ISSN 0031-0301, Paleontological Journal, 2011, Vol. 45, No. 4, pp. 358–369. © Pleiades Publishing, Ltd., 2011.
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Mollusks in Phanerozoic Marine Communities: Implications from the Analysis of Global Paleontological Databases

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Received November 16, 2010

Abstract—Evolutionary history of three mollusk classes (Bivalvia, Gastropoda, and Cephalopoda), regarded as components of the Phanerozoic marine biota, is discussed based on the comparison of dynamics of quantitative parameters obtained from the analysis of the global paleontological databases. The main trends in the evolution of the role of mollusks in Phanerozoic marine ecosystems and relationships between the diversification of this group and biodiversity of paleocommunities are considered. Certain parameters show similarity between the diversity dynamics of mollusks and the whole marine biota, including the paleolatitudinal distribution of diversity. At the same time, mollusk classes differ considerably in certain aspects. The evolutionary history of Bivalvia, Gastropoda, and Cephalopoda was different and determined presumably by deep ecological divergence which occurred as early as the Early Paleozoic adaptive radiation. Bivalves and gastropods followed the trend of a gradual and constant increase in their role in marine communities; they are characterized by high and constantly growing duration of genera, high (and also growing) frequency in paleontological collections. Cephalopods show more chaotic macroevolutionary dynamics, relatively low mean duration of genera and low relative frequency.

Keywords: Mollusca, bivalves, gastropods, cephalopods, Phanerozoic, diversity dynamics, Paleontological databases.

DOI: 10.1134/S0031030111040125

INTRODUCTION

Mollusks belong to the most important taxonomic and functional groups of marine communities. In the modern fauna, it is the second most diverse phylum, which, according to some estimates, comprises more than 130 000 species (Skarlato et al., 1994) and is only inferior to arthropods. Most of these species inhabit the sea and some classes of this phylum have only been recorded in marine habitats. Mollusks are diverse in morphology and biomorphs, occupy various positions in the food chains, and participate in all types of marine communities (benthic, planktonic, nektonic, etc.). The ecological features listed are also traced in the geological past of the phylum Mollusca and species and ecological diversity of some classes (Cephalopoda, Monoplacophora) were much higher in the geological past than now (Clarke, 1996; Lindberg, 2009). At the same time, Cephalopoda still play a significant role in modern marine communities, although they almost disappeared from the fossil record, because taxa with a well-developed skeleton were replaced by taxa with a reduced skeleton.

The phylum is divided into several classes (9 or 10), some of which have become extinct (Tatarinov and Shimansky, 1984), phylogenetic relationships between which remain incompletely understood (Willmer, 1990; Sigwart and Sutton, 2007; Wägele et al., 2009). At the same time, the phylum Mollusca is likely a natural monophyletic group (Peterson et al., 2005; Giribet et al., 2007). The majority of mollusk classes, probably except for gastropods, are mostly homogeneous with reference to ecology. For example, the class Bivalvia includes mostly slow-moving benthic animals feeding on suspended particles (Nevesskaja, 2009) and all scaphopods (class Scaphopoda) are infaunal marine invertebrates feeding on foraminifers and other small organisms (Reynolds, 2002). As a part of the marine biota, mollusks evolved together with it, responding to evolutionary changes in other groups and, in turn, causing changes in other groups, since they were food objects and (or) consumers of various groups of marine animals.

The development of computer methods during the past decades allowed the creation of extensive paleontological databases with information on the global diversity of marine communities during the whole of Phanerozoic (Benton, 1999; Alroy et al., 2001). The use of databases of biological diversity in the geological past enables the use of quantitative methods for the study of diversity dynamics in both the whole biota and particular taxonomic (or ecological) groups of organ-

Table 1. General statistics of the data examined

Taxon	Number of genera	Number of collections	Number of occurrences	Frequency of genera (number of occurrences/number of genera)
Total number of mollusks	5954 (35%)	25628 (54%)	151900 (46%)	25.5
Bivalvia	1676	16666	80815	48.2
Cephalopoda	1865	8211	20451	11.0
Gastropoda	2192	9830	47194	21.5
Polyplacophora	31	79	105	3.4
Rostroconchia	25	190	211	8.4
Scaphopoda	22	1205	1463	66.5
Tentaculita	23	679	824	35.8
Other mollusk classes and genera of uncertain taxonomic position	120	597	837	7.0
Total (in biota)	**16977**	**47398**	**330820**	**19.5**

isms. In the present paper, we attempted to study the evolutionary dynamics of taxonomic and ecological diversity of mollusks in the Phanerozoic using quantitative methods of analytical paleobiology.

MATERIALS AND METHODS

We studied the combined database described in detail in the previous study (Markov, 2009). This is two combined databases with global data on mollusks:

(1) Sepkoski Database (SBD), containing stratigraphical intervals for more than 35 000 extinct marine genera (http://strata.geology.wisc.edu/jack/).

(2) Paleobiology Database (PBD), including detailed information on approximately 75000 paleontological collections of the whole world (http://paleodb.org/; Alroy et al. 2001). Each "collection" in PBD contains the data on fossils of the same age and the same locality and includes several "occurrences" (=list of taxa). Each "occurrence" is the recorded fact of the presence of certain genus in a collection (i.e., in a bed of the age and locality under consideration).

When studying the diversity dynamics, two different approaches are applied, using two major aspects of biological diversity, taxonomic and ecological. In the first case, the units analyzed are taxa of certain rank; in the second, they are certain ecological groups corresponding to the units of an ecological classification (for example, biomorphs, groups recognized based on the feeding mode, general mobility, etc.). In the present study, we consider both aspects.

The main unit in the analysis of diversity dynamics at the taxonomic level is genus. This is caused by the character of the databases used, which provide information primarily on genera rather than particular species. This is suitable for paleontological material, the nature of which (only partial preservation of fossilized parts of organisms, which restricts the opportunity of studying the variability of organisms in syntopic samples[1] and other aspects) makes the judgements of taxonomists concerning the boundaries of species less reliable than in the studies of neontologists, who use complete set of characters of particular organisms. Thus, in the present study, the term *diversity* corresponds to the number of genera in a certain sample (time interval, geographical zone, community, collection).

As the data from two sources (SBD and PBD) were combined, a list of 16977 genera of Phanerozoic marine organisms (animals and protozoans) was obtained, including 5954 mollusk genera, the data on which are present in both SBD and PBD (Table 1). Mollusks are present in more than half of all collections of PBD, containing a marine fauna; they comprise 46% of all generic occurrences and 35% of the total number of genera of marine organisms in the databases used. Such a wide diversity and frequency of mollusks in paleontological collections makes this phylum one of most important groups for a better understanding of general patterns of changes in biological diversity of the Phanerozoic marine biota.

In our analysis, classes are taken for taxonomic units of higher rank. We restricted ourselves to three largest classes of the phylum Mollusca, because other classes are represented by insufficient number of genera in the combined database (Table 1) and, hence, they are insufficient to provide sure outcome. In addi-

[1] A syntopic sample is a set of individuals sampled in certain time and habitat. This implies that all individuals from a syntopic sample lived contemporaneously and probably represented one population at a certain point. The study of syntopic samples is an important means for a taxonomist–neontologist dealing with mollusks (Vinarski and Andreeva, 2007).

tion, only the three classes are present in the fossil record during of the whole of the Phanerozoic, since the Early (Bivalvia, Gastropoda) or Late (Cephalopoda) Cambrian (Willmer, 1990).

