fossil taxa of aquatic beetles still remains unclear. For instance, the adult tibiae of *Chimaerocoleus aenigma* Ponomarenko, 1985 from the Jurassic of the Kuznetsk Basin (Chernyi Etap I) were provided with a fringe of long swimming hairs (Fig. 5). Elytra with alternating rows of more or less large punctures, as in this species, are found in representatives of different suborders of Coleoptera, including aquatic beetles, such as Haliplidae Brullé, 1835 (Adephaga), Helophoridae Leach, 1815, and Hydrophilidae Latreille, 1802 (Polyphaga). However, the shape of the mid- or hind leg with the tarsomeres subequal in length does not make it possible to consider *C. aenigma* close to any of these families.

No taxon of family rank has been proposed for any genera of hydrophiloid beetles (*Hydrophilopsia* Ponomarenko, 1987, *Laetopsia* Fikáček et al., 2012, *Cretotaenia* Ponomarenko, 1977) that belong to the helophoroid lineage of the superfamily. *Memptus* Handlirsch, 1906 and *Necronectulus* Ponomarenko, 1977, the exact taxonomic position of which remains unclear, may belong to Dytiscoidea.

Fig. 2. Permian beetles with smooth and sulcate elytra: (a) Rhombocoleidae, *Erunakicupes grossus* Ponomarenko, holotype PIN, no. 3840/440, cells transforming into punctures; European Russia, Isady; Middle Permian; (b–f) Schizophoridae: (b, c) *Hadeocoleus calus* Ponomarenko, 1969, holotype PIN, no. 1361/59, direct impression shows rows of ring-shaped columellae; counter impression shows smooth surface of elytron; Kyrgyzstan, Ketmen'; Upper Triassic; (d–f) *Dicerocoleus calus* Lin, holotype NIGP, no. 70704, photograph and dorsal and ventral views; China, Yinping; terminal Middle Permian; (g–h) *Archisyne permiana* Ponomarenko et al.; holotype NIGP, no. 158312, photograph and dorsal and ventral views; China, Yinping; terminal Middle Permian; (i) *Permosyne dentate* Ponomarenko, holotype PIN, no. 3446/10; European Russia, Aristovo; Upper Permian, Vyatkian Stage; (j) *Permosyne rasnitsyni* Ponomarenko, holotype PIN, no. 5103/264; European Russia, Vyazniki; Upper Permian, Vyatkian Stage.
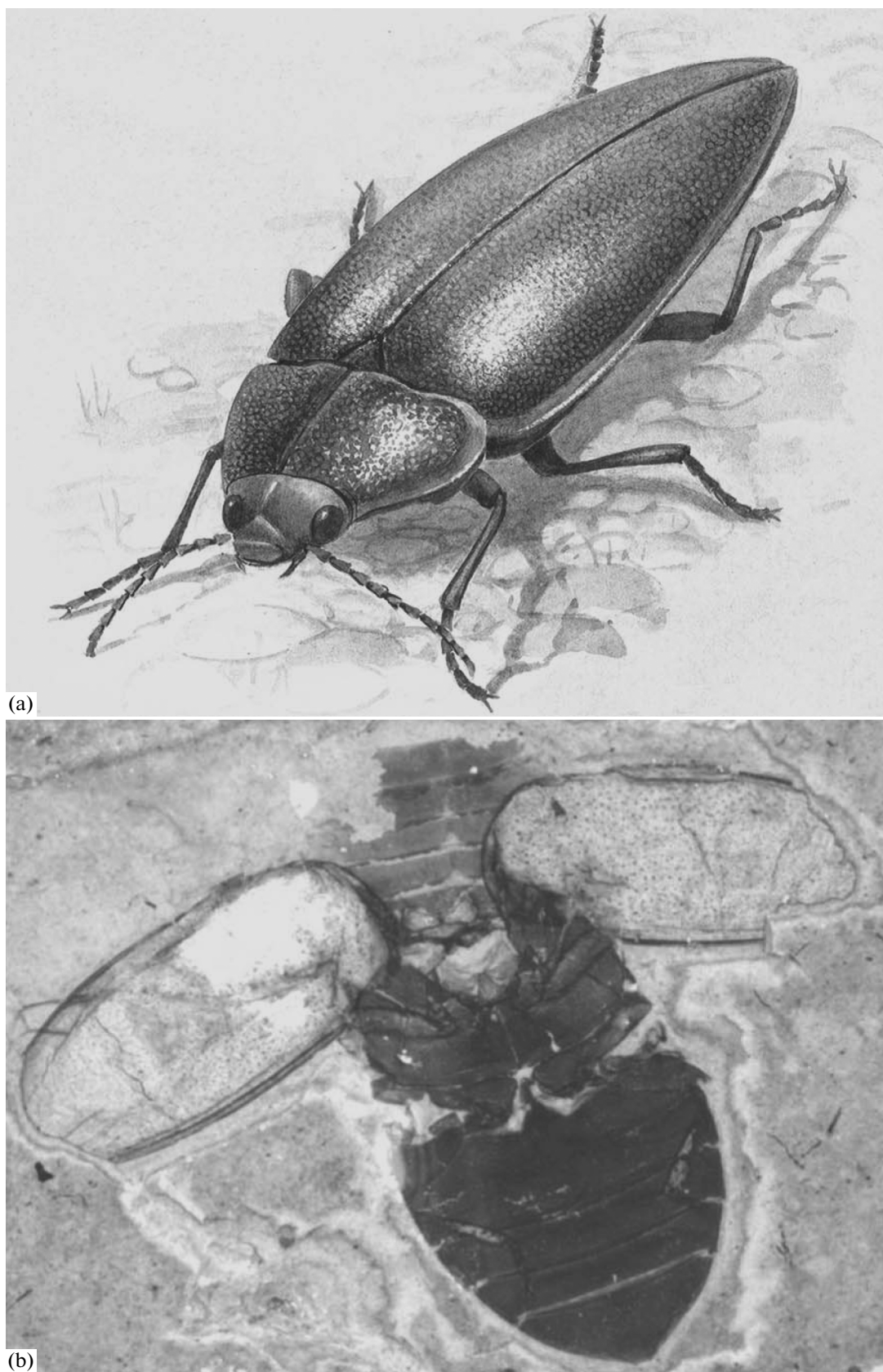
Fig. 3. Beetles of the family Schizophoridae: (a) reconstruction of *Hadeocoleus* sp., Kyrgyzstan, Fergana, Madygen; Upper Triassic; (b) gen. sp., CNU COL LB 2009143, China, Yixian; Lower Cretaceous.
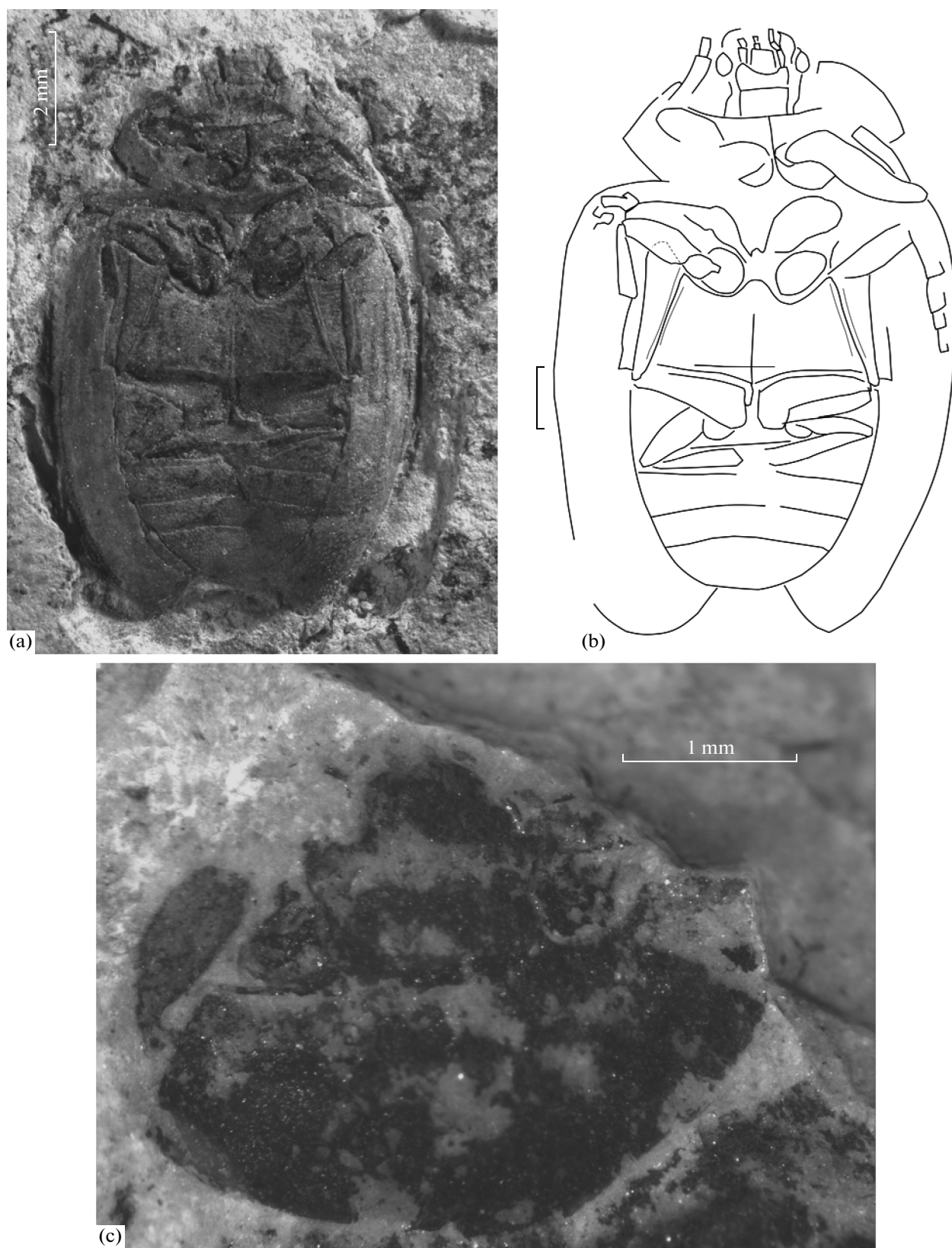
Fig. 4. *Catinius pelta* Ponomarenko: (a, b) holotype PIN, no. 2384/634, photograph and ventral view; (c) paratype no. 2066/2575, head, pronotum, fossorial foreleg; Kazakhstan, Karatau; Upper Jurassic.
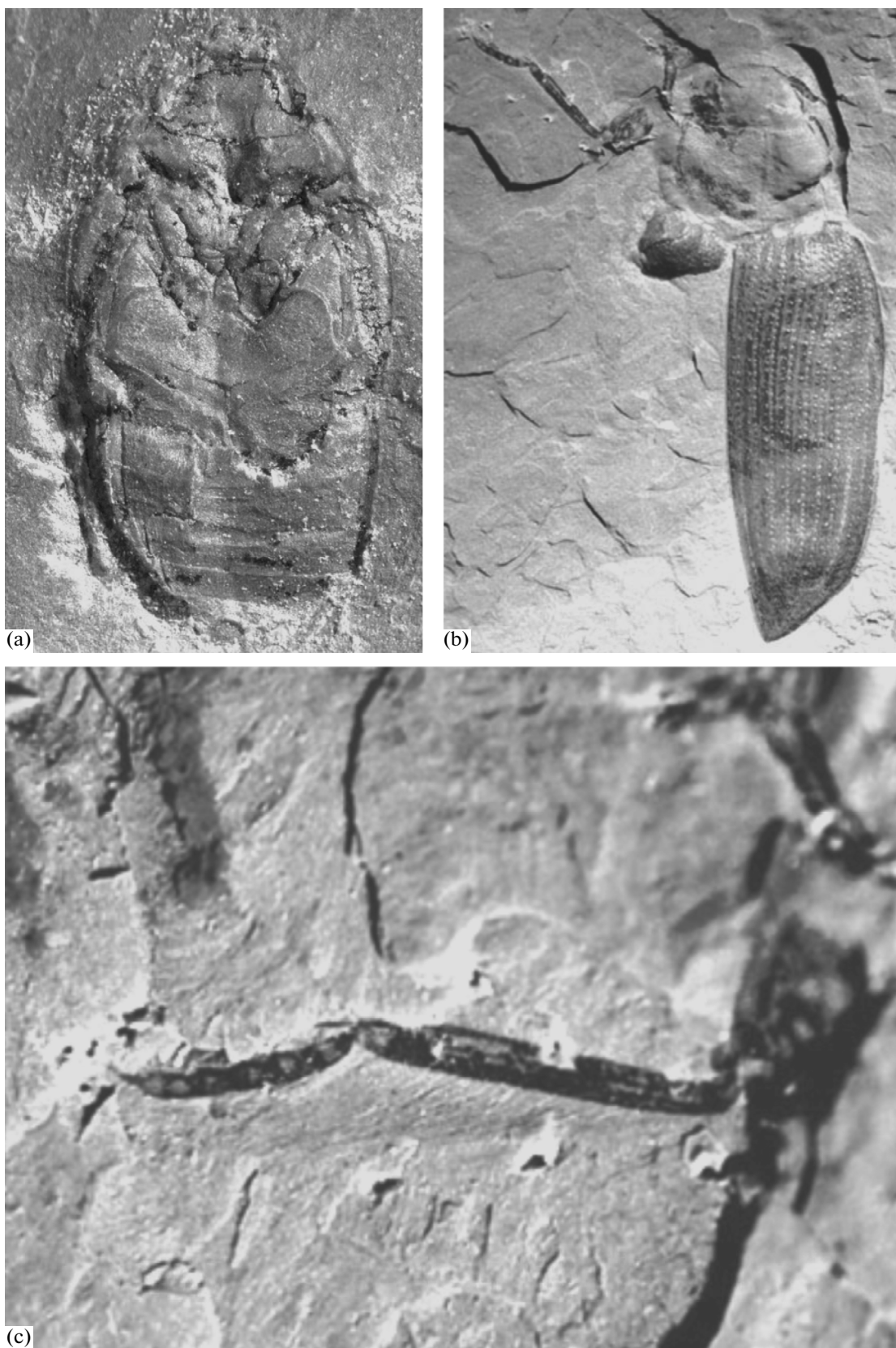
Fig. 5. (a) *Necronectulus avus* Ponomarenko, 1977, holotype PIN, no. 1362/47, Upper Triassic, eastern Kazakhstan; (b, c) *Chimerocoleus aenigma* Ponomarenko, holotype PIN, no. 2791/11*;* Siberia, Kuznetsk Basin, Chernyi Etap I; Jurassic.

