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Ecological evolution of beetles (Insecta: Coleoptera)

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Abstract. The most ancient life style of beetles is xylomycetophagy; xylophagy and rhizophagy appeared in the Jurassic and flourished in the middle of Lower Cretaceous but before angiosperms diversification; the same is true about carnivorous beetles living under loose bark. In the Triassic and Jurassic the most common xylophagous beetles were Cupedidae, from Mid-Cretaceous to Eocene – Buprestidae, and later on Cerambycidae. Spermatophagy existed from the Triassic and became common from the Upper Jurassic in tropical and subtropical regions (possible connection with bennettites). Palynophagous forms were common in the Upper Jurassic too. Phyllophagous beetles are unknown prior to angiosperm expansion in the Middle Cretaceous. Terrestrial carnivorous beetles existed from Triassic and did not differ essentially from the Recent ones. History of water beetles is distinctive. They lived under the water for a long time but did not swim. Most of Upper Mesozoic beetles lived in upper layers of the water (bentic forms are rare). Many ecological types of Mesozoic water beetles became extinct and have no Recent analogues. Ecological diversity of beetles became close to the Recent ones only after the end of Paleogene.

Key words: fossil, beetles, ecology, evolution.

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I. INTRODUCTION

The geological history of beetles is one of few advanced areas in palaeoentomology (CROWSON 1974; PONOMARENKO 1995). Large collections of fossil beetles from all epochs and continents are accumulated but not studied. Several thousand extinct species were described, but true patterns of beetle evolution are not elucidated yet. Most previous descriptions are out of date, and revisions of types are very rare. The status of palaeocoleopterology has not improved in recent times, and future does not hold much hope. Most of palaeocoleopterological papers state only that some beetles' remains were found in some locality. Descriptions of species are more rare. Speculations on ecology of the ancient beetles are even more rare. Beetles are usually omitted in special monographs on the fossil insects of some localities. There is a single part of palaeoentomology with a very advanced research of palaeoecology – study of Pleistocene beetles (ELIAS 1994). The main goal of this paper is to draw attention of palaeoentomologists to studying fossil beetles.

Coleoptera is one of the most diverse insect orders in taxonomy and ecology. The diversity dynamics of beetles (Fig. 1) is most close to that of all insects and also to the marine fauna (ALEXEEV et al. 2001). The more diverse is ecology of the group, the more similar is its diversity dynamics to the dynamics of marine faunas.

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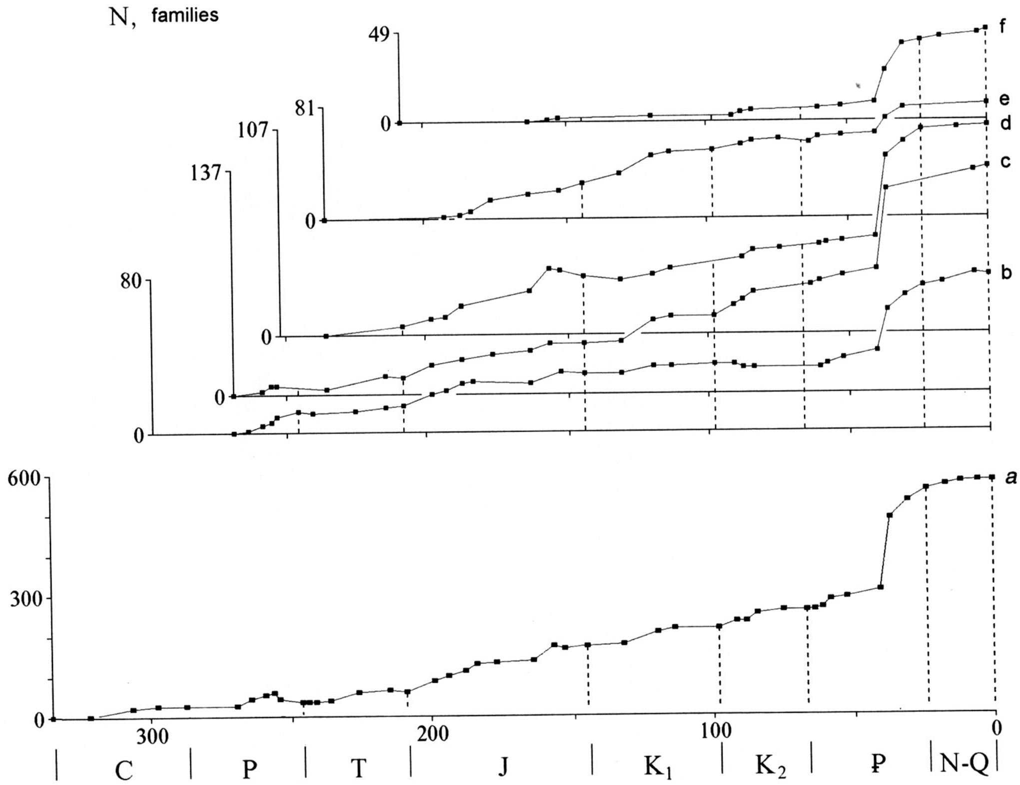

