Insect Diversity from the Carboniferous to Recent

V. Yu. Dmitriev[a], *, D. S. Aristov[a, e], A. S. Bashkuev[a], D. V. Vasilenko[a, e], P. Vřanský[b],
A. V. Gorochov[c], E. D. Lukashevitch[a], M. B. Mostovski[d], A. G. Ponomarenko[a], Yu. A. Popov[a, †],
A. P. Rasnitsyn[a], N. D. Sinitshenkova[a], I. D. Sukatsheva[a], M. M. Tarasenkova[a],
A. V. Khramov[a], and A. S. Shmakov[a]

[a]*Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia*
[b]*Geological Institute, Academy of Science of Slovakia, Bratislava, 84005 Slovakia*
[c]*Zoological Institute, Russian Academy of Science, St. Petersburg, 199034 Russia*
[d]*Tel Aviv University, Tel Aviv, 6997801 Israel*
[e]*Cherepovets State University, Cherepovets, 162600 Russia*
*e-mail: vyudmi@mail.ru
Received December 26, 2016

Abstract—Changes in insect biodiversity in terms of the number of families throughout the history of the class are described. The results are compared with those published recently by other researchers and possible reasons for observed differences are discussed. The main stages in the evolution of insect diversity are recognized. The per-family rates of the appearance and extinction of families, the mean longevity of families existing during certain periods of the geological time, and the rates of renewal of entomofauna are considered.

Keywords: Insecta, diversification, rates of evolution

The first generalizations of the data on changes in insect diversity at the family level during the entire history of this group were published by Labandeira and Sepkoski (1993; see also Labandeira and Eble, 2001; Labandeira, 2005) and somewhat later in the same year by Jarzembowski and Ross (1993). An improved version of the second work was prepared three years later (Jarzembowski and Ross, 1996). Both researches provide diagrams showing the currently known number of families in each geological age in the first research and in each epoch in the second. The diagrams of this kind provide a general understanding of diversification of the group throughout long time periods, but are of little use for estimation of changes in diversity within an age (or epoch, as in Jarzembowski and Ross, 1996) (Dmitriev and Ponomarenko, 2009).

The diagrams showing documented changes in the number of insect families within geological ages were first published by Dmitriev and Ponomarenko (Alekseev et al., 2001; Dmitriev and Ponomarenko, 2002) based on the data provided by researchers of the Laboratory of Arthropods of the Borissiak Paleontological Institute of the Russian Academy of Science (PIN), experts on the main groups of fossil insects. In connection with incomplete and very nonuniform understanding of ancient entomofaunas, the treatment of

such diagrams as directly reflecting the evolution of diversity is not always reliable.

Labandeira (1994) published a list of families of fossil insects, provided with the age of the first and last occurrences, which were the basis for the paper prepared by him and Sepkoski. This allowed a comparison of the diagrams based on the data of Labandeira and the Laboratory of Arthropods (Alekseev et al., 2001, p. 37). Having significant differences in the initial material, considerable distinctions between the diagrams were observed in five age intervals. All of them appeared to be connected with different datings of the same large insect localities. In addition it was concluded that different treatment of the system of the group had a little effect on the shape of diagrams.

The intense accumulation of new data after the publications cited above justifies repetition of these studies, allowing improvement of conclusions and comparison with the previously obtained results. Recently, the dissertation of Nicholson (2012), which generalizes the data published by the end of 2009 appeared in the Internet. Not numerous changes and specification accumulated by the end of 2011 were included in his list of families somewhat later (Nicholson et al., 2014, 2015).

In the Laboratory of Arthropods of PIN, the data on the first and last occurrences of insect families have been renewed beginning from the end of 2012. Both

† Deceased.
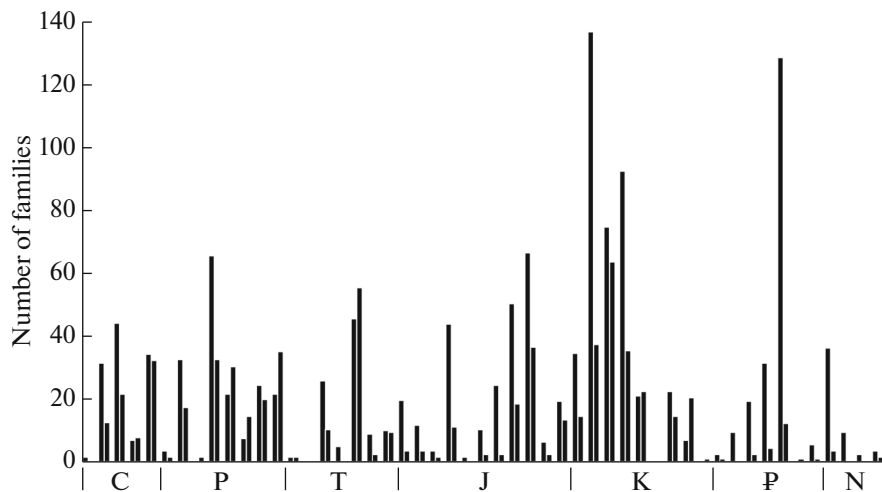
Fig. 1. Number of families that appeared and became extinct. For each age interval, the left column shows the number of appearing families (first occurrences of their representatives) and the right column is the number of extinct families (last occurrences). Summarized data are shown for the Berriasian and Valanginian, Hauterivian and Barremian, Albian and Cenomanian.

published data and unpublished identifications of large collections housed in PIN and some foreign collections investigated by employees of the laboratory were taken into account. The diagrams illustrating the results of this work are given below. A preliminary variant of the diagrams was published earlier by Ponomarenko (2016). Subsequently, the list of families used in this work was revised essentially. The list of families and data on localities of fossil insects are available from the site of the laboratory (http://palaeoentomolog.ru/bibl/fam.html), which also provides substantiation of datings accepted here of some Cretaceous localities of Central Asia (http://palaeoentomolog.ru/bibl/entomocomplex.html).

