

Taxonomic Diversification of Normal-Marine Bivalve Mollusks in the Phanerozoic

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Abstract—The dynamics of the taxonomic diversification of normal-marine bivalve mollusks and that of the entire fossil marine skeletal fauna are compared. A major Early Permian turnover has been revealed. The changes in the proportions of the bivalve mollusks to the entire marine fauna during the Phanerozoic are studied.

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This paper continues the series of papers (Dmitriev, 2004, 2005) on the changes in the taxonomic diversity of major groups of fossil marine animals during the Phanerozoic in the context of the diversification of marine fauna as a whole. The methods used are described in these previous papers. The study is based on data on the age of the first and last appearances of representatives of fossil bivalve genera available from the literature and on our own data on the Cenozoic bivalves. Data on the stratigraphic ranges of as many as 1812 genera of fossil bivalves have been used. Comparative material on the entire fossil marine fauna has been taken from the compendium by Sepkoski (2002), in which the ranges of 35638 genera are listed. In Sepkoski's compendium some bivalve genera are provided with more detailed ranges than in our database. Those of Sepkoski's dates that are consistent with our data (250 of 3167) have been used to correct our dates.

Sepkoski's compendium provides data on 2844 genera of bivalve mollusks, i.e., it contains 1032 genera more than our database, which in turn provides data on 162 genera absent from Sepkoski's list. These are predominantly recently described genera and a number of genera from the territory of the former USSR. Thus, there are 1650 genera common to both lists. These differences in the number of genera are mainly due to the fact that genera in Sepkoski's list have a narrower scope rather than to the completeness of Sepkoski's fossil material. Many of the genera that he believed to be independent are synonyms or subgenera. In addition, Sepkoski's list includes many genera that are not normal-marine.

Because of differences in understanding of genera (along with inevitable differences in the treatment of available global data), many dates in our database differ from those provided by Sepkoski. Of genera common to both lists, 431 genera are extant, i.e., there are 2869 dates of appearance and extinction, of which 570 dates are

different. Most of the chronological discrepancies are due to differences in the system of genera. In order to use such an index as the number of taxa for studying the evolution of biodiversity of fossil organisms, we should determine how variations in the system adopted in the study may affect the general character of conclusions (Maxwell and Benton, 1990; Dmitriev, 2001). In our case the differences in initial material are very considerable; thus, comparison between the results of investigations based on both data sets may be of considerable interest not only for the evolution of bivalve mollusks.

The graphs showing the relationship between the numbers of appeared (Fig. 1a) and extinct (Fig. 1b) genera of bivalve mollusks and the respective numbers of appeared and extinct genera of all marine animals known in the fossil state during the entire history of this group are almost independent of the material used. Although the curves constructed based on our data (upper graphs in Figs. 1a, 1b) and those based on Sepkoski's data (lower graphs in the same figures) are similar, the latter are slightly more concave. However, this difference does not affect the major structural features that all the four graphs have in common: a Paleozoic part that forms a gently curving arc from the beginning of the Arenigian to the end of the Sakmarian (for the appearance of new genera) or Leonardian¹ (for the extinction of genera) ages (Cambrian bivalves are poorly represented and cannot be analyzed quantitatively) and a nearly straight part from the end of the Sakmarian (appearance) or Leonardian (extinction) ages to the Recent. The graphs of extinction (Fig. 1b) clearly show a Maastrichtian step that divides the Per-

¹ Sepkoski divided the Permian System into the Asselian, Sakmarian, Leonardian, Guadalupian, Djulfian, and Dorashamian stages. The Leonardian Stage, which according to Sepkoski's (now outdated) correlation corresponds approximately to the Artinskian and Kungurian stages of the East European scale.