Fig. 1. Diversity (number of families in particular epochs) of Insecta (a) and Hemiptera (b), Coleoptera (c), Diptera (d), Hymenoptera (e), Lepidoptera (f). From ALEXEEV et al. 2001, with changes.

II. PERMIAN

Coleoptera is one of the most ancient orders of Oligoneoptera. The oldest beetles were Tshekardocoleidae from the Lower Permian of Moravia (Artinskian) and Chekarda, Ural (Kungurian) (Fig. 2). Most probably they lived in rotten wood. This speculation is based on the life mode of modern Cupedidae and Micromalthidae and on hypothetical life mode of the initial oligoneopterans. Upper Permian Permocupedidae and Taldycupedidae in the cupedoid stem and Asiocoleidae in the schizophoroid stem possibly had the same habits (PONOMARENKO 1969).

Some schizophoroid beetles went into the water in Upper Permian. They had special adaptations for life under the water (but not for swimming), a closing device on the border of elytra and the abdomen. This structure is seen on the fossil elytra as the longitudinal groove, or "schiza"(ROHDENDORF 1961) along the outer margin. Now only water beetles have this feature. Among Permian schizophoroids there were detritophagous or algophagous (mostly) and carnivorous (rare) forms.

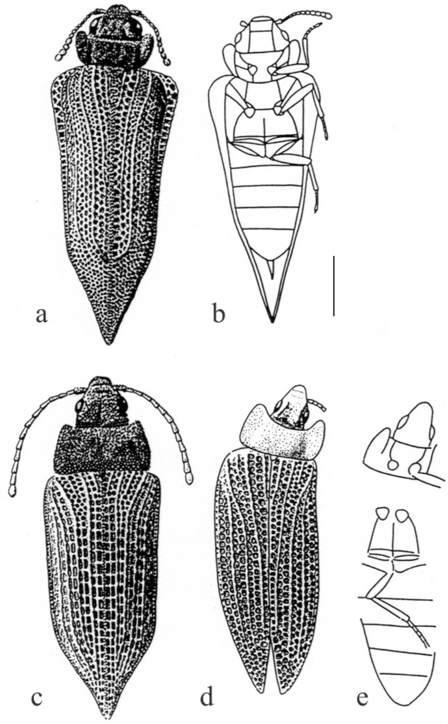

Fig. 2. Cupedoid Archostemata: a, b – *Sylvacoleus sharovi* PONOMARENKO 1963 (Tchekardocoleidae), Lower Permian; c – *Permocupes sojanensis* PONOMARENKO 1963 (Permocupedidae), Upper Permian; d, e – *Archicupes reichardti* ROHDENDORF 1961 (Permocupedidae), Upper Permian. Scale bar = 1 mm.

That type of elytrae was rare in the first half of Upper Permian but dominated in second one. The "typical" beetles elytrae with punctated grooves and smooth areas between them appeared in the end of Permian and dominated in some localities. This modification can be interpreted as an adaptation to water life, too. Ecological innovations occurred possibly parallel to taxonomical ones (Fig. 3).

