

European Russia				Kuznetsk Basin		
Lower Triassic	Olenekian		Tikhvinskoe		Babii Kamen'	
		Vetlugian				
	Induan	Vokhmian	Nedubrovo			Sosnovaya Fm.
						Maltseva Fm.
Upper Permian	Tatarian	Upper Tatarian	Vyatikian	Aristovo	Erunakova Gr.	
			Severodviniian			Novo-Aleksandrovka
		Lower Tatarian	Urzhumian	Kargala		Il'inskoe Gr.
	Kazanian	Upper Kazanian		Kityak	Kuznetsk Gr.	Kaltan
		Lower Kazanian		Soyana		Starokuznetsk

Fig. 2. Main stratigraphic units and beetle localities in European Russia and Kuznetsk Basin.

elytral disc are often obscured by superimposition onto the body structures. Thus, in complete fossil beetles, the structure of the elytra is poorly studied and described, and isolated elytra are usually impossible to place in the natural system. Nevertheless, the study of isolated beetle elytra may produce quite positive results, as we will try to demonstrate below.

The most complete succession of Late Permian beetle assemblages is known in the Kuznetsk Basin (for the accepted correlation of the mentioned Upper Permian

and Lower Triassic localities of European Russia and the Kuznetsk Basin, see Fig. 2). In the Kuznetsk Basin, the share of beetle specimens in the total number of fossil insects increased by several tens of times during the Late Permian (Fig. 3), and beetles are present in almost every assemblage. In the Balakhonka Group (which is older than Kuznetsk Group), however, beetles have not been found, although many other insects have been collected. Hence, Late Permian beetles have no prehistory in the Kuznetsk Basin and should be considered immigrants. In the sequence of the Late Permian assem-

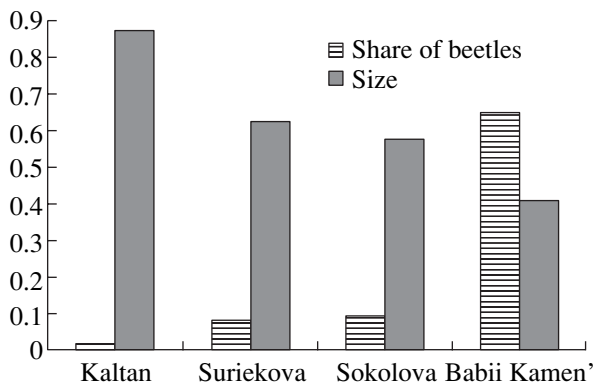


Fig. 3. Share of beetles in Permian and Lower Triassic insect faunas of the Kuznetsk Basin and average size of beetles (elytron length multiplied by 6).

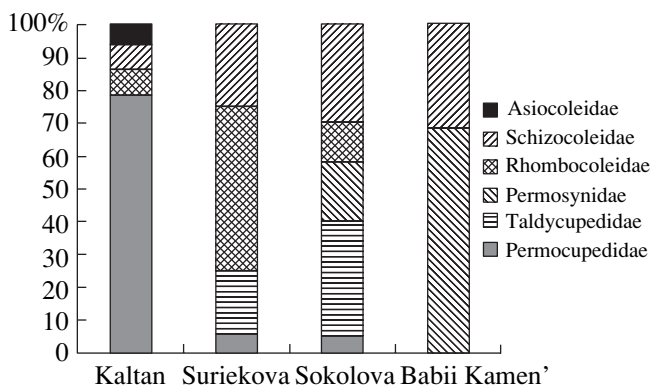


Fig. 4. Family composition (%) of Permian and Lower Triassic beetle assemblages of the Kuznetsk Basin.

