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A Complete Diversity of Fossils: Perspectives

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Abstract—A method allowing estimation of the total diversity of fossil organisms is described and illustrated, using the examples of the Permian ammonoids of the Pamir, Permian brachiopods of Texas, and Tithonian marine animals.

Keywords: evolution of taxonomic diversity, methods

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INTRODUCTION

The diversity curves commonly used to illustrate changes in communities (i.e., the number of genera and families) of marine skeletal animals are based on counting these taxa (Sepkoski, 1984, 1992, 1996, 2002). Modern studies mainly focus on quantitative analysis of selective samples, which usually shows a considerably different general pattern of changes in diversity. Detailed recent publications provide a relatively comprehensive account of the history of studies in this area and show the current situation in this field (Alroy, 2010; Vilhena and Smith, 2013; Silvestro et al., 2014; Brocklehurst, 2015).

Any diversity curve correctly shows the actual changes in biodiversity, if the accepted numbers of the appearing and extinct skeletal genera constitute the same share of the total number of appearing and extinct genera (i.e., are confined to a narrow interval around this value). In that case, the number of genera at the stage borders constitute the same share of the total diversity; the curves of the counted and total diversities are similar and, in the dimensionless form, coincide (nondimensional curves can be conveniently produced by dividing the diversity at the stage borders by the number of extant taxa known in the fossil state). To make sure that the curves are similar, it is necessary to demonstrate the constancy of the above share throughout time, for which a knowledge of the complete diversity is needed. Without that, none of the interpretations of diversity evolution can be verified. However, a complete account of the total diversity is clearly impossible and it needs to be inferred from the existing data.

Below I describe a method for evaluating the total diversity. The method is based on a well-known basic fact: in the course of long-term collection of fossils belonging to the same assemblage, sooner or later a time comes when novel genera or species of this assemblage are no longer found. A curve showing the relationship of the number of recognized taxa and the number of specimens collected asymptotically approaches a constant value that is equal to the total number of taxa in the studied assemblage. This method was tested on two regional faunas: Permian ammonoids of the southeastern Pamir and Permian brachiopods of Texas. Its use for the reconstruction of the total diversity is illustrated using an example of Tithonian marine animals.

PERMIAN AMMONOIDS OF THE SOUTHEASTERN PAMIR

The material of ammonoids from the Kotchusu and Shindy formations of the southeastern Pamir (Leonova and Dmitriev, 1989), from the Bostere Assemblage (Kungurian) is used here, as it is very familiar to the author. The collection has 5274 specimens identified to genus; a total of 38 genera. If specimens are randomly selected from the collection, all genera fall in a sample constituting less than a half of the collection. The generic composition can be considered exhaustively studied, at least, it can be expected that further studies of this material will not add more than one or two new genera.

The number of species is more interesting. The collection contains 68 species and 4965 specimens identified to species. These were randomly divided into 17 groups of 276 each and one (18th) group with 273 specimens. The graph in Fig. 1a shows an increase in the number of species in a sample, as the number of groups increases.