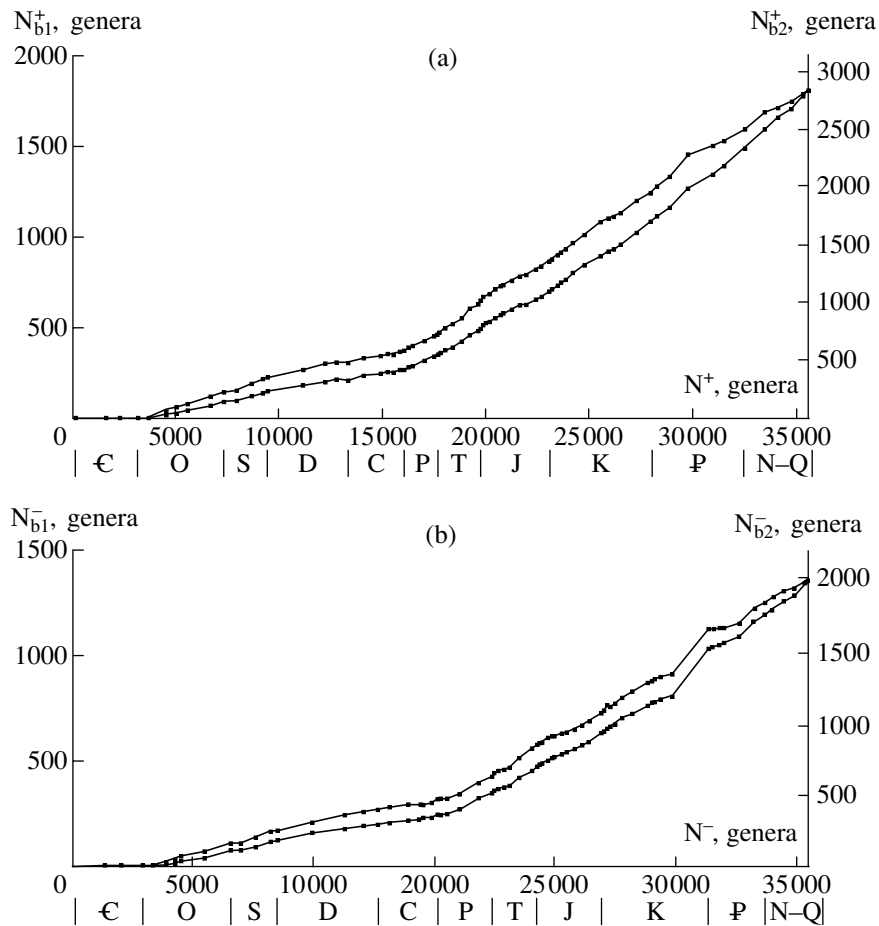


Fig. 1. Appearance and extinction of genera of bivalve mollusks in the Phanerozoic: (a) appearance of genera and (b) extinction of genera. The number of genera of all marine animals that appeared (N^+) and became extinct (N^-) from the beginning of the Cambrian is plotted along the horizontal axis, the same is plotted along the vertical axis for bivalve mollusks. On both graphs the upper curve is constructed based on our own data (scale on the left, N_{b1}^+ , N_{b1}^-); the lower curve, on Sepkoski's data (scale on the right, N_{b2}^+ , N_{b2}^-). Figures 2 and 3 have the same designations.

mian–Mesozoic–Cenozoic parts into pre-Maastrichtian and Cenozoic parts.

Each of the two intervals in the development of the group is represented in greater detail in Figs. 2 and 3. Figure 2 shows both the Paleozoic and Triassic parts. Although the transition from the Paleozoic to Permian–Mesozoic–Cenozoic interval is slightly flattened, it is sufficiently clearly seen in three of the four curves. The intervals where the curves of the appearance and extinction of genera in the Paleozoic constructed based on our and Sepkoski's data deviate from linearity almost coincide. For the Permian–Mesozoic–Cenozoic interval in Fig. 3b, both data sets yield virtually identical curves of extinctions: there are two linearity intervals that fairly accurately coincide with the interval from the end of the Leonardian to the Maastrichtian and that of the Cenozoic, which are divided by a distinct Maastrichtian step. The curve of the appearance of new genera constructed based on our data (Fig. 3a) closely approximates a linear relationship from the Permian to

the Recent, with the most marked deviation in the Eocene. In contrast, the graph constructed based on Sepkoski's data is slightly concave; thus, this time interval cannot be approximated by a linear relationship. This graph shows no clearly defined bends; nevertheless, it may be divided into two almost linear parts with a boundary located at the beginning of the Campanian.

Thus, both data sets studied clearly show a close relationship between the diversification of bivalve mollusks and the evolution of the taxonomic diversity of the entire marine fauna. For bivalve mollusks this relationship was previously proposed by Miller and Sepkoski (1988), who arrived at their conclusions based on circumstantial evidence, by analyzing exclusively the evolution of the biodiversity of bivalves. Direct correlation of the diversification of bivalve mollusks with that of the entire marine fauna supports their opinion and, in addition, makes it possible to find out the form of this relationship.