The present paper describes the results of direct calculations based on the family list with datings of the first and last occurrences. The diagrams always display the number of families at the boundaries of geological ages. Preliminary preparation of the material consisted only of the distribution of families dated to the age intervals (Anisian−Ladinian, etc.) that appeared and became extinct throughout the ages of this interval proportional to the number of first occurrences and extinctions precisely established in them. In some cases, this age interval was considered without division. We used the time scale accepted by the Geological Congress in 2012 (Gradstein et al., 2012). In connection with extensive material from the Middle Permian of Russia accumulated during the last years, the East European Urzhumian (=Wordian) and Severodvinian (=Capitanian) stages are more convenient; the Upper Permian completely corresponds to the East European Vyatkian Stage. In the Eocene and Miocene, localities are dated to subseries.

The number of first and last occurrences of representatives of families over the stages (subseries in the Eocene and Miocene) is illustrated by the histogram in Fig. 1. It distinctly reflects extremely nonuniform distribution of data over the time. In particular, in the Aalenian, reliable first and last occurrences of families are absent, whereas in the Toarcian, 44 families appeared and ten became extinct. This agrees with the rich material coming from the Toarcian (seven large localities, mainly in Germany) and absence of large collections from the Aalenian. He same picture is true of other ages.

The nonuniform knowledge of entomofaunas differing in age means an incomplete understanding of the fauna as a whole. Since the number of taxa established in particular time intervals is directly connected with the abundance of collections from this interval, standardization of samples has recently become popularity for estimation of the expected number of taxa in respective time intervals (Alroy, 2010). For insects (as for other fossil groups), these methods show a picture of diversification rather different from that obtained by direct calculations based on a usual list of families (Clapham et al., 2016), which does not allow the use of standardized samples. However, the studies using both the list and standardized samples have the same restriction; both preclude estimates of the extent to which the diagrams obtained correspond to the required valid picture of changes in diversity (Dmitriev, 2016). In contrast to the standardization of samples, work with the lists is not connected with additional assumptions and depends only on the currently known number of taxa, showing a true picture of actual diversity (Newell, 1959).

In the cited publications, various aspects of the evolution of insect biodiversity are discussed in detail. New data basically confirm the main conclusions of these studies. Nevertheless, the question of stability of
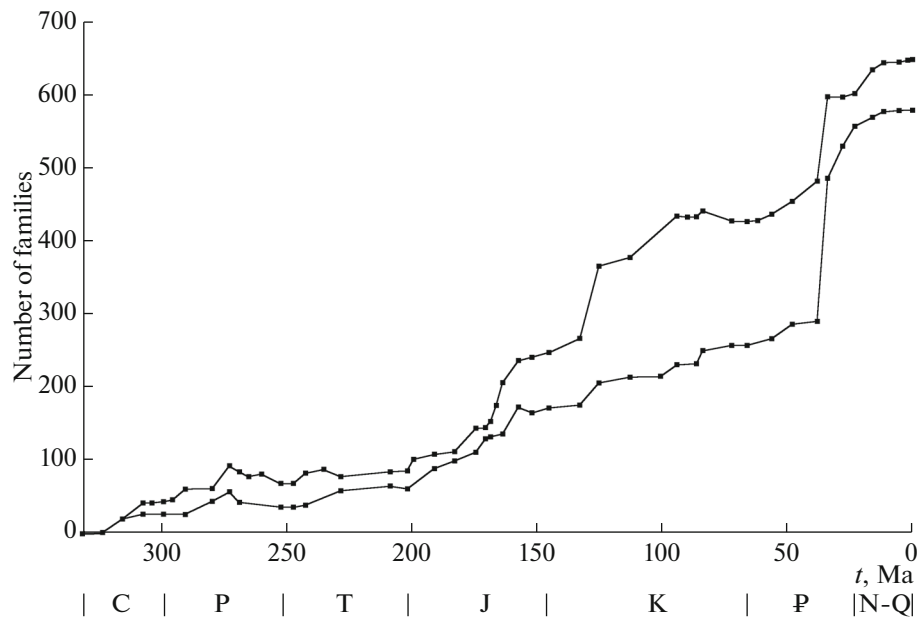
Fig. 2. Comparison of the diagrams showing changes in the number of insect families based on the former and modern data of the Laboratory of Arthropods. The lower diagram is the former results (Alekseev et al., 2001; Dmitriev and Ponomarenko, 2002) and the upper diagram is the last results.

the main results with accumulation of new data on ancient entomofaunas remains urgent. First of all, it is expedient to compare the new and previous results (Fig. 2) obtained by researchers of the Laboratory of Arthropods (Alekseev et al., 2001; Dmitriev and Ponomarenko, 2002).

More than 15 years of studying in the 21st century resulted in significant changes in the general picture. An increase in the number of families in the modern material due to accumulation and description of new collections and also taxonomic revisions is quite natural. A more important point is the absence of similarity of the diagrams. The most pronounced changes are observed within the interval of 50–150 Ma, that is, mostly in the Cretaceous. This is accounted for by intense accumulation of the data on insects from Cretaceous ambers (Rasnitsyn et al., 2016). As a result, the relative size of a step in the Late Eocene decreases significantly (Fig. 2), since many families previously found for the first time in the Baltic amber are presently recorded in the Cretaceous. In general, it should be noted that the ideas concerning the evolution of insect biodiversity have not yet come to a definite state and significant accumulation of new data may result in essential changes in the final results. Thus, each subsequent generalization provides a picture of diversification of insects, as it looks at the present state of knowledge, without insisting on the finality of conclusions. The sequence of such generalizations apparently approaches an adequate description of the process, although it is difficult to predict the number and duration of required studies.