The dynamics of taxonomic diversity at the level of mollusk subclasses or orders is difficult to analyze because of the absence of a generally accepted taxonomic system of the three classes considered, Gastropoda (Barker, 2001; Bouchet and Rocroi, 2005), Bivalvia (Nevesskaja, 2009), and Cephalopoda (Nesis, 1996). The concepts of the taxonomic position of extinct taxa are based almost exclusively on the study of shell characteristics; as a result, the systems of extant and extinct representatives of the same class are contradictory (Nesis, 1996). Simultaneous use of morphological and molecular data for taxonomic reconstructions also gives inconsistent results (see, for example, Lindgren et al., 2004). In particular, these contradictions are seen in the databases analyzed in the present study, in which incompatible systems of the same class are used.

We used the absolute dates of stratigraphical boundaries (Gradstein et al., 2004). Calculations were performed based on the stratigraphic scale used in SBD. This scale divides the Phanerozoic into 167 intervals with the mean duration of 3.25 m.y., most of which correspond to substages. For comparison, a rougher scale was also used, which was used by some authors for the analysis of PBD and divides the Phanerozoic into 49 almost equal intervals (on average about 11 m.y.) (Alroy et al., 2001). As was shown in our previous study (Markov et al., 2010), the diagrams constructed based on either scale are similar, suggesting that results are independent of the time scale.

The following parameters are calculated:

Absolute diversity (*N*), that is, the number of genera of a taxon existing in the time interval considered. A genus is regarded as existing within an interval even if it has not been recorded there but is known from the preceding and succeeding intervals. As *N* is divided by the total number of genera in the biota, the *relative diversity* is obtained, characterizing the contribution of this taxon to the general generic diversity of the marine biota.

Relative frequency of mollusks in paleontological collections was calculated as the ratio of the number of generic occurrences of a taxon to the total number of generic occurrences for the entire marine biota in the time interval under study.

Duration of existence of genera, m.y. (*L*), was calculated as the time between the first and last occurrences of genera in the fossil record, following the method described in detail in the previous studies; in extant genera, expected duration of existence was calculated based on the extinction rates estimated for the Cenozoic (Markov, 2000, 2002, 2009).

Mean number of genera in the collections containing a given genus (*D*) is regarded as a rough estimate of adaptation of a genus to complex (or simple) biotic conditions, or to the life in communities with a high or low alpha diversity. These estimates are based on the assumption that true alpha diversity of paleocommunities is an important factor that influences the taxonomic diversity of paleontological collections (along with other factors, such as preservation of fossils, research effort, purposes and methods of collecting, etc.). The arguments for the benefit of legitimacy of the given assumption, were in detail discussed earlier (Markov and Korotayev, 2007; Markov, 2009). *D* was calculated for each of 16977 genera included in both PBD and SBD. Calculations involved not only genera characterized in SBD, but the total generic lists for each collection of PBD. The mean value of *D* in all genera existing in a given time interval is used as an estimate of the mean alpha diversity (generic abundance) of communities at that time (Markov and Korotayev, 2007; Markov, 2009). Hence, the mean *D* for all genera of a given taxon (phylum or class) reflects to some extent the heterogeneity of environments of members of this taxon during the geochronological interval considered.

The dynamics of the latitudinal gradient of diversity was analyzed based on the number of mollusk genera in each paleolatitudinal zone (of 15°) in each interval of the geochronological scale from PBD (see above). We used rectangular extrapolation of the data on spatial-temporal distribution of genera (Powell, 2009); the genus was considered to exist during the whole interval of existence (according to SBD) in all paleolatitudinal zones, in which PBD gives evidence of true occurrences of members of this genus.

RESULTS AND DISCUSSION

1. Dynamics of generic diversity (*N*). Diversity dynamics of the phylum Mollusca during the Phanerozoic generally agrees with the general biotic trend towards an increase in biodiversity with time (Fig. 1). This trend was recognized analytically as early as the mid-1970s and repeatedly corroborated by different research teams (Bambach, 1977; J. Sepkoski, 1978, 1979, 1984; Lane and Benton, 2003; D. Sepkoski, 2005).

The diagrams based on geochronological scales from SBD and PBD, time intervals in which differ in duration by three times, look rather similar (Figs. 1a, 1b), suggesting that time resolution has an insignificant effect on the results. The most significant distinction is a weaker decrease in *N* after extinction at the Cretaceous–Paleogene boundary in the diagram which is based on a "rough" scale from PBD. This probably results from relatively rapid restoration of biotic diversity in the Paleogene. In the case of rough periodization, time intervals with sharply different diversity are combined and give an "averaged signal."

In the phylum Mollusca, diversity grows with time much smoother than in the whole biota. This is particularly prominent in the Paleozoic, when the marine biota showed sharp periodical fluctuations of generic diversity. In mollusks, these fluctuations are expressed to a much lesser extent, the minima and maxima in the diagrams are smoothed. This distinguishes mollusks from many other phyla of marine invertebrates, for example, echinoderms, which show very sharp fluctuations of taxonomic diversity in the Paleozoic. After the Permian extinction, in the Meso-Cenozoic time, the diagrams of diversity dynamics of the biota and phylum Mollusca become almost isomorphic, so that sharp reduction of diversity in the biota corresponds to almost equally sharp reduction of mollusk diversity.

Thus, the history of mollusk diversity in the Phanerozoic is divided into two main stages: before and after the great Permian extinction. Before extinction, mollusks constantly increased their taxonomic diversity, although this process was very slow. At the same time, Mollusca did not show considerable rises and falls in the diversity curve, in contrast to the biota as a whole (Fig. 1). In the Meso-Cenozoic, the diversity dynamics of Mollusca became almost the same as that of the biota; moreover, diversity grows at a higher rate than in the Paleozoic.

These changes are possibly connected with changes in taxonomic and ecological structure of Meso-Cenozoic marine communities. The modern taxonomic structure of the phylum Mollusca developed in the Carboniferous, when the youngest mollusk class, Scaphopoda, appeared (Reynolds, 2002). By that time, small-sized mollusk classes had become extinct, they did not continue into the Mesozoic (rostroconches, tentaculites); this extinction began even earlier, in the Devonian (Tatarinov and Shimansky, 1984). The same is characteristic of the whole marine biota, the taxonomic composition of which at the level of phyla and classes remained almost constant in the Meso-Cenozoic (appearance in the marine fauna of secondarily aquatic tetrapods was probably the most prominent exception), although diversity, abundance, ecological significance, and taxonomic composition at the order level changed considerably. In general, after the great Permian extinction, at the level of macrotaxa, the biota acquired almost the Recent appearance.

Sharp fluctuations of generic diversity of the marine biota in the Paleozoic were largely connected with periodic extinctions of large and diverse taxa (such as archaeocyathans, graptolites, some classes of Paleozoic echinoderms, etc.), which were replaced by new taxa. In the phylum Mollusca, Paleozoic macroevolutionary processes were not so sharp, because the primary adaptive radiation of the phylum and division into the basic phylogenetic lineages, corresponding to subphyla and classes, occurred much earlier, probably at the end of the Proterozoic, in the Ediacaran Time (Willmer, 1990; Fedonkin and Waggoner, 1997).