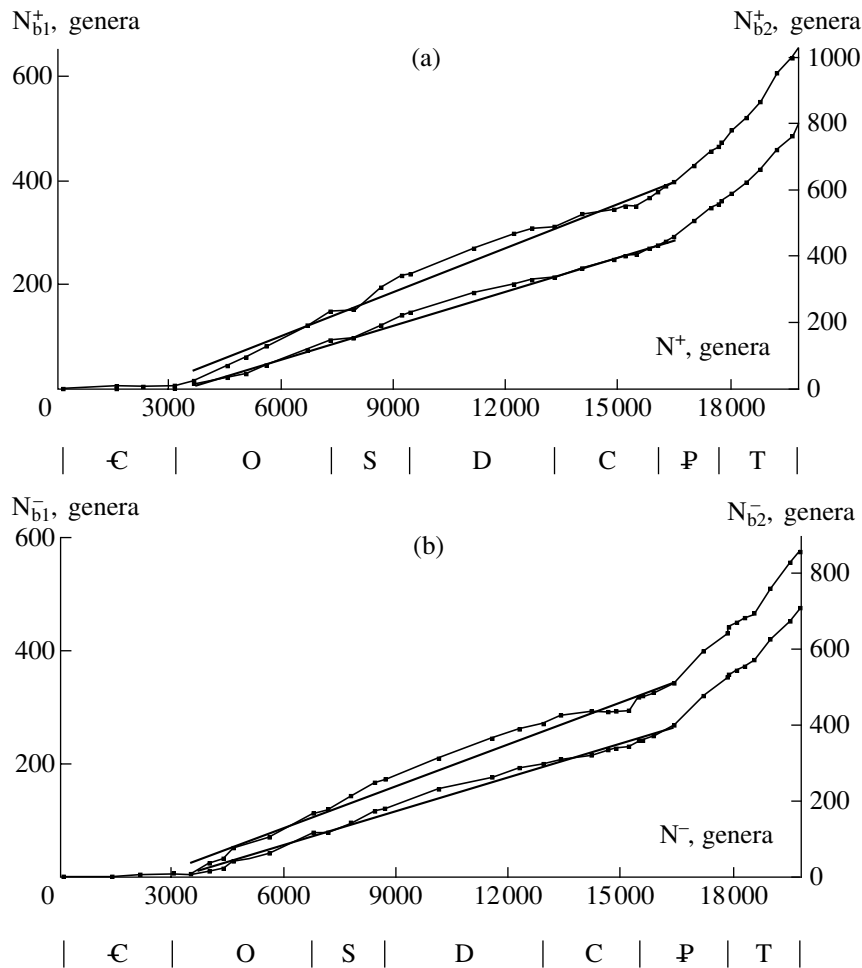


Fig. 2. Appearance and extinction of genera of bivalve mollusks in the Paleozoic and Triassic.

Table 1 shows the ratios (in percent) of the bivalve genera that appeared and became extinct to all fossil marine genera that appeared and became extinct (the parenthesized ratios are given according to Sepkoski). In the middle and terminal Early Permian these ratios increased from 2.8% (3.4%) up to 7.5% (10.4%) for appeared new genera and from 2.6% (3.0%) up to 6.5% (9.3%) for extinct genera, i.e., by a factor of 2.5–3. According to Sepkoski's data, the ratio of new bivalve genera to all marine genera appeared in the Campanian, Maastrichtian, and Cenozoic was greater than those appeared during the end of the Permian and most of the Mesozoic by 40% (increased from 10.4 up to 14.7%). The existence of this phenomenon, which according to Sepkoski is six to eight times less important than the major Permian turnover, is not supported by our material. This invites further investigations, although this may most likely be attributed to differences in the selection of data: Sepkoski's list includes genera that lived under nonmarine conditions, whereas our database does not include them. Since such genera are better identified

from the Cenozoic, it is this interval that shows the most marked differences in the respective data.

Thus, the relationship between the diversification of bivalve mollusks and the evolution of the taxonomic diversity of marine animals as a whole may be divided into two well-defined phases with a boundary between them running through the Permian. The Maastrichtian extinction divides the Mesozoic–Cenozoic history of bivalves into two parts; however, the ratio of extinct bivalves to all extinctions did not change. Our data show that this ratio is 6.5% in the Mesozoic and 6.3% in the Cenozoic, Sepkoski's data yield 9.3 and 12.0%, respectively; i.e., it increased by 30%; however, this may be again caused by differences in data selection concerning the genera inhabiting environments different from normal-marine ones.

The change in the regime of diversification of bivalve mollusks that occurred in the Permian bears no relation to any evident turnover in the taxonomic or ecological composition of the group. The ordinal affiliation of the genera appeared during the Permian shows