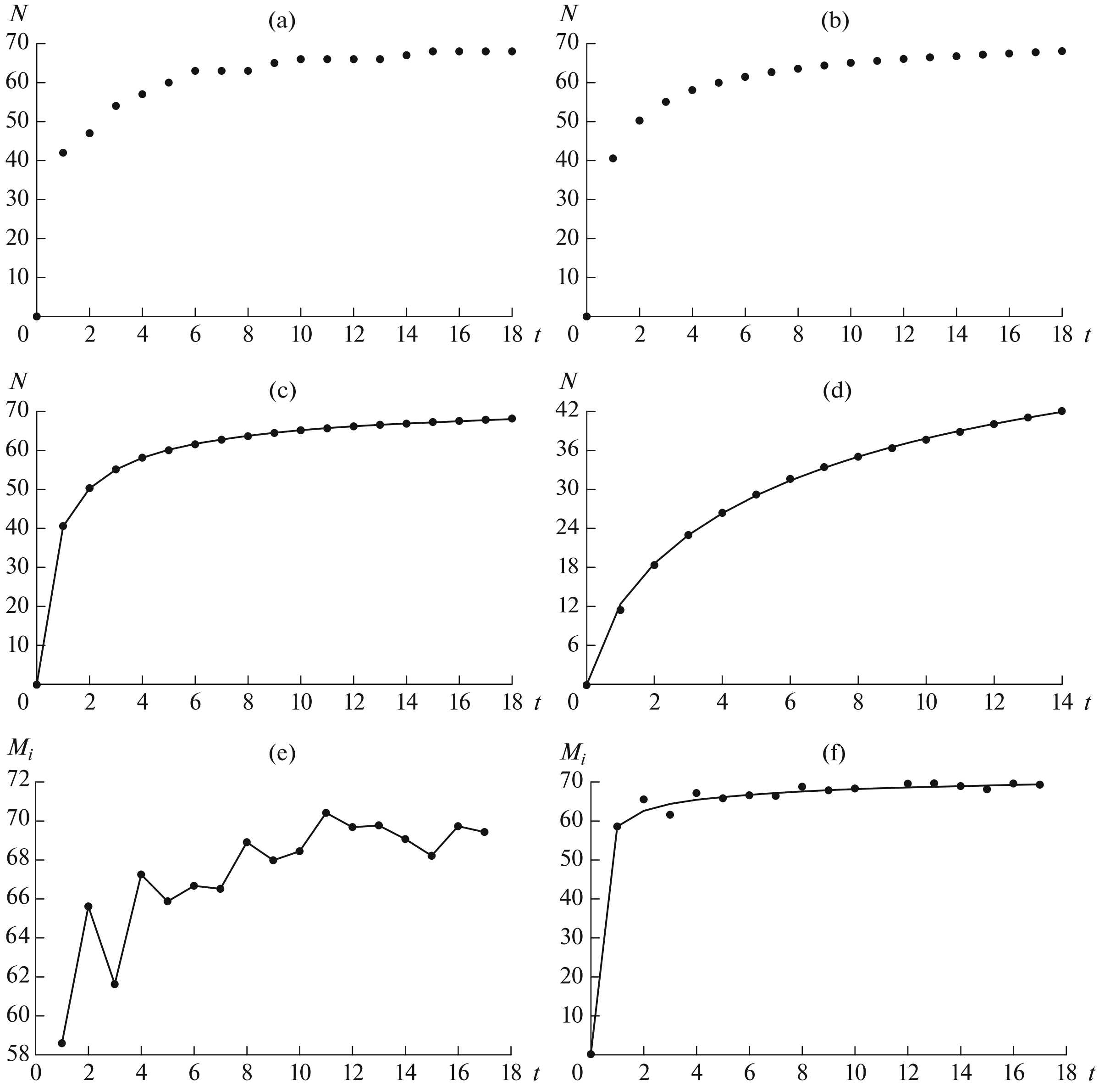

Fig. 1. Prediction of the number of the ammonoid species in the Bostere Assemblage: (a–c) number of species in random samples of increasing size: (a) number of species in a single sequence of groups; (b) mean number of species after 400 reshuffles of groups; (c) the same with the result of calculation using equation (1) (solid line, the same in Figs. 2 and 3), $M = 72$ species; (d) number of species in assemblages of smaller groups in a case of one of the large groups, $M_I = 56$ species; (e) increase in the predicted number of species for the increasing number of large groups, at $t = 1$, the mean value of M_I is given for the large groups; (f) the same, with the result of calculations using equation (1), $M = 73$. Explanations (Figs. 1–3): (t) number of groups, (N) number of taxa (species in Fig. 1, genera in Figs. 2 and 3), (M_i) expected number of taxa.

This graph is not suitable for an equation describing the ratios observed in this study. It describes an increase in the number of species for succession of sums arranged according to their numbers from 1 to 18, i.e., it shows only one of the possible group sequences. It would be more interesting to mean-test the behavior of this relationship for a random sequence of groups. This is easily achieved by averaging out the results of a large number of random changes (randomization). The graph in Fig. 1b shows the situation after 400 reshuffles.