When considering Phanerozoic diversity dynamics of three largest mollusk classes, sharp distinctions between them are recognized. Bivalves and gastropods

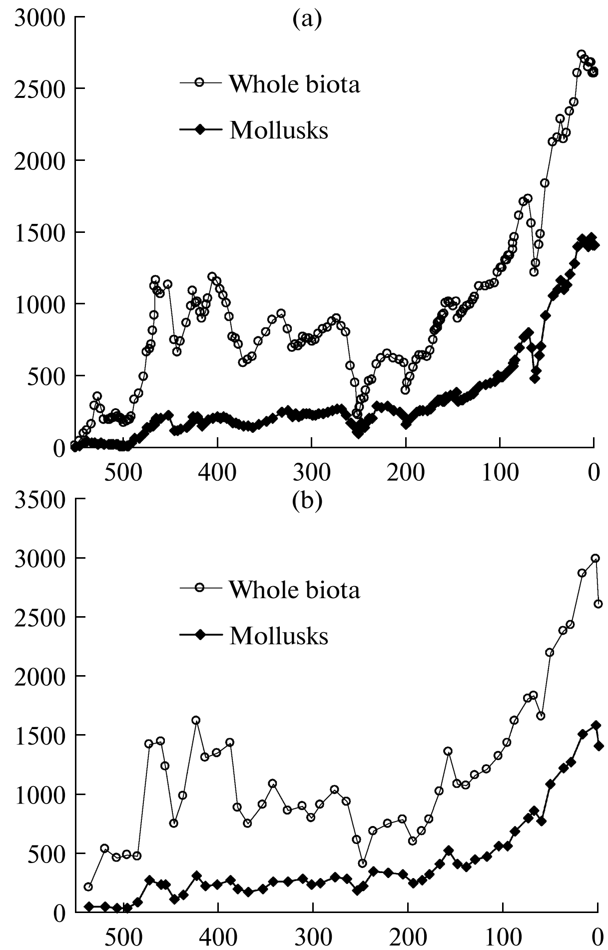

Fig. 1. Dynamics of absolute generic diversity of mollusks in the Phanerozoic. Abscissa is time (Ma), ordinate is the number of genera: (a) based on the time scale from SBD (mean duration of time units is 3.25 m.y.) and (b) on the PBD time scale (mean duration of units is 11 m.y.).

successfully survived two greatest Phanerozoic extinctions (at the Paleozoic–Mesozoic and Mesozoic–Cenozoic boundaries), whereas cephalopods (at least those with a well-preserved shell) showed an obvious decline in the Cenozoic. Cenozoic diversity dynamics of this class strongly differs from that of the phylum Mollusca and biota as a whole (Fig. 2). Probable causes of a sharp decrease in cephalopod diversity in the Cenozoic were repeatedly discussed. According to one version, as early as the Jurassic, teleosts began to compete successfully with cephalopods in marine ecosystems, gradually occupying the position of large marine predators at the top of the food chain (Clarke, 1996). This primarily concerns forms with an external shell (ammonites, nautiloideans), whereas forms with an internal shell (octopuses, squids) have retained relatively high taxonomic diversity and abundance up to the present time.

The diagrams of generic diversity dynamics of Bivalvia and Gastropoda in the Phanerozoic are simi-

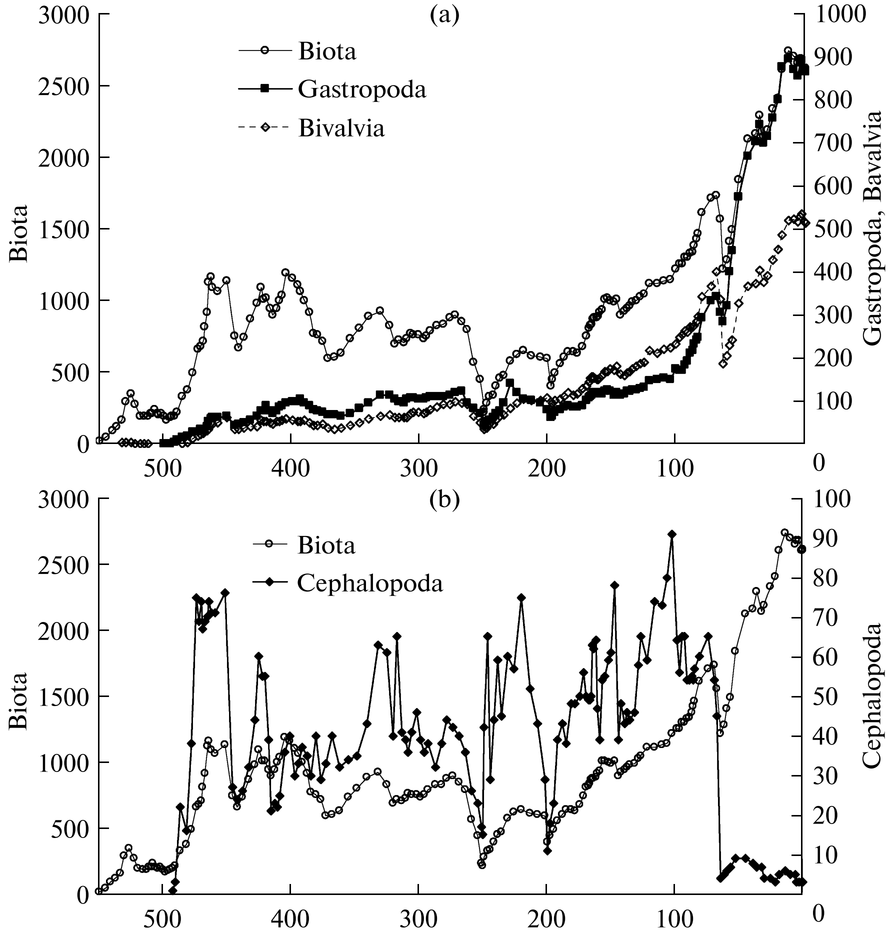

Fig. 2. Phanerozoic dynamics of diversity of three most abundant classes of the phylum Mollusca (Gastropoda, Bivalvia, and Cephalopoda), using geochronological scale from SBD. For designations, see Fig. 1.

lar to each other and the diagram of changes in generic diversity of the whole biota (Fig. 2). Our results agree with the results obtained previously in the study of generic diversity dynamics of bivalves and gastropods in the Phanerozoic; both classes show increasing generic diversity during the Phanerozoic; decreases in diversity during great extinctions were less significant than in the majority of other groups of marine animals (Amitrov et al., 1981; Miller and Sepkoski, 1988). In particular, a decrease in diversity during the great Permian extinction was expressed in gastropods and bivalves to a lesser extent than in the whole biota. At the Cretaceous–Paleogene boundary, gastropods show a less significant extinction than bivalves and their diversity grows more rapidly at the end of Cretaceous and in the Cenozoic; as a result, in the modern fauna, gastropods are superior to bivalves in the number of both species and genera.

In general, it is possible to regard these classes as an example of evolutionarily stable taxa, the diversity of which grew during the Phanerozoic, following a stable trajectory, which is close in bivalves to exponential growth and, in gastropods, to a hyperbolic curve (Markov and Korotayev, 2007). Mass extinctions only slightly influenced this trajectory, showing accelerated diversification in the post-crisis periods, which could have been connected with extinction of competitors, providing free ecological space (Miller and Sepkoski, 1988). This resulted in a large number of species and genera in these classes because of their wide adaptive radiation and ecological plasticity. Of all mollusk classes, only these two were able to invade the freshwater basins; moreover, gastropods came on land and underwent there explosive taxonomic diversification. The Recent fauna of terrestrial gastropods comprises about 35 000 species (Barker, 2001).