A comparison of our new diagram with that constructed in a similar manner based on the list provided by Nicholson is of great interest (Fig. 3). The lists differ considerably (Table 1). Nevertheless, the general patterns of diagrams in Fig. 3 are very similar (coefficient of correlation is 0.995). However, it is necessary to pay attention to different courses of diagrams in some ages (the most essential distinctions are shown in Table 2). The differences revealed may depend on three causes, the role of which varies in particular cases:

(1) Different datings of the same localities.

(2) Different involvement of global paleoentomological material.

(3) Different taxonomic systems of the group at the family level.

The effect of different datings can be excluded, as the ages of localities in the list used by Nicholson are changed according to that accepted in the Laboratory of Arthropods. Table 3 and Fig. 4 show the results of substitution. As a result, only in four ages, the course of diagrams remained essentially different. Thus, most of the discrepancies shown in Table 2 and Fig. 3 actually depended on datings.

The divergence of results in the Artinskian Age is determined by the fact that Nicholson assigned to this age the Brazilian Irati Formation, where according to his data, six families appear. In our list, these families appear in younger deposits, while the Irati Formation is absent, since it is dated Kungurian and all families recorded by Nicholson in this formation are considered to appear for the first time in other localities. In
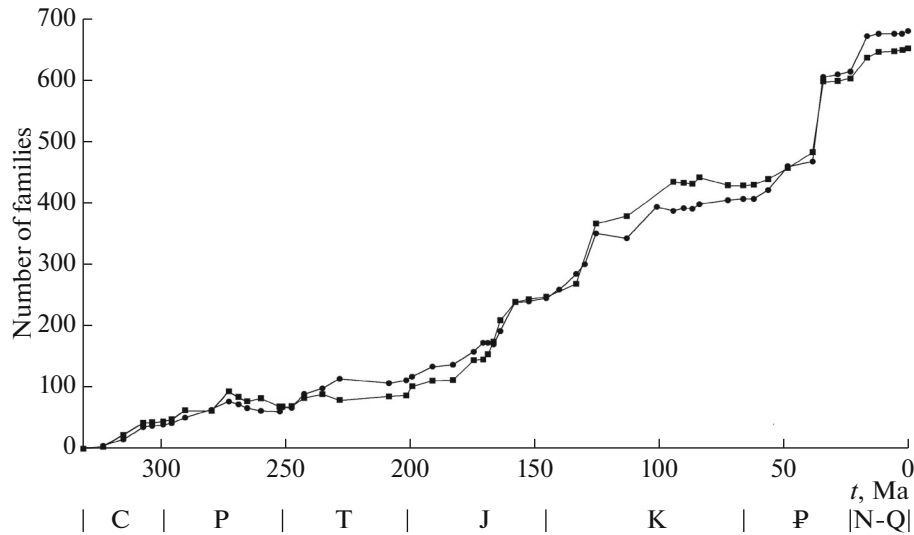
Fig. 3. Comparison of the diagrams showing temporal changes in the number of insect families based on the data of the Laboratory of Arthropods (squares) and the data of Nicholson (circles).

other words, in this case, the determining factor is also differences in dating.

The situation is different with Vyatkian faunas. The Laboratory of Arthropods possesses large collections with many last occurrences of representatives of Paleozoic families (Aristov et al., 2013; etc.), which were not taken into account by Nicholson. During the Vyatkian Time, insect diversity decreased significantly whereas Nicholson indicated the first occurrences of 12 families in Vyatkian deposits, which did not become extinct in the same age, with a general increase in the number of families. In our collections, two of them occur in more ancient Severodvinian deposits; four appeared in the Jurassic and Cretaceous, one is considered to appear and become extinct in the Vyatkian Time, and remaining five are absent in the list of the Laboratory of Arthropods. Only ten families out of 75 in the complete list of families from the

Vyatkian Stage (where both shared families and families only represented in one of the two family lists) suggest that there was influence of different understanding of their taxonomic composition. Hence, the main distinction of the results for the Vyatkian Stage follows from two factors, with the taxonomic disagreements playing a secondary role.

For the Carnian, the difference in increments is 15 families. Three families that according to Nicholson appeared in the Carnian are presently known from the Permian, which he probably could not take into account. Both compared lists include 81 families, which appeared in the Carnian and passed upward or appeared before the Carnian and became extinct in this stage. Eight families are only present in one list; in 40 families, the moments of appearance or extinction do not coincide. Thus, the difference of 12 families is

Table 1. Comparative characteristics of the data of the Laboratory of Arthropods and Nicholson

	Laboratory of Arthropods	Nicholson	Coincidences
All families			1117* (88%**)
Datings of the first occurrence	1270	1421	519 (41%)
Localities of the first occurrence			556 (44%)
Datings and localities of the first occurrence			394 (31%)
Extinct families			544 (88%)
Datings of last occurrence	621	757	251 (40%)
Localities of last occurrence			269 (43%)
Datings and localities of last occurrence			170 (28%)

  * Synonyms specified in Nicholson's list.
** Share in the list of Laboratory.

Table 2. Changes in the number of insect families in some ages according to the data of the Laboratory of Arthropods and Nicholson

Age	Laboratory of Arthropods	Nicholson
Artinskian	−1	+12
Kungurian	+33	+12
Severodvinian	+5	−4
Vyatkian	−14	+1
Induan	0	+6
Carnian	−10	+17
Norian	+6	−8
Rhaetian	0	+5
Aalenian	0	+15
Bajocian	+8	0
Bathonian	+22	−1
Aptian	+11	−8
Albian−Cenomanian	+57	+34
Campanian	−14	+8

Table 3. The same as in Table 2, after substitution in list Nicholson of datings of the localities accepted by Laboratory of Arthropods

Age	Lab. Arthropods	Nicholson
Artinskian	−1	+6
Vyatkian	−14	+8
Carnian	−10	+5
Campanian	−14	+8

of the laboratory, and 16 are present in both. The difference between the lists depends basically on the different taxonomic ideas, as in the case of the Carnian.

