



Insects during the Time around the Permian–Triassic Crisis

A. G. Ponomarenko

Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: aponom@paleo.ru

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Abstract—Dramatic changes in ancient biotas usually interpreted as ecological crises or mass extinctions are treated in many publications of every sort, and yet our notions about such events remain insufficient. The data of fossil insect studies about the Permian–Triassic crisis, thought to be the greatest in the Phanerozoic, are reviewed here.

Keywords: Permian–Triassic crisis, insects, ancient biotas, mass extinctions

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Considerable and dramatic changes in ancient biotas have long attracted the attention of researchers. One example is the evolutionary event of the terminal Permian and basal Triassic. The boundary between the Permian and Triassic periods became also the boundary between the Paleozoic and Mesozoic eras. The Permian–Triassic event is treated in numerous studies of every sort. A large bibliography can be found in summarizing works, such as the books by Benton (2003) and Erwin (2005). Nevertheless, there is still no unified notion about this evolutionary crisis, its dating, causes, course, and consequences. The varying notions about this crisis are probably especially different in Russian literature, although the majority of experts now believe that the event was caused by abundant eruptions of basalts from Siberian Traps of the Tunguska Basin, i.e., by an event that took place in a territory that now is part of Russia. Strangely, no systematic and detailed study has been performed to investigate what happened there. As a matter of fact, all research on the deposits of the Siberian Traps has been limited to geological survey and did not include detailed specialized geological or paleontological work aimed precisely at comprehensive study of the transformations of the biota in the area of trap basalt eruptions. The crisis was studied in Europe, South Africa, and even Antarctica, but almost all that we know about the Siberian Traps results from the work of many years—and almost the entire life—of Sadovnikov (1981, 2008, 2015a, 2015b; Sadovnikov and Orlova, 1994, etc.).

The existing notions remain contradictory. Benton (2003) entitled his book *When Life Nearly Died*, whereas Rasnitsyn (2012) entitled his paper, published in the popular science journal *Priroda*, “When Life Did not Even Think of Dying.” The duration and scale of eruptions of the traps and of the crisis itself and

influence of eruptions on climate and landscapes differ considerably in estimations provided by different authors. Unfortunately, there is no hope that the situation will change considerably, because the potential of geological and paleontological field studies has decreased catastrophically.

The changes were global. Literally everything changed: not only the biota, but also the landscapes and climate (Zharkov and Chumakov, 2001; Chumakov and Zharkov, 2003). The changes of the living world were part of a single process of changes in the inorganic component of the biosphere. It was the greatest ecological crisis in all Phanerozoic history. When ecological crises happen, the ecosystems that are more complex, more diverse, and more stable under stable conditions are usually the first to become destroyed and the most difficult to regenerate. In the geological past, high diversity ecosystems were replaced by low diversity ones. Detailed analysis of crisis situations of the geological past has shown that the diversity of life decreases not so much from mass extinctions as from decreased rate of appearance of new forms that replace extinct ones under normal, crisis-free conditions. Regeneration of ecosystems can take tens of millions of years. It took two geological periods for the diversity of marine ecosystems to reach its pre-crisis levels after the Permian crisis. Not only newly appeared forms participate in the regeneration of diversity: an even greater role may be played by the so-called “Lazarus taxa,” which resurrect like the biblical Lazarus, re-emerging in the fossil record at the end of a crisis. Unlike Lazarus, they did not really die, but only strongly reduced their geographical distribution and remained in rather few refugia or in landscapes remote from the taphonomic window.

The crisis itself was preceded by a rather long period of emergence of new forms that transformed

ecosystems, which resisted those changes because of their inherent homeostasis. The crisis was pending, and needed only a trigger to happen. It should be noted that trigger and cause of evolutionary changes are not distinguished in either popular or scientific literature. Moreover, only one-factor influences are usually considered. Such influences, external to the biota, as changes in geography and climate of the planet, strong volcanic eruptions, close supernova explosions, and collisions with asteroids are presented as causes of changes in life on Earth. All these events were used to explain the causes of the biotic crisis of the terminal Paleozoic–basal Mesozoic.

It appears that the main cause of the Permian–Triassic crisis of the biota was the transformation of the biota itself. The groups of the Permian biota traditionally studied include plants, mollusks, crustaceans, fishes, and tetrapods. One should turn to groups that are still little used in analyses of evolutionary changes, preferably groups of high diversity. Arthropods, especially insects, were the most diverse group of animals in the Permian (as they are now). Before we describe the changes that took place in insects and other arthropods near the P/T boundary, let us note one common feature of their Paleozoic fossil sites. They include extremely many fossil records of groups not found in the Mesozoic and Cenozoic, although they exist to this day and are often quite abundant, e.g., mites and spiders. Carboniferous and Lower Permian localities often include fossil remains of arachnids, diplopods, and monurans. They also occur, although rarely, in the Upper Permian (Fet et al., 2011; Aristov, 2013), and then almost disappear from the fossil record, although their actual diversity and abundance most probably remained unchanged. The only explanation is that in the Paleozoic they could have different modes of life, which increased the probability of their fossilization. In waterbodies, insects are usually fossilized rather far from the bank; surface currents could hardly transport such rapidly sinking wingless insects as monurans, to say nothing of the larger and heavier myriapods. Therefore, they should have been transported by large floating objects. One interesting peculiar feature of these insects is that they are morphologically similar to the larvae rather than adults of their closest relatives. Almost nothing is known about Late Permian chelicerates and myriapods (Carboniferous ones are much more fully represented in the fossil record). Only sporadic records are known, most of them undescribed. It has to be noted that all Permian eurypterids, rather few and known only until the Kazanian, were freshwater animals.

This review is based not only on published data (Aristov, 2013 and many others), but also on preliminary examination of the large collections of fossil insects accumulated at the Arthropoda Laboratory, Borissiak Paleontological Institute, Russian Academy of Sciences. The Permian is represented in these collections by many times as many specimens as in all

collections from the rest of the world. Unfortunately, for the most part they remain unexamined.