In contrast to bivalves and gastropods, cephalopods showed very sharp fluctuations of generic diversity (Fig. 2). The close similarity of Phanerozoic diversity dynamics of gastropods and bivalves and dissimilarity with that of cephalopods are partially attributable to ecological factors. Notwithstanding sharp distinctions in feeding mode (bivalves are filter-feeders, while gastropods are active scrapers, phytophages, or predators), bivalves and aquatic gastropods are mostly benthic and relatively weakly mobile organisms. On

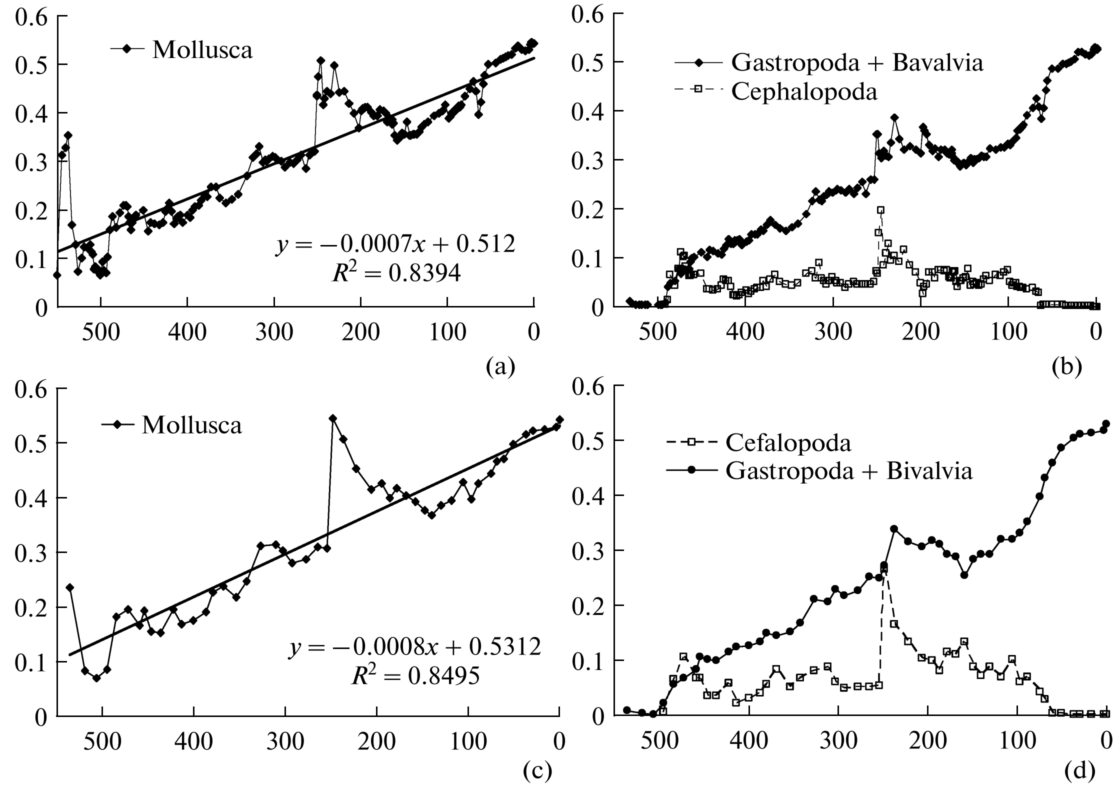

Fig. 3. Dynamics of relative mollusk diversity in the Phanerozoic: (a, b) on the SBD scale; (c, d) on the PBD scale. Abscissa is time (Ma) and ordinate is relative diversity (number of genera in the group under study divided by the number of genera in the whole marine biota); curves (a, c) are accompanied by regression equations and confidence factor of approximation (R^2).

the contrary, almost all cephalopods are actively swimming predators pursuing prey and, hence, having essentially different, high level of development of the nervous system and locomotor apparatus. However, it is hardly possible that this factor alone explains key differences between mollusk classes in their evolutionary response to hanging natural conditions. Thus, the macroevolutionary dynamics of brachiopods is more similar to that of cephalopods than bivalves, although, in ecology, brachiopods are undoubtedly more similar to bivalves. The macroevolutionary dynamics of teleosts, which presumably occupied in the Cenozoic many ecological niches of Mesozoic cephalopods with external shell, is closer to that of bivalves and gastropods than cephalopods (Markov, 2002). These sharp distinctions are probably connected with different evolutionarily–ecological "universality" of the body plan of the groups considered, which resulted in distinctions in the mean level of ecological specialization of their genera. Apparently, cephalopods with external shell (as brachiopods) had a less universal body plan and narrower (on average) ecological specialization and, hence, were forced to respond to environmental changes by in general more profound changes in morphology (including the skeleton structure) than bivalves and gastropods (or teleosts); this caused differences in the rate of changes in generic composition and amplitude of fluctuations of generic diversity.

Taking into account the similarity in diversity dynamics between Gastropoda and Bivalvia, in further analysis they are taken for an united group (Bivalvia + Gastropoda).

2. Dynamics of relative diversity (proportion of mollusks in the generic composition of the marine fauna). The relative diversity of the phylum Mollusca (proportion of mollusks in the total generic diversity of the marine biota) constantly grew throughout the Phanerozoic, notwithstanding sharp periodic fluctuations (Fig. 3). In modern marine communities, mollusks compose more than half of all genera (considering only taxa that are well represented in the fossil record and included in the databases analyzed) and display the maximum relative diversity in the whole history of the marine biota. During the Phanerozoic, the proportion of mollusks in the total generic diversity of the marine biota showed an almost linear growth. The Spearman correlation coefficient (r_S) for relative mollusk diversity and geological time ($1-t$) is 0.89 ($p = 0.00$). The almost linear growth of the proportion of mollusks in the generic composition of the fauna, from low values at the beginning of the Paleozoic to 54% at the end of the Cenozoic, is an important general trend in the macro-