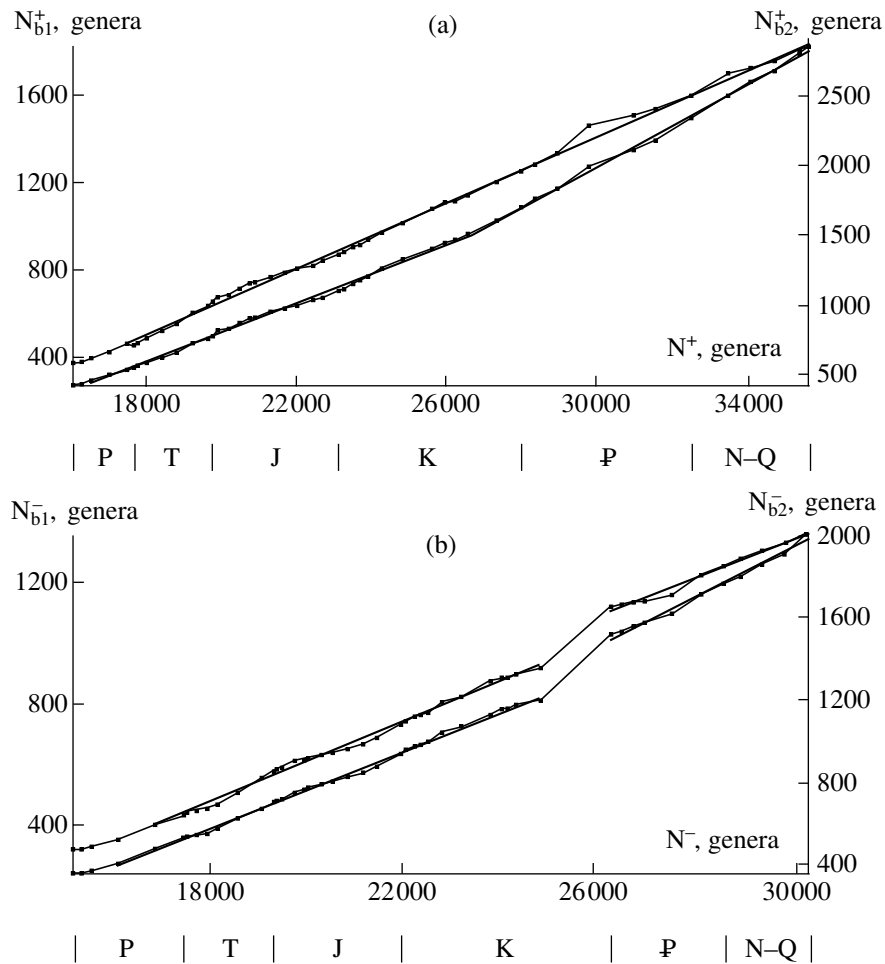


Fig. 3. Appearance and extinction of genera of bivalve mollusks from the beginning of the Permian to the Recent.

no marked changes. The most salient feature in the ecological history of bivalve mollusks was an increased importance of infauna: detritivores with siphons from the orders Venerida and Pholadomyida (Stanley, 1981; Neveeskaja, 2003). This is most clearly seen in the Cenozoic and does not coincide with the changes in the contribution of bivalves to the appearance of marine

animal genera. The Permian shift in the evolution of the group may be due to some general changes in the structure of biotic relationships of marine animals that created favorable conditions for a wider expansion of bivalve mollusks rather than to evolutionary transformations of bivalves themselves. In particular, the second half of the Early Permian marked the beginning of a general decline in the taxonomic diversity of marine animals, including most brachiopod groups, major competitors of bivalve mollusks in the Paleozoic (Afanasjeva and Neveeskaja, 1994; Afanasjeva et al., 1998; Neveeskaja, 2003).

Table 1. The ratios of the marine bivalve genera that appeared and became extinct to those of the entire marine fauna (in percents)

	Appearance	Extinction
Arenigian–Sakmarian	2.8 (3.4)	–
Arenigian–Leonardian	–	2.6 (3.0)
Leonardian–Recent	7.5	–
Leonardian–Santonian	(10.4)	–
Guadalupian–Campanian	–	6.5 (9.3)
Campanian–Recent	(14.7)	–
Danian–Recent	–	6.3 (12.0)

The changes in the number of genera of bivalve mollusks compared with those of all marine animals known in the fossil state are shown in Fig. 4. The graphs constructed for bivalves based on our and Sepkoski's data virtually coincide up to the Oligocene, after which the differences in the selection of genera other than normal-marine presumably become increasingly important. The Paleozoic parts of the graphs show a gradual increase in the importance of bivalve mollusks in the marine fauna and coincidence of the major minima of