Moreover, even the relatively scant (compared to the actual insect diversity) data that are available are not used properly. They are barely discussed in the above-mentioned monograph by Benton (2003). Even the large special study on the Permian–Triassic insects by Béthoux et al. (2005) contains many mistakes and inconsistencies. As a result, the editors of a special volume on the emergence of the biota from the P/T crisis came in their introductory chapter to the strange conclusion that there is a huge gap of about 15 million years around the P/T boundary, from which no insect fossils whatsoever are known (Bottier and Gall, 2005). This is certainly not true. Insect fossils from the nearest environs of the P/T boundary are known since the early 20th century, and the number of localities known from that time constantly increases. Fossil insects have been found also in intertrappean deposits of the Tunguska Basin, i.e., clearly in the immediate environs of the boundary. Let us quote some erroneous statements of that study: “Historically, the Late Permian deposits that have been the most intensively studied are located in the region of Perm (Russia), Central North America, Moravia. ...Those from the Triassic are from France, Central Asia, Australia, South Africa and North America” (Béthoux et al., 2005, p. 613). As a matter of fact, only two localities of France are discussed in that study, Lodève and the Vosges, both quite distant from the boundary. Actually, Late Permian insects were first described from Australia, then from European Russia (not only from the region of Perm) and Siberia—the monograph *Paleozoic Insects of the Kuznetsk Basin* (Rohdendorf et al., 1961) is 706 pages long—as well as from South Africa and Brazil. They have also been recently recorded in China. In North America and Moravia, only Early Permian insects have been recorded.

In reality, Permian insect localities are numerous and known from all modern continents. Most of the larger localities are situated in Russia. Localities of Middle Permian insects are numerous, although widespread; fossil insects have been found both in continental and marine deposits. Fossil insects of the same age are known in Eastern and Western Europe, Siberia, South America, South Africa, and Antarctica, but fewer fossil insects have been recorded on all these continents taken together than in any of the larger deposits of European Russia. Although geographically remote, Kazanian assemblages of insects found on all these continents show surprisingly little difference. It should be noted that a number of studies has been published recently that profoundly analyze both biotic and abiotic components of historic changes in the Earth’s biosphere. The most important part of this work is the attempt to provide a more precise notion of the stratigraphic relations between different deposits. In biostratigraphy, such publications include both traditional studies using ostracodes, conchostracans (Kozur and

Weems, 2011), and plants and analyses of new groups, such as insects (Rasnitsyn et al., 2013). New methods have found widespread application, e.g., isotope analysis in paleoecology, paleoclimatology, and stratigraphy (Arefev et al., 2015), paleomagnetic studies (Newell et al., 2012), and studies of fossil soils (Retallack, 2013); it turned out that marine and continental deposits could be synchronized using ash (Grasby et al., 2011) or carbon spheres that spread all over the globe after explosive eruptions.

Until recently, very few Late Permian insects were known, but now a number of localities have been discovered, including some in European Russia. Insects have been found in both Vishkilian (Severodvinian) and Vyatkian deposits. The very rich Mutovino (Isady) locality has been found near the boundary between these deposits, i.e., between the Middle and Upper Permian (Aristov, 2013). It is the largest known Upper Permian locality: a total of over 4000 insect fossils have been found here to date, along with fossil remains of other animals and plants. The sequence Aristovo–Vyazniki–Nedubrovo is known for Upper Vyatkian deposits, immediately adjacent to the P/T boundary. The last of these three localities contains intermediate entomofauna. These records make it possible to describe the preparation to changes near the P/T boundary in rather much detail (Fig. 1).

The study of fossil insect localities in the intertrappean deposits of the Tunguska Basin is especially important. Since it is believed that volcanic eruptions and outflow of trappean basalts were the cause of the P/T crisis, there is no doubt that the insects the fossil remains of which are found in the intertrappean deposits lived under crisis conditions. Insect records are known here beginning with the Early Carboniferous Kata Formation, from coal-bearing deposits that formed before the eruptions, from tufa sedimentary deposits of the early stages of the eruptions, and from intertrappean deposits of the time of the basalt outflow. Insects are also known from intertrappean deposits of Babii Kamen', Kuznetsk Basin, at the edge of the volcanism zone; unfortunately, they remain very poorly studied.

Fossil insects from the Tunguska and Kuznetsk basins (intertrappean deposits), earlier considered Early Triassic, now are treated by most experts as originating from the terminal Permian. More and more studies have been published recently on insects of the terminal Permian to basal Triassic. They include both descriptions of numerous insects from various localities and analyses of changes in all insects over the time interval in question (Rasnitsyn et al., 2013; Aristov and Rasnitsyn, 2015).

Insects in the Late Permian changed extremely rapidly, but nevertheless insects living on continents situated in different hemispheres remained quite similar. Flight capacity allows insects to disperse very rapidly, and even in rather remote territories they emerge simultaneously on the geological scale of time. There

are reasons to believe that changes in insects on different continents were homotaxal and most probably synchronous. The Permian was a rather clearly pronounced period in the evolution of insects. The majority of Carboniferous insects belonged to extinct orders, whereas the majority of Permian insects belonged to extant orders. Representatives of a total of 26 insect orders are known from the Permian; only eight of them are extinct. Not a single insect order is known exclusively from the Permian. At the same time, almost all families, and thus, of course, almost all genera and species described from the Permian are extinct. Extant Permian families are mostly coleopteran. The number of insect families started to decrease in the Middle Permian, decreasing especially strongly from the Kazanian (71 families) to Tatarian (64 families of six orders, which included only two that are now extinct); at most one-third of all families became extinct at the P/T boundary; the families that became extinct by the Jurassic went extinct sharply; 90% of Kazanian insects became extinct by the Jurassic; the proportion of such insects at the P/T boundary is only 40%. The main ecological achievements of insects during the Permian and Triassic were the spread of holometabolans, the larvae of which are perfectly adapted to developing within their food substrate, such as wood, and the spread of insects that suck juices from vascular tissues of plants. The latter group shows no decrease in diversity at the P/T boundary. The insects most typical of the Permian are odonates, blattinopseids, hypoperlids, auchenorrhynchans, miomopterans, cockroaches, and especially scorpionflies and grylloblattodeans. Among them, only auchenorrhynchans evolved in the Permian; the others appear in the Carboniferous. Three insect orders became extinct during the Permian, and only three other orders became extinct during the rest of the history of insects. Palaeodictyopterans and related groups, all so typical of the Paleozoic, did not survive into the Upper Permian. The Permian was a turning point in the evolution of insects: it was during this period that most extant orders appeared and insects typical mainly of the Carboniferous became extinct. The diversity of insects at the family level decreased during the entire Late Permian (Fig. 3); in many groups extinction rate visibly grows at the middle of the Kazanian. The drop of diversity near the P/T boundary was relatively small; extinction was compensated by the appearance of rather many new families in some groups. Palaeoptera, now represented by two orders, mayflies and odonates, already existed in the Permian; odonates played more or less the same role as now or could be even more important, as the only flying predators. Mayflies were rare in the Permian, represented by only one family; their occurrence somewhat increases by the terminal Permian. By contrast, odonates were abundant and quite diverse. Permian odonates were no longer so large animals (for insects) as they were in the Carboniferous, although they