Thus, the major cause of different results in some ages in the comparison of insect diversification between the data of the Laboratory of Arthropods and Nicholson is different datings of some large localities (12 of 14 distinctions). For Vyatkian assemblages, an essential role is played by new materials; however, the different understanding of families is also significant and only in two cases (Carnian and Campanian) it is probably determining.

When characterizing insect diversification in the geological past, the rates and per-family rates of appearance and extinction are of great interest. Unfortunately, the extremely nonuniform knowledge of entomofaunas over the ages precludes reliable estimates of rates within short time intervals, although it is possible to obtain a generalized picture within a long time interval. Figure 5 shows accumulated number of first occurrences and extinctions of families (rates of appearance and extinction of families determine the inclination of curves). In the case of the roughly gener-

primarily accounted for by different understanding of families.

As for Campanian insects, the data of the Laboratory of Arthropods are presently, after new generalization of entomofaunas from Cretaceous ambers (Rasnitsyn et al., 2016) are most detailed. They strongly differ from the data provided by Nicholson. The two compared lists include a total of 47 families appearing or becoming extinct in the Campanian; of them 18 are only present in Nicholson's list, 13 are only in the list
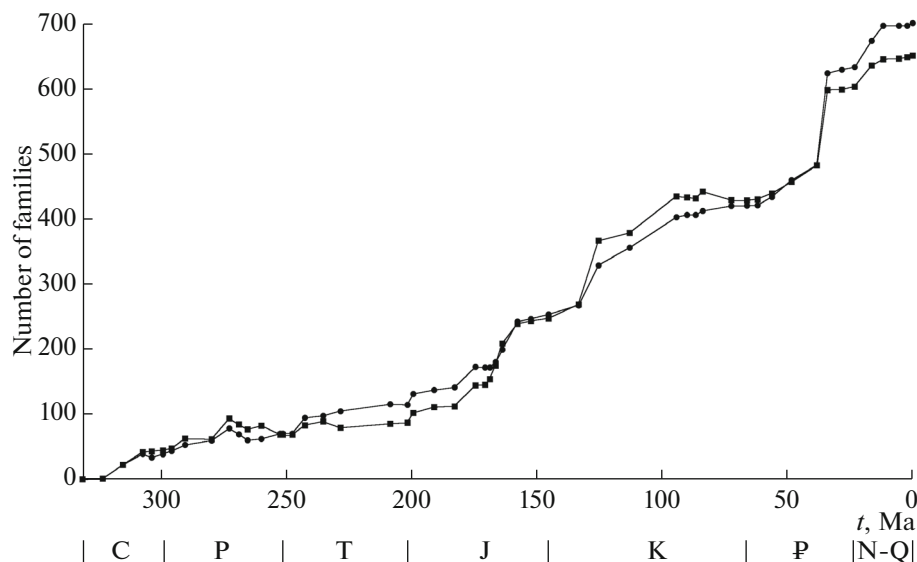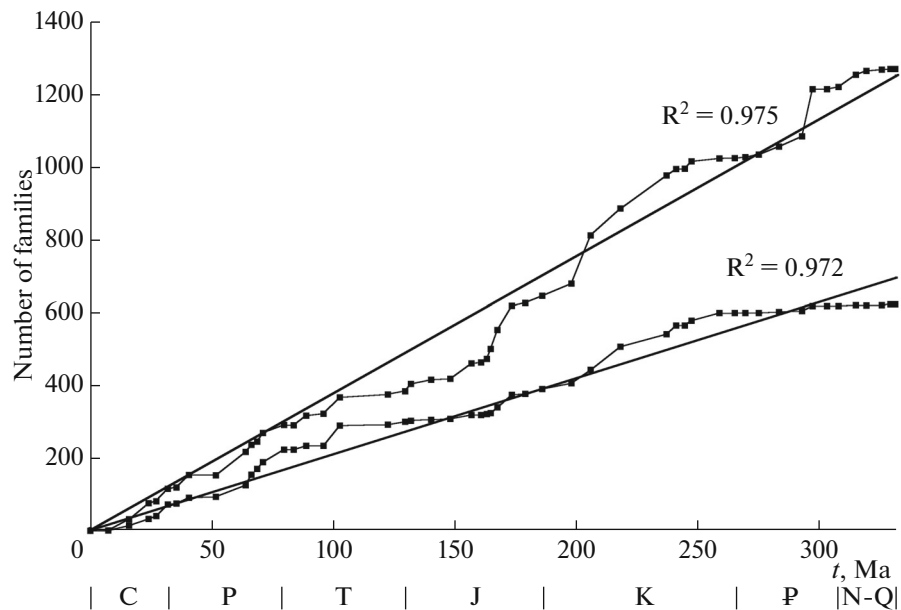