An averaged curve is better suited for this study. An increase in the number of species is observed in Fig. 1b for all 18 groups in contrast to Fig. 1a, where the four points on the right have an ordinate of 68 species, giving an impression of the position of an asymptote at the same level. To predict the total number of species N for the averaged correlation, it is proposed to use the equation obtained from the gamma distribution function by replacement of the scale parameter by a decreasing function:

$$N(t) = \begin{cases} 0, t \le 0 \\ \dfrac{M}{C}\displaystyle\int_0^t \frac{t^{s-1}}{(a+bt^r)^s}\exp\left(-\frac{t}{a+bt^r}\right)dt, t > 0 \end{cases} \quad (1)$$

$$C = \int_0^\infty \frac{t^{s-1}}{(a+bt^r)^s}\exp\left(-\frac{t}{a+bt^r}\right)dt,$$

where N is the number of species; $t = 0,1,2,...$, the number of groups proportional to the number of specimens in their groups; M is predicted number of species; and a, b, r, s are parameters.

The gamma distribution is used for sums of similarly distributed random variables. In the material examined, the numbers of specimens are added between the appearance in the increasing random sample of a previously unencountered species and the next appearance of a species also first recorded in the sample analyzed. As the list of the species encountered in the procedure grows, the distance (number of specimens) between the two adjacent occurrences of new species on average increases, which necessitates a replacement of the scale parameter of a usual gamma distribution by the function $1/(a + bt^r)$. Theoretically, this function is determined by the frequencies of species, but a successful prediction of the total number of species based on the empirical frequencies in most cases is unlikely to be possible. The function applied in this study (and in all below examples) gives good results, but this does not exclude the possibility of using other function. The equation should satisfy the following conditions: $N(0) = 0$, $N(t) \to M$ at $t \to \infty$, $N'(t) > 0$, $N''(t) < 0$, the actual number of encountered species $N^* \le M$. These five conditions strongly limit the possible evaluations of M, so at N^*/M nearing 1, even the functions $N(t)$ not adequate as models of samples examined would give a suitable prediction. If N^*/M is much lower than 1, it is necessary to describe the empirical data as precisely as possible.

Figure 1c shows the results of the calculation using formula (1) for species. The ordinate of the asymptote is 72 species. Here, the prognosis of the number of species is based on the total collection, but the estimate of M can depend on the sample size (Simberloff, 1972). This should be taken into account. All 4965specimens are randomly divided into 17 large groups (16 groups of 292 specimens and one group with 293 specimens) and each large group is divided into 14 smaller groups (12 groups of 21 specimens and 2 groups of 20 specimens; in the last large group, there are 13 groups with 21 specimens and 1 group with 20 specimens). Smaller groups in each large group were numbered. Then, frequencies M_1, M_2, ... were determined for assemblages of an increasing number of large groups, designated by the subindex of M. When large groups were united, small groups with the same numbers were considered as one small group.

Figure 1d shows a graph for an example of one large group. This graph was chosen to illustrate the results, because in this case, the calculation is least comparable with the actual values. The greatest deviation (0.95 of the total sum of absolute deviations 2.45) is shown for the number of species in the first small group. This happens frequently and, as discussed in the next section, is explained by a dispersion of the number of species (or genera, as in the two next sections), which is usually higher for the first group. The deviation of the calculated values from the factual values can also depend on whether or not the parameters are sufficiently optimized. The minimum of the criterion for optimization (in this case, sum of absolute deviations) was found by varying the parameters. The minimum thus found is not necessarily the lowest, but complete optimization would require a time-consuming scanning of the parameter space. In this case, as in the other examples below, this was not done, as the purpose of this study was to show the method, rather than the correct final result.

Figure 1e shows how M_i changes as the number of large groups increases. For one large group, there is a mean value of M_1 for all 17 large groups (59 species with the standard deviation of 4 species). No averaging out was performed for assemblages of large groups. As estimates of M_i increase with the growth of the sample size, the final value of $M = 73$ is received applying equation (1) to these values, i.e., for a indefinitely increasing sample size (Fig. 1f).

Compared to the previous estimate ($M = 72$), the difference of one species is insignificant. The precision can be improved by completing the optimization of the parameters, by multiple repeat of calculation and averaging out the resulting values of M. In this case, it is evident, even without all this, that the collection studied includes ca. 93–95% of all species of the Bostere Ammonoid Assemblage. Later, another four–six species can be discovered in addition to the presently known 68 species. It is possible that they are even represented in the collection by single or few specimens, but not identified as separate species.