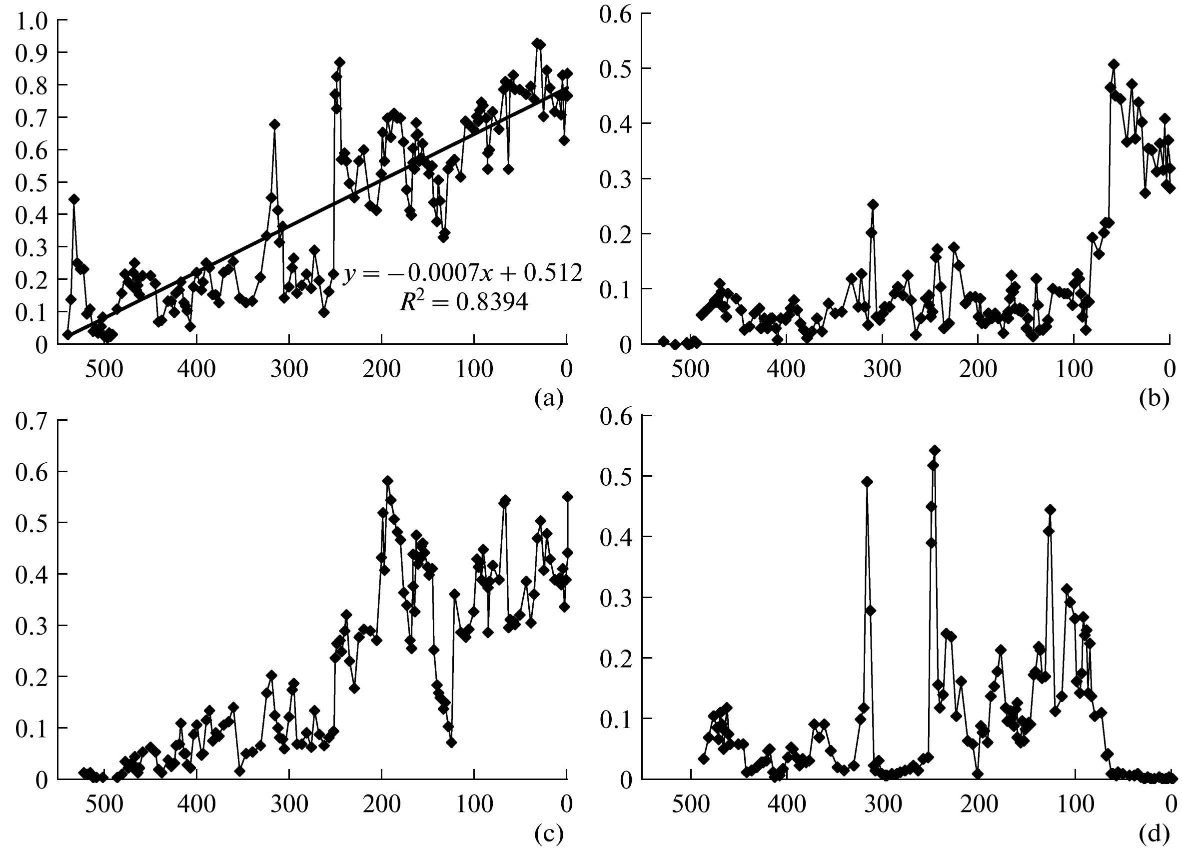

Fig. 4. Dynamics of relative frequency of the phylum Mollusca. Abscissa is time and ordinate is relative frequency (number of occurrences of particular mollusk taxa divided by the total number of occurrences of all marine genera), using the SBD scale: (a) all mollusks, (b) Gastropoda, (c) Bivalvia, and (d) Cephalopoda.

evolutionary dynamics of the marine biota in the Phanerozoic.

The relative mollusk diversity grew in the Phanerozoic almost exclusively due to bivalves and gastropods (Fig. 3). Cephalopods made the greatest contribution to biotic diversity in the Triassic (approximately 250–220 Ma). This was the time of maximum taxonomic diversity of this class, which was connected with extremely rapid diversification of the order Ceratitida, which began soon after the great extinction at the end of the Permian. Subsequently, a decline began and continued to the present time. However, the growth rates of taxonomic diversity of gastropods and bivalves in the Late Mesozoic–Cenozoic were very high, even higher than in the previous time, resulting in continuing trend towards a linear increase in relative diversity of the phylum Mollusca, even when the contribution of cephalopods sharply decreased.

3. Frequency in collections. Mollusk genera are usually frequent in paleontological collections. The average number of occurrences of a mollusk genus in collections of PBD is 25.5 (Table 1), that is, mollusks were widespread in the Phanerozoic seas. In this parameter, they are superior to the majority of other phyla of marine invertebrates, including diverse taxa, such as echinoderms, arthropods, and bryozoans (Markov et al., 2010). Of the three major mollusk classes, bivalve genera are most frequent (on average, a genus of this class occurs in 48.2 collections), gastropods are less frequent (21.5 occurrences per genus), and cephalopods show a relatively low frequency (11.0 occurrences per genus). For cephalopods, the character of occurrences in collections is probably partly accounted for by postmortal transportation of shells, which were characterized by good floatation and capable of drifting with marine currents for a significant distance (Saunders and Landman, 2009). However, it is hardly possible to estimate quantitatively the effect of this factor on the taxonomic composition of collections.

The analysis of occurrence dynamics of mollusks confirms the previously obtained results (Fig. 4). In general, the phylum Mollusca shows constant growth of frequency in collections during the Phanerozoic; the maximum of this parameter was in the Late Paleogene, when the proportion of mollusk genera was more than 90% of the total generic occurrences in the marine fauna in collections of PBD. During the Phanerozoic, the relative frequency of mollusks changed very sharply, much sharper than fluctuations of absolute (Figs. 1, 2) and relative (Fig. 3) generic diversity. The amplitude of fluctuations of this parameter is more than 80%. The difference in amplitude of fluctuations is attributable mostly to the character of the values compared. As *N* and relative diversity were calculated, genera were taken for primary units, which are considered to exist during the whole period from the earliest to latest occurrence in the fossil record (according to SBD), including periods when a particular genus is absent from collections of PBD. As a result, the diagrams are smoothed compared to the diagrams of relative frequency, where the primary unit is occurrence of genus in a certain collection.

A sharp growth of relative frequency of Mollusca in the fossil record usually followed the periods of an extreme decrease in this parameter. The greatest decrease in mollusk frequency falls on the Permian Period, which is followed by a sharp increase in this parameter in the Triassic; this was connected primarily with rapid diversification of Ceratitida and, partially, bivalves soon after the great extinction. The increased frequency of mollusks just after the crisis apparently means that members of this phylum restored their number at a greater rate (do not confuse with generic diversity) than other macrotaxa of the marine biota, effectively using advantages given by reduction of the number of competing groups in marine communities.

Three largest mollusk classes sharply differ in frequency dynamics, in turn dominating marine communities during the Phanerozoic (Fig. 4). Until the Carboniferous, mollusks were relatively rare; in the Middle Carboniferous, the frequency of cephalopods in collections sharply increased. This class showed very sharp fluctuations of frequency during the Paleozoic–Mesozoic. In the Mesozoic, bivalves were the most frequent class of Mollusca, reaching the peak in the Middle Jurassic and remaining rather frequent up to the present time. This class also shows considerable fluctuations of frequency, although they are less pronounced than in cephalopods. The frequency of gastropods was rather low during the Paleozoic and Mesozoic; only in the Cenozoic, they became similar to bivalves in this parameter. A sharp growth of gastropod frequency in collections began from the Late Cretaceous and the maximum was achieved in the Paleocene; subsequently, it gradually decreased during the Cenozoic, although remaining almost as high as in bivalves. The changes were probably connected with changes in the structure of marine faunas, which followed the periods of mass extinctions, when ecological advantage was characteristic of various classes of the phylum Mollusca.

4. Dynamics of the mean duration of genera (*L*). In this parameter, the phylum Mollusca follows the general biotic trend; the diagrams are almost isomorphic, except for the period from the Early Triassic to the Early Jurassic, when the mean duration of genera in the biota was approximately 50 m.y. longer than in mollusks (Fig. 5a). This was connected with the prevalence among mollusks at that time of Ceratitida and other ammonoids, which are characterized by a very low mean duration of genera (high rate of changes in the generic composition). In the other epochs of the Phanerozoic, the mean duration of mollusk genera was similar to that in the whole biota (this is partially connected with the fact that, in some epochs, the proportion of mollusks reached 50% and more of the total generic diversity of the marine biota, the data on which are provided by the databases analyzed).