PERMIAN				TRIASSIC	
Guadalupian		Lopingian		Lower	
Roadian	Wordian	Wuchiapingian	Changhsingian	Induan	Olenekian
Biarmanian		Tatarian			
Kazanian	Urzhumian	Vishkilian (Severodvinian)		Vyatkian	
Upper		Lower	Upper	Lower	Upper
	Urzhumian	Sukhomian	Putyatnianian	Bykovian	Neftedovian
					Vokhmian
				Tikhvinskoe	
				Zalazna Sholga	
				Entola	
				Nedubrovo	
				Vyazniki	
				Aristovo	
				Beloshchel'e	
				Mutovino (Isady)	
				Opoki	
				Babintsevo	
				Kul'chumovo	
				Novoaleksandrovka	
				Kopylovo	
				Kargala	
				Kostovaty	
				Chepanikha	
				Kityak	
				Australia	
				Yaman-Us	
				Babii Kamen'	
				Tunguska	
				Belmont	
				Sokolova	
				Normandien	
				Suriekova	
				Karaungir	
				Bor-Tologoi	
				Kaltan	

Fig. 1. Main localities of insect fossils from the time around the P/T boundary set against the stratigraphic chart. The first column shows localities of European Russia; the second column shows localities of other regions.

belonged to the same groups. The wingspan of Carboniferous odonates almost reached one meter, whereas the largest Permian odonates were only one-fifth as large. The wings of the larger odonates were folded like paper fans to make them stronger. Large legs covered with strong spines facilitated capturing prey in the air. Along with these forms, still rather large, there were quite small damselflies similar to les-tids and coenagrionids that flutter near waterbodies today. Unlike recent odonates, Paleozoic ones probably did not have aquatic larvae.

Palaeodictyopteroidea, a mainly Carboniferous group of insects that became completely extinct during the Permian, consists of three orders, of which the

best-known one is Palaeodictyoptera. In the Carboniferous they were abundant—sometimes represented by up to half of all insect fossils—large (wingspan up to 40 cm) insects with a variegated coloration pattern of the wings. The wings of palaeodictyopterans were always stretched to the sides and could not be folded; in representatives of the order Diaphanopteroidea they were flatly folded on the abdomen. Representatives of the third order, Protohymenoptera, had wings that could not be folded and had a very fine venation; they were the very best fliers of their time. Some of them were functionally two-winged: the hindwings were very small and were not used for flight. The heavy abdomen was supported in flight by the long caudal fil-

aments. The females had cutting ovipositors and probably laid their eggs into plant tissues. They were phytophagous forms that sucked the contents of unripe ovules and sporangia. Palaeodictyopterans and protohymenopterans were very diverse in the Carboniferous; in the Permian their remaining relatives were small and had rather low abundance and diversity. The latest representatives of this group are known from the terminal Middle Permian (Isady). The gradual extinction of these orders was clearly unrelated to the P/T crisis.

Hemipterans are also sucking insects; most of them suck juices from cells and vascular tissues of plants, but some subsequently became predaceous, including those that are bloodsucking. This important group includes Auchenorrhyncha, Aphidoidea, Psylloidea, and Heteroptera; it appeared in the Permian and rapidly increased its diversity and role in ecosystems (Shcherbakov, 1984). During almost all the Early Permian, the only hemipterans were Archescytinidae, which were similar to Psylloidea and had very long proboscises and ovipositors; in the terminal Early Permian families of Auchenorrhyncha appeared and rapidly increased in number. The diversity of auchenorrhynchans increased very rapidly; there were as many as 12 families in the Kazanian and 15 families in the Tatarian; diversity barely decreased even in the terminal Permian; 11 families survived from the Permian into the Mesozoic. Many auchenorrhynchans had cryptic spotted coloration patterns of the wings; some forms are known that imitated the shape of leaves of contemporary plants. Forms intermediate between auchenorrhynchans and heteropterans appeared in the terminal Permian; they were extremely scant in the Mesozoic; few of them have survived to this day and occur only in Australia, South America, and New Zealand.

Holometabolan insects are those that have larvae quite dissimilar in appearance from the adults, almost always different from them in mode of life, and transforming into adults during the resting pupal stage. They now comprise the majority of all insects and include over ten orders. This group includes such universally known insects as beetles, butterflies and moths, true flies, and wasps and their relatives. Of all the above-listed insects, only beetles are known from the Permian. The majority of Permian holometabolans belong to the now scant neuropterans and scorpionflies. Permian megalopterans and caddisflies are also known. Beetles, neuropterans, and scorpionflies appeared in the basal Early Permian, whereas megalopterans and caddisflies appeared in the terminal Early Permian. No new orders appeared in the Late Permian. The order Miomoptera, recently also assigned to Holometabola, may have been ancestral to all other holometabolans, although, of course, it is unknown whether it also had the pupal stage. This order evolved in the terminal Carboniferous and was especially abundant and diverse in the Permian; rather

few of its representatives survived into the Jurassic. They outwardly resembled megalopterans but had cutting ovipositors and laid their eggs into plant tissues; it is believed that their larvae lived in immature cones of conifer trees. The geological history of another extinct order of this group, Glosselytrodea, is similar, except for the fact that it evolved in the mid-Early Permian. It comprises rather small slender insects with strange wings, similar in shape to badminton racquets; the fore- and hindwings were similar in shape. No other insect, extant or extinct, has wings of this shape.