blages of the Kuznetsk Basin, one can see a gradual increase in the share of beetles in the total number of insects and a shift of dominance from the cupedoid to schizophoroid archostematans (Fig. 4). In the cupedoid branch, the abundance of Permocupedidae diminished and the share of Taldycupedidae increased; in the latter family, elytron cells were gradually replaced by widening veins. Among schizophoroids, the only elytron with reticulate venation was found in the Kuznetsk Group (Starokuznetsk and Kaltan localities; for description of localities, see Rohdendorf *et al.*, 1961). The relative abundance of Rhombocoleidae among beetles increased up to the Il'inskoe Group (Suriekova) and decreased in the Erunakovo Group (Sokolova); the relative abundance of Schizocoleidae (the fossils of which possibly include some elytra of Adephaga) increased up to the Maltseva Formation. Elytra with punctate striae (for their Permian representatives, a formal family, Permosynidae, has been proposed) appear only in the youngest Erunakovo Group, where they are very rare, less than 10% of the total number of beetles. The observed paleosuccession may be interpreted not only as a gradual replacement of less advanced beetles by

beetles with elytra of a more perfect type but also as a reduction in the relative abundance of xylobiotic forms of beetles.

The next locality in the sequence of the Kuznetsk Basin is Babii Kamen'. There, insects have been found in the Maltseva Formation and lower Sosnovaya Formation. These formations have been traditionally considered to be Lower Triassic, although some experts in ostracods and some paleobotanists have long believed that the insect-bearing beds are Late Permian. Beetles constitute more than half of the fossil insects there. The composition of beetles differs markedly from that of the Erunakovo Group. Most have elytra of the permosynid type, schizophoroids are much rarer, and no reticulate elytra of presumably xylobiotic forms have been found. The formal composition at the level of parataxa that has been established for isolated elytra is closer to that of the terminal Permian (Aristovo and Belmont localities, see below). There are many complete beetle specimens, some of them identifiable up to natural taxa; namely, Archostemata: Ademosynidae and Schizocoleidae; Adephaga: Triaplidae and Trachypachidae; and Polyphaga: Hydrophilidae, Byrrhidae, and Elateroidea. Most of these taxa were previously known only from Late Triassic and younger beds. Such a diverse and advanced composition is not at all characteristic of the Early Triassic and even of most Middle Triassic localities. Although at first sight the beetles of the Babii Kamen' locality might appear to be markedly different from those of the Late Permian, they may be regarded as a direct continuation of the trend from the Kuznetsk to the Erunakovo beetles. However, the appearance among the Babii Kamen' beetles of forms previously known only from the Triassic should not be regarded as proof that the locality is of Triassic age. Remember that the composition of elytra in Babii Kamen' and in the latest Permian localities (Aristovo, Belmont) does not differ significantly. In the two latter, the beetles are represented only by isolated elytra, which can be evidence neither for nor against the hypothesis that the beetles belong to the above-mentioned advanced families. Another trend is a noticeable (nearly twofold by the beginning of the Triassic) decrease in the average beetle size (Fig. 3). This diminution is due to the extinction of the fairly large cupedoid and less advanced schizophoroid archostematans and the spreading of elytra of those types that belong to either advanced archostematans or to members of the higher suborders Polyphaga and Adephaga. In this index, the Babii Kamen' beetles also do not differ from those of the terminal Permian.

Another succession of Late Permian insect assemblages is known in the eastern part of European Russia, where beetles are quite rare but occur in localities from the Lower Kazanian up to the uppermost Tatarian (Figs. 5, 6). The share of beetles in the total number of fossil insects is much lower there than in the Kuznetsk Basin, eastern Kazakhstan, and Mongolia. In European Russia, the abundance of beetles increased, if slowly, from the Kungurian to the Upper Tatarian. The average