Sharp distinctions in the dynamics of *L* are characteristic of particular mollusk classes. The group Gastropoda + Bivalvia shows a gradual increase in the mean duration of genera (Fig. 5b), reaching the maximum in the Cenozoic (when the specific rate of extinction of bivalve and gastropod genera became very low). The class Cephalopoda shows an essentially different picture, in which the mean duration of genera remained short (much shorter than in the group Gastropoda + Bivalvia) until mass extinction of ammonoids and belemnites at the end of the Mesozoic. A sharp increase in *L* at the beginning of the Cenozoic is explained by the fact that, after a great extinction, the fossil record provides only a few representatives of poorly preserved groups (cuttlefish, octopuses) and isolated relict forms with external shell (nautiloideans), which rarely became extinct in the Cenozoic. These relict genera apparently dwelt under relatively stable conditions, like extant *Nautilus* (Saunders and Landman, 2009). Probably, only some short-lived genera became extinct (or new genera appeared at a very low rate), displaying deep intraclass differentiation of *L* rather than a true increase in this parameter within families and orders that previously had low values of *L*.

When considering the temporal dynamics of *D* (average number of genera in a collection), it is evident that respective diagrams in the phylum Mollusca and whole biota are almost identical (Figs. 5c, 5d). The growth of the mean value of *D* in mollusks shows that marine communities including mollusks became more and more complex with time (on average, showed greater generic diversity). This trend is also seen in individual classes of Mollusca, although dynamics of *D* in cephalopods showed considerable fluctuations. During the Late Paleozoic and all Mesozoic, cephalopods occurred in on average poorer fossil assemblages than bivalves or gastropods. This is probably partly connected with the swimming (nektonic) lifestyle of cephalopods, which were involved in taphocoenoses poor in other taxa with a firm skeleton, and with the fact that they were connected to a lesser extent with particular benthic ecosystems.

Mollusks, as the whole biota (Markov, 2009), show a positive correlation between *L* and *D* (Figs. 5e, 5f). In the phylum Mollusca, the Spearman correlation coefficient (r_S) of *L* and *D* is 0.53 ($p = 0.00$), that is, much higher than in the remaining part of the marine biota ($r_S = 0.22$; $p = 0.00$). Thus, mollusks make the

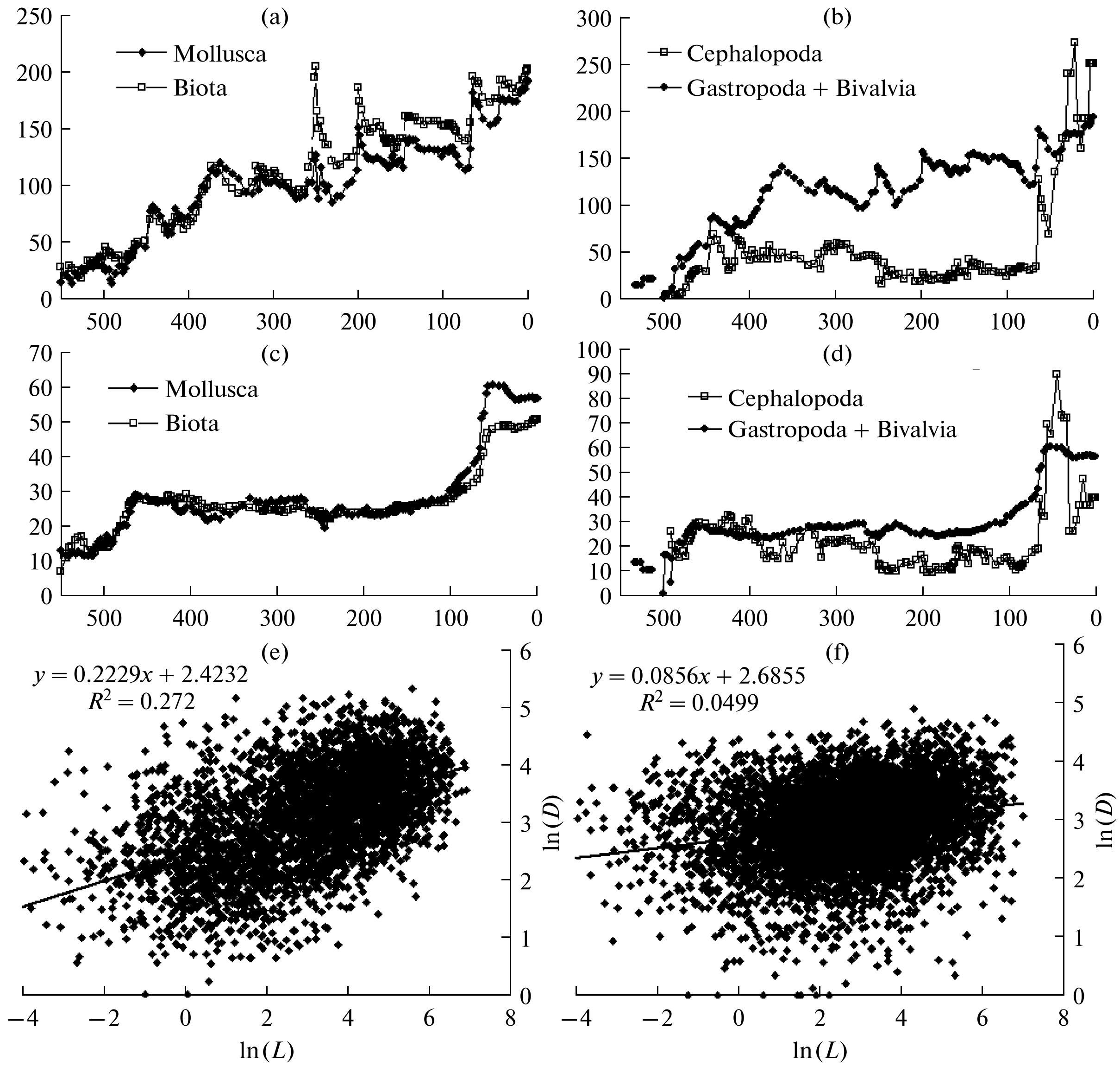

Fig. 5. Dynamics of L (mean duration of genera) and D (mean generic abundance of collections containing a genus in question): (a, b) changes in L; (c, d) changes in D; (e, f) ratio of L to D; the genera recorded in at least four collections of PBD are only taken into account (3607 mollusk genera and 5823 genera of other marine animals and protozoans).

main contribution to the previously established positive correlation between L and D in the whole marine biota (Markov, 2009). During the Phanerozoic, mollusks gradually passed to more and more diverse communities; this not only corresponds to the general biotic trend, but determines this trend to a great extent.

5. Paleolatitudinal distribution of mollusk diversity in the Phanerozoic. Like the whole marine biota, mollusks showed latitudinal gradient of diversity during the Phanerozoic (Fig. 6). In each period, the maximum generic diversity of mollusks was confined to one paleolatitudinal zone and decreased northerly and southerly with the distance from this zone. In the Paleozoic, it decreased monotonously, while, in the Mesozoic and Cenozoic, a secondary local maximum in the Southern Hemisphere was observed. The maximum diversity zone was not constantly near the equator, but moved from the south to the north. In the Ordovician, Silurian, and Devonian, the maximum mollusk diversity was in the tropical latitudes of the Southern Hemisphere (15°–30° S). In the Carboniferous and most of the Permian, the zone of the maximum diversity was somewhat northerly, in the equatorial zone of the Southern Hemisphere (0°–15° S). From the end of the Permian to the beginning of the Jurassic, the maximum mollusk diversity gradually moved to the north. At the end of the Permian, this zone passed from the