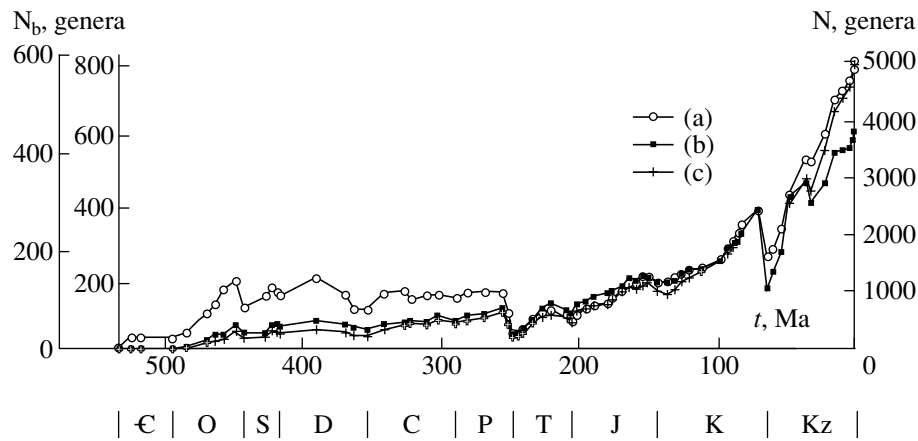


Fig. 4. Changes in the generic diversity of bivalve mollusks during the Phanerozoic compared with those of all fossil marine animals: (a) and (b) bivalve mollusks; (a) our data, (b) according to Sepkoski (2002); and (c) all marine animals (Sepkoski, 2002). Designations: N_b is the number of bivalve genera (scale on the left of the axis shows our own data, scale on the right of the axis shows Sepkoski's data), N is the number of genera in the entire fossil marine fauna.

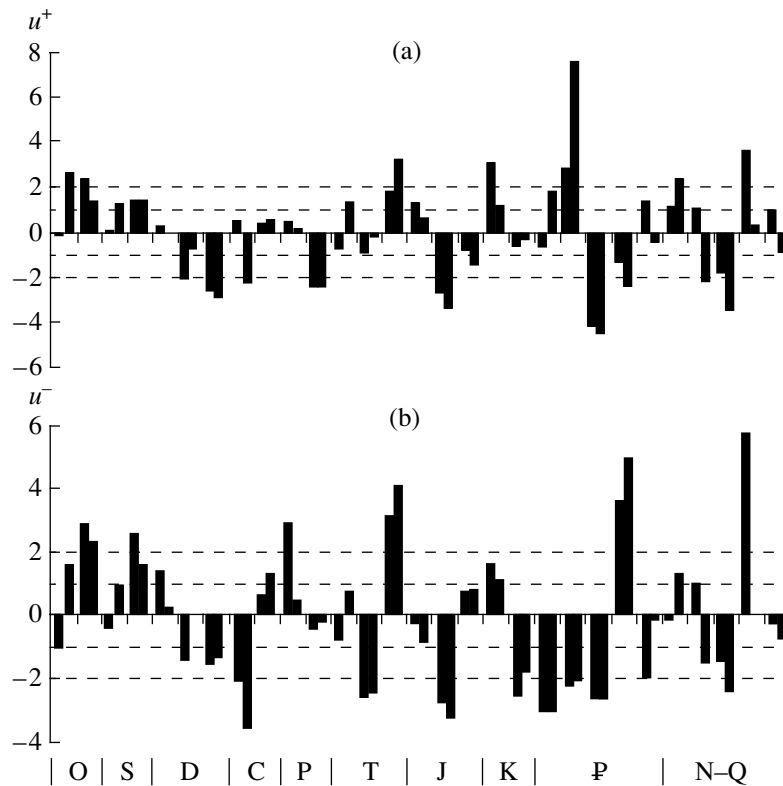


Fig. 5. Standardized deviations from the established number of appearances and extinctions of genera of marine bivalve mollusks for each epoch: (a) appearance of genera and (b) extinction of genera. For each epoch the deviations calculated based on our own and Sepkoski's data (2002) are given on the right and left, respectively. In Fig. 5b the Late Cretaceous is shown without considering data on the Maastrichtian.

diversity. The Mesozoic parts of all three graphs are virtually identical. Pairwise comparisons of the graphs show that the degree of linear association is highest for bivalve mollusks (correlation coefficient 0.99) and is slightly lower for all marine animals compared with Sepkoski's (0.98) and our (0.96) data on bivalves. Con-

siderable differences in the initial data on bivalve mollusks do not give rise to considerable differences in the results obtained.

Contrastingly, the analysis of deviations from the linear relationship could hardly be expected to yield