III. MESOZOIC

The beetles' assemblages consisted of xylophilous forms throughout the most part of Permian and in the end of Permian evolved into water forms, which were characteristic of the Mesozoic. Remains of water beetles, mainly their larvae, dominated in many Mesozoic localities (except for the Upper Cretaceous) and there are many Mesozoic localities where only water beetles were found. In the Palaeozoic and Cainozoic such assemblages are unknown.

T r i a s s i c. In the Lower Triassic all fossil insects, including the beetles, are scarce. Diversity of beetles (like that of all insects) decreased near the P/T boundary (Fig. 1). Usually only few specimens of 1–3 beetle species in a Lower Triassic locality can be found. In 2001 a quite rich beetle fauna (ca. 80 specimens) was collected for the first time from a lowermost Triassic locality (Babiy Kamen', Kuznetsk Basin, Siberia). It is more diverse than all remaining Lower Triassic faunas combined and is dominated by beetles with punctato-striated elytrae. Beetles with cellulate elytrae, both cupedoid and schizophoroid, are absent. There should be some beetles that connect Permian and Mesozoic xylophilous forms, but were not found till now. The absence of xylophilous forms coin-

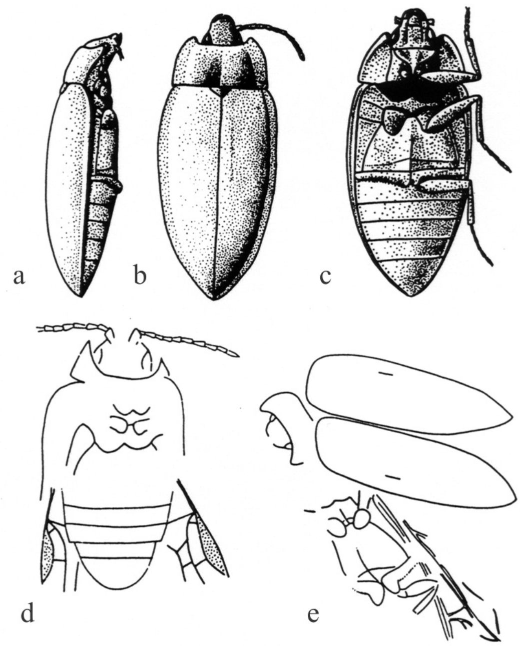

Fig. 3. Schizophorid Archostemata: a, b, c – *Hadeocoleus gigas* PONOMARENKO 1969, Upper Triassic; d – *Tersus karatavicus* PONOMARENKO 1968, Upper Jurassic; d, e – *Schizophoroides glaber* PONOMARENKO 1969, Upper Triassic.

cided chronologically with the gap in coal deposition (RETALLACK et al. 1996). Most of the Lower Triassic plant fossil assemblages were dominated by lycopsids (*Pleuromeia* CORDA et.al., 1852*)* that, in my opinion, were floating forms. Water schizophoroids (and possibly Myxophaga), most primitive Adephaga (both aquatic and terrestrial) and hydrophiloid Polyphaga constitute the majority of beetles in the beginning of Mesozoic. Most beetles in many Lower and Middle Triassic localities (but not in Babiy Kamen') have smooth elytra with "schiza". Xylomycetophagous Cupedidae – the oldest extant family of beetles – appeared in the Middle Triassic and became numerous (about third part of collections) in the Upper Triassic (Fig. 4). There is one family of schizophoroids with cellulate elytra, possibly xylophilous Tricoleidae, most common in the Ladinian and not so abundant in the Upper Triassic. Some schizophoroids were very similar to carabids and possibly had the same habits. Probably in the Upper Triassic there appeared algophagous Triaplidae and Hydrophilidae, carnivorous water beetles *Triadogyrinus* PONOMARENKO, 1977 and *Colymbothetis* PONOMARENKO, 1993, xylodetritophagous primitive elateriform Polyphaga, bryophilous Byrrhidae, possibly spermatophagous rhynchophorous Obrieniidae and carnivorous terrestrial Staphylinidae. *Colymbothetis* (probably close or identical to *Mormolucoides* HICHCOCK*,* 1858) is the first known water beetle larva with metapneustic type of breathing under the water, but without swimming adaptations. For a long time beetles lived under the water but had no adaptation for swimming, only for walking. Water beetle larvae appear in the fossil assemblages at the same time when the larvae of other water insects became much more common. In the Triassic and lowermost Jurassic larvae of water beetles did not constitute such an important part of communities as in the Middle-Upper Jurassic and, especially, in the Lower Cretaceous.