Fig. 4. The same as in Fig. 3 after substitution in Nicholson's list of datings of localities according to that accepted in the Laboratory of Arthropods.
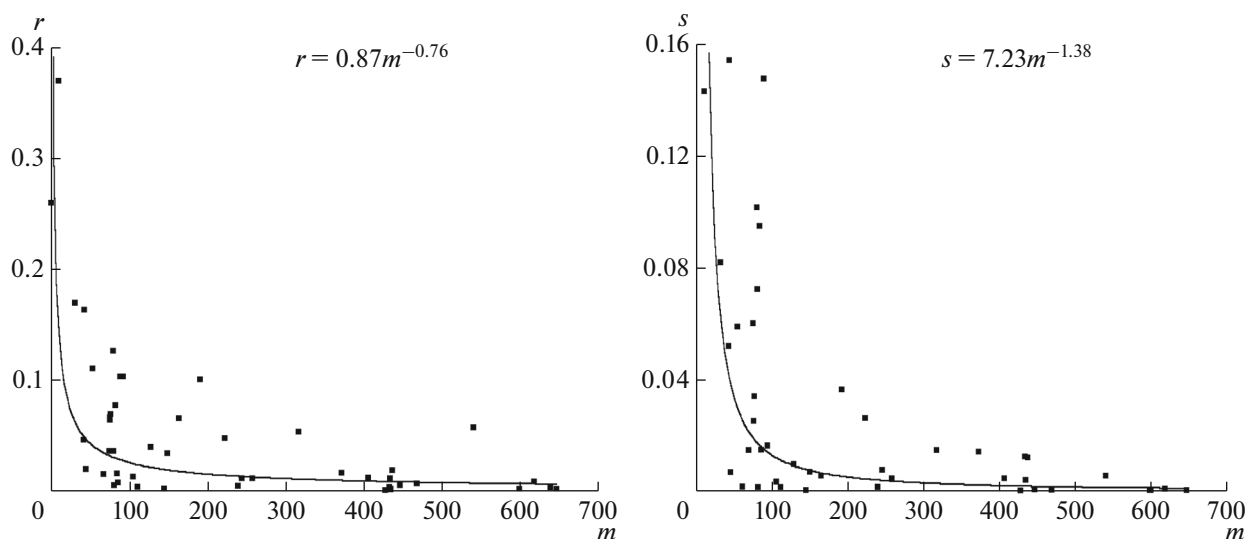
Fig. 5. Appearance and extinction of insect families. Ordinates are the number of families that appeared (upper curve) and became extinct (lower curve) beginning from the appearance of true insects in the Serpukhovian Age. The coordinate origin is placed at the lower boundary of the Serpukhovian.

alized approach, both processes can be close to linear. Any regular changes in the rates are absent. They vary about a constant value with significant fluctuations: throughout the history of insects, the mean rates of appearance and extinction are 3.77 and 2.10 fam./m.y., respectively. Consequently, the per-family rates of appearance and extinction of families at this level of generalization are on average inversely proportional to diversity (total number of families). This is an important result, since for a particular family, the probability of extinction or appearance of a descendant family within short time intervals is proportional to respective per-family rate. A decrease in both per-family rates in time was illustrated by Nicholson (2012, text-figs. 3–6). In the present paper, Fig. 6 shows the same as function of the number of families. A wide dispersal of empirical estimates does not mask the obvious general decrease in both per-family rates with the growth of insect diversity. The empirical exponents are −0.76 for the appearance of families and −1.38 for extinction. The theoretical exponent in both cases, proceeding from the average constancy of the rates at a high value of the criterion for conformity R^2, is −1. The difference of empirical values from −1 characterizes the general accuracy of quantitative estimates of the material based on fossil insects (24 and 38%).

A result of a decrease in the per-family rates is an increased mean duration of the existence of families and delay in renewal of the entomofauna. Half of all families are present in the modern fauna. The duration of their existence is not known. Therefore, the first consequence cannot be supported by a direct investigation. However, it is also seen in an increase in the mean longevity of families existing during a certain time interval. Actually, the mean longevity of families before the Kungurian is at most 15 m.y., whereas modern families known in the fossil record are almost 100 m.y. of mean longevity. This obvious phenomenon can be illustrated for the entire history of the group (Fig. 7). In this figure, in some cases, the mean longevity of families existing at the beginning of some ages decreases. This is caused by the presence of large localities of fossil insects with many first occurrences of families shortly before the respective age. In particular, a decrease in the mean longevity of families existing at the beginning of the Middle Permian is connected with extensive collection material from Kungurian deposits (Chekarda and Elmo localities); at the beginning of the Vyatkian Age, with the material from Severodvinian deposits. The same concerns families at the Carnian−Norian boundary, with extensive Carnian collections at the Barremian−Aptian boundary after the fauna from the Chinese Yixian Formation and some Mongolian localities, the Eocene−Oligocene boundary after Baltic amber. There is a decrease in the latter half of the Middle Jurassic and in the Late Jurassic prior to the Tithonian, which is connected with rich material from Haifanggou, Daohugou, and Karatau localities. In general, the mean longevity of families increases by 260 thousand years per each million years of insect history.

A decrease in the rate of renewal of entomofaunas as the second consequence of a decrease in per-family rates can also be illustrated. A convenient quantitative indicator is the period of half-renewal of the list of families. It means the time required for families exist-

Fig. 6. Dependence of the per-family rates of appearance (r) and extinction (s) of insect families on their diversity m (mean number of families in each age).
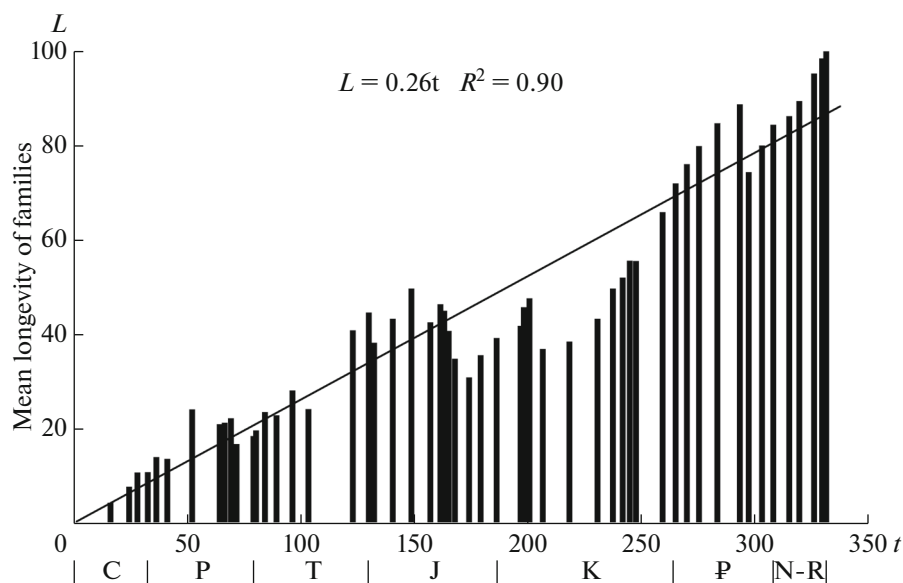