Coleoptera, or beetles, the subject of my own special interest, have low diversity in the Permian; in the Early Permian they are represented by a single family, Tshekardocoleidae. During most of the Middle Permian, the only coleopteran suborder is also Archostemata, but in the very terminal Middle Permian beetles have been recorded that have characters of the two higher suborders (Fig. 2): Adephaga (two extant families) and Polyphaga (abundant elytra some of which may be polyphagan). Such an early appearance of extant families is unknown in other insects. Because of their strong integuments, fossil remains of beetles are well transported by water and therefore can be more abundant in localities than the beetles themselves were in their natural environment. In the Mesozoic and Cenozoic beetles are a flourishing, abundant, and diverse group; now it includes more known species than all other plants and animals—except other insects—taken together. In the Early Permian all beetles were consumers of decomposing wood; aquatic and terrestrial detritivores and predators appeared by the terminal Permian. Six families are known from the Late Permian. Taxa of the family and genus ranks had extremely wide geographical distribution; species recorded in Brazil, South Africa, and European Russia differ very little and include those described in the same genera. The larvae of these beetles lived in wood; galleries attributed to them have been recorded in fossil wood from the Kazanian (Naugolnykh and Ponomarenko, 2010). The similarity of Gondwanaland and Angaraland beetles is very strange, taking into account the difference between the floras of the two continents. In the terminal Permian, beetles, the larvae of which probably lived in wood, disappear from deposits, and their direct descendants appear only in the Middle Triassic. Similarly, new groups appear earlier than the boundary event and then disappear from the fossil record in the Early Triassic to re-appear beginning with the Middle Triassic. In the Lower Triassic, only rather scant fossil remains of beetles with smooth elytra are known, similar in body shape to water beetles. The P/T event temporarily decreased the abundance and ranges of many groups but had no considerable effect on the course of the evolutionary process itself and did not lead to any considerable changes in the taxonomic structure of beetles.

The relatively small order Neuroptera appears in the basal Early Permian and becomes rather diverse by

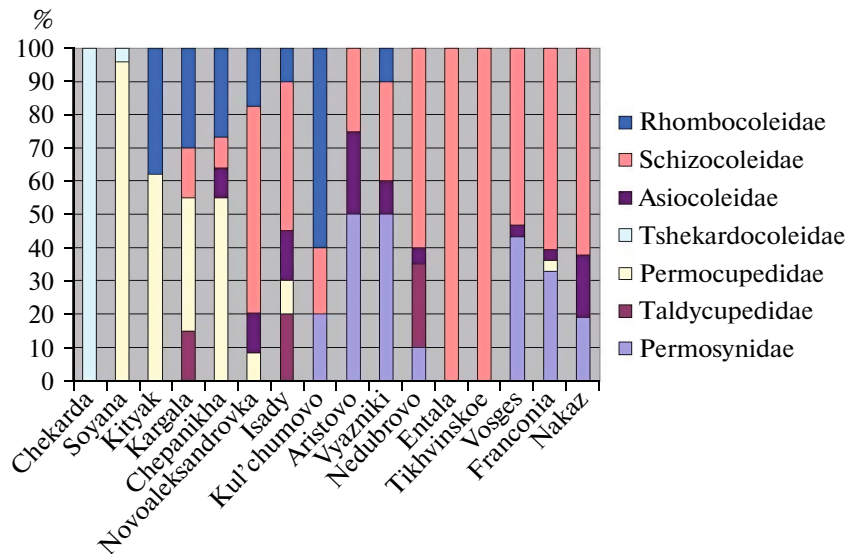


Fig. 2. Family composition of coleopteran fossils in different localities. It can be seen that dendrophiles are reduced, and aquatic forms and possible polyphagans appear as early as the Vyatikian in the Permian. Lower Triassic fossils supposedly belong to aquatic forms. In the Anisian, dendrophiles and representatives of higher groups re-emerge in the fossil record.

the terminal Early Permian. The shape and venation of their wings are strongly variable, but the species constitute a continuum that cannot be divided into supraspecific taxa separated by distinct hiatuses. The order remains in this state until the terminal Middle Permian, after which the abundance and diversity of neuropterans decreases. In contrast to Coleoptera, typical Mesozoic groups of Neuroptera do not appear in the terminal Permian.

Scorpionflies (Mecoptera), so called because of the scorpion-like manner in which males raise the tip of their abdomens, exist to this day as a group of low diversity but rather abundant and widespread (Novokshonov, 1997; Bashkuev, 2013). The order was especially diverse in the Late Permian: it included 11 families, one of them represented in almost every locality and making up 80–100% of all scorpionfly specimens in large collections. The peak diversity of this order was in the Kazanian. Each oryctocenosis usually contains only one or two scorpionfly families; the Australian locality Belmont is quite outstanding in containing six families, three of them known only from this locality. Four scorpionfly families survived into the Triassic; one genus has been recorded both in the Permian and Late Triassic.

The large group of orthopteroid insects (Gryllones) is divided into three subgroups: Blattidea, Gyllidea (Orthopteroidea s.str.), and Perlidea. The subgroup Blattidea includes cockroaches (Blattodea), which exist since the Carboniferous, as well as termites (Isoptera) and mantises (Mantodea), which evolved rather late from cockroaches. Paleozoic cockroaches show little difference from recent ones, except for the protruding ovipositor of females. In some Paleozoic localities, the vast majority of insect fossils represent

cockroaches, but in the Late Permian cockroaches almost disappear in temperate zones of the Earth, in both the Northern and Southern hemispheres. In the Middle to Upper Permian of the Kuznetsk Basin, where many thousand fossil insects have been collected, not a single cockroach has been found, although cockroaches were common in Lower Permian localities of the same area and made up almost all fossil insects in Carboniferous localities of that area. Cockroaches re-appear in the fossil record at the very end of the terminal Permian. The absence of cockroaches at high latitudes is usually explained by temperate climate, but the period of zonal climate with low temperatures at high latitudes ended in the mid-Early Permian, and therefore the opposite effect should have been expected.

Gryllidea are now treated as comprising the large order Orthoptera (which includes the well-known crickets, katydids, and grasshoppers) and Phasmatoidea (phasmids). Primitive orthopterans are rather common in the Permian; they all outwardly resemble katydids and also had a sound-producing apparatus. The songs of these insects were most probably the first sounds that echoed through Paleozoic forests. By contrast, phasmids were very rare in the Permian.

The extant Perlidea include such dissimilar insects as stoneflies (Plecoptera), tender insects associated with water, and earwigs (Dermaptera), which resemble staphylinid beetles. Their ancestors, Proleptoptera, existed in the Permian and were even more similar to Coleoptera. It is often impossible to conclude from isolated forewings to which of these quite distantly related orders they belonged. Stoneflies are rather scant in the Permian; they mostly occur only in the Late Permian. The larvae of all recent stoneflies

live in rapidly flowing water rich in oxygen, in most cases on stones. Interestingly, in the Permian and in the Mesozoic stonefly larvae are often found in lake deposits; they are so abundant and well-preserved that their presence cannot be explained by transport from some mountain rivers or brooks. In some Jurassic localities stonefly larvae occur far more frequently than all other insects. Although these stoneflies show little difference from recent ones in body morphology, it has to be concluded that they had quite different modes of life.