beetle size almost halved from the Kungurian to the Upper Tatarian and, then, changed little up to the Middle Triassic (Nakaz locality; Fig. 5). No fossil beetles have been found from the Ufimian (including Solikamskian) of the Pechora Basin or the Urals, whereas they occur regularly (though rarely) in the Kungurian. In the Kazanian of European Russia, beetle finds are about as rare as in the Lower Permian. Beetles do not form a distinct evolutionary sequence there. As in many other insect groups, Lower and Upper Kazanian beetles markedly differ in composition. The last occurrences of many insect groups have been recorded in Lower Kazanian localities. The most primitive and almost exclusively Early Permian family, Tshekardocoleidae, has been recorded from the Upper Permian only in the Lower Kazanian Soyana locality (Arkhangel'sk region) (Ponomarenko, 2000). The other beetles from this locality belong to the family Permocupedidae, but, in contrast, they belong to the genus that is most advanced in the elytral structure, *Permocupes*. Although the collections grew larger, the diversity did not increase: almost all new finds belong to the most common species, *P. sojanensis* Ponomarenko, 1963. Asymmetric occurrence usually indicates that the most common species have already been collected. This situation is scarcely accidental, because beetles from a remote locality of similar age, Tikhie Gory in Tatarstan, also belong to this genus. As a rule, advanced beetles have not been recorded from Lower Kazanian localities. *Permocrossos elongatus* Martynov, 1932, which was found in Soyana and described as a permosynoid elytron, belongs to Protelytroptera.

Upper Kazanian (Kityak locality, Kirov region) and Lower Tatarian (Kargala locality, Kuzminovskie dumps, Orenburg region) beetles from European Russia are similar in composition. The family Permocupedidae dominates, while the other beetles belong to Rhombocoleidae. Taldycupedidae, Permosynidae, and Schizocoleidae are absent.

The Upper Tatarian insect localities of European Russia are few in number. Among them, only Novo-Aleksandrovka has yielded a fairly high number of fossil beetles (Orenburg region; 15 specimens collected in 2002). They belong almost exclusively to schizophoroids (Rhombocoleidae, Schizocoleidae). Permocupedidae are represented by a single specimen. All the specimens found in the latest Permian (Vyatkian) locality, Aristovo, belong to the most advanced beetles, permosynids (Ponomarenko, 2003). Moreover, the numerous setigerous pores that entirely cover one of these elytra indicate that this elytron should belong to a beetle from the higher suborder Polyphaga.

Thus, the paleosuccession of beetles in the Permian of European Russia may be divided into four stages, which show almost no continuity. In the Kungurian, beetles are represented only by tshekardocoleids. In western Europe, even more primitive tshekardocoleids appeared in the Sakmarian; the systematic position of

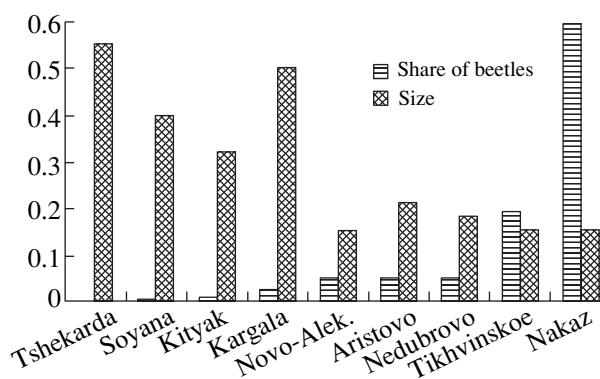


Fig. 5. Share of beetles in Permian and Triassic insect faunas of European Russia and average size of beetles (elytron length multiplied by 6).

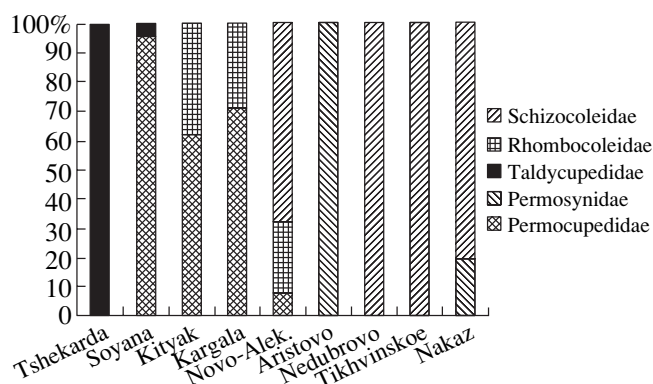


Fig. 6. Family composition (%) of Permian and Triassic beetle assemblages of European Russia.