Fig. 7. Middle longevity (L) of families existing at the lower boundary of ages (in m.y., beginning from the Moscovian Age; extreme right column shows the mean longevity of modern families known as fossil). The coordinate origin is placed at the lower boundary of the Serpukhovian; t is the time from this boundary prior to the beginning of respective age (m.y.).

ing at a certain moment reached half of the entire entomofauna (whereas the second half of families appeared after that moment). Figure 8 shows the period of half-renewal of insect families existing from the Moscovian to Albian. After the Albian up to the Recent, faunas renewed by half are absent. The observed time of half-renewal of entomofauna is characterized by significant fluctuations; therefore, its linear growth shown in Fig. 8 is questionable; in general, the increase in the half-cycle is rather distinct. Before the Norian, it is particularly strongly pronounced,

whereas in the Jurassic and Cretaceous before the Aptian, it is masked owing to a decrease in the time of renewal for the families existing at the beginning of some ages. The accelerated renewal of the family composition observed in some cases can be determined by the presence of large localities with a number of first and last occurrences of families soon after the age, in which the time of half-renewal of fauna is determined.

In particular, the acceleration of renewal of Artinskian and Kungurian entomofaunas is apparently

$$T = 0.23t \quad R^2 = 0.30$$
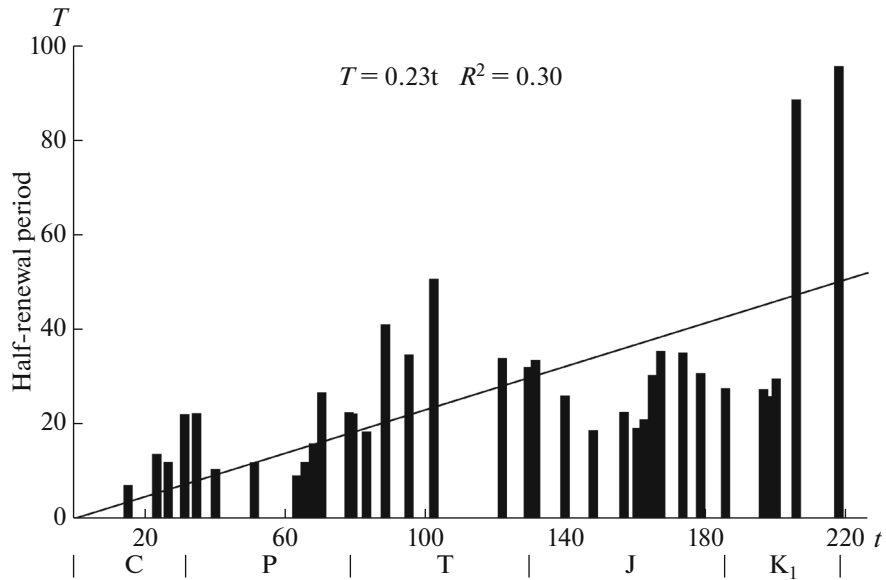
Fig. 8. Time of half-renewal (T) of the composition of families existing at successive boundaries of ages; t is the time from the beginning of the Serpukhovian (m.y.).

connected with the extensive collection material from Kungurian deposits, Induan–Anisian insects from the Anisian of Voges, the insects existing at the beginning of the Carnian with Carnian collections. The same concerns Plinsbachian and Toarcian insects, which is likely determined by the abundant West European Toarcian material and, in the Tithonian and Berriasian, by Early Cretaceous material from Central Asia.

Both consequences of a decrease in the per-family rates suggest that, with the growth of diversity, entomofaunas become more stable. For marine animals, a decrease in the per-family rate of extinction during the Phanerozoic is known since the 1980s (Van Valen, 1984); the same is true of the per-family rate of the appearance of new taxa, as was shown later (Alekseev et al., 2001). Thus, the stability of the entire biota increases in time, which is one of the main properties of the evolution of biodiversity as a whole.

In the changes in insect diversity, five characteristic intervals are recognized (Fig. 9).

It is noteworthy that the diversity rapidly and constantly grew from the Serpukhovian up to the beginning of the Middle Permian, when the number of families reached 93. The mean rates of the appearance and extinction during this time are 3.4 and 1.9 fam./m.y., respectively; the mean rate of diversifications is 1.5 fam./m.y. The knowledge of insects of the Kasimovian, Asselian, and Artinskian ages is limited and actual diversity of the group changes only slightly during these ages.

In the Middle and Late Permian, there was a general decrease in the number of families (at a rate of 1.6 fam./m.y.) to 68 at the boundary with the Triassic; the rate of appearance was 4.7 fam./m.y., that is,

higher than within the Serpukhovian–Kungurian, but the rate of extinction was even higher, 6.3 fam./m.y. On this background, the number of families increased somewhat in the Severodvinian (from 77 to 82), so that a small additional minimum of actual diversity is observed at its lower boundary. A thorough analysis of Middle–Late Permian transformations of the entomofauna, based on the data on particular local insect assemblages, was performed by Aristov et al. (2013).

