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Beetles (Insecta, Coleoptera) of the Late Permian and Early Triassic

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Abstract—Permian beetle fossils are usually represented by isolated elytra. In the Early and early Late Permian, when their forewings were being transformed into elytra, taxa based on the elytral structure were quite natural. By the second half of the Late Permian, different beetle lineages had evolved elytra of a similar structure, thus preventing their use in reconstructing their phylogeny and developing a natural system. However, the assemblages of isolated elytra turn out to be good for characterizing the evolutionary stages of beetles as a whole. By comparing the sequences of beetle assemblages in Angaria, Subangaria, and Gondwana, we have revealed that these sequences are homotaxal and that, most probably, their similar stages are synchronous. New taxa of the families Permocupedidae, Rhombocoleidae, and Schizocoleidae are described from European Russia.

Fossil beetles are one of the most interesting objects in paleontological and stratigraphical research, but they remain poorly understood, as they are difficult to study. Beetles constitute the largest and most ecologically diverse insect order, and regularities in their diversity dynamics correspond most closely to those in the entire class Insecta and in marine faunas (Alekseev *et al.*, 2001). It is also important that, due to their hard skeleton, fossil beetles are more widespread than other insect fossils and occur more often in facies that are favorable for burial of plants and vertebrates. Beetles, as well as other insects, spread rapidly, colonizing different parts of the Earth almost synchronously. In the well-known Paleocene–Eocene locality Fur (Denmark), many insects were buried in marine sediments hundreds of kilometers offshore. Thousands of specimens have been collected, and the frequency of finds compares well with the richest localities in continental facies. Even thousands of kilometers of open sea are not an insuperable obstacle for insects. Thus, one can assume that similar beetles appear in different, even very remote, regions of the Earth almost synchronously, and the correlation potential of beetles is quite high. The problem is only one of data acquisition: they are as yet poorly studied and, therefore, require much skilled work. Beetles have another peculiarity that hinders their study: beetle fossils are often mistaken for seeds and, hence, are either ignored when collecting fossil insects or come with plant megafossils; sometimes, beetle elytra have even been described as seeds (e.g., *Carpolithes mainachensis* Chelebaeva, 1984 from the Eocene of Kamchatka represents, in fact, an elytron of a beetle of the genus *Calosoma*).

One of the most important processes in the early evolution of beetles was the transformation of their forewing into a light and stiff two-layered structure, its upper surface being formed by widened veins, so that the cells were reduced to hollow pillars (columellae). These transformations are evident in Late Permian beetles; by the end of the Permian, their elytra became indistinguishable from those of modern beetles (Ponomarenko, 1969, 2002). This process took place in two ways (Fig. 1): In one lineage, among cupedoids, the veins of pre-elytron were first organized into a mechanically perfect lattice structure; only then did the veins forced the cells out, transforming the wing spaces into punctate striae. In the second lineage, among schizophoroids, the forcing of cells proceeds rapidly, on the basis of little specialized venation. It is necessary to note that no strict dichotomy is observed and that the elytra with a smooth surface develop in parallel in many groups. Smooth elytra may have appeared during adaptation to life in the water.

On this basis, one can see that the study of elytral morphology in different fossil beetles leaves different possibilities for classifying them. For ancient beetles of cupedoid lineage, a classification that is based on their elytral venation may be quite close to the natural classification, since there is reason to believe that it is the improvement of the arrangement of veins as strengthening ribs of the elytron that was the main morphogenesis in their evolution. These beetles are quite diverse in elytral structure and not much different in other characters. The later (Mesozoic) cupedoids, as well as all remaining beetles, can be classified based on their elytral structure only formally, since similar elytra sometimes occur in unrelated forms that are dissimilar in most other characters. Therefore, during the studies of coleopteran phylogeny, only beetles of cupedoid lineage have been described properly. Moreover, only isolated elytra could be examined in detail. When a complete fossil beetle is diagenetically compressed, the anterior elytral spaces set at the body sides become jammed and impossible to see, whereas the details of