There are still no paleontological data on the families Torridincolidae Steffan, 1964, Aspidytidae Ribera et al., 2002, Meruidae Spangler et Steiner, 2005, Amphizoidae Lacordaire, 1854, Epimetopidae Zaitzev, 1908, and Cneoglossidae Champion, 1897 and the subfamily Platypsyllinae Ristema, 1869 of the family Leiodidae Fleming 1821. For families living mostly under rheophilic and hygropetric conditions (Torridincolidae, Aspidytidae, Meruidae, Amphizoidae, Cneoglossidae) and commensals of aquatic mammals (Platypsyllinae), this can be explained by the low fossilization probability of remains. At the same time, findings of fossil Epimetopidae can well be expected.

In the table below we provide data on the earliest records of fossil representatives of Recent families (in some cases, subfamilies and tribes), indicating the taxa, localities, and their age. If the taxon has not been described, the table contains a reference to the published source of the record. If we doubted the correctness of the family assignment of the taxon (?), we provided additional references to records from the earliest localities.

Extinct families of undoubted aquatic beetles are known to date only in the suborder Adephaga and distributed mainly in the Mesozoic. All extant aquatic beetle subfamilies of this suborder—Haliploidea, Dytiscoidea, and Gyrinoidea—may have evolved as early as the Permian. We provide below a brief review of the geological ranges of extinct families and our notion about the modes of life and evolution of their representatives. A detailed review of the taxonomic composition and distribution of fossil beetles is provided at the site of the Zoological Institute of the Russian Academy of Sciences (Kirejtshuk and Ponomarenko, 2014).

Family Triaplidae Ponomarenko, 1977. Two species have been described from the Triassic Madygen Formation: *Triaplus macroplatus* Ponomarenko, 1977 (Madygen), *T. laticoxa* Ponomarenko, 1977 (Fig. 6), and *Triaplus sibiricus* Volkov, 2013 from the Babii Kamen' locality (Upper Permian, Mal'tsevo Formation); the last probably represents Dytiscoidea. At the same time, a real *Triaplus*, not yet described has been found in this locality. The family is viewed as an archaic taxon within Haliploidea and hence considered aquatic, although triaplids display no specific adaptations typical of aquatic beetles (Ponomarenko and Prokin, 2013).

Family Colymbothetidae Ponomarenko, 1993 is described for larvae of *Colymbotethis antecessor* Ponomarenko, 1993 (Fig. 7) from the Kenderlyk locality (Upper Triassic, Norian). The same subfamily is probably represented by larval *Mormolucoides articulatus* Hitchkock, 1858 from the Upper Triassic (Carnian) to Lower Jurassic of the United States. The species *Colymbotethis antecessor* had spiral thickenings of the tracheae, probably used as a hydrostatic apparatus, but the legs of this species were not yet adapted for swim-

ming, which is also confirmed by the weakly distinguished thoracic segments. In addition to the short and thick urogomphi, these characters suggest that the family (and possibly Dytiscoidea as a whole) emerged at the stage of transition from ambush to nektonic predation of larvae (Ponomarenko and Prokin, 2013).

The superfamily Dytiscoidea may have evolved earlier than the Triassic, if the undescribed adult from the Middle Permian Yinping locality and *Triaplus sibiricus* Volkov, 2013 belongs to this superfamily.

Family Coptoclavidae Ponomarenko, 1961 (Fig. 8). The earliest coptoclavid larval *Protonectes germanicus* Prokin et Ponomarenko, 2013 is known from the Upper Triassic (Carnian) of Germany (Prokin et al., 2013b); hind wings of beetles of this family have also been described from there (Fedorenko, 2014) as well as other copoclavid remains; the earliest known remains of adult coptoclavids are known from Buntsandstein (Anisian) of Germany (Ponomarenko et al., 2015). The fossils described belong to two coptoclavid subfamilies, Timarchopsinae and Coptoclaviscinae. In addition, coptoclavids have been recorded in the Upper Ladinian of the Alps (Strada et al., 2013). *Holcoptera* Handlirsch, 1906 from the Upper Triassic to Lower Jurassic of England and the United States probably belongs to Coptoclaviscinae. The great diversity and abundance of coptoclavids as early as the Triassic and their appearance in the fossil record in the Lower Anisian, when the restoration of beetle diversity following the Lower Triassic minimum had barely started, suggests that the family emerged as early as in the terminal Permian.

In the Jurassic and Early Cretaceous, coptoclavids were diverse and widespread over the globe, avoiding, however, high latitudes, although the climate of the Earth was equable at that time. Coptoclavid remains are abundant in deposits of algal–bacterial platforms; in Solnhofen, they are represented by specific genera not known from continental water bodies. One coptoclavid record is known from Upper Jurassic pelagic sediments. In the Jurassic, adult coptoclavids are diverse and usually represented in localities by several genera and species, while their rather scant larvae are so similar to each other that they still cannot be divided even into species, to say nothing of genera. Both adults and larvae are abundant and diverse in Lower Cretaceous localities of Europe, whereas in localities with the East Asian Jehol fauna, coptoclavids are represented by a single abundant species.

The latest known representative of the family, *Coptoclava longipoda* Ping, 1928, is distributed from the Khutuliyn Khira locality (Upper Jurassic–Lower Cretaceous, Ulugei Formation of Mongolia) to Bon Tsagan locality (Lower Cretaceous, Barremian–Aptian, Bon Tsagan Group, Khurilt Member of Mongolia). This species was recently recorded from the Jinji Formation in South Korea, from deposits believed to be much earlier than those containing the Jehol biota (Park et al., 2013). *C. longipoda* was the most typical

Table 1. The earliest records of fossil representatives of Recent aquatic beetle families (subfamilies, or tribes)

| Family (subfamily/tribe)	Earliest known taxon or source of record	Locality, age
Lepiceridae Hinton, 1936	*Haplochelus georissoides* Kirejtshuk et Poinar, 2006 *Lepiceroides pretiosus* Kirejtshuk et Poinar, 2013	Burmese amber (Lower Cretaceous, Upper Albian)
Sphaeriusidae Erichson, 1845	*Burmasporum rossi* Kirejtshuk, 2009	Burmese amber (Lower Cretaceous, Upper Albian)
Hydroscaphidae LeConte, 1874	*Hydroscapha jeholensis* Cai, Short et Huang, 2012	Yixian (Upper Jurassic–Lower Cretaceous, Tithonian–Berriasian)
Haliplidae Brullé, 1835	*Haliplus cretaceus* Prokin et Ponomarenko, 2013	Bon Tsagan (Lower Cretaceous, Barremian–Aptian, Bon Tsagan Group, Khurilt Member)
Gyrinidae Latreille, 1810	*Angarogyrus minimus* Ponomarenko, 1977	Iya (Lower Jurassic, Cheremkhovskaya Formation)
Paelobiidae Regimbart, 1878	*Hygrobia cretzschmari* (Heyden et Heyden, 1866)	Rott (Upper Oligocene or Lower Miocene)
Noteridae Thomson, 1860	Noteridae sp. (Mitchel and Wighton, 1979)	Pascapu (Paleocene, Torrejonian–Tiffanian)
Dytiscidae Leach, 1815	*Palaeodytes gutta* Ponomarenko, 1987	Karatau (Upper Jurassic, Karabastau Formation)
Hydrophilidae Latreille, 1802	*Protochares brevipalpis* Fikáček et al., 2012	Talbragar (Upper Jurassic, Oxfordian–Tithonian)
Hydrochidae Thomson,1859	*Cretohelophorus cupedoides* Ponomarenko, 1987	Bon Tsagan (Lower Cretaceous, Barremian–Aptian, Bon Tsagan Group, Khurilt Member)
Helophoridae Leach, 1815	*Helophorus inceptivus* Fikáček et al., 2012	Shar Teg (Upper Jurassic)
Spercheidae Erichson, 1837	*Prospercheus cristatus* Prokin, 2009	Shar Teg (Upper Jurassic)
Georissidae Laporte, 1819	? *Georissites negev* Ponomarenko, 2008	Gerofit (Upper Cretaceous, Turonian)
	Georissus magnus Haupt, 1956	Geiseltal (Middle Eocene)
Hydraenidae Mulsant, 1844	*Ochthebiites altus* Ponomarenko, 1977	Novospasskoe (Middle Jurassic, Ichetui Formation)
Scirtidae Fleming, 1821	? *Angarolarva aquatica* Ponomarenko, 1985	Ust'-Balei (Lower Jurassic, Cheremkhovskaya Formation)
	Scirtidae sp. (Jell, Duncan, 1986)	Koonwarra (Lower Cretaceous)
	Scirtidae sp. (Kirejtshuk, Azar, 2008)	Lebanese amber (Lower Cretaceous, Barremian–Aptian)
Elmidae Curtis, 1830	*Potamophilites angustifrons* Haupt, 1956	Geiseltal (Middle Eocene)
Dryopidae Billberg, 1820	*Dryops eruptus* Wickham, 1911	Florissant (Lower Oligocene)
Lutrochidae Kasap et Crowson, 1975	*Lutrochites lecontei* Wickham, 1912	Florissant (Lower Oligocene)
Limnichidae Erichson, 1846	*Palaeoersachus bicarinatus* Puetz, Hernando et Ribera, 2004	Baltic amber (Upper Eocene)
Heteroceridae MacLeay, 1825	*Heterocerites magnus* Prokin et Ren, 2011	Yixian (Upper Jurassic–Lower Cretaceous, Tithonian–Berriasian)
Psephenidae Lacordaire, 1854	*Eubrianax* sp. (Bertrand, Laurantiaux, 1963)	Aude (Eocene)
Ptilodactylidae Laporte, 1836	*Aphebodactyla rhetinae* Chatzimanolis, Cashion, Engel et Falin, 2012	Burmese amber (Lower Cretaceous, Upper Albian)
Eulichadidae Crowson, 1973	Eulichadidae sp. (Yan et al., 2013)	Daohugou (Middle Jurassic)
Donaciinae Kirby, 1837	Our unpublished data	Altan Ula (Upper Cretaceous, lower beds of the Barun Goyot Formation)
Tanysphyrini Seidlitz, 1887	? *Pissodes effossus* C. Heyden, 1858	Sieblos (Middle Oligocene)
	Tanysphyrus deletus Oustalet, 1874	Aix (Upper Oligocene)
Bagoini C.G. Thomson, 1859	*Bagous palintonus* Foerster, 1891	Brunstatt (Oligocene)
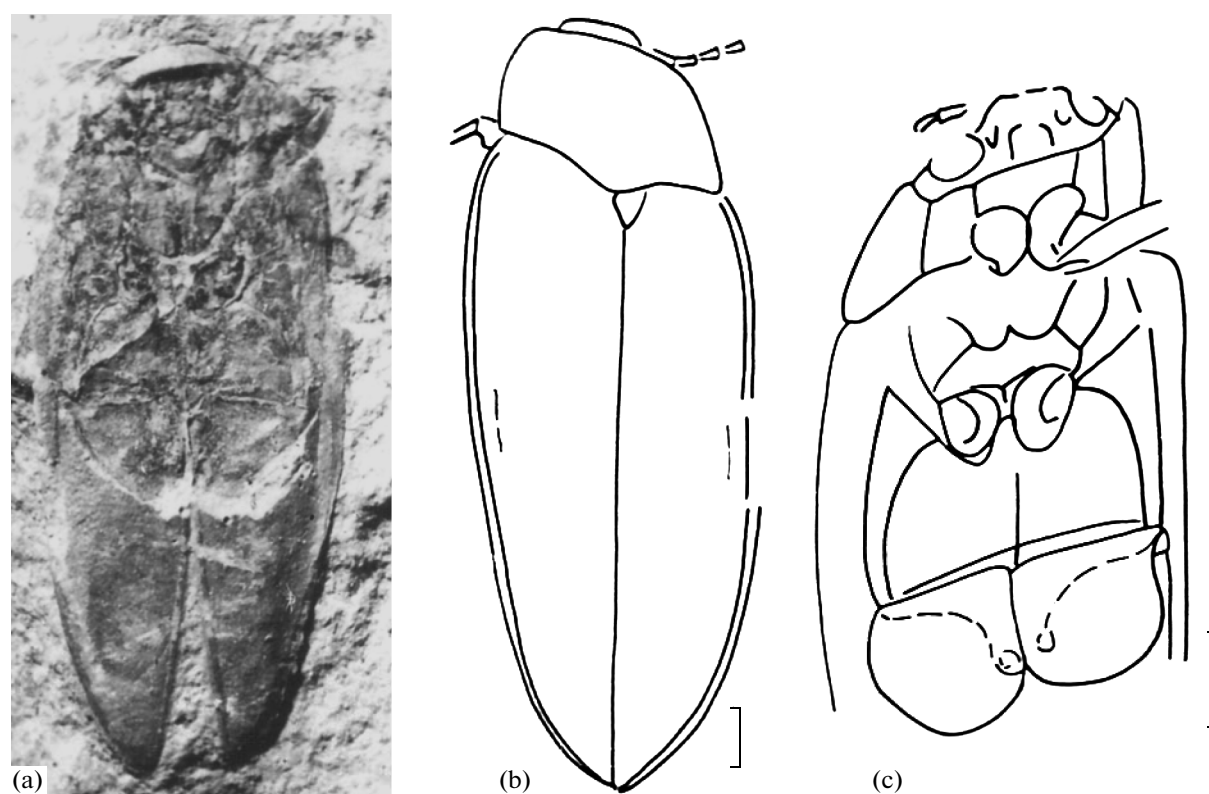
Fig. 6. Beetles of the family Triaplidae: *Triaplus macroplatus* Ponomarenko, holotype PIN, no. 2971/104: (a) photograph and (b, c) dorsal and ventral views; Kyrgyzstan, Fergana, Madygen; Upper Triassic.