In the Paleozoic, a most important role was played by Paraplecoptera (Grylloblattida), which resembled stoneflies but in most cases probably had no aquatic larvae. They have survived to this day as rather scant and rare wingless relicts, but in many Permian localities they make up the majority of insect fossils. They exist since the Late Carboniferous, but the group is mainly Permian (Storozhenko, 1990; Aristov, 2009a, 2009b). Only three families are known in the Carboniferous; two of them survived only into the Permian; in the Permian 19 families are known. In the Middle to Late Permian paraplecopterans remained a substantial component of the entomofauna and were represented by 11 families known from all continents of that time and recorded in South Africa, Europe, Siberia, Central Asia, and Mongolia; Five families disappeared in the Kazanian and only three disappeared in the Tatarian. The most diverse fauna of Paraplecoptera is known from the Late Permian of Europe and Asia, especially from the Kazanian of European Russia. Thus, ten families, 19 genera, and 32 species of Paraplecoptera are known from the locality Soyana in Akhangelsk Region. In Tatarian localities the diversity of paraplecopterans visibly decreases. The boundary between the Paleozoic and Mesozoic is crossed by three paraplecopteran families. There is one interesting family of this order, Chaulioditidae, fossil remains of which are in most cases found in localities close to the Permian–Triassic boundary. Rare representatives of this family are known from the late Tatarian to the beginning of the Middle Triassic, and in the Early Triassic they were the most important component of ecosystems. It would seem that they could be considered a typical taxon of catastrophes, but they started to spread long before rather than during the crisis.

In addition to these, rather clearly delimited groups, there are several other insect orders, most of which became extinct already in the Paleozoic. Some of these orders comprise the most primitive winged insects. These insects also include some extant orders, such as Thysanoptera, Embioptera, and Psocoptera, three orders that appear in the Permian. The most typical Permian representatives of this group of insects were Caloneuroidea, Hypoperlida, and Blattinopseida. Most of them were rather small insects with long legs and wings. They did not even survive to the terminal Permian. Most of these insects, as shown by studying the contents of their digestive systems, fed on pollen.

Permian insects are also rather peculiar ecologically. Up to one half of insects in the Carboniferous were forms that sucked the contents of unripe plant ovules. In the Permian the proportion of such insects sharply decreased and by the Late Permian they all became extinct. They were replaced by the newly evolved insects that lived in wood and those that sucked juices from the vascular system of plants. The second most important group, insects that fed on remains of dead animals and plants, above all represented by Blattodea, Mecoptera, and Protoblattodea, retain in the Permian more or less the same value as they had in the Carboniferous. Insects the larvae of which lived within plant tissues, in cones or wood, represented by Coleoptera and Miomoptera, became much more abundant in the Permian. Many Permian insects fed on spores and pollen of plants, as shown by direct examination of their gut contents. Finally, flying predators, namely odonates, retained their ecological role in the Permian but probably switched to preying on smaller insects. Permian insects were on average markedly smaller than Carboniferous ones, although they were probably still larger than recent ones. This is also true of representatives of the same groups. For instance, Carboniferous odonates that had a wingspan of about one meter and Carboniferous palaeodictyopterans that had a wingspan of about half a meter were 5–10 times as large as their Permian relatives. In some groups, e.g., beetles, such diminution continued also in the Permian. The largest Permian beetles lived in the Early Permian; they were almost ten times as large as terminal Permian beetles. This diminution was clearly associated with ecological transformations. Thus, Permian insects can be considered a group rather unified both taxonomically and ecologically.

Finally, we should discuss the main ecological achievements of insects during the Permian and interrelations of insects and plants in that period. Among phytophagous insects, consumers of plant ovules—Palaeodictyopteroidea—first became much less prominent and then became completely extinct; many groups that consumed pollen and microsporophylls also became less prominent; the abundance of gnawed plant leaves considerably decreased. At the same time, hemipterans appeared, which sucked juices from the vascular system of plants and became the main group of phytophagous insects. Predaceous beetles that could already start competing with arachnids appeared at the very end of the terminal Permian. Only odonates, although they became smaller than in the Carboniferous, remained almost unchanged. Only parasitic and bloodsucking insects were still absent in the Permian, and, in addition, more or less large-scale colonization of fresh waters by insects started only by the terminal Permian.

The study of fossil insects cannot play any major part in biostratigraphy yet, mainly because they remain very poorly known; however, the part they play visibly increases. Stratigraphical usage of data on

insects is hindered above all by the insufficient number of paleoentomologists, compared to the colossal diversity of fossil insects. Insect remains can be used for quite broad correlations, because the main trends in evolution of diversity were essentially similar in insects and marine animals. Marine deposits of insects are far from rare, and many Permian localities of fossil insects formed in sea lagoons. In the Late Permian insects evolved extremely rapidly, as will be shown below. Flight capacity allows insects to disperse very quickly; even in quite remote areas they appear simultaneously on the geological timescale. All these factors increase the potential of using insects for stratigraphical correlations, including intercontinental ones.

The Permian Period constitutes a rather distinct stage in the evolution of insects. Most Carboniferous insects belonged to extinct orders, but most Permian insects belonged to extant orders. At the same time, almost all families known from the Permian are now extinct. The majority of recent insects are holometabolous. They also appeared in the Permian, although many holometabolous orders appeared much later. Of the orders dominant today, only beetles are known from the Permian, while the majority of Permian holometabolans belonged to the now scant orders Neuroptera and Mecoptera. Other quite widespread Permian insects, such as auchenorrhynchans, cockroaches, paraplecopterans, and katydids, crossed into the Permian from the Carboniferous and survive to this day. A total of 26 insect orders are known from the Permian; six of them became extinct during the Permian Period. A total of 175 families are known from the Permian, only one of which probably survives to this day. Most Permian insects were saprophagous; phytophagous forms (mostly sucking, such as auchenorrhynchans, and palynophagous; very few phytophagous forms had chewing mouthparts) and predators were rarer. Palaeodyctiopteroid palaeopterans that had sucking mouthparts and were typical of the Carboniferous survived until the Kazanian. Aquatic insects were considerably more numerous than in the Carboniferous but not so diverse as in the Triassic.