Table 2. Appearance of genera of marine bivalve mollusks

	<i>n</i>	<i>n</i> *	σ	<i>u</i>	Δ	$\Delta/n, \%$
Early–Middle Ordovician	111 (102)	86 (103)	9.3 (10.1)	2.7 (–0.1)	–16 (0)	14 (0)
Late Ordovician	24 (32)	18 (21)	4.2 (4.6)	1.4 (2.4)	0 (–6)	0 (19)
Early Silurian	46 (47)	38 (46)	6.2 (6.8)	1.3 (0.1)		
Late Silurian	29 (35)	22 (27)	4.7 (5.2)	1.5 (1.5)		
Early Devonian	49 (60)	49 (58)	7.0 (7.6)	0 (0.3)		
<i>Middle Devonian</i>	27 (24)	31 (37)	5.6 (6.1)	–0.7 (–2.1)	0 (7)	0 (29)
Late Devonian	15 (21)	31 (37)	5.6 (6.1)	–2.9 (–2.6)	11 (10)	73 (48)
Early Carboniferous	38 (70)	54 (65)	7.3 (8.1)	–2.2 (0.6)	9 (0)	24 (0)
Middle–Late Carboniferous	27 (31)	24 (29)	4.9 (5.4)	0.6 (0.4)		
Early Permian	52 (72)	51 (68)	7.1 (8.2)	0.1 (0.5)		
Late Permian	34 (51)	51 (71)	7.1 (8.4)	–2.4 (–2.4)	10 (12)	29 (24)
Early Triassic	33 (31)	26 (36)	5.1 (6.0)	1.4 (–0.8)		
Middle Triassic	57 (73)	58 (81)	7.6 (9.0)	–0.1 (–0.9)		
<i>Late Triassic</i>	100 (119)	72 (100)	8.5 (10.0)	3.3 (1.9)	–20 (0)	20 (0)
Early Jurassic	81 (116)	75 (103)	8.7 (10.1)	0.7 (1.3)		
Middle Jurassic	59 (96)	92 (127)	9.6 (11.3)	–3.4 (–2.7)	23 (19)	39 (20)
Late Jurassic	73 (109)	86 (118)	9.3 (10.9)	–1.4 (–0.8)		
Early Cretaceous	141 (220)	129 (178)	11.4 (13.3)	1.1 (3.2)	0 (–29)	0 (13)
Late Cretaceous	235 (377)	239 (388)	15.5 (19.7)	–0.3 (–0.6)		
Paleocene	89 (135)	73 (142)	8.5 (11.9)	1.9 (–0.6)		
Early Eocene	124 (154)	63 (122)	7.9 (11.0)	7.7 (2.9)	–53 (–21)	43 (14)
Middle Eocene	47 (119)	89 (174)	9.4 (13.2)	–4.5 (–4.2)	33 (42)	70 (35)
<i>Late Eocene</i>	27 (73)	43 (85)	6.6 (9.2)	–2.4 (–1.3)	9 (0)	33 (0)
Oligocene	69 (156)	72 (139)	8.5 (11.8)	–0.4 (1.4)		
Early Miocene	92 (155)	72 (141)	8.5 (11.9)	2.4 (1.2)	–12 (0)	13 (0)
<i>Middle Miocene</i>	31 (100)	46 (90)	6.8 (9.5)	–2.2 (1.1)	8 (0)	26 (0)
<i>Late Miocene</i>	24 (76)	48 (93)	6.9 (9.6)	–3.5 (–1.8)	17 (0)	71 (0)
<i>Pliocene</i>	52 (133)	50 (97)	7.1 (9.8)	0.3 (3.7)	0 (–26)	0 (20)
Pleistocene	16 (45)	20 (39)	4.5 (6.2)	–0.9 (1.0)		

Note: Designations: *n* is the number of observed appearances of genera, *n** is the mathematical expectation of the number of appearances of genera, σ is the root-mean-square deviation, *u* is the standardized deviation, Δ is the number of genera that should be added to (+) or subtracted from (–) the observed number of genera to make the standardized deviations equal to 1, $\Delta/n, \%$ the same expressed as a percentage of the established number of appeared genera. The parenthesized values are given according to Sepkoski. Table 3 has the same designations for extinct genera.

an equally high degree of similarity for each epoch (Tables 2, 3; Fig. 5). Indeed, the correlation coefficient of the standardized deviations is 0.7 with a 95% confidence interval of 0.5–0.8. Twenty-one of the 58 deviations are given in bold type as worthy of further study. Thirteen of these 21 deviations are given in Roman typeface. These are deviations that have been estab-

lished based on both our and Sepkoski's data: the deficiency of appearances in the Late Devonian, Late Permian, Middle Jurassic, and Middle Eocene; the excess of appearances in the Early Eocene; the deficiency of extinctions in the Early Carboniferous, Middle Triassic, Middle Jurassic, Paleocene, and the Early and Middle Eocene; and the excess of extinctions in the Late Trias-