and abundant top consumer species in Lower Cretaceous lakes of eastern Asia from Transbaikalia to South China for almost 20 m.y. This is probably an unprecedented case of such long dominance of an insect species over a large area; it underlines the principal differences in ecosystem organization between Mesozoic lakes, and biomes in general, and Recent lakes.

The principal direction of coptoclavid evolution was adaptation first to nektonic and, then, to hyponeustonic predation in larvae and to peustonic predation in adults. Morphologically, this manifested itself in gradual flattening of the mid- and hind legs in larvae, development of swimming hairs on these legs, and in divergence of forelegs, which became prehensile, in strengthening of spiral thickening of the tracheae used as a hydrostatic apparatus, and in the shift of mandibles with a groove via the development of the retinaculum to mandibles with several large teeth, which were probably optimal for feeding on the surface film, as in Recent larvae of *Hydrophilus* O.F. Müller, 1764 (Hydrophilidae).

A trend that can be noted in the evolution of Coptoclavidae includes specialization of forelegs as prehensile and mid- and hing legs as swimming and separation of two pairs of eyes. The legs of neustonic coptoclavid larvae, absolutely unfit for movement on land, in combination with the presence on the mesothorax and on all abdominal segments of preserved stigmata,

which could function only in the air, suggests that they pupated in cradles of plants above the water surface, like gyrinids (Ponomarenko and Prokin, 2013, 2014). The large spiracles of Coptoclavidae, situated in the posterior membranous part of tergite 8, were covered in submerged larvae by urogomphi raised to the plane of the body and drawn to each other. When the larva rose to the water surface to fill its tracheae with air, the urogomphi separated and the spiracles became open (Prokin et al., 2013b).

It should be noted that many coptoclavids, such as *Coptoclavisca*, have ambulatory legs as both adults and larvae, although they preserved two pairs of eyes. Possibly, they lived on the surface of floating plant aggregates, like beetles of the Recent genus *Amphiops* Erichson, 1843 (Hydrophilidae), in which eyes are separated into the upper and lower parts and which live on the lower surface of plants floating on the water, such as *Azolla*, *Nymphoides*, and others. A life form not found in Recent aquatic beetles was typical of *Hispanoclavina* Soriano et al., 2007 and *Hoyaclava* Soriano et al., 2007. These beetles filtered zooplankton, using combs of setae on their forelegs (Soriano et al., 2007)

Family Parahygrobiidae Ponomarenko, 1977 was established for the species *Parahygrobia natans* Ponomarenko, 1977 (Fig. 9) from the Uda locality (Jurassic, Uda Formation). This species is similar in the structure of its head to primitive coptoclavids; it is also
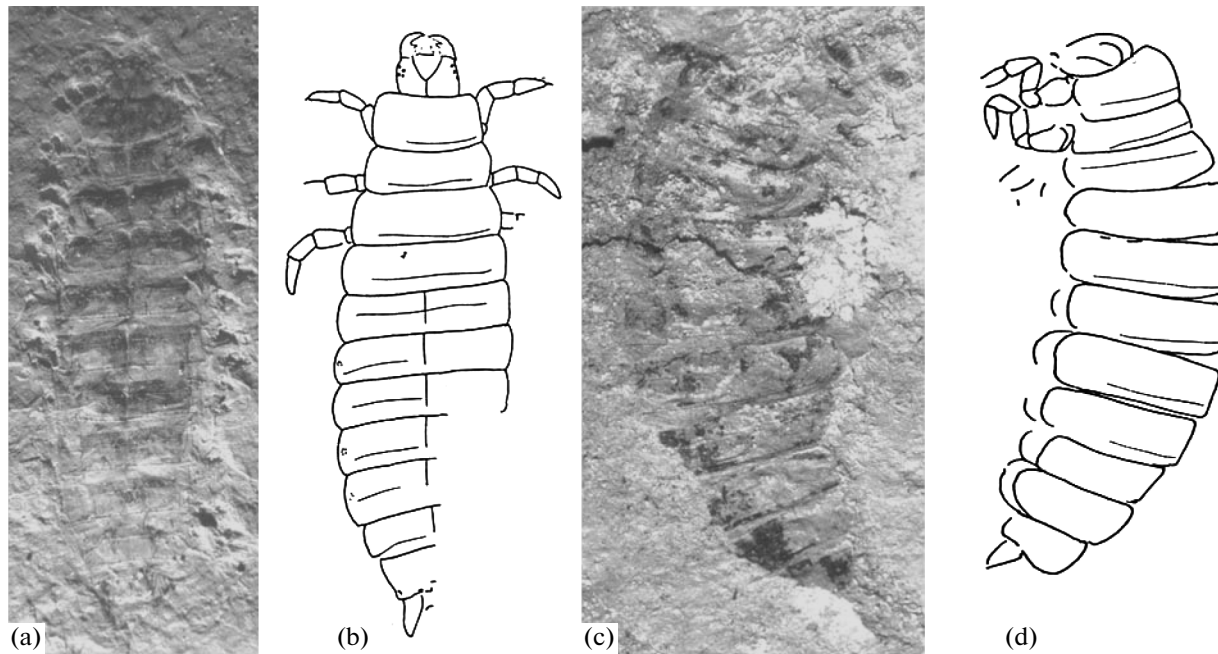
Fig. 7. Beetles of the family Colymbothetidae: *Colymbothetis antecessor* Ponomarenko: (a, b) holotype PIN, no. 2497/13, photograph and dorsal view; (c, d) paratype no. 2497/14, photograph and lateral view; Kazakhstan, Kenderlyk; Upper Triassic.

similar to them as well as to Recent Aspidytidae in rather well-developed abdominal segment 10. At the same time, the strong and sparse swimming setae on legs and secondarily segmented urogomphi are a unique combination of characters, which makes it impossible to assign this species to any known family of Dytiscoidea. Many-segmented urogomphi are known among dytiscoids only in the coptoclavid *Megacoptoclava longiurogompha* Ponomarenko et Martinez-Delclos, 2000 from the Las Hoyas locality (Spain, Lower Cretaceous, Barremian), which is distinguished from other species of the family by the life form, which resembles rheophilic and hygropetric stoneflies and mayflies; possibly, it should also be assigned to a separate family or transferred to Parahygrobiidae.

Family Liadytidae Ponomarenko, 1977. Liadytids occur from the Lower Jurassic of Siberia—*Liadytes avus* Ponomarenko, 1963 (Ust'-Balei)—to the Glushkovo Formation of the Upper Jurassic: *L. crassus* Ponomarenko, 1977 (Unda), *L. longus* Ponomarenko, 1977 (Fig. 10), and *L. dajensis* Ponomarenko, 1987 (Daya). *Liadytes aspidytoides* Prokin et al., 2013 was described from Shar Teg (Upper Jurassic, Oxfordian–Tithonian of Mongolia). Larval *Angaragabus jurassicus* Ponomarenko, 1963 (Ust'-Balei) possibly belongs to the same family. The adult is similar in morphology to the Recent Aspidytidae and differs from them in the following characters visible in fossil specimens: closely positioned mesocoxae with the metathorax bearing no process (Prokin et al., 2013a) and the structure of the scape and pedicel. Larval *A. juras-*

sicus differs from extant dytiscids of the subfamily Agabinae Thomson, 1867 only in the shortened urogomphi. If we accept that it belongs to Liadytidae, then, this family is an example of mosaic evolution, with the larva more morphologically advanced than the adult (Prokin et al., 2013a). An opposite case of mosaic evolution among dytiscoids was described earlier for the coptoclavid *Daohugounectes primitivus* Wang, Ponomarenko et Zhang, 2009.

Judging from the nonflattened hind legs without swimming hairs and with long tibiae and from the small area of the metacoxae, liadytids were poor swimmers, incapable of synchronously paddling with both hind legs (Prokin et al., 2013a). At the same time, they probably turned to the nektonic mode of life, since the species *Liadytes aspidytoides* Prokin et al., 2013 had a coloration adaptive for this mode of life: pale venter and dark dorsum (Prokin et al., 2013a). Larval *A. jurassicus* was probably nektonic–benthic and, judging from the morphology of its legs and the tracheal system, could pupate in the soil, suggesting that the paleowater body of the Ust'-Balei locality had a stable shoreline.