Thus, the algorithm of the evaluation of the total number of taxa is described below:

1. All material in a collection is randomly divided into large groups of equal size.

2. Large groups are divided into the same number of smaller groups, which are numbered. It is desirable for smaller groups to include as much as possible of the material in the collection. This limits the number of smaller groups, but their number should not be too small. It is sufficient to have about 15 large and 15 smaller groups.

3. Two, three, and other large groups are successively assembled. Smaller groups with the same num-

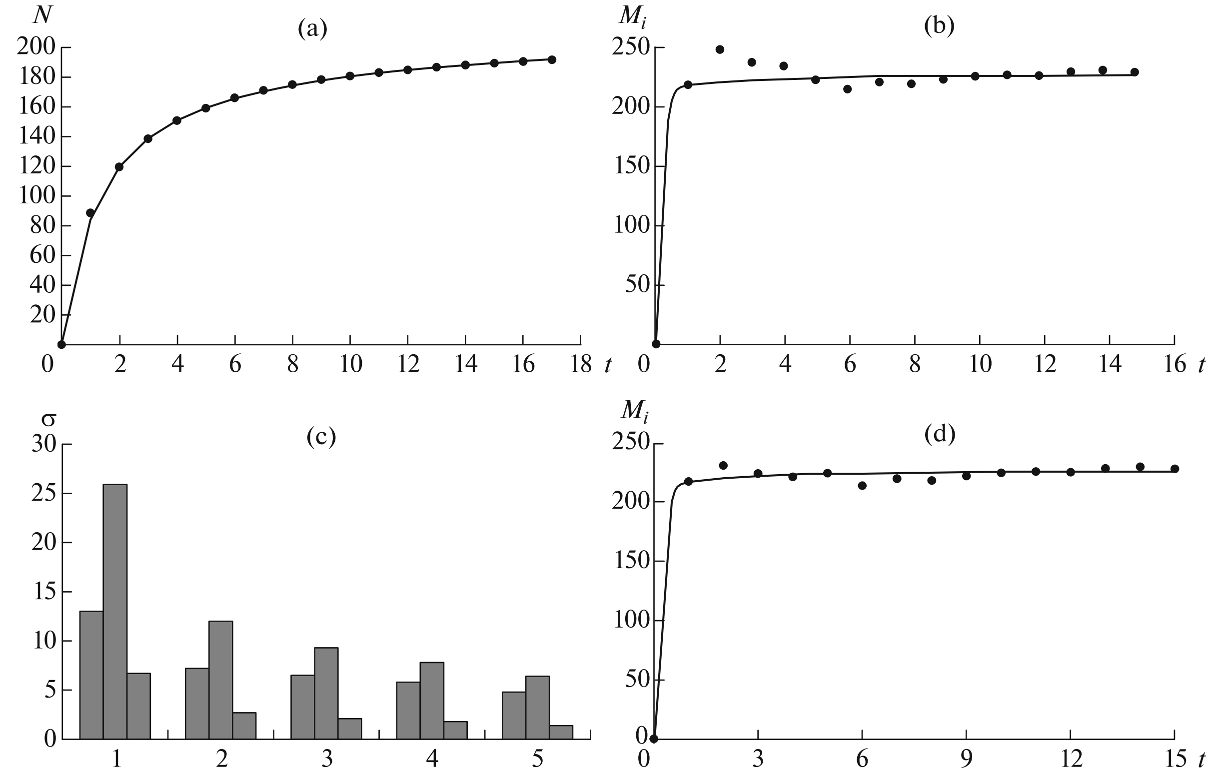

Fig. 2. Predicted number of genera of Permian brachiopods of Texas: (a) increase in number of genera in six large groups of Texas brachiopods for an increasing number of smaller groups; (b) an increase in the predicted number of genera for an increasing number of large groups, at $t = 1$, the mean value M_1 for large groups, $M = 229$ genera, the actual number of described genera $N^* = 211$, $N^*/M = 0.92$; (c) standard deviation (σ) of the actual number of described genera (in each three, left column), predicted number of genera (middle column), and of the mean values of the predicted number of genera (right column); figures in the horizontal axis are the number of assembled large groups; (d) the same as in Fig. 2b, with M_2, M_3, M_4, M_5 replaced by their mean values, $M = 228$ genera, $N^*/M = 0.925$.

ber should also be united with groups with the same number.