beetles reported from the Asselian of Germany (Hörschemeyer, 1999) is unknown. Only a restricted number of tshekardocoleids survived into the Early Kazanian stage, but permocoleids should be considered immigrants, since their advanced elytral structure prevents them from being derived directly from tshekardocoleids. The following Late Kazanian–Early Tatarian fauna is likewise alien, because it can in no way be a descendant of the more advanced Early Kazanian fauna, which therefore should go extinct. The latest (Vyatkian) beetles likewise cannot be regarded as a product of autochthonous evolution, because their evolutionary precursors, Taldycupedidae, have not been recorded within this area.

There are two Lower Triassic localities: Nedubrovo (Vologda region), which is assigned to the most basal Triassic horizons (Lozovsky *et al.*, 2001) and, in considerable part, shows a still end-Permian composition of insects and plants, and Tikhvinskoe (Yaroslavl region), which belongs to the late Early Triassic. Beetles are extremely rare and their diversity is poor: notwithstanding the fact that insects were a subject of spe-

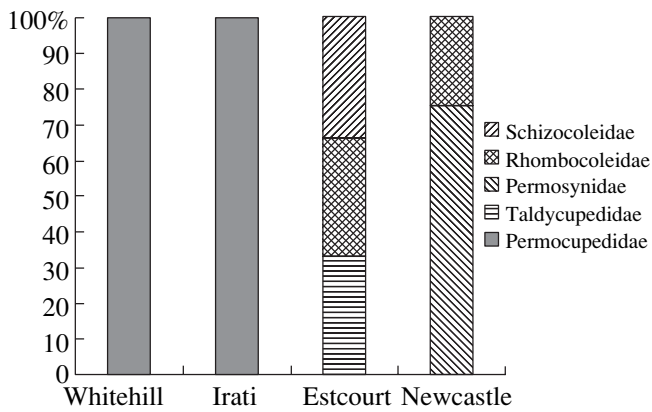


Fig. 7. Family composition (%) of Permian beetle assemblages of Gondwana.

cial collecting by paleoentomologists, only two beetle specimens were found in each locality. All these specimens are quite short and markedly convex smooth elytra in which the schiza is poorly visible or entirely absent. These elytra may belong to aquatic beetles of the suborder Adephaga. They are completely dissimilar to Vyatikian beetles (which include no schizophoroids with smooth elytra), resemble each other and are significantly larger than Severodvinian schizophoroids. In addition, Nedubrovo has yielded a fragment of an elytron without punctate striae but with sparse diffuse large punctures that is elongate (as judged from the preserved part) and similar to an elytron of *Schizocoleus* (specimen PIN, no. 4811/24, Pl. 11, Fig. 10). In the Triassic, the succession characteristic of the East European Permian continued, and the difference between the faunogenetic stages was mostly of a migrational rather than an evolutionary nature.

Recently, one more succession of Late Permian Coleoptera, that of Gondwana, has become available for analysis. Gondwanian beetles show no specificity as compared to European ones, and they belong to the same genera. The succession begins with beetles from the Irati Formation in Brazil and the Whitehill Formation in Natal, South Africa (Fig. 7). The former is correlated with the Kazanian; the latter is attributed to the lower part of the Ecca Group (dated in different parts from Artinskian to Changhsingian). Two beetles have been found in the former locality and only one in the latter; all three belong to the permocupedids. Specimens that are indistinguishable in their elytral structure from the genus *Permocupes* have been found in both localities: that from Irati has been described as *Protocupoides* (Pinto, 1987), and that from Whitehill has been described as *Afrocupes* (Geertsema, van den Heever, 1996). Another beetle from Irati has been described as *Kaltanicupes*. It seems impossible that *Permocupes* already existed in the Early Permian, all the more so as, in the other Gondwanian locality, it is known from the Kazanian, which is exactly synchro-