Some morphological changes can be traced at the Mesozoic stage of the evolution of Dytiscidae (Fig. 11) associated with the transition to swimming, using simultaneous strokes of the mid- and hind legs (Prokin et al., 2013b), which determined evolutionary success of this family as nektonic predators. Unfortunately, adults and larvae of Dytiscidae from the Koonwarra locality (Lower Cretaceous of Australia) (Jell and Duncan, 1986) have not yet been studied. They display
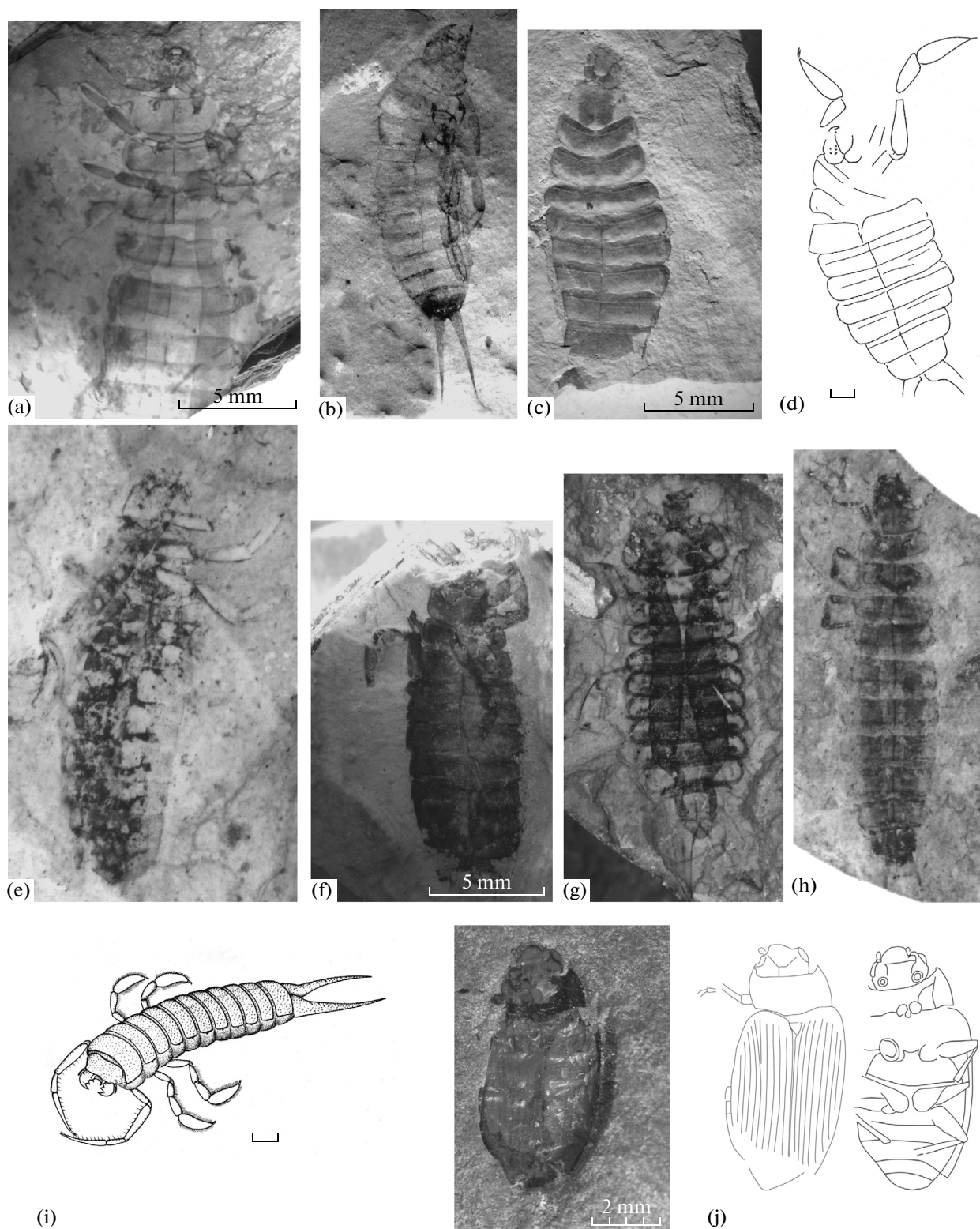
Fig. 8. Beetles of the family Coptoclavidae: (a, b) *Stygeonectes jurassicus* Ponomarenko: (a) paratype PIN, no. 3000/925, photograph, (b) paratype PIN, no. 3000/975; (c, d) *Bolbonectes occidentalis* Ponomarenko: (c) paratype PIN, no. 3000/3205, photograph; (d) paratype, PIN, no. 3000/3241, drawing, dorsal view, Transbaikalia, Novospasskoe; Jurassic; (e) *Daohugounectes primitivus* Wang et al., paratype NIGP, no. 20099081, China, Daohugou; Jurassic; (f) *Bolbonectes intermedius* Ponomarenko, paratype PIN, no. 3920/83, photograph; Transbaikalia, Bolboi; Jurassic; (g–i) *Coptoclava longipoda* Ping, (g–h) undescribed larvae, NIGP, no. 20099047, 2009049; China, Yixian; Lower Cretaceous; (i) reconstruction of larva; (j) *Coptoclavella jurassica* Ponomarenko, holotype PIN, no. 2470/1007, photograph and drawings, dorsal and ventral views; Mongolia, Shar Teg; Jurassic.
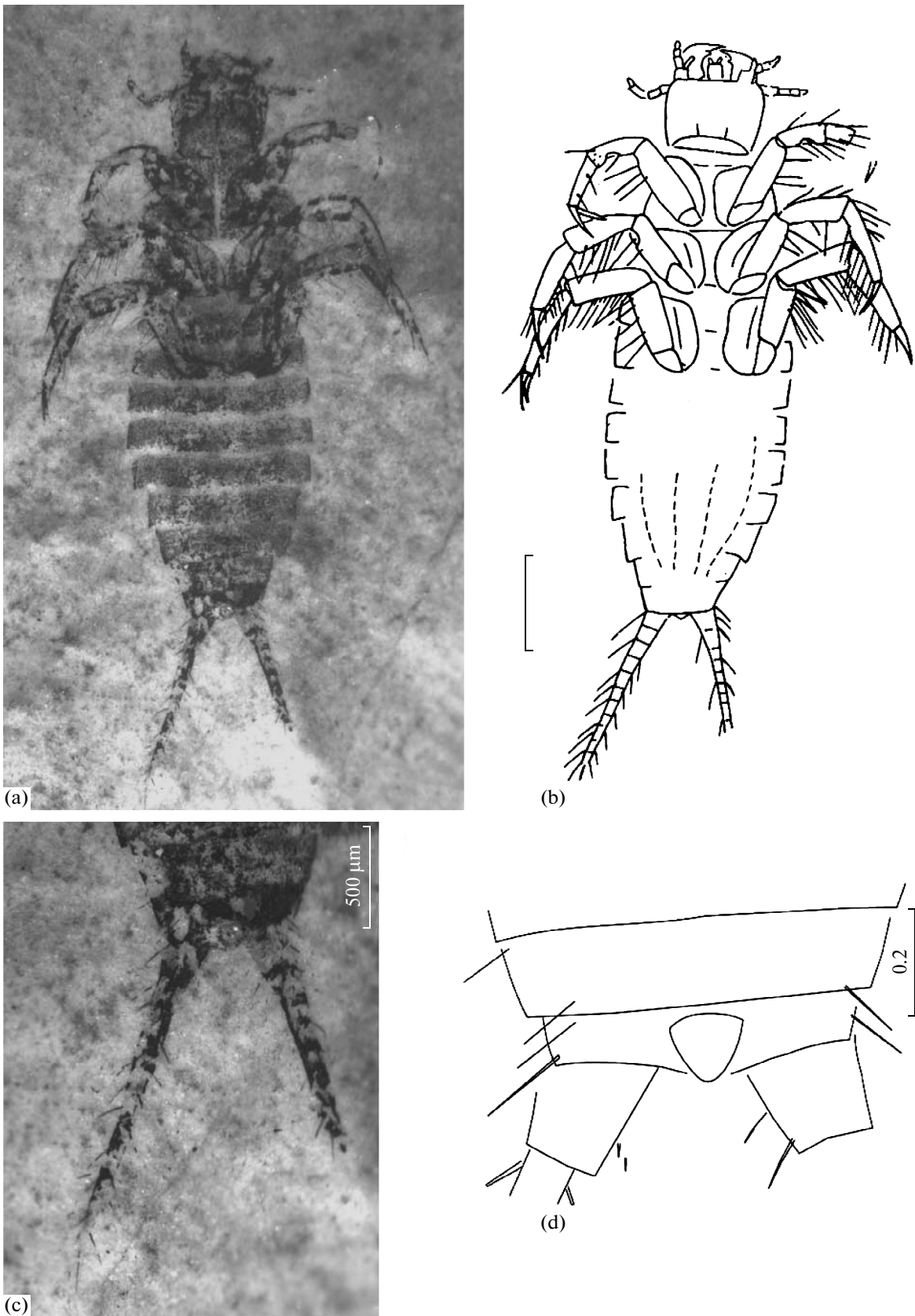
Fig. 9. Beetles of the family Parahygrobiidae: *Parahygrobia natans* Ponomarenko: (a, b) holotype PIN, no. 3053/423: (a) photograph and (b) drawing, ventral view; (c, d) holotype PIN, no. 3053/423: (c) photograph and (d) drawing, ventral view; Transbaikalia, Uda, Upper Jurassic.
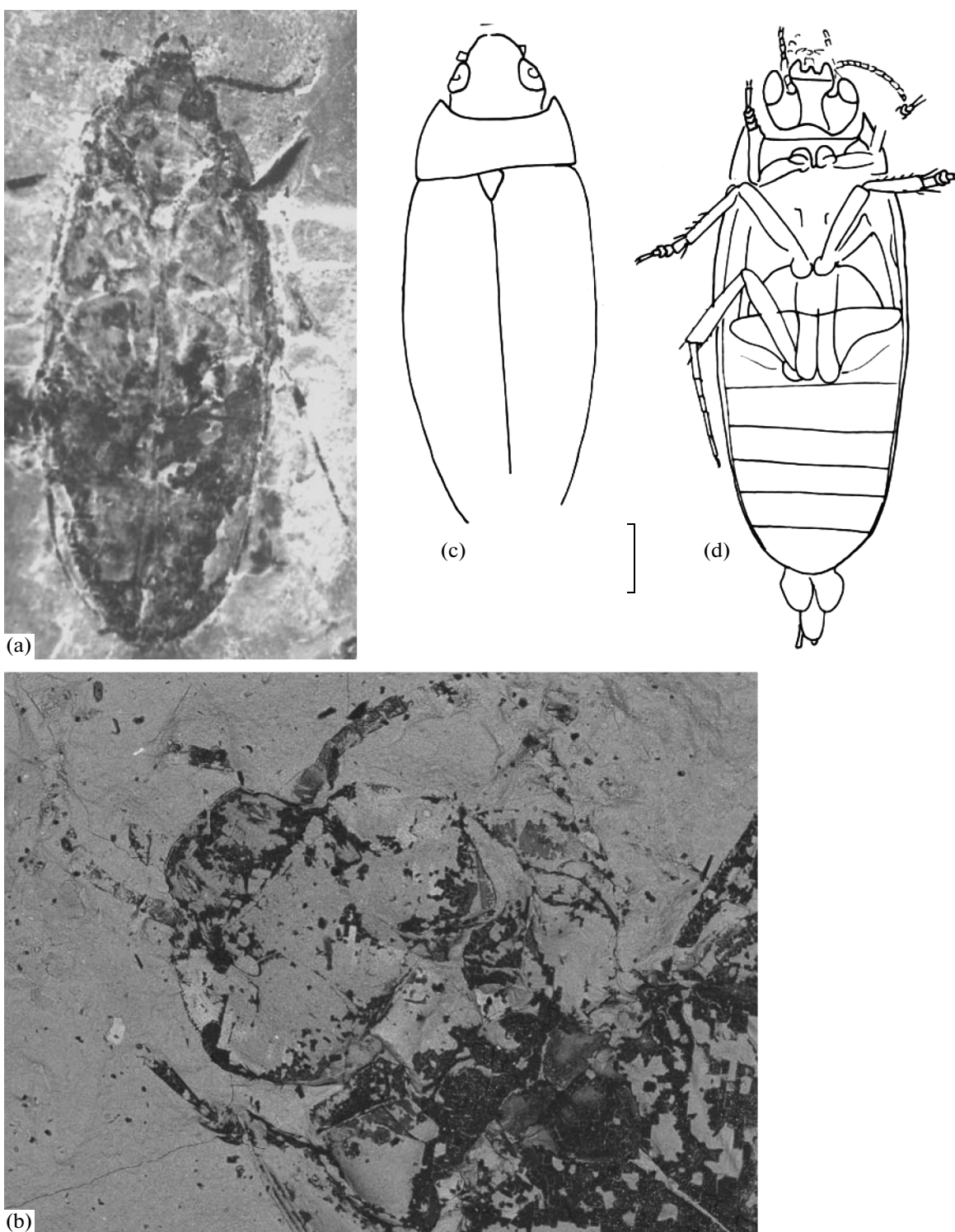
Fig. 10. Beetle of the family Liadytidae, *Liadytes longus* Ponomarenko, holotype PIN, no. 3063/736: (a, b) photograph: dorsal view and (b) details of head and prothorax; (c, d) drawings: (c) dorsal and (d) ventral views; Transbaikalia, Daya, Upper Jurassic.

some advanced features compared to the known Mesozoic dytiscids. For instance, the adults probably already moved using simultaneous strokes and the morphological level of the larvae probably corresponds to that of extant Agabinae or Colymbetinae.

The extinct subfamily Palaeogyrininae Schlechtendal, 1894 occurring in the Miocene should also be studied.

The origin of aquatic Adephaga is not at all as clear as usually believed. The most widespread notion is that aquatic adephagans evolved from terrestrial ones,
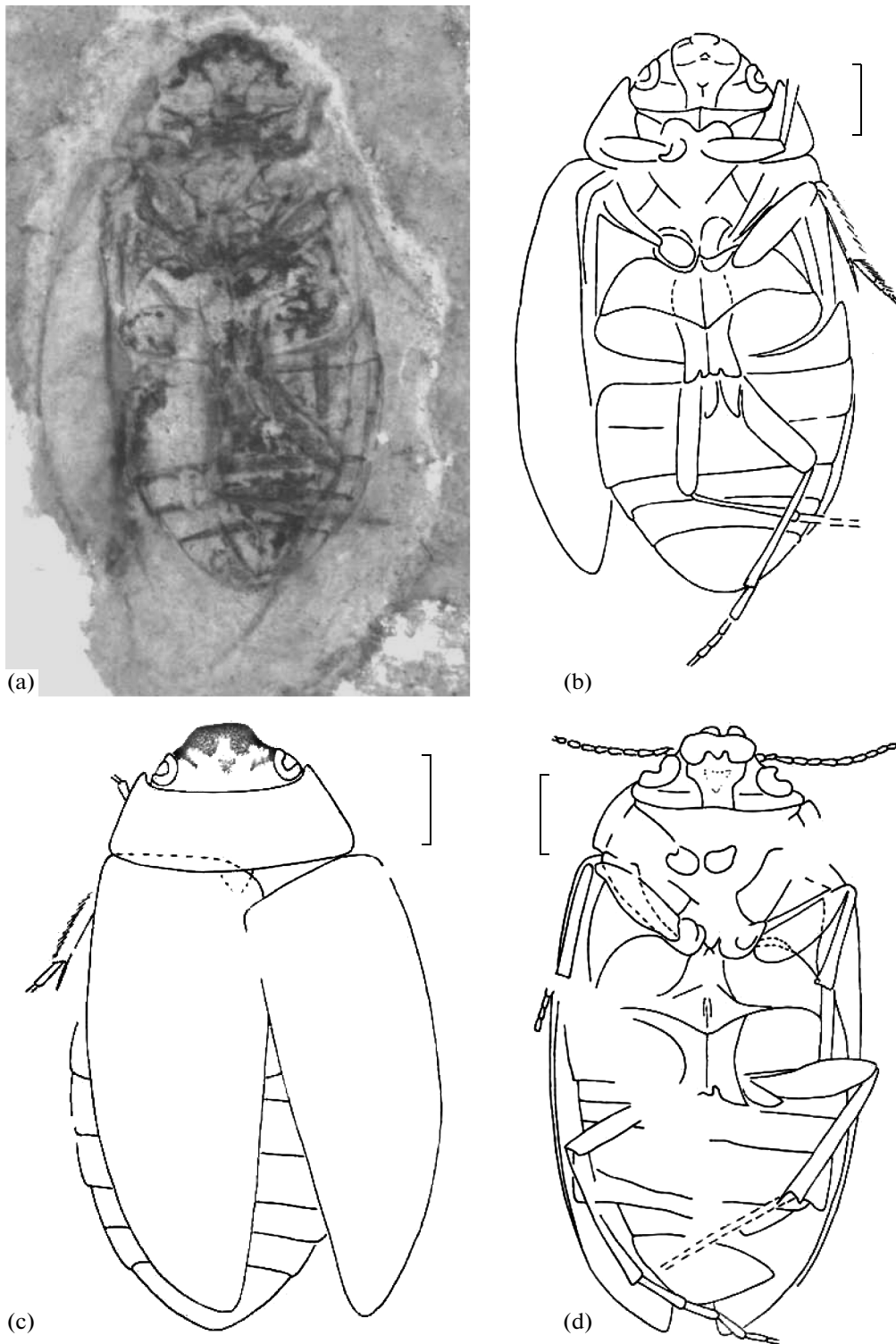
Fig. 11. Beetles of the family Dytiscidae: (a–c) *Liadytiscus cretaceus* Prokin et Ren, holotype CNU COL LB 2009028, China, Yixian; Lower Cretaceous, photograph and drawings; (d) *Liadytiscus longitibialis* Prokin et Ren, holotype CNU COL LB 2009026, China, Yixian; Lower Cretaceous, drawing.