J u r a s s i c. Beetles from the lowermost Jurassic are similar to those from the Uppermost Triassic ones. In England the same species of beetles are known from the Uppermost Triassic and lowermost Jurassic localities (they are found in marine deposits, and their stratigraphical position is

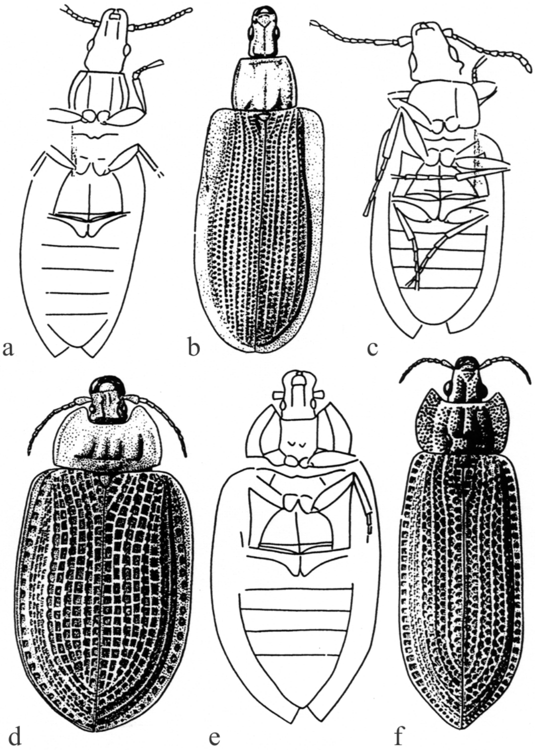

Fig. 4. Cupedids beetles: a – *Tetraphalerus maximus* PONOMARENKO 1968, Upper Jurassic; b – *Brochocoleus aphaleratus* (PONOMARENKO 1969), Lower Jurassic; c – *Omma jurassicum* PONOMARENKO 1968, Upper Jurassic; d, e – *Zigadenia nigrimonticola* (PONOMARENKO 1968), Upper Jurassic; f – *Notocupoides triassicus* PONOMARENKO 1969, Upper Triassic.

controlled by ammonites). This fact is very interesting, because the insect diversity decreased near the T/J boundary (as the diversity of marine faunas did), as a result of some extinction event at this time. The second interesting aspect of these fossil assemblages is connected with the presence of extant genus *Omma* NEWMAN, 1839 (Cupedidae) (CROWSON 1962). All Recent cupedids live on angiosperms only. This genus was found in Solite locality in North America (FRASER et al. 1996) but Carnian appear to be too old age for beetles assemblage from the locality.

Xylophagous Cupedidae (Fig. 4) were numerous in hot regions during the Jurassic, and were not found in Siberia with temperate gingko-czekanowskiales forests until climate warming in the Callovian. Also other xylophagous groups were not abundant there. Share of cupedids was less significant in the end of Jurassic than in the beginning. A new xylophagous group, Buprestidae (Fig. 5), appeared in the Middle Jurassic but were very rare until middle of Cretaceous (ALEXEEV 1999).