In the Triassic and up to the Toarcian, an essential increase in the number of families has not been recorded. It grew from 68 at the boundary with the Permian to 111 at the end of the Plinsbachian, with the
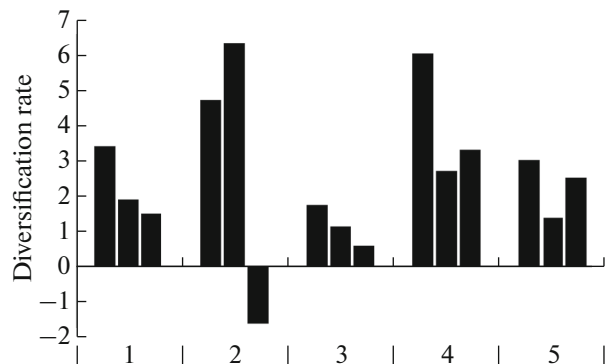
Fig. 9. The mean rates (fam./m.y.) of appearances (left columns in each group), extinctions (middle columns), and changes in diversity (right columns) of insects at the main stages of their diversification: (1) Carboniferous–Early Permian, (2) Middle–Late Permian, (3) Triassic–Plinsbachian, (4) Toarcian–Santonian, (5) Campanian–Recent.
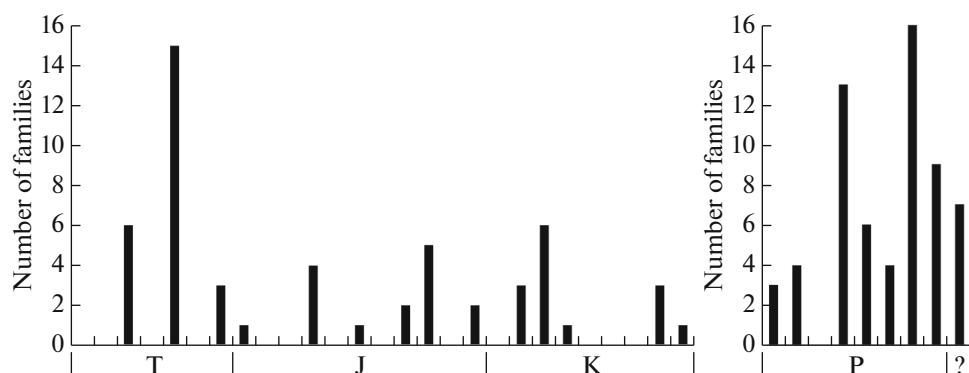
Fig. 10. Extinction in the Mesozoic from the Induan to Campanian of families that appeared in the Carboniferous and Permian (left histogram) and appearance in the Permian of families that became extinct in the Mesozoic (right histogram); question mark designates intertrappean deposits of the Tunguska Basin with uncertain Vyatkian−Induan age.

mean rate of 0.6 fam./m.y. The mean rates of appearance and extinction are 1.75 and 1.15 fam./m.y., respectively. During this interval, changes in actual diversity were weakest in the history of insects. This is probably caused by a poor understanding of Triassic insects compared to that of other periods. In particular, first occurrences and extinctions of families in the Early Triassic have not been revealed, but collections from the deposits of this age are very poor. Ladinian, Norian, and Rhaetian insect assemblages are also insufficiently investigated.

Unexpectedly, in Carnian material, the last occurrences prevail over the first occurrences, with a decrease in the number of families from 88 to 78. This may be caused by the abundance in the Carnian of the families appearing in the Paleozoic and found here for the last time (Fig. 10, left histogram). In the Permian, the greatest number of families that became extinct after the Paleozoic is found in the Kungurian and Severodvinian (Fig. 10, right histogram). The most abundant Permian and Triassic collections come from the Carnian, Kungurian, and Severodvinian. In the diagnostics of the taxonomic position of genera, an important role is usually played by taxonomic conservatism (to assign a genus to a known family is a less responsible action than the description of a new family), this, along with the volume of collections, is responsible for a decrease in the number of families in the Carnian. In any event, before resolution of this problem, we should not attach great significance to it.

After the Early Jurassic, any great events in the history of insect diversity have not been recorded. The actual number of families in general constantly grows with a varying rate. Transition to this growth of diversity in general corresponds to the beginning of a great expansion of insects with complete metamorphosis (Nicholson et al., 2015). The entomofauna of some ages is investigated insufficiently, as reflected, in particular, in a few first or last representatives of families found in these ages (Fig. 1). Only two points deserve

special attention. First, the absence in the middle of the Cretaceous of a minimum of insect diversity is corroborated (Alekseev et al., 2001; Dmitriev and Ponomarenko, 2002; Rasnitsyn et al., 2016), which was presumed previously (Zherikhin, 1978; Dmitriev and Zherikhin, 1988; Rasnitsyn, 1988) in connection with reorganization of vegetation at the transition from the Mesophytic to Cenophytic. Second, in the Campanian, after generalization of the data on Cretaceous ambers (Rasnitsyn et al., 2016), a decrease in the number of families was revealed. However, a poor understanding of Maastrichtian and Danian insects prevents the judgment of changes in insect diversity at the Mesozoic−Cenozoic boundary. If the families found for the last time in the Campanian continued to exist later, the observed prevalence of the last occurrences in this age may result from the poor data on the Maastrichtian.

The rate of the appearance of families from the beginning of the Toarcian to Recent is retained with significant fluctuations about the mean value of 4.7 fam./m.y., whereas the rate of extinction varies considerably within Toarcian−Santonian (2.7 fam./m.y.) and Campanian−Recent (0.5 fam./m.y.). In the first interval, the mean rate of the appearance of families is 6.0 fam./m.y.; on the second, 3.0 fam./m.y., and the rates of diversification are 3.3 and 2.5 fam./m.y., respectively. A sharp deceleration of extinctions in the last interval was recorded previously (Zherikhin, 1978, etc.). It clearly distinguishes insects from other large groups of modern animals and requires special interpretation. The Cenozoic deceleration of extinctions may at least partly depend on taxonomic preferences of paleoentomologists, who are frequently inclined to assign fossil insects to modern families, and result from the above-mentioned "taxonomic conservatism."

A remarkable feature of observed diversification of insects is existence only one confidently established minimum of their diversity close to the Permian−Triassic boundary.