although there is no evidence of that, either comparative morphological (except for the functional spiracles of larvae in aquatic families) or paleontological. Moreover, rather advanced aquatic adephagans are probably known from earlier deposits than terrestrial ones. The earliest beetle fossil that can be considered representing Adephaga is known from the terminal Capitanian (Yinping, Middle Permian). Its preserva-

tion is mediocre, but in appearance it is most similar to dytiscoids. The earliest known terrestrial adephagan, *Ademosinoides asiaticus* Martynov, 1936 of the family Trachypachidae (Ponomarenko and Volkov, 2013), is known from the terminal Permian (earlier considered Lower Triassic) of the Babii Kamen' locality in the Kuznetsk Basin. Certainly, this order of appearance in the fossil record cannot be considered a serious proof that aquatic adephagans evolved earlier than terrestrial ones, but nevertheless it makes the origin of the former from the latter somewhat less likely (Ponomarenko, 2002). If Dytiscoidea diverged from Caraboidea or from the common stem of Adephaga, their divergence can be associated with living on floating plant aggregates, widespread in Mesozoic lakes (Ponomarenko, 1996). The opposite scenario was proposed earlier: the origin of Caraboidea from Dytiscoidea (Ponomarenko, 2002).

Further evolution of the superfamily Dytiscoidea was connected with adaptation to the nektonic and neustonic modes of life; the former proved more promising. Extinction of coptoclavids, hyponeustonic at the larval stage and pleustonic at the adult stage and often occupying the position of top predators in Mesozoic lakes, was probably associated with the disappearance of floating aggregates, in which they probably pupated, and with reorganization of aquatic trophic networks associated with the spread of angiosperms (Ponomarenko and Prokin, 2013) and diatoms.

Whirligigs (Gyrinidae) underwent very few evolutionary changes since they appeared in the fossil record. The Mesozoic whirligigs do not constitute a distinct taxon that could be distinguished from the Cenozoic whirligigs (Ponomarenko, 1977), although the Mesozoic ones typically have poorly developed metacoxae and preserved derivative of the metaventral suture, as in Recent Heterogyrininae. The only taxon described as close to whirligigs from the Upper Triassic Garazhovka locality (*Triadogyrus sternalis* Ponomarenko, 1977) is probably rather distant from whirligigs (Fig. 12), although Beutel et al. (2013) in their review included it in Gyrinidae. Interestingly, the neustonic mode of life and pupation in cradles of plants above the water did not prove to be dead-end adaptations in whiriligigs, in contrast to dytiscoids. This is probably explained by the smaller size of whirligigs, greater division of niches between adults and larvae, and ability to secrete substances protecting from fish predators.

Gyrinids were no less abundant than dytiscids in the Mesozoic and very abundant in the Early Cenozoic. The earliest known gyrinid, *Angarogyrus minimus* Ponomarenko, 1977, has a thorax and coxae most adapted to the pleustonic mode of life, which makes it close in the level of morphological perfection to the Recent genera *Dineutus* and *Porrorhynchus*. A similar picture is found in Dytiscidae: the earliest representatives of the genus *Palaeodytes* Ponomarenko, 1987 appear to have been better swimmers than all later Mesozoic taxa (Prokin et al., 2013).

Peculiar features of *Mesogyrus* Ponomarenko, 1973 and *Baissogyrus* Ponomarenko, 1973, above all the narrow metaventral suture, suggest that they could be ancestors of Heterogyrininae+Gyrininae. *Cretotortor zherichini* Ponomarenko, 1973 can probably be considered the earliest of all known Gyrinini Latreille, 1810; and Pliocene *Mesodineutes amurensis* Ponomarenko, 1977 from Arkhara can be considered the earliest representative of Spanglerogyrininae or a closely related extinct group.

The earliest known representative of Orectochilini Régimbart, 1882 is *Gyretes giganteus* (Piton, 1940) from the Menat locality (Paleocene of France); it was originally described in the genus *Dineutus* and subsequently correctly transferred to this tribe based on the genitalia (Nel, 1989). The assignment to the genus *Gyretes* Brullé, 1835 should be indicated above all by the hidden scutellum, which, however, is not clearly seen in the impression of the holotype. This genus is currently distributed exclusively in the New World; the closely related genus *Orectogyrus* Régimbart, 1884 is African and most species of the closely related genus *Patrus* Aubé, 1838 occur in Asia and the Oriental region, with one species in central Africa (Miller and Bergsten, 2012). Thus, the modern distribution of the *Gyretes—Orectogyrus—Patrus* group of genera, to which *G. giganteus* doubtlessly belongs, shows that it is very old.

In our opinion, the most primitive superfamily of Adephaga is Haliploidea; this is confirmed by the unique morphology of the abdomen in adult Haliplidae, which also have preserved the helical folding pattern of hind wing apices typical of Archostemata and Myxophaga (Ponomarenko, 1977), larval legs with one simple claw, and well-developed abdominal segment 10 in later instar larvae of *Haliplus* and *Brychius*. The haliplid found in the Lower Cretaceous and belonging to an extant genus confirms the very old age of this family. At the same time, *Haliplus cretaceus* Prokin et Ponomarenko, 2013 has a sutural elytral groove, which is on the whole atypical of *Haliplus*. Probably this species should, after all, be assigned to a separate genus, since the loss of the sutural groove is a synapomorphy of Haliplidae, except for the most primitive genus *Peltodytes* (Beutel and Ruhnau, 1990), which also has an embryonized larva with long gills during the entire larval development, as in first-instar larvae of *Haliplus* (Fig. 13).

Larvae feeding on algae are good indirect evidence that the family is relatively ancient, probably evolved even before angiosperms appeared and colonized the aquatic environment (Prokin and Ponomarenko, 2013). Beetles with elytral punctation typical of haliplids and large femoral plates of metacoxae have been found in the Upper Permian Babii Kamen' locality (Prokin and Ponomarenko, 2013). The very old age of Haliplidae and its proximity to Myxophaga could give evidence of its origin from Archostemata (Schizophoroidea) independently of other Adephaga; how-
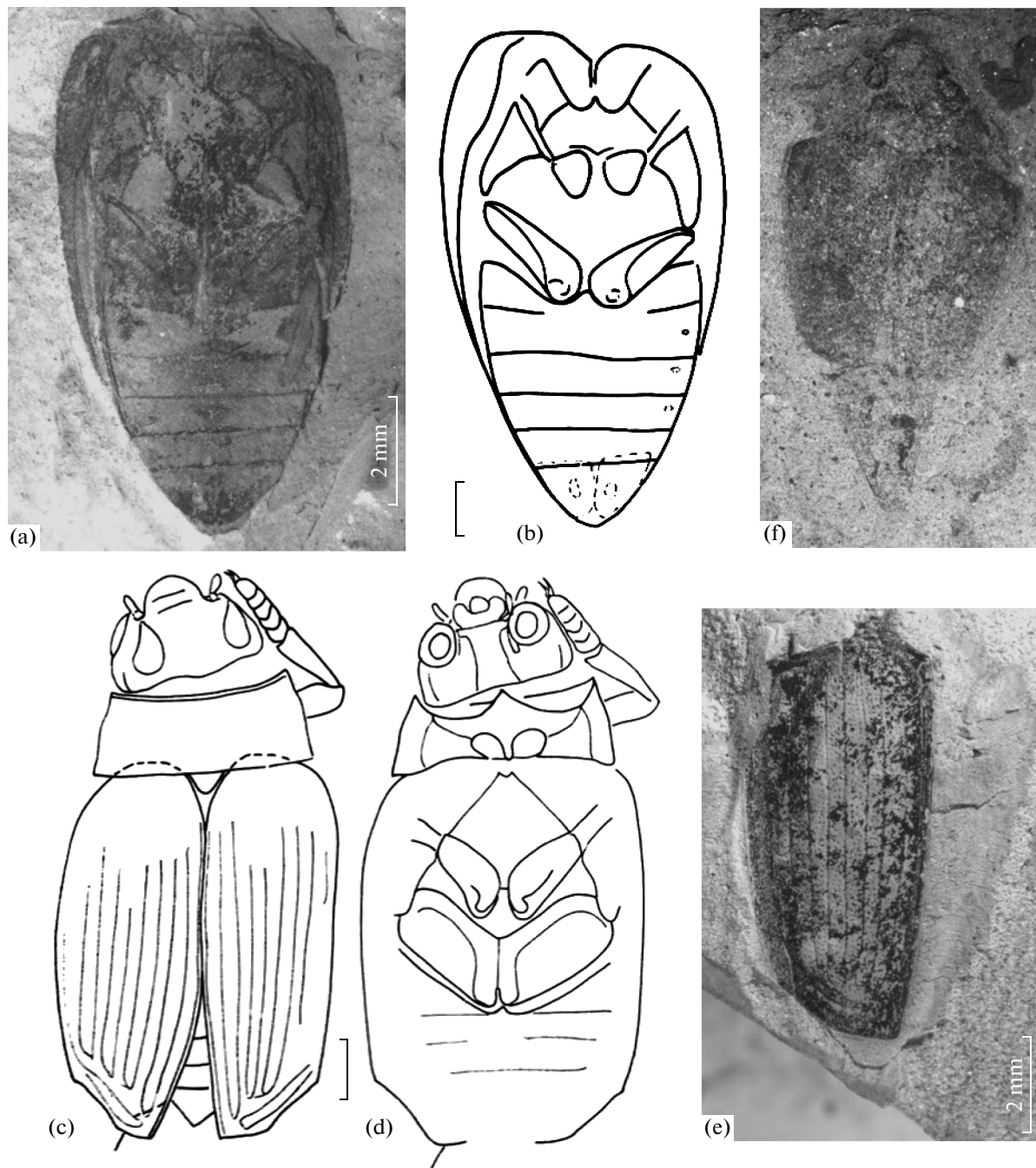
Fig. 12. Beetles of the family Gyrinidae and *Triadogyrus* (familia incerta): (a, b) *Triadogyrus sternalis* Ponomarnko, holotype PIN, no. 3320/13, photograph and drawing, ventral view; Ukraine, Garazhovka, Upper Triassic; (c, d) *Cretotortor zherichini* Ponomarenko, PIN, no. 2383/212, drawings, dorsal and ventral views; Kazakhstan, Kzyl-Dzhar; Upper Cretaceous, Turonian; (e) undescribed gyrinid elytron, specimen PIN, no. 3429/252, Russian Far East, Biamo; Eocene; (f) *Gyretes giganteus* (Piton), holotype IPM R-06998, France, Menat; Paleocene.