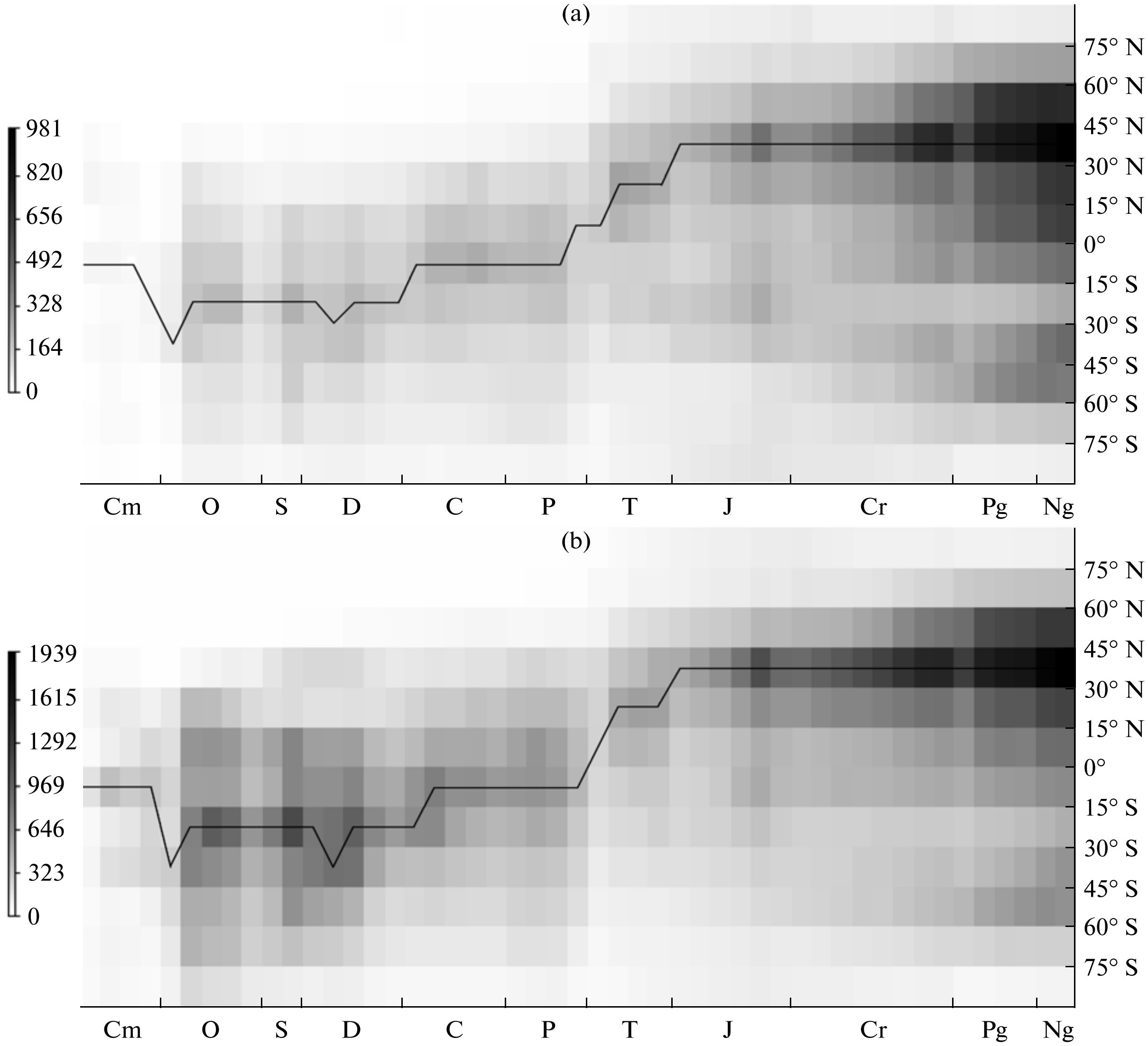

Fig. 6. Paleolatitudinal distribution of generic diversity in the Phanerozoic: (a) mollusks and (b) whole marine biota. Abscissa is geological time and ordinate is paleolatitudinal zone; gray colors of different brightness show generic diversity in each 15-degree paleolatitudinal zone in each interval of the geochronological scale. The scale from PBD (see *Material and Methods*) was used. Thin lines indicate the positions of latitudinal zones with the maximum diversity.

Southern Hemisphere to the Northern Hemisphere and, at the beginning of the Jurassic, it was in the middle latitudes of the Northern Hemisphere (30°–45° N). The general northerly displacement of the maximum mollusk diversity zone (Fig. 6a) is the same as in the whole marine biota (Fig. 6b). At the end of the Triassic, the zone of secondary mollusk diversity in tropics of the Southern Hemisphere (15°–30° S) appeared; in the Late Cretaceous–Cenozoic, it was displaced in the southern temperate latitudes (30°–60° S). The Meso-Cenozoic secondary southern maximum of diversity was also characteristic of the whole marine biota; however, it is better pronounced in mollusks. The shift of the maximum diversity zones is apparently accounted for by the global tectonic processes, which resulted in the displacement of the continental shelf (Powell, 2009).

CONCLUSIONS

In a number of quantitative parameters, diversity dynamics of the phylum Mollusca and whole marine biota are in general similar, including similarity in the dynamics of paleolatitudinal distribution of mollusk diversity and remaining marine fauna. This is probably connected with a uniform evolutionary response of mollusks and whole biota to changes in ecological conditions. General laws of macroevolutionary dynamics of the marine fauna apparently include the prevalence of positive correlations between alpha diversity of communities and the rate of appearance of new genera (Markov et al., 2010). On the other hand, some parameters show profound distinctions between the main classes of the phylum Mollusca. The classes Bivalvia, Gastropoda, and Cephalopoda differ in the evolutionary fate, which was probably predetermined by deep ecological differentiation even during the Early Paleozoic adaptive radiation. Bivalves and gastropods followed a pathway of a slow, continuous increase in their role in marine communities and, in doing so, members of the two classes retained a relatively low and stable level of organization. Throughout their history, they differed in the high and constantly growing mean duration of genera; they are also characterized by high (and also growing) frequency in paleontological collections. On the contrary, cephalopods were early to reach a high level of organization connected with their lifestyle and, to the terminal Mesozoic, showed profound changes in the taxonomic composition, which were manifested in expansion of new groups with considerably changed body plan and ecological and taphonomic characteristics. During most of their historical development, cephalopods showed a low duration of genera and relatively low frequency in collections (communities), as compared with other mollusk classes. Due to the huge diversity and abundance, mollusks determine in many respects the previously established general biotic laws of changes in taxonomic diversity, as they are an important component of the total sample and one of the basic components of marine communities.

ACKNOWLEDGMENTS

The study was supported by the programs of the Presidium of the Russian Academy of Sciences "Biodiversity and Dynamics of Gene Pools" and "Origin of Biosphere and Evolution of Geobiological Systems," Subprogram 2, and the Russian Foundation for Basic Research (project nos. 09-05-01009 and 10-05-00342).

REFERENCES

Alroy, J., Marshall, C.R., Bambach, R.K., et al., Effects of Sampling Standardization on Estimates of Phanerozoic Marine Diversification, *Proc. Nat. Acad. Sci. USA*, 2001, vol. 98, pp. 6261–6266.

Amitrov, O.V., Blank, M.Ya., Gorbach, L.P., et al., Gastropod Mollusks, in *Razvitie i smena mollyuskov na rubezhe mezozoya i kainozoya* (Development and Replacement of Mollusks at the Mesozoic–Cenozoic Boundary), Moscow: Nauka, 1981, pp. 72–123.