4. The preparation of the material for calculation is a repeated randomization of smaller groups in each assembly of large groups with averaged results.

5. Using equation (1), asymptotes M_1, M_2, ... are determined for one large group and assemblages of two, three, etc. large groups.

6. Using the sequence M_i also using equation (1), the final value of M (predicted number of taxa in the material) is determined.

7. The higher precision of the material preparation and determination of the confidence interval for M can be made by repeated procedures 1–6 and averaging of received values of M.

PERMIAN BRACHIOPODS OF TEXAS

The material of Permian brachiopods of Texas is described in a very large monograph on Texas (Cooper and Grant, 1977). I used the data from the monograph, which are included in the Paleobiology Database (www.paleodb.org), lists of brachiopods from 511 sites. In this case, it is impossible to determine the number of specimens of each genus and species, so it is interesting to use the number of sites instead of the number of specimens. The preparation of the material for calculation includes repeated randomization of smaller groups with averaging the results; hence, not only the number of taxa is averaged, but also the number of specimens in the groups. After randomization, the number of specimens in each smaller group is near the average, equal to the number of all specimens in assemblages of large groups divided by the number of smaller groups, but it remains unknown (unlike the preceding example of Pamir ammonoids).

For Texas brachiopods, the number of genera was studied. All 511 sites are randomly distributed across 15 large groups (14 groups with 34 sites and the last group with 35 sites). Small groups (17 in each larger group) contain two sites each and only one smaller group in the last large group contains three sites.

Equation (1) describes all isolated cases with a high degree of precision. An example of the graph (Fig. 2a) shows an assemblage of six large groups. This case is chosen for illustration, hence, the agreement of the calculation with real data is at the worst (the relative deviation at $t = 1$ equals 5%).

Figure 2b shows the result of using equation (1) for the sequence of isolated evaluations of M_i. Considerable deviations of M_2, M_3 and M_4 are noticeable. To understand the nature of these deviations, M_2, M_3, M_4, and M_5 were determined 20 times for different random assemblages of two, three, four, and five groups. After that, the average and standard deviations were calculated (Fig. 2c).

All standard deviations decrease with an increase in the sample size. This explains the usual connection of the largest deviations of calculated values from the actual number of genera (or species, as in the Pamir material) with the first group. For $i > 5$, the variance should be low and averaging will not lead to a significant change in M_i (relative deviation of M_5 from its average is less than 3%).

The result of the replacement of M_2, M_3, M_4, and M_5 by their average values is shown in Fig. 2d. The replacement did not lead to a significant change in the prediction (see the caption to Fig. 2), hence, in this case, the estimates of M_i for $i > 4$ play the major role. For the Permian brachiopods of Texas, it is possible to expect the discovery of another 20 genera (using the same criteria for genus). The determination of M in large groups without their subdivision into smaller groups and estimates of M_i gives 229 genera; for the ratio N^*/M near 1, a satisfactory prediction of the total number of taxa can be made only for the large groups (the same in the Pamir material). However, as shown in the next section, this is not the case, if N^*/M is considerably lower than 1.

TITHONIAN MARINE ANIMALS

For quantitative study of the evolution of biodiversity for each stage, it is necessary to have the data on the number of taxa at its lower or upper boundary and also on the number of taxa appearing and becoming extinct. If two successive stratigraphic intervals with N_1 taxa in the first, N_2 in the second, and N_{1+2} taxa in these two intervals together, the number of taxa at their boundary is as follows:

$$N_{1|2} = N_1 + N_2 - N_{1+2}. \qquad (2)$$

The data from the Paleobiology Database (www.paleodb.org) at the beginning of 2015 are used to examine the number of genera of marine animals of Tithonian. I used all the data on marine localities for five intervals: Anisian–Kimmeridgian, Anisian–Tithonian, Tithonian–Eocene, Berriasian–Eocene, Anisian–Eocene. The first four intervals are ca. 100 m.y. Such long intervals are taken for the maximum completeness of the material. About 97% of all genera existed not more than 100 m.y., so that, in intervals of such duration, almost all genera available to paleontologists are taken into account. This eliminates difficulties of working in short stratigraphic intervals, connected with the presence of genera known only in these localities on the basis of limited material, the distribution of which should not be considered known, and also genera not found in a narrow interval, but present in earlier and later beds.