Fig. 13. Beetles of the family Haliplidae: (a) *Haliplus* sp., extinct, 1st instar larva, Yaroslavl Region, Nekouzskii District, near the village of Borok, Latka River; (b–e) undescribed beetle, possibly of the family Haliplidae, specimen PIN, no. 4887/91: (b, c) ventral view and SEM image; (d, e) dorsal view and SEM image; Siberia, Kuznetsk Basin, Babii Kamen'; terminal Permian; (f, g) *Haliplus cretaceus* Prokin et Ponomarenko, PIN, no. 3559/6371, photograph and SEM image; Mongolia, Bon Tsagan; Lower Cretaceous.
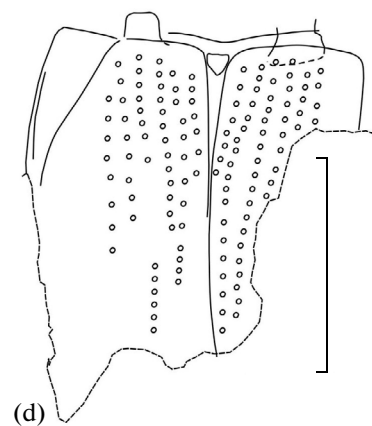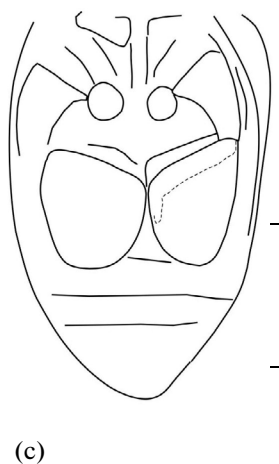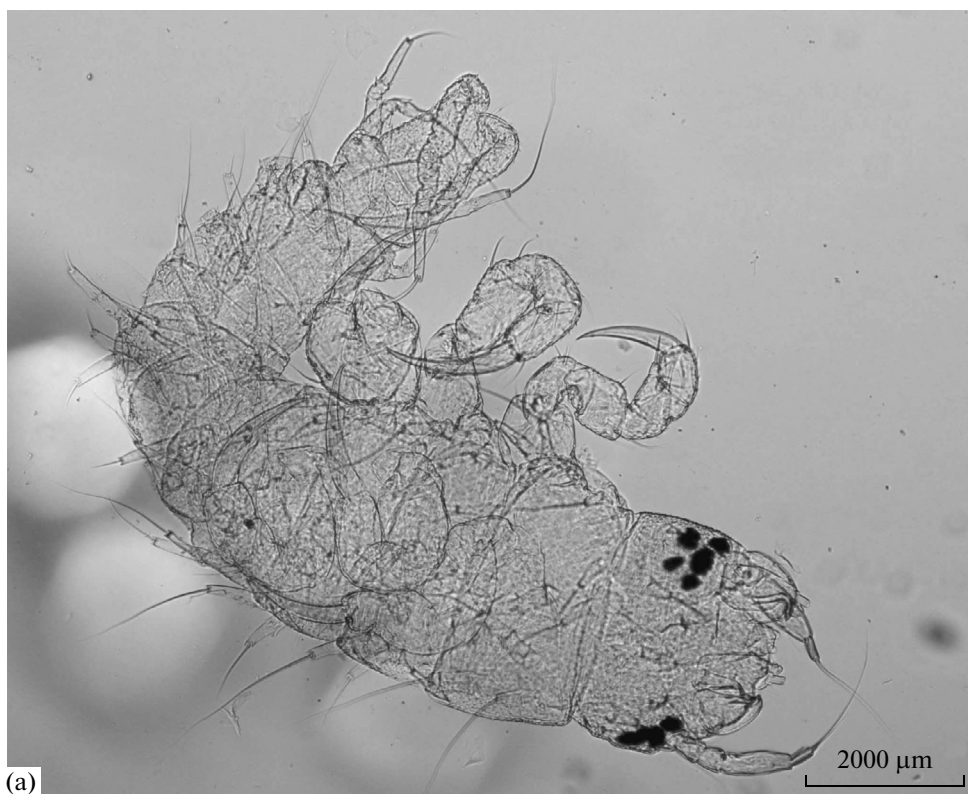
ever, their hind wing venation shows synapomorphies with Dytiscoidea and Gyrinoidea, confirming the single origin of Hydradephaga: the broad hind wing with *rml* wider than *mcl* and apex of MP_{3+4} curved anteriad (Fedorenko, 2009), which confirms the basal position of Haliplidae in this very group.

The suborder Myxophaga is poorly represented in the fossil record because of their small size, but their origin and evolution appear very important for understanding the history of the order Coleoptera as a whole. It is possible that undescribed fossils from intertrappean Permian deposits of the Tunguska Basin belong to Myxophaga (Fig. 14). Many signs of reduction, which set myxophagans apart, are in our opinion explained by their small size, and it is most likely that this suborder (if we accept it as a separate suborder) evolved from representatives of the superfamily Schizophoroidea Ponomarenko, 1968 (Ponomarenko, 2002).

Known Jurassic and Cretaceous representatives of the suborder Polyphaga usually belong to extant taxa up to the level of tribe in the family Hydrophilidae (Prokin et al., 2010; Fikáček et al., 2014) and even genus in the family Helophoridae (Fikáček et al., 2012a, 2012b) (Fig. 15). The extant genus *Helophorus* is known as early as the terminal Jurassic (Fikáček et al., 2012a) and the Recent species *Helophorus sibiricus* (Motschulsky, 1860), arctoboreal according to the zonal component of its range, has been found in the Early Miocene of Kartashevo (Ombinsk Formation) (Fikáček et al., 2011). Judging from fish remains and fossil flora, this locality was formed under a warm temperate or subtropical climate (Ponomarenko and Prokin, 2013), which makes it possible to consider this species, which currently lives mostly at high latitudes of the Palearctic, as a displaced ecological relict. The evolutionary stability of this species, and Helophoridae in general, is probably associated with shortening of larval development and low trophic specialization of detritophagous adults, which makes it possible to use ephemeral and temporary water bodies, like phyllopods, also known for their high evolutionary stability (Mantovani et al., 2004; Fikáček et al., 2011).

The basal groups of helophoroid hydrophiloids had an aquatic mode of life at the adult stage, judging from the presence of swimming hairs on the tarsi of *Hydrophilopsia longitarsalis* Ponomarenko, 1987. In addition, the hypothetical common ancestor of Hydrophiloidea should have had many groups of trichobothria and a cover of hydrophobic hairs on the venter, which points to the aquatic mode of life (Fikáček et al., 2012b). Unfortunately, these data are still ignored and it is believed that ancestral hydrophiloids were terrestrial (Song et al., 2014).

At the same time, larval *Cretotaenia pallida* Ponomarenko, 1977, which probably corresponds to adult *Laetopsia baissensis* (Ponomarenko, 1987) (Zherikhin et al., 1998), had a holopneustic breathing system with open spiracles and dorsal eyes, which gives evidence of living mostly in a terrestrial—aerial environment. Floating plant aggregates of Mesozoic lakes could have well been a fitting habitat for such larvae; in these aggregates, the larvae could prey on small inhabitants of those mats and surface film. This suggestion is also confirmed by the mode of life of some Recent hydrophiloid larvae. For instance, larvae of the genus *Enochrus* (Hydrophilidae), which we collected in algal mats on the surface of Orog Lake in Mongolia, remained active without water for about 24 hours.

Known Mesozoic fossils of other polyphagous families, Hydraenidae and Heteroceridae, still cannot be reliably distinguished from Recent taxa and are therefore described in formal genera. The appearance of family-group taxa of aquatic beetles of the suborder Polyphaga is shifted to the terminal Permian; elytra with puncture grooves typical of representatives of this suborder are dominant in localities of that age. However, such elytra of the *Hydrobiites* morphotype subsequently become very rare not only in the Permian, but also in the Middle Triassic.

The appearance of phytophilous water beetles is associated with the expansion of angiosperms in the Cenophytic. The appearance of elytra of Donaciinae in the fossil record coincides with the appearance of Hadrosauridae, which had teeth adapted for chewing food that contained abrasive matter. It is likely that this food consisted of shore helophytes; Donaciinae feed on such plants, and it is possible that hadrosaurids accidentally consumed these beetles with highly abrasive matter that stuck to them (Ponomarenko, 2006, 2010). Donaciinae probably evolved from Sarginae (Borowiec, 1984) as a result of the shift of larvae from developing inside stems to living on plant roots and at leaf bases underwater (Bieńkowski and Orlova-Bienkowskaja, 2004) in the mid- or terminal Cretaceous. The analysis of mitochondrial and nuclear DNA dates the appearance of Donaciinae to 75—100 Ma (Kölsch and Pedersen, 2008). The earliest donaciine species described from the Paleocene of the Amur Region (Arkhara) belongs to the genus *Donacia* and subgenus *Donacia* sensu stricto or *Cyphogaster* (Bieńkowski, 2015) (Fig. 16). The existence of an extant subgenus of Donaciinae in the Paleocene shows that the evolution and dispersal of Donaciinae were extremely rapid, since in about 40 m.y. they dispersed almost globally, except for South America and Antarctica, and reached the modern level of morphological development.

Extant genera of aquatic beetles (except for the most conserved family Helophoridae, which appeared even earlier, as noted above) probably appeared at the Cretaceous—Cenozoic boundary or even earlier, at the boundary between the Mesophytic and Cenophytic, but their appearance is usually documented only beginning from the Eocene. In oryctocenoses of Lower Paleocene localities, fossil gyrinids appear no less or even more frequently than dytiscids. In the Eocene, the composition of taxocene also acquires
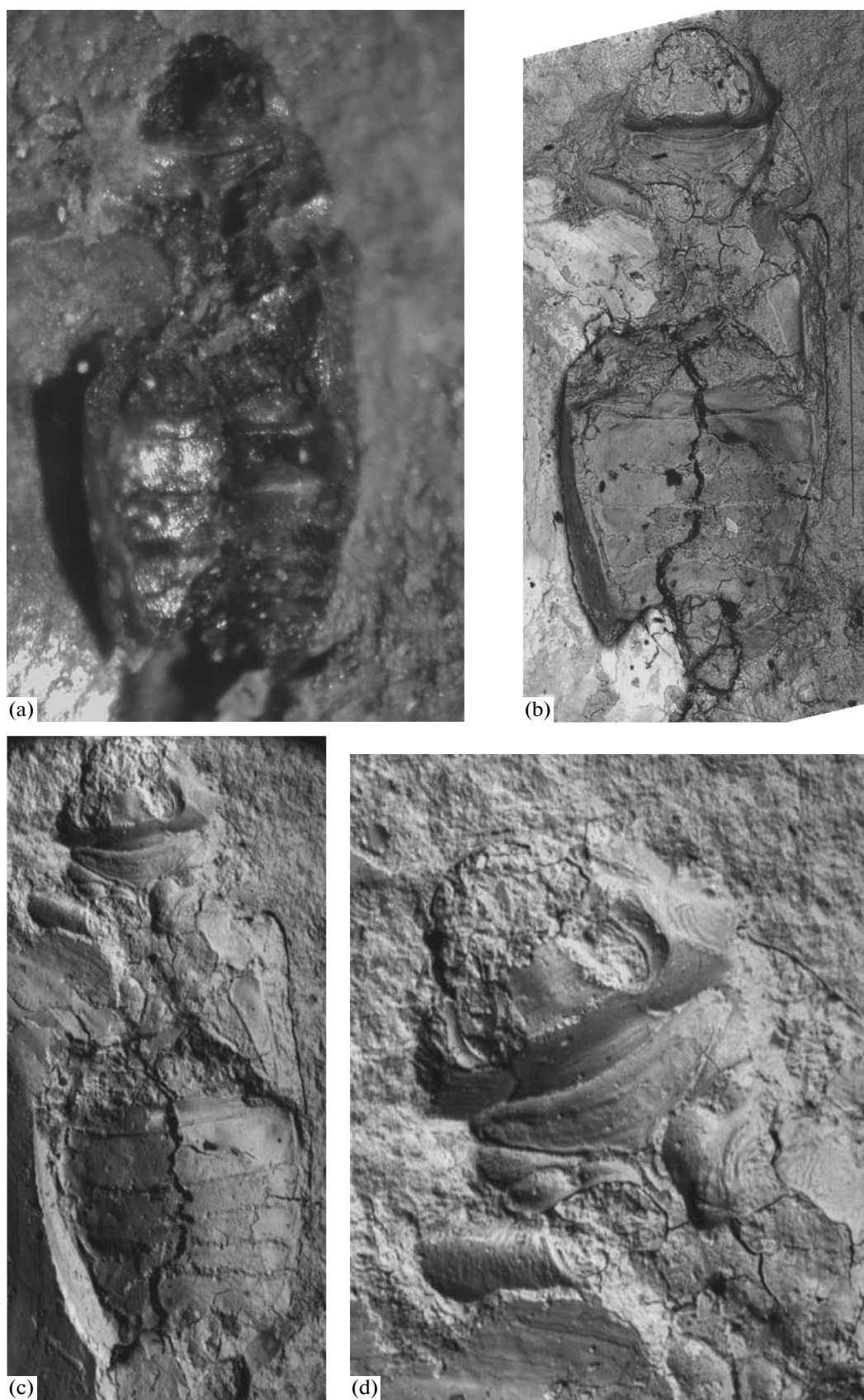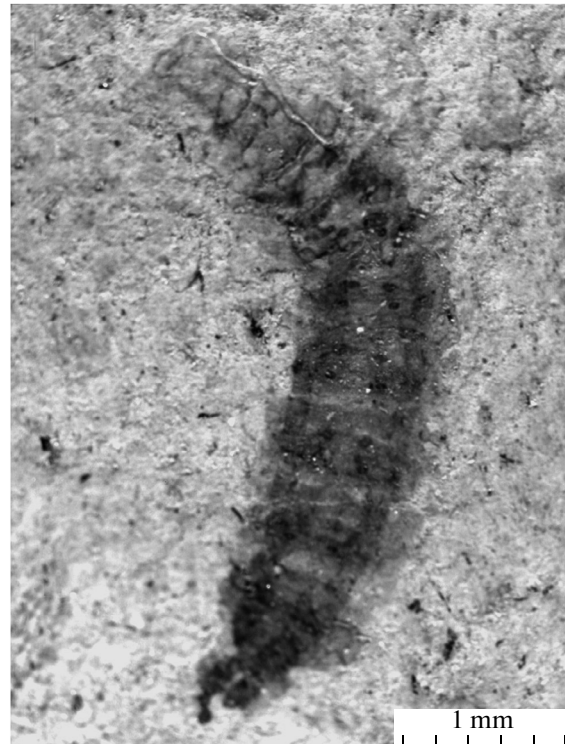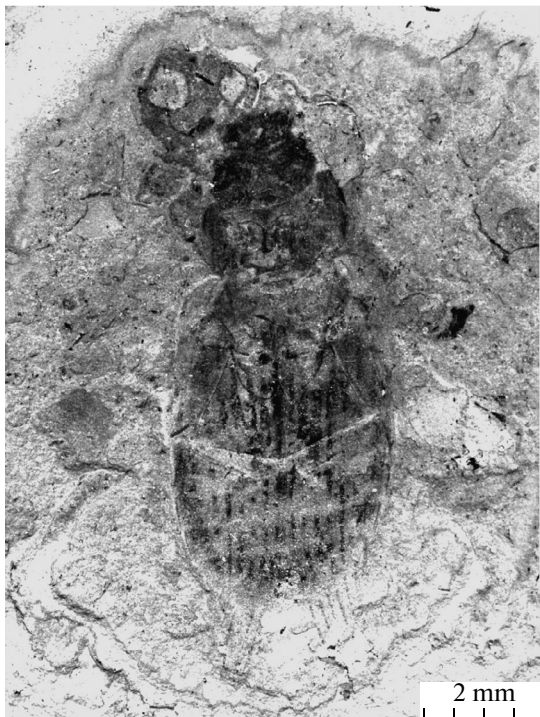
Fig. 14. Undescribed beetle, possibly of the suborder Myxophaga: (a) photograph; (b–d) SEM images of adult, specimen PIN, no. 2757/1; Siberia, Tunguska Basin, intertrappean deposits, Untuun; terminal Permian.