C r e t a c e o u s. First and very rare cerambycids are not known before the Upper Cretaceous, and became common in the end of the Paleogene (STATZ 1952; LINSLEY 1942). Beetles of extant cupedid genera *Tetraphalerus* WATERHOUSE, 1901 and *Omma* were very common during Late Jurassic and more rare in Early Cretaceous. Elaterids, like cupedids, were very common in hot regions (DOLIN 1980) and rare in temperate Siberia. They could take part in wood decomposition. First Upper Jurassic and Lower Cretaceous scarabaeoids were most probably xylomycetophagous, not coprophagous (NIKOLAJEV 1992); thus the picture from well-known English TV-series "Walk-

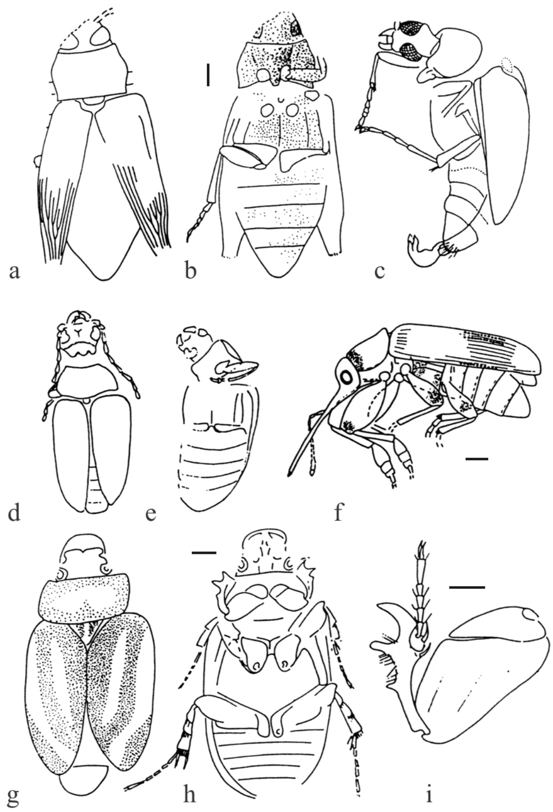

Fig. 5. Mesozoic phytophagous beetles: a, b – *Pseudothyrea oppenheimi* HANDLIRSCH 1906 (Buprestidae), Upper Jurassic; c – *Jurallecula grossa* MEDVEDEV 1969 (Tenebrionidae), Upper Jurassic; d, e – *Pseudomegamerus grandis* MEDVEDEV 1968 (Chrysomelidae), Upper Jurassic; f – *Archaeorrhynchus paradoxopus* L. ARNOLDI. 1977 (Belidae), Upper Jurassic; g, h – *Holcorobeus vittatus* NIKRITIN 1977 (Scarabaeidae), Lower Cretaceous; i – Scarabaeidae gen. sp., Lower Cretaceous. Scale bar = 1 mm.

ing with Dinosaurs" presenting numerous scarabaeids in Jurassic dinosaurian dung seems unrealistic. The first coprophagous ichnofossilien in dinosaurian dung are known since the Upper Cretaceous (Campanian) (CHIN & GILL 1996). Anthophilous-like beetles appeared and played an important role in coevolution of entomophilous proangiosperms and insects. Spermatophagous rhynchophorous forms were numerous and diverse in hot areas and are not found in Siberia (ARNOLDI 1977; GRATSHEV & ZHERIKHIN 1995). Phyllophagous beetles were rare; the moss-eating byrrhids were more common among them but they possibly lived on water liverworts. Most Recent Chrysomelidae are phyllophagous, whereas all Jurassic–Lower Cretaceous Protoscelinae lived probably in pachycaulous stems as their Recent relatives Aulacoscelinae do (MEDVEDEV 1968). Phytophagous Curculionidae *sensu stricto* and Buprestidae are very characteristic of the end of Lower Cretaceous.

The distribution of terrestrial predaceous beetles was asymmetrical, too. Caraboids (Trachypachidae, Carabidae) (Fig. 6) were more common in hot areas, while Staphylinidae in more temperate climate. The share of Trachypachidae gradually decreased and that of the Carabidae increased, but in Siberia Trachypachidae were more common in the end of Jurassic. Cleroid and cucujoid beetles numerous in the Cretaceous (KIREJTSHUK & PONOMARENKO 1990) were carnivorous and dwelled under the loose bark.