One feature of Permian insects important for stratigraphy is the wide geographical distribution of many forms. Insects of Kazanian localities of European Russia and insects of the Irati Formation of Brazil, considered approximately of the same age, mostly belong to the same genera, which in most cases existed no longer than one geological age. Insects could be used as the foundation for rather broad correlations; the only problem is that they remain very poorly known. Insects are quite abundant in the Permian of European Russia, in the Tunguska and Kuznetsk basins, but unfortunately they have been studied in rather much detail only in the Kuznetsk Basin. Triassic entomofaunas similarly show high degrees of similarity. Only insects from the Newcastle Formation of Australia are distinguished by high levels of endemism in some groups and surprisingly depleted other groups.

The faunas of northern continents considered synchronous with Newcastle display no such features.

Several methods have been proposed for mathematical analysis of changes in taxonomic diversity. They have been discussed earlier (Alekseev et al., 2001); it was shown in the same publications that those methods could be successfully applied to analyzing the evolution of diversity in insects. Different methods have different advantages and drawbacks. The graphs of those changes, compiled by V.Yu. Dmitriev from new data, are shown below. The first method, proposed by Sepkoski (1978), is based on counting taxa known from some stratigraphical unit, usually geological age. As a result, the long-known fact of the unevenness of evolution was given a mathematical foundation, and moments of considerable drops in diversity were revealed. Unfortunately, this method strongly depends on the incompleteness of the fossil record (Fig. 3). Let us discuss the dynamics of insect families during the time around the P/T boundary as they are characterized by momentary diversity of families, i.e., the number of families that cross the boundaries between ages (Fig. 4–6). This method was proposed by V.Yu. Dmitriev (Dmitriev et al., 1995; Dmitriev and Ponomarenko, 2002). The number of families in the basal Permian was the same as in the terminal Carboniferous; by the Middle Permian it became approximately twice as great; the greatest number of families that cross boundaries between ages is found at the boundary between the Ufimian and Kazanian; then this number begins to decrease, especially rapidly from the Kazanian to Tatarian; after the very beginning of the Triassic it remains almost at the same level until the Anisian. Only a small decrease in diversity can be seen at the Permian–Triassic boundary, compared to the boundaries between the Kazanian and Tatarian or Olenekian and Anisian. In the Anisian diversity begins to increase, but fails to reach in the Triassic the record highest—Kazanian—level of the Paleozoic. This record is not broken until the Jurassic. Thus, in comparison with marine organisms, the diversity of which dramatically drops near the P/T boundary, the diversity of insects begins decreasing much earlier, does not fall as low, and regenerates also much earlier. Moreover, both the fall and regeneration of this diversity are by far less dramatic than in marine faunas. The number of insect families decreased by the P/T boundary by less than one-third, while the number of families in the marine faunas decreased by more than half. Although the transition from the Paleozoic to Mesozoic was characterized by a considerable drop in the family diversity of insects—the greatest such drop in history—this change was not catastrophic. The P/T boundary is nothing special in comparison with adjacent boundaries, and the drop of diversity is much smaller than it was after peaking in the Kazanian.

The dynamics of taxonomic diversity in insects has a somewhat different aspect in accumulated values, i.e., if we consider the number of families that existed

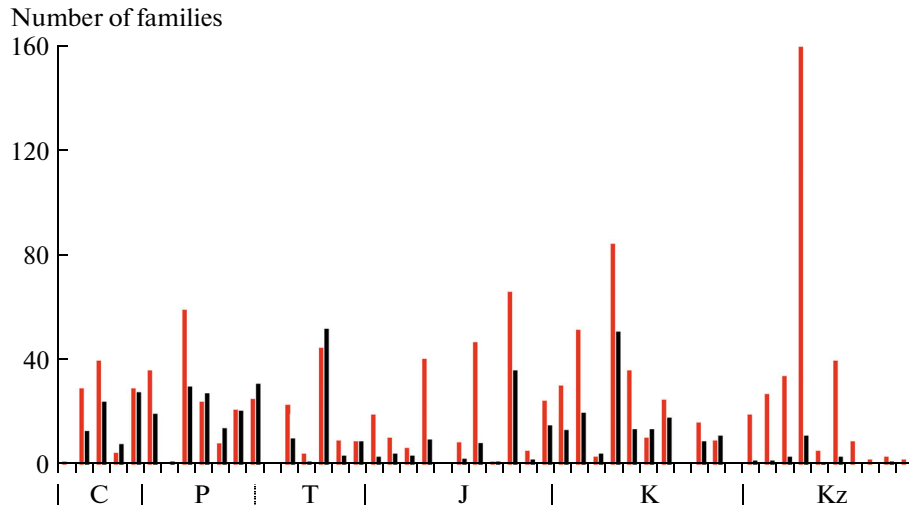


Fig. 3. Initial data. The light column for each age is the number of insect families that appeared in that age; the dark column is the number of families that became extinct. It can be seen that the faunas have been studied very unevenly. One common trend is that appearance is almost invariably higher than extinction. Notation in Figs. 3–7: C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Kz, Cenozoic; time is measured in millions of years ago.