Bambach, R.K., Species Richness in Marine Benthic Habitats through the Phanerozoic, *Paleobiology*, 1977, vol. 3, pp. 152–167.

Barker, G.M., Gastropods on Land: Phylogeny, Diversity and Adaptive Morphology, in *The Biology of Terrestrial Molluscs*, Wallingford: CABI Publ., 2001, pp. 1–146.

Benton, M.J., The History of Life: Large Databases in Palaeontology, in *Numerical Palaeobiology: Computer-based Modelling and Analysis of Fossils and Their Distributions,* New York: John Wiley and Sons, 1999, pp. 249–283.

Bouchet, P. and Rocroi, J.-P., eds., *Classification and Nomenclator of Gastropod Families*, Hackenheim: Conch Books, 2005.

Clarke, M.R., The Role of Cephalopods in the World's Oceans: An Introduction, *Phil. Trans. R. Soc. Ser. B*, 1996, vol. 351, pp. 979–983.

Fedonkin, M.A. and Waggoner, B.M., The Late Precambrian Fossil *Kimberella* Is a Mollusc-like Bilaterian Organism, *Nature*, 1997, vol. 388, no. 6645, pp. 868–871.

Giribet, G., Dunn, C.W., Edgecombe, G.D., and Rouse, G.W., A Modern Look at the Animal Tree of Life, *Zootaxa*, 2007, vol. 1668, pp. 61–79.

Gradstein, F.M., Ogg, J.G., Smith, A.G., et al., *A Geologic Time Scale 2004*, Cambridge: Univ. Press, 2004.

Lane, A. and Benton, M.J., Taxonomic Level As a Determinant of the Shape of the Phanerozoic Marine Biodiversity Curve, *Am. Natur.*, 2003, vol. 162, no. 3, pp. 265–276.

Lindberg, D.R., Monoplacophorans and the Origin and Relationships of Mollusks, in *Evolution: Education and Outreach*, 2009, vol. 2, pp. 191–203.

Lindgren, A.L., Giribet, G., and Nishiguchi, M.K., A Combined Approach to the Phylogeny of Cephalopoda (Mollusca), *Cladistics*, 2004, vol. 20, pp. 454–486.

Markov, A.V., The Return of the Red Queen, or the Law of the Growth in the Mean Duration of the Existence of Genera during Evolution, *Zh. Obshch. Biol.*, 2000, vol. 61, no. 4, pp. 357–370.

Markov, A.V., Mechanisms Responsible for the Increase in the Taxonomic Diversity in the Phanerozoic Marine Biota, *Paleontol. Zh.*, 2002, no. 2, pp. 3–13 [*Paleontol. J.*, vol. 36, no. 2, pp. 121–130].

Markov, A.V., Alpha Diversity of Phanerozoic Marine Communities Positively Correlates with Longevity of Genera, *Paleobiology*, 2009, vol. 35, no. 2, pp. 231–250.

Markov, A.V., Bondarev, A.A., and Vinarski, M.V., Relationship between the Alpha Diversity of Communities and the Appearance Rates of New Genera in the Evolution of Phanerozoic Marine Biota, *Paleontol. Zh.*, 2010, no. 5, pp. 3–14 [*Paleontol. J.*, 2010, vol. 44, no. 5, pp. 477–488].

Markov, A.V. and Korotayev, A.V., Phanerozoic Marine Biodiversity Follows a Hyperbolic Trend, *Palaeoworld*, 2007, vol. 16, pp. 311–318.

Miller, A.I. and Sepkoski, J.J., Modeling Bivalve Diversification: The Effect of Interaction on a Macroevolutionary System, *Paleobiology*, 1988, vol. 14, no. 4, pp. 364–369.

Nesis, K.N., The System of Recent Cephalopods: The Critical Analysis of Newly Proposed Improvements Using the Characters of the Reproductive System, *Zool. Zh.*, 1996, vol. 75, no. 3, pp. 335–349.

Nevesskaja, L.A., Principles of Systematics and the System of Bivalves, *Paleontol. Zh.*, 2009, no. 1, pp. 3–13 [*Paleontol. J.*, 2009, vol. 43, no. 1, pp. 1–11].

Peterson, K.J., McPeek, M.A., and Evans, D.A.D., Tempo and Mode of Early Animal Evolution: Inferences from Rocks, Hox, and Molecular Clocks, *Paleobiology*, 2005, vol. 31, suppl. 2, pp. 36–55.

Powell, M.G., The Latitudinal Diversity Gradient of Brachiopods over the Past 530 Million Years, *J. Geol.*, 2009, vol. 117, no. 6, pp. 585–594.

Reynolds, P.D., The Scaphopoda, *Molluscan Radiation—Lesser-known Branches*, London: Academic Press, 2002, pp. 137–236 (Advances in Marine Biology, vol. 42).

Saunders, W.B. and Landman, N.H., Eds., *Nautilus: The Biology and Paleobiology of a Living Fossil*, Dordrecht: Springer, 2009.

Sepkoski, D., Stephen Jay Gould, Jack Sepkoski, and the 'Quantitative Revolution' in American Paleobiology, *J. Hist. Biol.*, 2005, vol. 38, pp. 209–237.

Sepkoski, J.J., A Kinetic Model of Phanerozoic Taxonomic Diversity: I. Analysis of Marine Orders, *Paleobiology*, 1978, vol. 4, no. 3, pp. 223–251.

Sepkoski, J.J., A Kinetic Model of Phanerozoic Taxonomic Diversity: II. Early Phanerozoic Families and Multiple Equilibria, *Paleobiology*, 1979, vol. 5, no. 3, pp. 222–251.

Sepkoski, J.J., A Kinetic Model of Phanerozoic Taxonomic Diversity: III. Post-Paleozoic Families and Mass Extinctions, *Paleobiology*, 1984, vol. 10, no. 2, pp. 246–267.

Sigwart, J.D. and Sutton, M.D., Deep Molluscan Phylogeny: Synthesis of Palaeontological and Neontological Data, *Proc. R. Soc. Ser. B*, 2007, vol. 274, pp. 2413–2419.

Skarlato, O.A., Starobogatov, Ya.I., Lobanov, A.L., and Smirnov, I.S., Databases on Zoological Systematics and Data on Higher Taxa of Animals, *Zool. Zh.*, 1994, vol. 73, no. 12, pp. 100–116.

Tatarinov, L.P. and Shimansky, V.N., eds., *Spravochnik po sistematike iskopaemykh organizmov* (Reference Book on the Systematics of Extinct Organisms), Moscow: Nauka, 1984.

Vinarski, M.V. and Andreeva, S.I., To the Question of Species in Freshwater Mollusks: History and Modern State, in *Teoreticheskie i prakticheskie problemy izucheniya soobshchestv bespozvonochnykh: pamyati Ya.I. Starobogatova* (Theoretical and Practical Problems of the Study of Invertebrate Communities: In Memory of Ya.I. Starobogatov), Moscow: KMK, 2007, pp. 130–147.

Wägele, W., Letsch, H., Klussmann-Kolb, A., et al., Phylogenetic Support Values Are not Necessarily Informative: The Case of the Serialia Hypothesis (a Mollusk Phylogeny), *Frontiers in Zoology*, 2009, vol. 6, no. 12. (http://www.frontiersinzoology.com/content/6/1/12).

Willmer, P., *Invertebrate Relationships: Patterns in Animal Evolution,* Cambridge: Univ. Press, 1990.