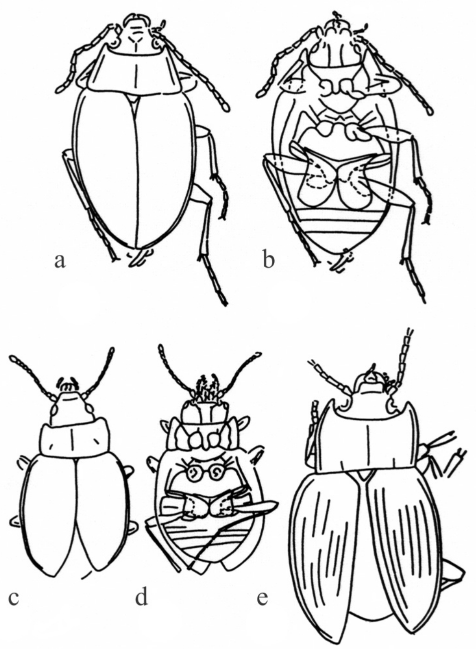

Fig. 6. Mesozoic caraboid beetles: a, b – *Psacodromeus gutta* PONOMARENKO 1977 (Trachypachidae), Upper Jurassic; c, d – *Unda cursoria* PONOMARENKO 1977 (Trachypachidae) Upper Jurassic; e – *Protorabus planus* PONOMARENKO 1977 (Carabidae), Upper Jurassic.

Among water beetles appeared the first beetles with swimming adaptations both in adult and larva (Gyrinidae, Parahygrobiidae, Coptoclavidae, Dytiscidae). Coptoclavids were most common in the Upper Jurassic and, especially, in Lower Cretaceous. Gyrinids were not numerous but their remains are found regularly. The most common beetle in geological history was the Lower Cretaceous *Coptoclava longipoda* PING 1928 (Fig. 7). Many thousands of larvae and hundreds adults of this beetle were found in numerous localities in East Siberia, Mongolia and China. The oldest of them comes from about the J/C boundary (possibly Uppermost Jurassic), the last ones from the Lower Aptian. The morphology and palaeoecology of both adult and larva of this beetle is known in detail including internal structures and genitalia. It was dytiscoid according to its systematic position, but ecological adaptation of the adult was more close to gyrinid one. The adult beetle had two pair of eyes, catching fore legs and swimming middle and hind ones with short flatted and widened segments. They lived on surface of water and collected chaoborid midges and insects which fell on water. Larvae had catching mandibles, catching and swimming legs, metapneustic type of breathing and robust tracheal hydrostatic mechanism. It was a nectic predator. Abundance of coptoclavids was correlated with that of chaoborid midges. Remains of this beetle species were described many times under different names, but attempts to divide this huge and long-lived species had no success. Dytiscids in the Mesozoic (including the Upper Cretaceous) were much more rare than gyrinids, in the Cainozoic this ratio was opposite. Larvae of dytiscids are not found in Mesozoic, and those of gyrinids are absent in the fossil record at all. Most water beetles lived on and under the surface or in the floating plant-islands. Like modern gyrinids, the coptoclavids had two pair of eyes (for air and for water). It is strange but some coptoclavids had four eyes but not swimming legs. In some lake ecosystems such coptoclavids dominated. Some coptoclavids were very common in marine lagoonal localities such as Solnhofen, but their larvae are never found in these localities. Most Mesozoic hydrophilids (Fig. 8) were probably microalgophagous at adult stage and lived under the water

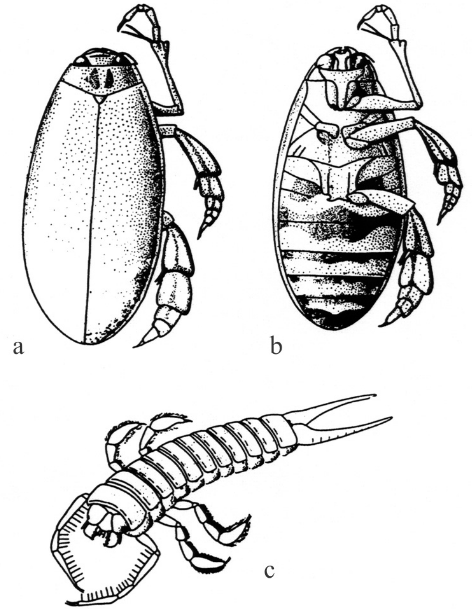

Fig. 7. *Coptoclava longipodai* PING 1928 (Coptoclavidae), Lower Cretaceous: a, b – imago, c – larva.