The data from the Paleobiology Database are incomplete and spatially heterogeneous. For example, for the Anisian–Eocene interval, there are data on 7370 collections from the United States, 3438 collections from France, 2252 collections from the United Kingdom, and only 2119 collections from the vast territory of the former USSR, and 2665 collections from Africa, also very unevenly distributed across the countries. A separate number in the collection from the Paleobiology Database is given to a list of taxa from one locality published in a paper; hence, several collections may come from one locality. Nonmarine animals, plants, ichnogenera, nomina dubia and, where possible, parataxa are excluded from the lists from the database. Synonyms and homonyms are also taken into account.

The material of the above intervals includes the following. Anisian–Kimmeridgian (Fig. 3b): Altogether 25722 collections divided into 15 large groups (12 groups with 1715 collections and 3 groups with 1714 collections). In each large group, there are 17 smaller groups. Large groups with 1715 collections contain 15 smaller groups with 101 collections each and two with 100 collections; groups with 1714 collections contain 14 smaller groups with 101 collections each and three with 100 collections. Anisian–Tithonian (Fig. 3c): 25858 collections with 15 large groups (13 groups with 1724 collections and 2 groups with 1723 collections). Each large group contains 15 smaller groups. Large groups with 1724 collections contain 14 smaller groups with 115 collections and one with 114 collections; groups with 1723 collections contain 13 smaller groups with 115 collections each and 2 with 114 collections. Tithonian–Eocene (Fig. 3d): 22104 collections: 14 large groups (12 groups with 1579 collections and 2 groups with 1578 collections). Each large group contains 17 smaller groups. Large groups with 1579 collections contain 16 smaller groups with 93 collections and one with 91 collections, groups with 1578 collections contain 15 smaller groups with 93 collections, one with 92, and one 91 collections. Berriasian–Eocene (Fig. 3e): 20255 collections; 14 large groups (11 groups with 1447 collections and 3 groups with 1446 collections). Each large group contains 17 smaller groups. Large groups with 1447 collections contain 15 smaller groups with 85 collections and two with 86 collections, groups with 1446 collections contain 16 smaller groups with 85 collections and one with 86 collections. Anisian–Eocene (Fig. 3f): 46 112 collections; 15 large groups (13 groups with 3074 collections and 2 groups with 3075 collections). Each large group contains 15 smaller groups. Large groups with 3074 collections contain 14 smaller groups with