REFERENCES

Alekseev, A.S., Dmitriev, V.Yu., and Ponomarenko, A.G., *Evolyutsiya taksonomicheskogo raznoobraziya* (Evolution of Taxonomic Diversity), Moscow: GEOS, 2001.

Alroy, J., Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates, *Paleontol. Soc. Pap.,* 2010, vol. 16 (Quantitative Methods in Paleobiology, Alroy, J. and Hunt, G., Eds.), pp. 55—80.

Aristov, D.S., Bashkuev, A.S., Golubev, V.K., et al., Fossil insects of the Middle and Upper Permian of European Russia, *Paleontol. J.,* 2013, vol. 47, no. 7, pp. 641—832.

Clapham, M.E., Karr, J.A., Nicholson, D.B., et al., Ancient origin of high taxonomic richness among insects, *Proc. Roy. Soc. B: Biol. Sci.,* 2016, vol. 283. http://dx.doi.org/10.1098/rspb.2015.2476

Dmitriev, V.Yu., Early Cretaceous insect assemblages of Central Asia, *Electronic Resource.* URL: http://palaeoentomolog.ru/bibl/entomocomplex.html.

Dmitriev, V.Yu., A complete diversity of fossils: Perspectives, *Paleontol. Zh.,* 2016, no. 6, pp. 3—10.

Dmitriev, V.Yu. and Ponomarenko, A.G., Dynamics of insect taxonomic diversity, in *History of Insects,* Rasnitsyn, A.P. and Quicke, D.L.J., Eds., Dordrecht: Kluver Acad. Publ., 2002, pp. 325—331.

Dmitriev, V.Yu. and Ponomarenko, A.G., Diversity curves revisited, *Paleontol. Zh.,* 2009, no. 2, pp. 102—105.

Dmitriev, V.Yu. and Zherikhin, V.V., Changes in diversity of insect families based on the method of accumulated occurrences, in *Melovoi biotsenoticheskii krizis i evolyutsiya nasekomykh* (Cretaceous Biocoenotic Crisis and the Evolution of Insects), Ponomarenko, A.G., Ed., Moscow: Nauka, 1988, pp. 208—215.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M., Eds., *Geologic Time Scale 2012,* Amsterdam: Elsevier, 2012.

Jarzembowski, E.D. and Ross, A., Time flies: The geological record of insects, *Geology Today,* 1993, vol. 9, pp. 218—223.

Jarzembowski, E.D. and Ross, A.J., Insect origination and extinction in the Phanerozoic, *Geol. Soc. Spec. Publ.,* 1996, no. 102 (Biotic Recovery from Mass Extinction Events, Hart, M.B., Ed.), pp. 65—78.

Labandeira, C.C., A compendium of fossil insect families, *Contrib. Milwaukee Publ. Mus. Biol. Geol.,* 1994, no. 88, pp. 1—71.

Labandeira, C.C., The fossil record of insect extinction: New approaches and future directions, *Am. Entomol.,* 2005, vol. 51, no. 1, pp. 14—29.

Labandeira, C.C. and Eble, G.J., The fossil record of insect diversity and disparity, *Santa Fe Inst. Work. Pap.,* 2001, vol. 121 (Gondwana Alive: Biodiversity and Evolving Biosphaere, Anderson, J., Thackerey, F., Van Wyk, B., and De Wit, M., Eds.), pp. 1—54.

Labandeira, C.C. and Sepkoski J.J, Jr., Insect diversity in the fossil record, *Science,* 1993, vol. 261, pp. 310—315.

List of families of fossil insects, *Electronic Resource.* URL: http://palaeoentomolog.ru/bibl/fam.html.

Newell, N.D., Adequacy of the fossil record, *J. Paleontol.,* 1959, vol. 33, no. 3, pp. 488—499.

Nicholson, D.B., *Fossil perspectives on the evolution of insect diversity,* 2012, pp. 1—421. URL: http://etheses.whiterose.ac.uk/3713/1/DB_Nicholson_PhD_Thesis.pdf.

Nicholson, D.B., Mayhew, P.J., and Ross, A.J., Changes to the fossil record of insects through fifteen years of discovery, *PLoS. ONE,* 2015, vol. 10, no. 7, pp. 1—61.

Nicholson, D.B., Ross, A.J., and Mayhew, P.J., Fossil evidence for key innovations in the evolution of insect diversity, *Proc. Roy. Soc. B,* 2014, vol. 281, no. 1793, pp. 1—7. http://rspb.royalsocietypublishing.org/content/suppl/2014/08/26/rspb.2014.1823.DC1.

Ponomarenko, A.G., Insects during the time around the Permian—Triassic crisis, *Paleontol. Zh.,* 2016, no. 2, pp. 68—81.

Rasnitsyn, A.P., Problem of the global crisis of terrestrial ecosystems in the middle of the Cretaceous Period, in *Melovoi biotsenoticheskii krizis i evolyutsiya nasekomykh* (Cretaceous Ecosystem Crisis and Evolution of Insects), Ponomarenko, A.G., Ed., Moscow: Nauka, 1988, pp. 191—207.

Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., et al., Sequence and scale of changes in terrestrial biota during the Cretaceous (based on materials from fossil resins), *Cret. Res.,* 2016, vol. 61, pp. 234—255.

Sohn, J.-C., Labandeira, C., Davis, D., and Mitter, C., An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the World, *Zootaxa,* 2012, vol. 3286, pp. 1—132.

Van Valen, L.M., A resetting of Phanerozoic community evolution, *Nature,* 1984, vol. 307, pp. 50—52.

Zherikhin, V.V., Development and changes in Cretaceous and Cenozoic faunal assemblages (tracheates and chelicerates), *Tr. Paleontol. Inst. Akad. Nauk SSSR,* 1978, vol. 165, pp. 1—198.

Translated by G. Rautian