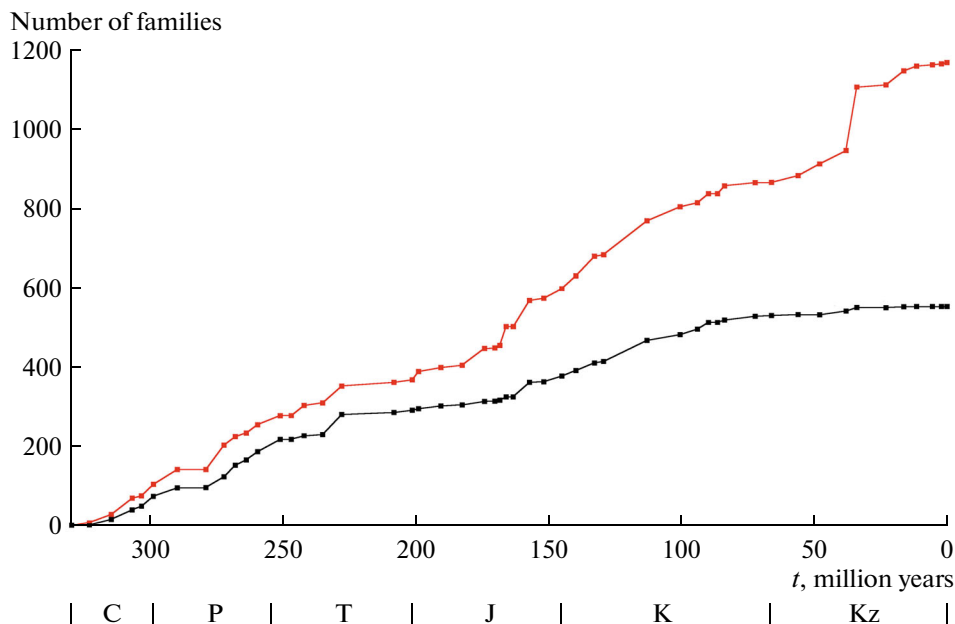


Fig. 4. Accumulated number of appearances (light curve) and extinctions (dark curve) of insect families. It is clear that there was no pronounced growth in appearance and extinction rates of families during the entire history of the group, while the number of families increased by over two orders of magnitude (the rates are represented by slopes of the graphs).

during some time interval, such as geological age or period (Fig. 5). As mentioned above, a total of 175 families are known from the Permian, but only 105 families are known from the Triassic. This difference is quite great, compared to momentary values of diversity; it is determined by a much higher rate of faunal turnover, compared to the Triassic. A total of 71 families are known from the Kazanian Stage, ten of them endemic. The Kazanian Age is also distinguished

by the greatest extinction of insects at the order level. The latest records of six insect orders are known from Kazanian deposit; only two orders that became extinct later crossed the boundary between the Kazanian and Tatarian; one of them became extinct before the terminal Permian; the other became extinct in the Jurassic. A total of 63 insect families are known from the Tatarian Stage, only four of them endemic of the Tatarian Age. Insect diversity drops from the Kazanian

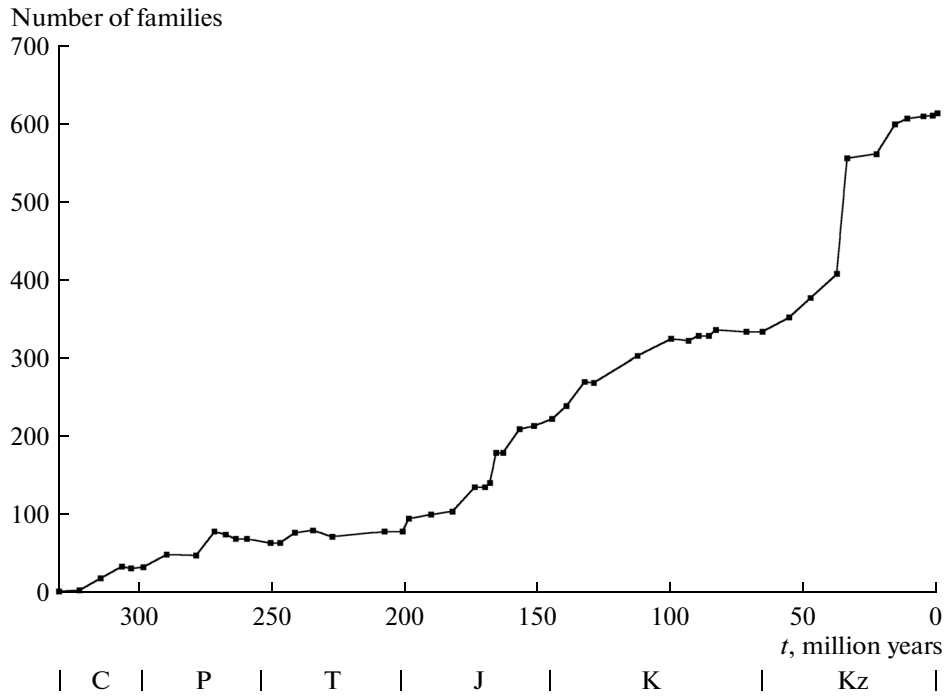


Fig. 5. Changes in the number of insect families (difference between ordinates of corresponding points in Fig. 4).

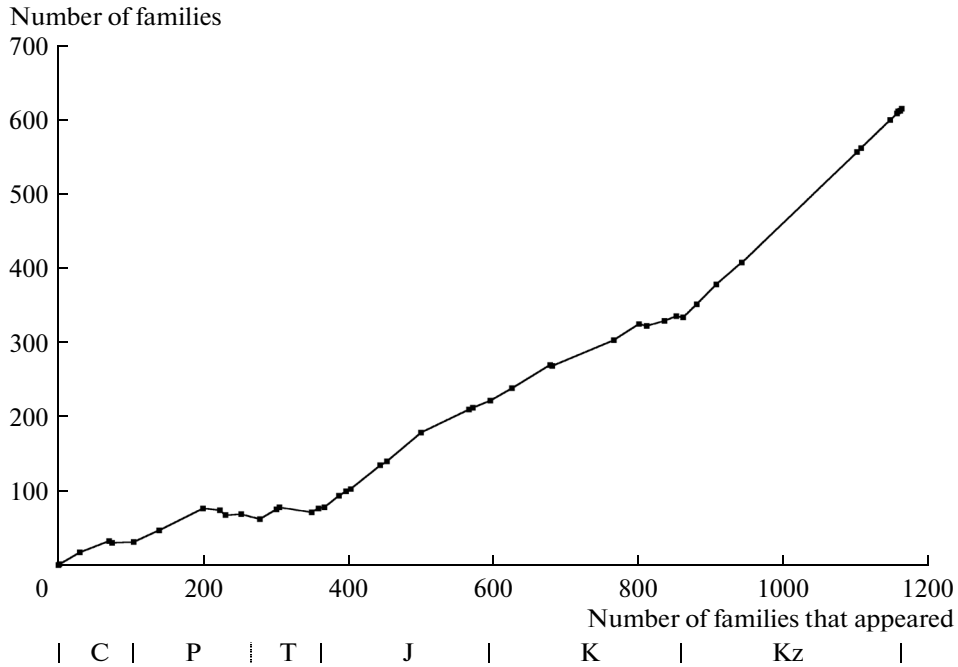


Fig. 6. Changes in the number of insect families. In contrast to Fig. 4, abscissa shows the accumulated number of families that appeared, rather than time.