nous to Europe. Assuming that homotaxal changes in composition of the beetle assemblages in the Northern and Southern Hemispheres were synchronous, one should correlate both these formations with the Kazanian or, less probably, Lower Tatarian. The next stage is represented by two localities of the Estcourt Formation, Beaufort Group (Balgovan and Lidgetton), Natal, South Africa. They are of similar age (van Dijk, 1997); thus, the beetles found there may be considered as a single assemblage. There are only three beetles, each of a different family. The beetles from Balgovan belong to the families Taldycupedidae and Rhombocoleidae. Lidgetton has yielded the best-preserved and earliest known representative of Schizocoleidae (isolated elytra of possible representatives of this family are known also from older strata). If three beetles constitute an assemblage, this assemblage should correlate with the beetles from the Severodvinian of European Russia and the Erunakovo Group of the Kuznetsk Basin. The locality Belmont (Newcastle Coal Measures, Australia), which completes the succession, differs markedly from all the other Gondwanian localities both in the general composition of insect fauna and in the composition of beetles but resembles the Vyatikian localities of European Russia. Four isolated beetle elytra found there have been described as four species of the genus *Permosyne* from the monotypic family Permosynidae (Tillyard, 1924). In fact, all of them are quite dissimilar. One species (*P. pincombeae*) was transferred into the genus *Karakanocoleus* of the family Schizocoleidae (Rohdendorf, 1961), and, subsequently, into the family Rhombocoleidae (Ponomarenko, 1969). The others can be treated as representatives of different organ-genera in the formal family Permosynidae, which is interpreted as an association of isolated elytra with punctate striae. In the Kuznetsk Basin, such beetles have been recorded only from the Erunakovo Group; even there, they constitute a minor component. The elytra from the Vyatikian locality Aristovo are of the same type. Therefore, the Gondwanian succession turns out to have been homotaxal to those of the Northern Hemisphere, and the stages of these successions may coincide in time. Thus, the successions of geographically remote regions, as well as of essentially different climatic zones (Zharkov and Chumakov, 2001), have proven to be similar.

Each of the other regions (eastern Kazakhstan, Transbaikalia, Mongolia, and China) is represented by a single beetle locality. In the Karaungir locality of eastern Kazakhstan, which is considered to be Vyatikian on the basis of conchostracans, the beetle assemblage is dominated by permocupedids and rhombocoleids (more than one-third each), schizocoleids are less abundant, and taldycupedids are even rarer (Fig. 8). These beetles represent a strange mixture of taxa; the most similar forms occur throughout the sequence of the Kuznetsk Basin (from the Kuznetsk Group to the Erunakovo Group), but advanced permosynids are

absent. Therefore, the Karaungir assemblage shows no features characteristic of the end-Permian beetles.