Table 3. Extinction of genera of marine bivalve mollusks

	<i>n</i>	<i>n</i> *	σ	<i>u</i>	Δ	$\Delta/n, \%$
Early–Middle Ordovician	66 (55)	54 (63)	7.3 (7.9)	1.6 (–1.0)		
Late Ordovician	40 (51)	28 (34)	5.3 (5.8)	2.3 (2.9)	–7 (–11)	18 (22)
Early Silurian	31 (27)	26 (30)	5.1 (5.5)	1.0 (–0.5)		
Late Silurian	32 (42)	24 (28)	4.9 (5.3)	1.6 (2.6)	0 (–8)	0 (19)
Early Devonian	37 (51)	36 (42)	6.0 (6.5)	0.2 (1.4)		
Middle Devonian	36 (32)	36 (42)	6.0 (6.5)	0.0 (–1.5)		
Late Devonian	27 (31)	35 (41)	5.9 (6.4)	–1.4 (–1.6)		
Early Carboniferous	20 (37)	44 (52)	6.6 (7.2)	–3.6 (–2.1)	17 (8)	85 (22)
Middle–Late Carboniferous	27 (27)	21 (24)	4.6 (4.9)	1.3 (0.6)		
<i>Early Permian</i>	<i>24 (42)</i>	<i>22 (27)</i>	<i>4.7 (5.2)</i>	<i>0.4 (2.9)</i>	<i>0 (–10)</i>	<i>0 (24)</i>
Late Permian	88 (123)	91 (129)	9.5 (11.4)	–0.3 (–0.5)		
Early Triassic	21 (21)	18 (25)	4.2 (5.0)	0.7 (–0.8)		
Middle Triassic	16 (26)	30 (43)	5.5 (6.6)	–2.5 (–2.6)	8 (11)	50 (42)
Late Triassic	109 (137)	74 (105)	8.6 (10.2)	4.1 (3.1)	–27 (–21)	25 (15)
Early Jurassic	38 (60)	44 (62)	6.6 (7.9)	–0.9 (–0.3)		
Middle Jurassic	32 (56)	57 (81)	7.5 (9.0)	–3.3 (–2.8)	17 (16)	53 (29)
Late Jurassic	80 (111)	73 (104)	8.5 (10.2)	0.8 (0.7)		
Early Cretaceous	94 (138)	84 (120)	9.2 (11.0)	1.1 (1.6)		
Cenomanian–Campanian	87 (121)	107 (153)	10.3 (12.4)	–1.9 (–2.6)	0 (20)	0 (17)
Paleocene	12 (33)	29 (56)	5.4 (7.5)	–3.1 (–3.1)	11 (16)	92 (48)
Early Eocene	6 (15)	14 (27)	3.7 (5.2)	–2.2 (–2.3)	4 (7)	67 (47)
Middle Eocene	20 (47)	36 (69)	6.0 (8.3)	–2.7 (–2.7)	10 (14)	50 (30)
Late Eocene	69 (105)	38 (74)	6.2 (8.6)	5.0 (3.6)	–25 (–22)	36 (21)
Oligocene	28 (41)	29 (56)	5.4 (7.5)	–0.2 (–2.0)		
Early Miocene	27 (40)	21 (41)	4.6 (6.4)	1.3 (–0.2)		
Middle Miocene	26 (61)	28 (54)	5.3 (7.3)	–0.4 (1.0)		
Late Miocene	20 (44)	29 (55)	5.4 (7.4)	–1.7 (–1.5)		
<i>Pliocene</i>	<i>28 (96)</i>	<i>28 (54)</i>	<i>5.3 (7.3)</i>	<i>0.0 (5.8)</i>	<i>0 (–35)</i>	<i>0 (36)</i>
Pleistocene	4 (10)	6 (11)	2.4 (3.3)	–0.8 (–0.3)		

sic and Late Eocene. The other eight deviations, expressed in italics, have only been established in one of the two data sets.

Changes in the proportion of genera of bivalve mollusks within the composition of marine fauna during the Phanerozoic are shown in Fig. 6. Here again the results obtained based on the two data sets are in good agreement (correlation coefficient 0.94). The proportion of bivalves generally increased throughout the Paleozoic and Triassic. It is worth noting that in all episodes in which the diversity of either the marine animals as a whole or bivalve mollusks diminished (Fig. 4) the proportion of the group increased. Thus, as in the

example of foraminifers and gastropods (Dmitriev, 2004, 2005), the increase in the proportion of the group is not restricted to any specific episode and cannot be used for the causal analysis of separate events. In the Paleozoic the one exception is a degree of decline in the proportion of bivalve mollusks in the Late Carboniferous, when a general decrease in marine biodiversity was poorly defined and not quite reliably established. In contrast to all other Paleozoic episodes, the general increase in the proportion of bivalves in the Givetian–Late Devonian was not uniform: the Famennian and Norian show a degree of decline in the proportion of the group.