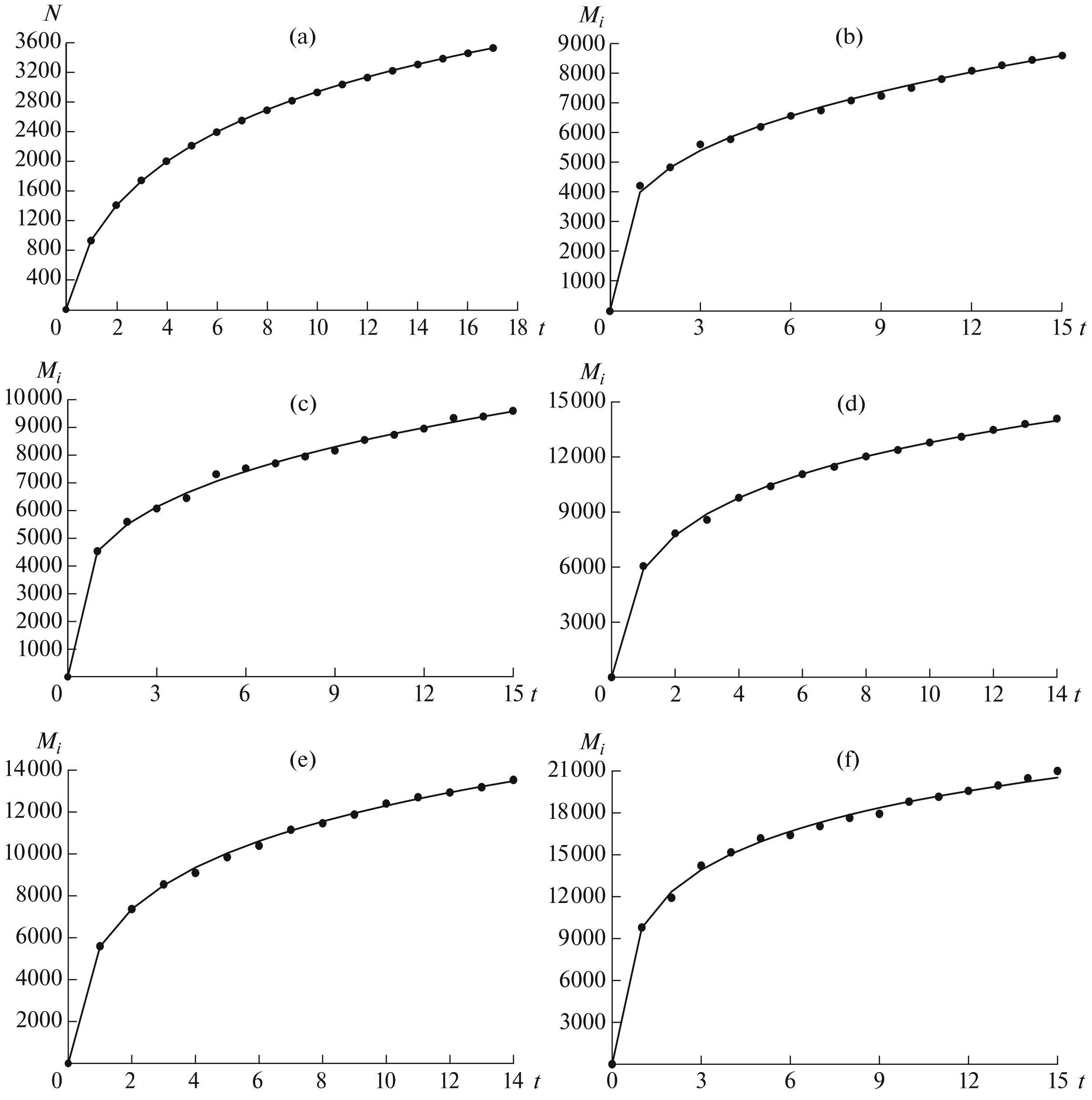

Fig. 3. The material used for estimation of the diversity of Tithonian marine animals: (a) relationship of $N(t)$ in Anisian–Kimmeridgian for assemblage of four large groups; (b–f) relationships $M_i(t)$: (b) for Anisian–Kimmeridgian, $M \approx 17000$ genera (value close to the optimum 16 839, hereinafter given in parentheses after M); for point M_1, the mean determined for all 15 large groups (4223 ± 46 genera, relative precision of the mean is 1.1%); (c) for Anisian–Tithonian; $M \approx 18\,000$ (17854); $M_1 = 4538 \pm 95$ (2.1%); (d) for Tithonian–Eocene, $M \approx 23000$ (23027), $M_1 = 6060 \pm 135$ (2.2%); (e) for Berriasian–Eocene, $M \approx 22\,500$ genera (22380), $M_1 = 5591 \pm 132$ (2.4%); (f) for Anisian–Eocene, $M \approx 30500$ (30 391), $M_1 = 9791 \pm 75$ (0.8%).

205 collections and one with 204 collections; in the groups with 3075 collections, all 15 smaller groups contain 205 collections each.

In the studied material, at least several dozen new genera are encountered in smaller groups. Therefore, in contrast to the two above examples, for optimization of parameters for determining M_i, the use of the sum of absolute deviations was replaced by the use of a statistically more accurate χ^2-test allowing the evaluation of the probability of the correspondence of the calculated and actual values:

$$\chi^2 = \sum_i \frac{(n_i - n_i^*)^2}{n_i^*}$$

where n_i is the number of genera in a smaller group numbered i, not encountered in groups with lesser numbers, n_i^* is the same calculated using equation (1).

Values of M_I, mean M_1, and its standard deviation were determined for each time interval for all large groups. The results are illustrated by the graph $N(t)$ with the lowest correspondence of the actual date and calculation (Fig. 3a). Graphs in Figs. 3b–3f show the correlation of M_i with the number of large groups. The resulting prediction of the expected number of genera M (see the caption to Fig. 3) was calculated for the minimum of the sums of absolute deviations. M characterizes the total diversity of skeletal animals, i.e., includes those genera which existed, but are not available to study. These are the genera contained in deposits which are either destroyed or deeply buried.