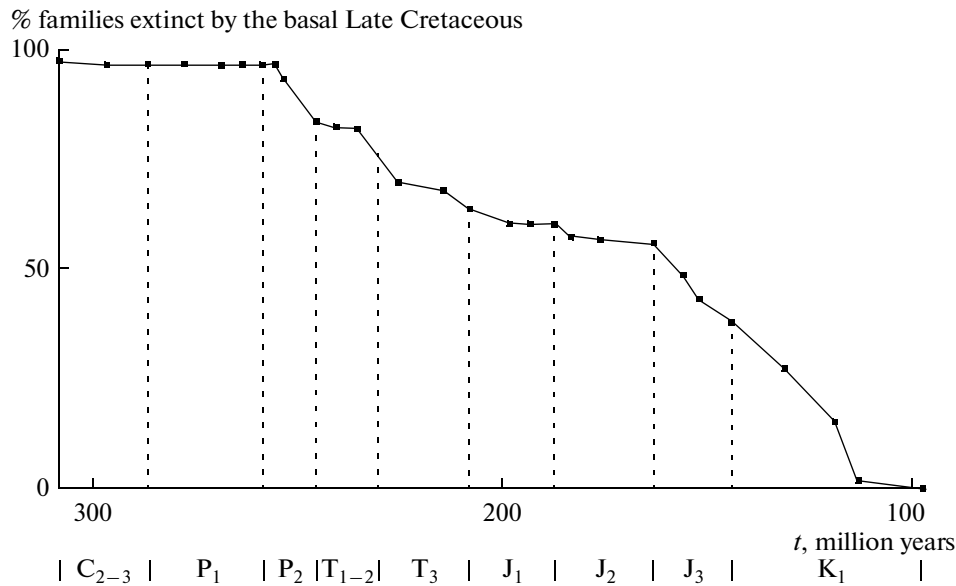


Fig. 7. Inverse Lyellian curve for insect families in the Permian and Triassic: percentage of families that became extinct from the basal Permian to the mid-Cretaceous.

to Tatarian not so strongly, but the rate of appearance of new taxa and the rate of faunal turnover decrease much more strongly. As usually observed in crisis situations, the decrease in diversity is determined by decreased rate of appearance of new taxa more than by increased rate of extinction. The boundary between the Permian and Triassic was crossed by 36 families, i.e., a little more than half of those that existed in the Tatarian.

Another possible method of analyzing the dynamics of insect diversity around the P/T boundary is based on the inverse Lyellian curve (Fig. 7), which can show the changes that took place during the Permian and Triassic in the percentage of families that became extinct by the mid-Cretaceous, i.e., the moment when the majority of Mesozoic insects became extinct. This modified method of C. Lyell was proposed for studying insects by V.V. Zherikhin. Until the boundary between the Ufimian and Kazanian ages, the parameter remains at a level slightly below 90%, then sharply drops to 40% by the P/T boundary, then changes little until the terminal Anisian, and then drops below 10% during the Ladinian. The Paleozoic entomofauna existed in a state close to dynamic equilibrium until the Kazanian, similarly to what was revealed for marine faunas using the kinetic model of Sepkoski (1978). After that, the entomofauna rather rapidly becomes almost entirely Mesozoic by the end of the Ladinian Age. The course of changes in family diversity around the P/T boundary in insects proved to be quite similar to the course of changes that accompanied the spread of angiosperm plants in the mid-Cretaceous. The trajectories of the inverse Lyellian curve are surprisingly similar in both cases. In the latter case, the proportion of extinct families also dropped very

sharply, which was followed by slow extinction around the time of the crisis itself, and then almost complete replacement of Mesozoic insect families by Cenozoic ones in the basal Late Cretaceous. Such rapid extinction as can be seen in the graphs gives evidence that it was practically (within one geological age) simultaneous even for localities situated on different continents: otherwise the extinction curve would necessarily be more even. It is shown for Cretaceous localities that the percentage of extinct families strongly correlates to the stratigraphic position of localities. Such relationship will most probably also prove true of the Late Permian to Early Triassic localities.

It can be stated that insects do not display such profound extinction at the Permian–Triassic boundary as usually believed (Looy, 2000). This not to say that there was no ecological crisis around the Permian–Triassic boundary. Although, as figuratively formulated by Rasnitsyn (2012), at that time “life did not even think of dying,” the composition of beetles in the Early Triassic dramatically changed compared to the terminal Permian. For instance, the Induan locality Entala and Olenekian locality Tikhvinskoe include only beetles with elytra of the schizocoleid morphotype, almost exclusively representing the genus *Pseudochrysomelites*, typical of the crisis interval. Such changes in the faunal composition give evidence of considerable changes in landscapes. The Permian diversity, which disappeared from the fossil record, began regenerating only in the basal Middle Triassic.

Let us formulate in brief the results of fossil insect studies important for understanding the P/T crisis:

In spite of the considerable growth in the amount of data on insects from the time around the P/T crisis,

the main features of changes in the taxonomic diversity as represented by curves of momentary accumulated diversity changed little, while the traditional curve, drawn by the method proposed by Sepkoski, changed considerably. It can be concluded that the former approach to analyzing biodiversity reflects more fundamental features of the evolution of biodiversity.

The actual drop in biodiversity during crisis situations was much weaker than usually accepted. The actual diversity in the eruption area of the Siberian Traps was not much smaller than normal elsewhere during a similar time. A crisis situation really took place, but the scale of extinction was far lower than usually accepted. Extinction rate was close to background values, but the emergence of new forms was decreased.

The decrease of the visible diversity in the Early Triassic resulted from a general drop in the abundance of many forms; as a result of this decrease in their abundance, many taxa temporarily dropped out of the fossil record to re-appear later. In addition, the taphonomic window of insect preservation became narrower because of changes in the main landscapes, which resulted in the spread of coarser sediments, unfavorable for preservation of insects.

There is no evidence of any increase in the appearance of new forms as a result of ecosystem destabilization, i.e., considerable changes in the landscape and phytocenoses. New groups characteristic of the Mesozoic appear as early as during the pre-crisis Permian times or after the end of the most dramatic phase of the crisis. Beetles of the most advanced suborders Adephaga and Polyphaga appear in the terminal Permian, rather than in the terminal Triassic as believed earlier, but they retain visible abundance only for a very short time, and then temporarily disappear from the fossil record.

The eruption area of the Siberian Traps has a rather typical entomofauna of the intermediate type, closer to the Permian entomofauna, if we take into account the groups that appeared during the late Vyatkian.

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