modern features: dytiscids and hydrophilids become dominant. Some localities (Bembridge, Upper Eocene) contain abundant adult scirtids. Many scirtids have also been found in Baltic amber. The Miocene beds have yielded almost exclusively extant genera; extinct ones, such as *Paleogyrinus* Schlechtendal, 1894 or *Schistomerus* Palmer, 1957, are rare exceptions, but the geographical distribution of beetles at that time still strongly differed from the modern distribution. For instance, the composition of dytiscids of the North Caucasus Miocene locality of Stavropol' is more similar to the Recent fauna of the Mediterranean and North Africa, and South Asian hydrophilids were present in Europe at that time.

The earliest aquatic beetles indistinguishable from extant species are known beginning from the Miocene. For instance, the tundra—taiga species *Helophorus sibiricus* Motschulsky has been found in the West Siberian Miocene locality of Kartashovo; however, fishes and plants described from this locality are subtropical. In the Pliocene, this species is already found in the typical Siberian fauna. Unfortunately, when Pleistocene beetles are studied, aquatic ones clearly attract insufficient attention, compared to both terrestrial beetles and other aquatic insects, especially such as chironomid larvae. Representatives of extinct species of aquatic beetles are unknown among the studied Pleistocene materials, at least in areas of Europe and North America that were subject to catastrophic glaciation. Studies of Quaternary deposits of Europe have shown considerable changes in ranges of aquatic beetles during glaciation and extinction of many populations (Abellán et al., 2011). At the same time, faunal restoration was very rapid and efficient, since the beetle fauna of the British Isles, which were repeatedly completely covered by glaciers, now shows very little difference from the continental fauna. Studying Pleistocene insects of Europe, the eminent paleocoleopterist Coope (1970, 2004) came to the conclusion that, first, all Pleistocene beetles belong to extant species and second, the current distribution of beetles shows no signs of their pre-Pleistocene distribution (Coope, 1970, 2004). These statements have proved to be too maximalist. Fossil species have been found not in those areas in which environmental conditions underwent the greatest changes during the Pleistocene, but in those areas in which conditions were relatively stable, e.g., in the extreme northeast of Asia, where there were almost no glaciation because of the extremely low precipitation, and in the warm temperate Japan, where a thorough study of donaciine remains from

peat has revealed considerable numbers of extinct species and subspecies (Hayashi, 1998, 1999).

DISCUSSION

It is possible that the family Lasiosynidae Kirejtshuk et al., 2010 (Fig. 17) led an amphibiotic mode of life, with relatively rheophilic larvae, which therefore are not represented in the fossil record, like members of the family Eulichadidae Crowson, 1973 closest to it.

Judging from the abundance of adults of the family Mesocinetidae Kirejtshuk et Ponomarenko, 2010 (Fig. 18) in the Shar Teg locality, they possibly inhabited liverwort—algal aggregates of this lake (Ponomarenko et al., 2014) from above, like the true bug subfamily Enicocorinae Popov, 1980 (Ryzhkova, 2012, 2015), from below, like *Coptoclavisca*, or inside aggregates, like larval *Cretotaenia pallida* Ponomarenko, 1977 from the Baissa locality. Probably, during the existence of Mesocinetidae, the families of Scirtoidea had not yet diverged into consumers of decaying plant matter by larvae mostly in water (Scirtidae Fleming, 1821) and on land (Eucinetidae Lacordaire, 1857).

If this is the case, the list of 37 families of aquatic beetles provided by us can be supplemented not only by Schizophoridae, but also by these two families. Taking into account the fact that some aquatic beetles have not yet been referred to a taxon above the generic rank (*Chimaerocoleus aenigma* Ponomarenko, 1985) or a particular family (*Memptus* Handlirsch, 1906, *Hydrophilopsia* Ponomarenko, 1987, *Laetopsia* Fikáńek et al., 2012, *Cretotaenia* Ponomarenko, 1977), the total list of families of aquatic beetles, including extinct taxa, possibly consists of more than 40 names.

Available data suggest that, in the evolution of aquatic superfamilies of the suborder Adephaga, a number of parallelisms can be recognized in the course of repeated adaptation of larva or adult to nektonic or neustonic and pleustonic mode of life.

In adults, adaptation for the nektonic mode of life resulted in the acquisition of (1) the streamlined body, with isolation of the subelytral cavity and various mechanisms of connection between the prothorax and mesothorax (with the process of the prothorax inserted into the process of the metathorax between the mesocoxae, or without such a lock); (2) swimming legs with weak differentiation of the forelegs as prehensile; (3) type of movement with synchronous or alternating strokes of the mid- and hind legs; (4) adaptive coloration with the darker dorsum. Nektonic larvae probably

Fig. 15. Beetles of the superfamily Hydrophiloidea: (a–d) *Prospercheus cristatus* Prokin (Spercheidae), holotype PIN 4270/1012, photograph and drawings, Mongolia, Shar Teg; Upper Jurassic; (e–h) *Helophorus* (*Mesosperchus*) *inceptivus* Fikáček et al. (Helophoridae), holotype PIN, no. 4270/1008, photograph and drawings, Mongolia, Shar Teg; Upper Jurassic; (i) *Laetopsia mongolica* (Ponomarenko) (Hydrophiloidea, familia incerta, holotype PIN, no. 3664/1567, photograph; Mongolia, Shin Khuduk; Lower Cretaceous; (j) *Baissalarva hydrobioides* Fikáček et al., (Hydrophilidae, Hydrobiusini), holotype PIN, no. 3064/6977, photograph; Transbaikalia, Baisa, Lower Cretaceous.
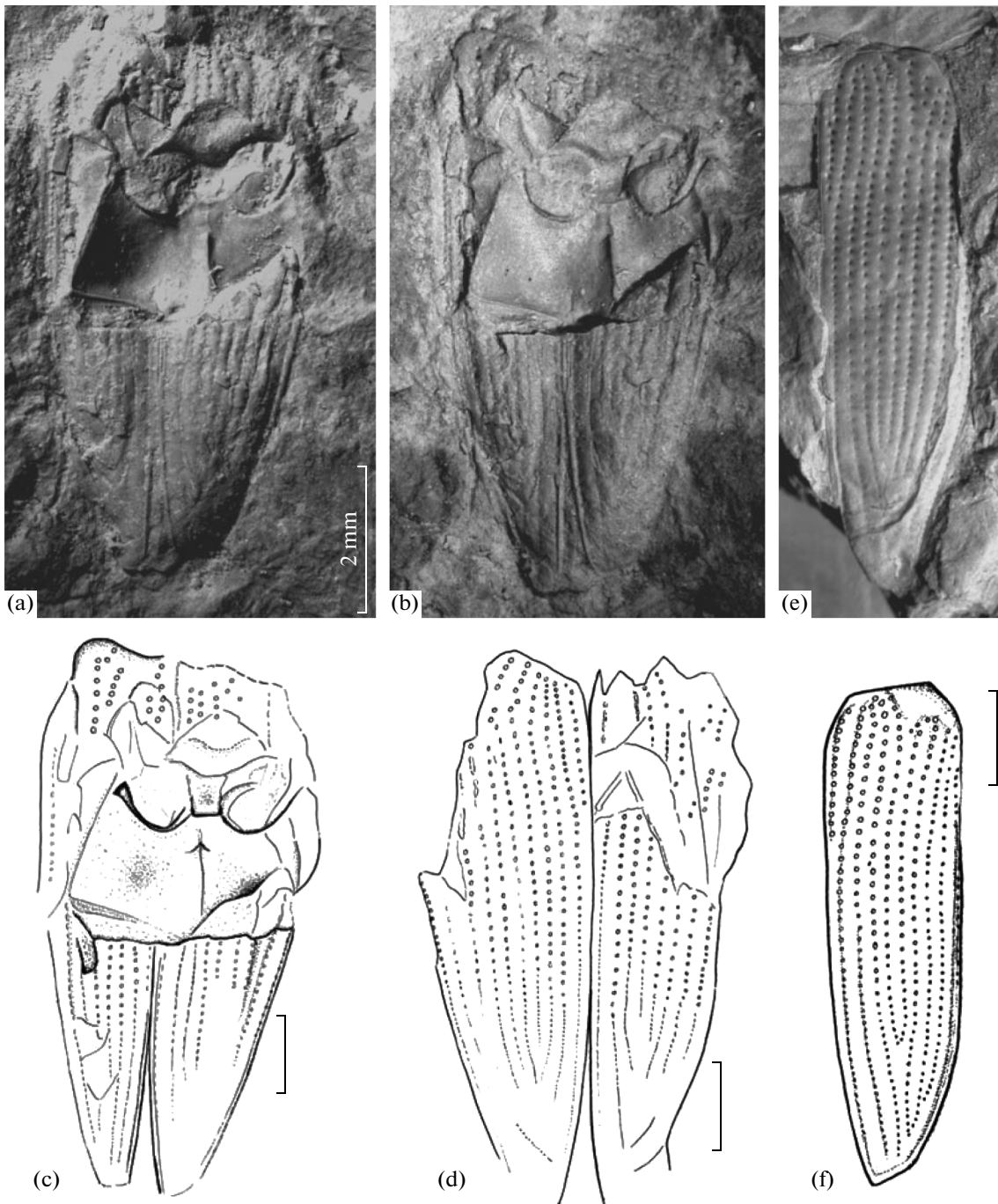
Fig. 16. Beetles of the family Chrysomelidae, subfamily Donaciinae: *Donacia anetae* Bienkowski: (a–c) holotype PIN, no. 2055/164, positive impression of elytra and negative impression of metathorax; (d) paratype PIN, no. 2055/36; (e, f) paratype PIN, no. 2055/124; Amur Region, Arkhara; Lower Paleocene.

independently acquired the following characters: (1) mandibles with the internal canal and (2) ability to pupate in soil.