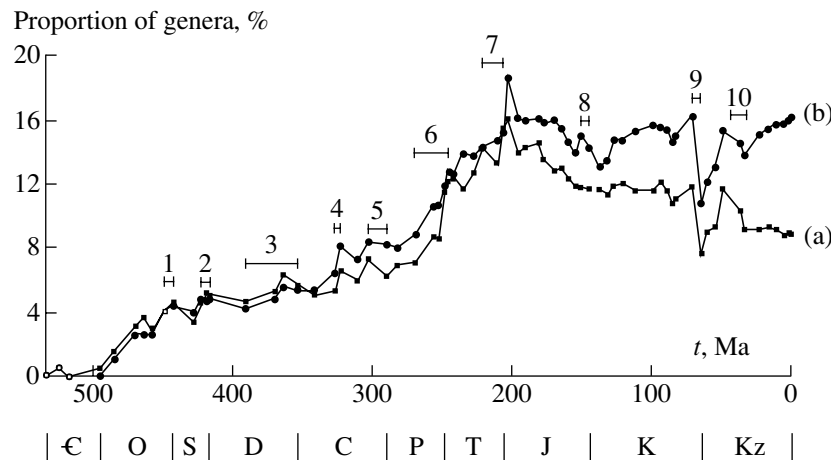


Fig. 6. Changes in the contribution of genera of bivalve mollusks to the composition of marine fauna during the Phanerozoic: (a) our data and (b) according to Sepkoski (2002). Designations: (1) Ashgillian, (2) Late Silurian, (3) Givetian–Late Devonian, (4) Serpukhovian, (5) Late Carboniferous, (6) Leonardian–Induan, (7) Norian–Rhaetian, (8) Tithonian, (9) Maastrichtian, and (10) Late Eocene.

After the Triassic the contribution of bivalve mollusks to the composition of marine fauna decreased at least to the Hauterivian. This previously unknown fact is of interest. During the Late Jurassic, Maastrichtian, and Late Eocene episodes of the decrease in taxonomic diversity, the proportion of bivalve mollusks diminished especially abruptly at the end of the Cretaceous. From the Oligocene to the Recent, the proportion of bivalves has been slightly diminishing according to our data and increasing according to Sepkoski. This difference is apparently due to the previously mentioned difference in the selection of genera other than normal-marine.

CONCLUSIONS

These results support the conclusions made earlier based on data on the development of foraminifers and gastropods that there is a close connection between the development of major groups of fossil animals and the entire marine biota (Dmitriev, 2004, 2005). In addition, it is established that reconstructions of the general patterns of the development of taxonomic diversity are independent of the system of the group (Maxwell and Benton, 1990; Dmitriev, 2001).

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REFERENCES

1. G. A. Afanasjeva and L. A. Nevevsckaja, “The Analysis of Cause and Effect of Various Consequences of Crisis Sit-

uations Using Articulate Brachiopods and Bivalves as an Example,” in *Turnovers in Ecosystems and the Evolution of the Biosphere, Issue 1* (Nedra, Moscow, 1994), pp. 101–108 [in Russian].

2. G. A. Afanasjeva, I. P. Morozova, L. A. Viskova, and L. A. Nevevsckaja, “Consequences of the Permian Crisis for Various Invertebrate Groups,” in *Turnovers in Ecosystems and the Evolution of the Biosphere, Issue 3* (Nedra, Moscow, 1998), pp. 30–37 [in Russian].
3. V. Yu. Dmitriev, “Diversity Curves,” in A. S. Alekseev, V. Yu. Dmitriev, and A. G. Ponomarenko, *Evolution of Taxonomic Diversity: Turnovers in Ecosystems and the Evolution of the Biosphere, Issue 5* (GEOS, Moscow, 2001), pp. 19–67 [in Russian].
4. V. Yu. Dmitriev, “Quantitative Analysis of the Taxonomic Diversification of Foraminifers,” in *Turnovers in Ecosystems and the Evolution of the Biosphere, Issue 6*, Ed. by I. S. Barskov, T. B. Leonova, and A. G. Ponomarenko (Paleontol. Inst. Ross. Akad. Nauk, Moscow, 2004), pp. 40–50 [in Russian].
5. V. Yu. Dmitriev, “Taxonomic Diversification of Marine Gastropods,” *Paleontol. Zh.*, No. 3, 13–24 (2005) [*Paleontol. J.* **39** (3), 236–247 (2005)].
6. W. D. Maxwell and M. J. Benton, “Historical Tests of the Absolute Completeness of the Fossil Record of Tetrapods,” *Paleobiology* **16** (3), 322–335 (1990).
7. A. I. Miller and J. J. Sepkoski, Jr., “Modeling Bivalve Diversification: The Effect of Interaction on a Macroevolutionary System,” *Paleobiology* **14** (4), 364–369 (1988).
8. L. A. Nevevsckaja, “Morphogenesis and Ecogenesis of Bivalves in the Phanerozoic,” *Paleontol. Zh. (Suppl. 6)* (2003) [*Paleontol. J.* **37** (Suppl. 6), S591–S741 (2003)].
9. J. J. Sepkoski, Jr., “A Compendium of Fossil Marine Animal Genera,” *Bull. Am. Paleontol.*, No. 363, 1–560 (2002).
10. S. M. Stanley, “Infaunal Survival: Alternative Functions of Shell Ornamentation of the Bivalvia (Mollusca),” *Paleobiology* **7** (3), 384–393 (1981).