The Bor-Tolgoi locality in southern Mongolia stands apart. More than two hundred beetle specimens have been collected there (almost one-quarter of the total number of fossil insects). A considerable number of them are more or less complete beetles. The fossil insects originate from the Tsanhi and Tavan-Tolgoi formations, which have been assigned to the Upper Kazanian and Lower Tatarian on the basis of plant megafossils. However, both formations contain the same species, thus implying that they only slightly differ in age, and the difference between the respective floras is explainable by differences in the environment: the Tsanhi Formation was deposited in the water bodies of a flat, slightly arid plain, whereas the Tavan-Tolgoi Formation is coal-bearing. The locality has yielded palaeodictyopterans and some other insect groups that are known nowhere later than the Early Kazanian. The flora has been considered to be Angarian, but, in the Tsanhi Formation, there are plants with Cathaysian and Gondwanian relationships. Recently, it has been proposed to assign the locality to Subangaria (Durante and Luvsantseden, 2002). According to O.A. Betekhtina (pers. comm.), bivalves of Bor-Tolgoi are most likely to be Gondwanian; more detailed identifications have failed because of poor preservation. The geographical position of the locality remains unclear: did it form at the southern edge of Angaria, in Amuria, or within a more southerly isolated terrain? This locality is remarkable for an exceptional abundance of beetles: more specimens have been collected than in all other Permian localities combined. The insects, including beetles, show few specific relationships with those of the Kuznetsk Basin, being closer to the eastern European insects. The terrestrial xylophagous cupedoids are less often represented by complete specimens than the aquatic and near-water schizophoroids. Unfortunately, state of preservation is far from perfect. All Permian beetle families, except for Permosynidae, are represented; schizophoroids dominate (almost two-thirds), Permocupedidae subdominate (about one-quarter), and Asiocoleidae (previously known only from the Mitino Formation of the Kuznetsk Group) and the forms transitional between them and Tricoleidae are unusually numerous (the latter have not been known from beds younger than the Middle Triassic) (Fig. 8). Unfortunately, this collection remains undescribed because of its great diversity (several tens of species). In terms of beetle composition, this locality, as well as Karaungir, turns out to be intermediate between the Kazanian and Early Tatarian localities and the only known Severodvinian locality in the European succession and between those of the Mitino Formation (Kuznetsk Group) and Kazankovo-Markino Formation (Il'inskoe Group) in the Angarian succession.

In China, the only beetle has been described from the Lungtan Group, Anhoi Province. It was assigned to cupedids (Lin, 1982), but, in fact, it is a schizophoroid

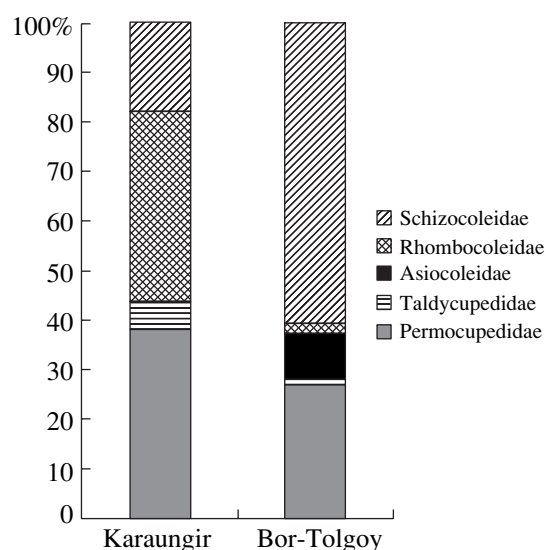


Fig. 8. Family composition (%) of Permian beetle assemblages of eastern Subangaria.

with large predaceous mandibles. Complete specimens of such beetles were previously known only from the Late Triassic, although isolated elytra of this type have occurred in the Kuznetsk Basin since the Mitino time. The Lungtan Group belongs to the Wuchiapingian Stage and roughly corresponds to the mid-Severodvinian; the presence of schizophoroids at that time corresponds to the general sequences.

The localities of the Tunguska Basin (including those possibly belonging to the Triassic) are dominated by schizophoroids; taldycupedids and permosynids are represented by a single find each.

From the above discussion it is clear that:

(i) the changes of Coleoptera in Angaria, Subangaria, and Gondwana follow quite similar homotaxal paleosuccessions;

(ii) the rate of changes in these paleosuccessions is quite high, so that the difference between successive stages exceeds that between the faunas of different biogeographic regions, and one may assume that the main stages of these paleosuccessions were synchronous;

(iii) the scarce data on tropical South China are not at variance with the data on paleosuccessions in temperate zones; and

(iv) the most significant changes in the composition of coleopterans took place at the end of the Late Permian in Angaria, Subangaria, and Gondwana.

SYSTEMATIC PALEONTOLOGY

Beetles from Upper Permian and Lower Triassic localities of European Russia are described below. All the specimens are represented by isolated elytra and can be ascribed only to formal taxa. Beetles of the family Permocupedidae and the formal family Permosyn-