The pleustonic mode of life of adults has led to the formation of the following characters: (1) two pairs of eyes; (2) strongly differentiated prehensile forelegs and swimming mid- and hind legs, which was reflected

in the structure of the musculature and in the relative development of structures of the metathorax. Morphologically different larvae of coptoclavids and gyrinids probably independently acquired the ability to pupate in cradles of plants above the water, which increased the survival rate of adults during their emergence from the pupa.
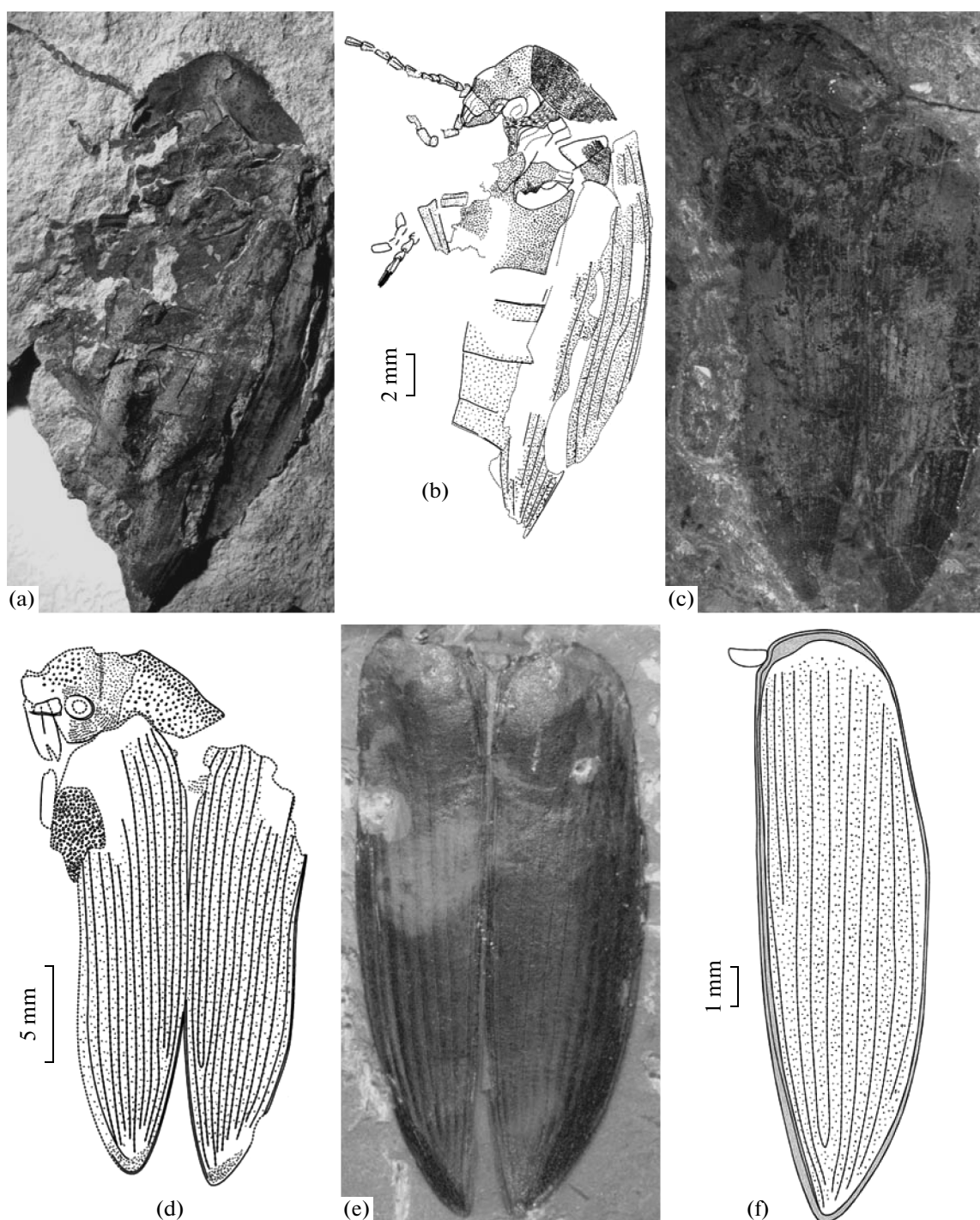
Fig. 17. Beetles of the family Lasiosynidae: (a, b) *Lasiosyne shartegiensis* Yan, holotype PIN, no. 4270/1246; (c, d) *L. insculpta* Yan, paratype PIN, no. 4270/1184; (e, f) *L. longitarsa* Yan, holotype PIN, no. 4270/1228; photograph and drawing; Mongolia, Shar Teg; Upper Jurassic.

The ability to perform simultaneous strokes with the mid- and hind legs found in the adults of most Dytiscoidea, pleustonic mode of life of adult Gyrinidae, and antimicrobial exocrinic secretion in adult Hydraenidae are considered as key innovations that determined the Recent high diversity of aquatic beetles in general (Dijkstra et al., 2014).

Our results give evidence of very different rates of evolutionary changes in various taxonomic groups of aquatic beetles. In the suborder Adephaga, all extant
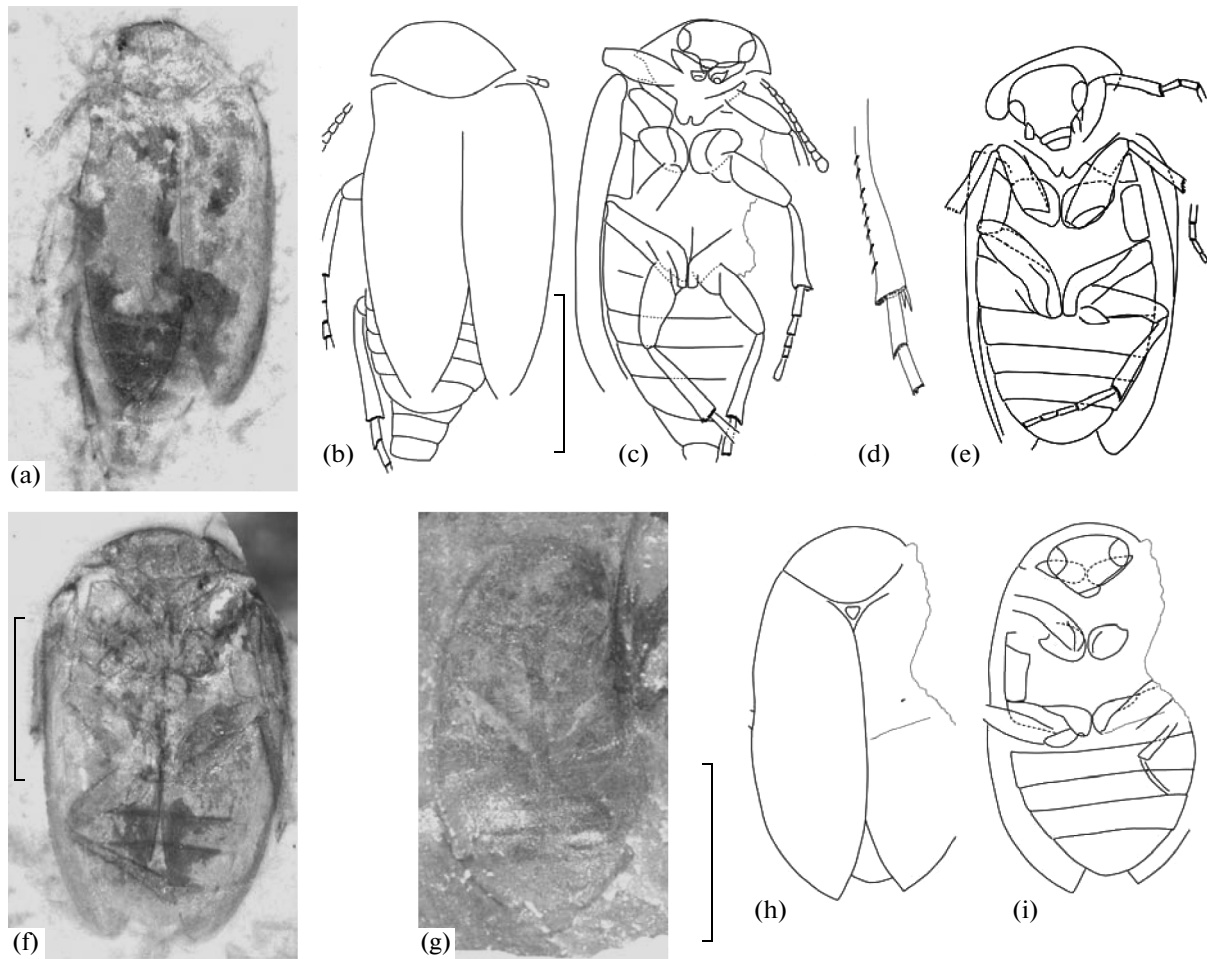
Fig. 18. Beetles of the family Mesocinetidae: (a–e) *Mesocinetes aequalis* Kirejtshuk et Ponomarenko: (a–d) holotype PIN, no. 4270/48; (e) paratype PIN, no. 4270/1071; (f) *Mesocinetes angustitibialis* Kirejtshuk et Ponomarenko, holotype PIN, no. 4270/1067; (g–i) *Shartegus transversus* Kirejtshuk et Ponomarenko, holotype PIN, no. 4270/1069; photograph and drawings; Mongolia, Shar Teg; Upper Jurassic.

aquatic superfamilies emerged in the Mesozoic; however, they include some known extinct family-rank taxa, including the highly taxonomically diverse Coptoclavidae. Evolutionary changes occurred in aquatic beetles of the suborder Adephaga in a complex way and included numerous parallelisms and heterochronies, characterizing this time as the period of "archaic variety" of the group, especially in the superfamily Dytiscoidea. At the same time, many known Jurassic and Cretaceous aquatic representatives of Polyphaga already belong to extant taxa at the level of tribes or even genera.

The Pleistocene chapter in the history of aquatic beetles shows that no considerable evolutionary events happened in those regions that were subject to the strongest influence of ecosystem reorganizations during glaciation, but changes in the geographical ranges of taxa considerably accelerated. At the same time, in those regions that did not undergo such profound

changes, intense speciation took place, as evidenced by fossil finds (Hayashi, 1998, 1999, etc.) and molecular data (Ribera and Vogler, 2004, etc.).

Consideration of the ecosystem organization of early continental water bodies, above all based on studying assemblages of aquatic beetles and others insects, has allowed us to formulate some general concept concerning the evolution of their ecosystems (Ponomarenko and Prokin, 2014). A brief abstract of these concept is provided below to make it known to those who cannot read in Russian.

The Mesophytic vegetation represented by spore-bearing plants and gymnosperms was probably less capable of preventing erosion of land than the Recent vegetation; the landscape was similar to Recent arid landscapes, independently of the level of precipitation (Ponomarenko and Kalugina, 1980). High concentrations of suspended substances caused low transparency of water and created light conditions that

reduced the volume of the photic zone. In the absence of a soil buffer under unstable conditions, any changes in the drainage area led to sharp changes in hydrochemical parameters and resulted, among other things, in suffocation of animals. Frequent catastrophic floods and washouts of substrate made freely floating or anchored aggregates and their consorting communities the most stable systems under such conditions. With the appearance of angiosperm helophytes, eutrophication of water bodies intensified as a result of easier decomposition of their tissues, compared to that of gymnosperms and the boundaries of water bodies became more clearly outlined. When dinosaurs fed first on floating aggregates and, then, on helophytes, their feces, similar to those of birds, i.e., with nitrogen higher than phosphorus, had to flow into the water. These feces had to result in especially strong development of predaceous cladocerans and copepods, as in seas (Andersen and Hessen, 1991; Sterner and Schulz, 1998; Tolomeev, 2006), rather than phytophagous cladocerans and rotifers, which develop if the water body is eutrophicated as a result of inflow of mammal feces, in which the phosphorus content is higher. The dominance of mammals has provided for shift towards phosphorus in the trophic networks of continental ecosystems, which has probably largely determined the modern habitus of the Earth, with a sharp boundary between land (including inland water bodies) and sea. Cooling began from the second half of the Eocene and had two favorable consequences for continental water bodies. It improved the supply of water with oxygen because of seasonal turnovers, and the cooler and seasonal dry climate led to the spread of the grass biomes, which successfully block erosion (Ponomarenko, 2010). Intensification of pedogenesis and accumulation of nutrients resulted in the formation of continental hydroecosystems of the modern type, having stabilized their boundaries and organized the flows of matter and energy from the drainage area by means of a soil buffer. The formation of boundaries of basins resulted in an increase in the diversity of freshwater fishes, which gradually replaced freshwater ecosystems with the "invertebrate control" to the periphery of succession series (temporary water bodies, wetlands) or to extrabasin ecosystems (such as some high-mountainous lakes), where under extreme conditions, heterotopic and amphibiont species still have advantage over homotopic hydrobionts. In those water bodies in which fishes became top predators, diversity increased and the average size of predaceous invertebrates decreased as a result of nonselective predation, according to the "top–down control" mechanism (Bezina, 1997).

Further study of aquatic beetle fossils is necessary not only for reconstructing the historical development of particular taxa, but also for understanding peculiar features of the evolution of aquatic ecosystems, as well as for a search for causalities in these processes.

CONCLUSIONS

(1) We believe that, during the entire history of beetles, some of them were associated with water to some extent, although special adaptations to the aquatic mode of life took longer to evolve and adaptations to swimming appeared only in the Mesozoic.

(2) Shifts from the terrestrial to aquatic mode of life and vice versa happened repeatedly.

(3) In the Mesozoic, the suborder Adephaga included markedly more specialized aquatic families, including extinct ones, than the suborder Polyphaga.

(4) In the Mesozoic, aquatic beetles included more pleustonic and nektonic forms and dwellers of floating plant aggregates. There were also special groups of beetles that colonized marine algal-bacterial platforms.

(5) Representatives of Adephaga and Polyphaga emerged as early as the terminal Permian; some extant families are known from that time, extant genera have been recorded in the Jurassic, and extant species are known beginning from the Miocene.

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