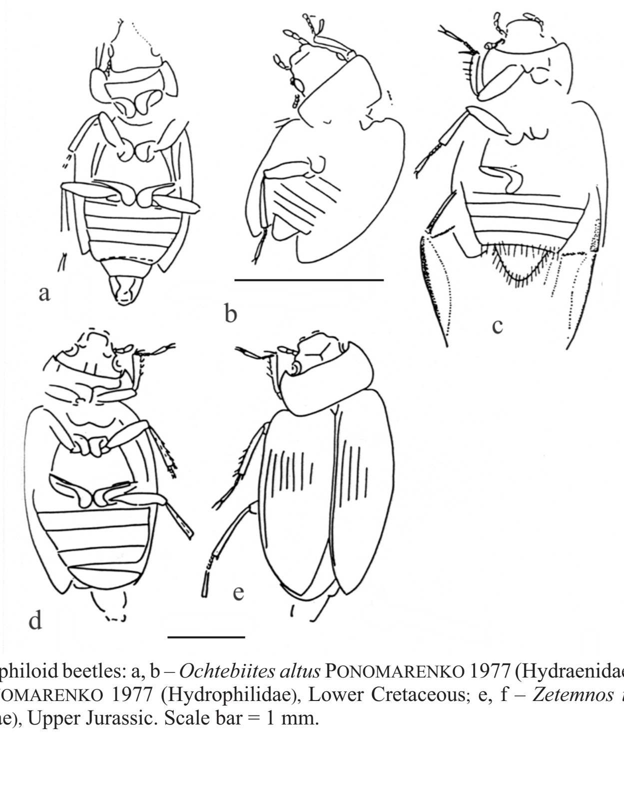

Fig. 8. Mesozoic hydrophiloid beetles: a, b – *Ochtebiites altus* PONOMARENKO 1977 (Hydraenidae), Upper Jurassic; d – *Mesydra elongata* PONOMARENKO 1977 (Hydrophilidae), Lower Cretaceous; e, f – *Zetemnos tarsalis* (PONOMARENKO 1977) (Hydrophilidae), Upper Jurassic. Scale bar = 1 mm.

surface, which is indicated by their leg structure. Their larvae are very rare in oryctocoenoses. Hydrophilids of the modern type appeared in the Lower Cretaceous, the fossils finds of their larvae being numerous in some localities. Legs of Mesozoic hydrophilid larvae had no swimming hairs.

Phyllophagous chrysomelids especially with water habits became very common in the second part of Upper Cretaceous. Specialized grass-eating dinosaurs with tooth battery evolved in the same time as the donaciin beetles living on water grass became common in oryctocoenoses. Coprolites of plant-eating dinosaurs with holes of coprophagous scarabaeids appeared in fossil record in the same time (CHIN & GILL 1996).

IV. CAINOZOIC

One of the most important steps in coevolution of plants, insects and vertebrates was the appearance of grazing ecosystems on grasses in the middle of Cainozoic. Balls of coprophagous scarabs were found in many localities in time with grass ecosystems and coprophagous forms were common in many Mid-Tertiary localities (STATZ 1952; ZHANG 1989). In the same time the diversity of water beetles increased in several times in macrophytous lakes according with increasing of their ecosystems stability. There were essential shifts of ecological role on the ground of morphological stability (STATZ 1939; RIHA 1974). Recent *Tetracha carolina* (LINNAEUS, 1758) was found in the Baltic amber (Eocene) (RÖSCHMANN 1999) and ASKEVOLD (1990) showed that water chrysomelid described from Florissant (Oligocene) as *Donacia primaeva* (WICKHAM, 1912) has not any real differences from recent *Plateumaris nitida* GERMAR 1811. The ecology of Neogene and Pleistocene beetles was very close to the recent one, but there is some ecological shift and their zoogeography was quite different (ELIAS 1994). There are few extinct Pliocene and Pleistocene species mainly among plant-eaters (HAYASHI 1999).

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