In total, at the Kimmeridgian–Tithonian boundary, the expected number of genera is near 9500, at the Tithonian–Berriasian $\approx$10000. In the Tithonian, around 1000 genera appeared (difference for the predictions for the Anisian–Tithonian and Anisian–Kimmeridgian) and ca. 500 became extinct (difference for the predictions for the Tithonian–Eocene and Berriasian–Eocene). The ratio $N^*/M = 0.32$ for the Anisian–Jurassic, 0.35–0.36 for the Tithonian–Berriasian to Eocene, and 0.40 for Anisian to Eocene. In this situation, extrapolation to infinity cannot give reliable results. The precision of these data can be increased to any desired level by the above method (see the end of the section about Pamir ammonoids), but the main resource to increase reliability is the most comprehensive inclusion of all available material suitable for quantitative estimation of the world's collections. A probable doubling of the number of the accounted collections should give considerably more reliable results. An evident method of verification of the results is the comparison of the existing estimates with the results received after the material studied is supplemented in the future by considerable amounts of new data. As the number of genera increases not only as a result of accumulation of new collections, but also due to taxonomic revisions of already existing material, only dimensionless values should be compared. The question of the appearance and extinction rates resolves itself.

The estimates obtained considerably exceed the known number of Tithonian genera (ca. 1200–1300 at the Tithonian boundaries, according to J. Sepkoski) and twice the number of modern genera known from fossils (ca. 5100). This does not overturn the Meso-Cenozoic increase in biodiversity, as the comparison in this case should be made with the number of extant genera, which could become fossils. In fact, these are all extant skeletal genera (except those remaining only as fragmented remains, as parataxa). An approximate estimate of the number of such genera can be obtained from a rough estimate of the number of skeletal marine species of 170–180 thousand (https://en.wikipedia.org/wiki/Marine_biology). By accepting that the mean number of fossil species in a genus is about five (Alekseev, 2001), we have approximately 35000 genera.

A decrease in diversity in the Tithonian, which is not supported by the above predicted results is an interesting problem. A decrease in the actual diversity (according to Sepkoski, by 150 genera, from 1318 to 1167) can be connected with a marine regression at the Jurassic–Cretaceous boundary. The deposits of the regressive phase are less available for paleontological study. Therefore, some genera that became extinct at that time will be found for the last time in older deposits, whereas the first occurrences of some new genera will be shifted to younger deposits. If the first and last occurrences of many genera are shifted, a false minimum of diversity can appear. Perhaps, such an artifact exists for the Tithonian.

The repeatedly used replacement of the exact time of the duration of taxa by the interval between the first and last occurrences of their representatives remains a weak point in the quantitative study of the evolution of biodiversity. This gives a lower estimate of the number of genera at the boundaries of all stages (Signor–Lipps effect is an example (Signor and Lipps, 1982)). If this error constitutes an approximately permanent proportion of genera, it does not affect the shape of the diversity curve and can be ignored. However, an even lower estimate of the minima of diversity is quite possible. Therefore, it is extremely desirable to remove this error. There are various proposals to determine the mathematically expected durations of taxa (Foote and Raup, 1996). They are based on calculations of the probabilities of the existence of the taxa outside their stratigraphic ranges. The probabilities are determined by the relation of the number of stages, which contain or do not contain occurrences of these taxa. The algorithm described at the end of the section on Permian ammonoids is desirable to use for more precise accounting of the durations of genera, after the following procedures:

(1) For each studied interval, mathematical expectation is determined of the number of genera which are (a) found last time in the older deposits and can be present in this interval and (b) found first time in the younger deposits and can be present in this interval.

(2) The number of genera corresponding to the mathematical expectation is selected from the lists of genera from the older and younger beds. The selection of genera can be random.

(3) These genera are randomly distributed in the lists of collections of the studied interval.

Unfortunately, no method exists so far to estimate the mathematical expectation applicable to marine animals represented by material with such extremely uneven stratigraphic distribution.

Only further results can show if the realization of the method described in this paper can bring satisfactory results.

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