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VARIABILITY OF FORAMINIFERS, SOME EVOLUTIONARY TRENDS, AND VALIDITY OF TAXONOMIC CATEGORIES

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Extensive creation of invalid names, as a result of extremely narrow interpretations of concepts of taxonomic category and inattention to biological laws is still a major problem in the foraminiferological literature. As a partial remedy the use of the taxonomic category "forma" is suggested for several lineages.

Key words: Foraminiferida, evolution, taxonomical categories.

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INTRODUCTION

Species are fundamental biological units. They are represented by populations that satisfy the following criteria: (a) they have a common origin; (b) they breed freely and yield fertile descendants; (c) all individuals exhibit morphological similarities and are connected with each other by transitional forms; (d) two different species may occupy the same area (although closely related species often have disjunct distribution), but two subspecies cannot coexist for a long time, because interbreeding would eliminate the subspecies differences. Although there are some rare exceptions to these rules (e.g., fertile interspecific hybrids are known in nature) the above mentioned criteria are essential for the definition of the concepts of species and subspecies. "Not more than one subspecies of any one polytypic species can exist in breeding condition in any one area" (Mayr *et al.* 1953: 30).

Free breeding is probably the most important of the criteria pointed out. However, as far as foraminifers are concerned, this criterion is difficult to assess for most Recent organisms and impossible to determine for the fossil ones. As a result, practically all the descriptions of new taxa are based on the morphology of the test.

Unfortunately, morphological traits have different implications in different groups of foraminifers and therefore it is not possible to use a particular change in morphology for the description of a given taxonomic category.

It is usually accepted that generic characters are: general form of the test, wall construction and location and character of the aperture. As Bugrova (1986) states, the number of morphologic parameters of benthic species can be as high as several dozens, but a much lower number is sufficient to discriminate infrageneric taxa. We can summarize that species characters usually consist of number of chambers, character of the supplementary skeleton, porosity, sutures, and periphery. Types of ornamentation and differences in size and in details of the shape are usually considered as subspecies traits.

It seems to me, however, that this determination of traits is worthwhile only for some relatively rare groups of foraminifers, because the intraspecific variability of foraminifers is considerably greater than is usually admitted. The traits that are considered by most foraminifero- logists as characteristic of the subspecies level, or even the species level, should be considered as characteristic of lower taxonomic categories.

I cited all these well-known and universally accepted concepts to taxonomic categories and reiterated some biological laws because the main goal of this article is a critical assessment of some conclusions where these principles have been disregarded.

VARIABILITY OF FORAMINIFERS

Foraminifera are subject to great variability which are related to the following causes:

(1) *Reproductive cycle.* The alternation of generations is well known in many species, especially the benthic ones. Two generations sometimes look so different that they were described not only as different species, but as different genera (Murray 1973), even as genera belonging to different families (Boltovskoy and Wright 1976).

(2) *Age.* Age dependant variability occurs to some degree in all species. However, in some species this variability can be notorious. For example, *Pyrgo* passes through a quinqueloculine stage and several quinqueloculinas show a tendency toward a *Triloculina*-type chamber arrangement. A good example of great morphological differences observed in the ontogeny of representatives of *Hauerina* is given by Serova (1960). Hemiplanktonic foraminifers show even greater differences (e.g., *Tretomphalus grandis*, which is pelagic state of the megalospheric *Cymbaloporella squamosa*). Young multilocular foraminifers have fewer chambers than the adult forms and their tests, obviously, are smaller.

(3) *Geological age.* Most foraminifers have a tendency to increase their size during their phylogeny (Boltovskoy 1984, 1988); in some species the size increase is considerable (up to 100%).

(4) *Environmental conditions.* Morphological changes related to environmental variations can be of great importance. Such factors as general shape, size, number of chambers, and even the character of the aperture, are subject to much variations in many species (Boltovskoy and Wright 1976).

The morphological variability of foraminifers was fully acknowledged in the last century and early 1900's. In fact, several micropaleontologists rejected the feasibility of the use of foraminifers for stratigraphic purposes.

INCREASE OF INVALID NAMES

During the second quarter of this century, significant advances in foraminiferal research, and especially in their use for biostratigraphy, stemmed from their increasing use by oil industry paleontologists. In order to achieve fine stratigraphic resolution, minor, obviously intraspecific, morphological differences were used and an enormous number of invalid taxa without zoological value were created. The foraminiferal nomenclature became overloaded with synonyms and the importance and the future of foraminiferology were seriously endangered (Boltovskoy 1965).

Unfortunately, due to the fact that many students of Recent foraminifers, following the example of many biostratigraphers, used very narrow definitions of species, the number of Recent foraminiferal taxa also began to increase alarmingly. A good example of this trend is given by work of McCulloch (1977), who described Recent foraminiferal assemblages from bottom samples of the Pacific Ocean, primarily its eastern part. This publication, undoubtedly, is a result of many years' work and is furnished with numerous excellent illustrations (199 plates). The volumes are excellently bound and the paper is of high quality. I cannot, however, agree with the author's very narrow interpretation of many new taxa. The number is really impressive, out of 2293 species, 1926 (i.e. 84%) were considered by McCulloch as new. Furthermore, 121 genera out of a total of 363 (i.e. 33%) were also described as new. In addition, 74% of the 367 taxa which were labeled with pre-existing names are placed in conditional nomenclature by the addition of "cf.". This means that almost all the taxa found by McCulloch in the Pacific Ocean were considered as new to science. McCulloch (1977: 3) writes that "excessive lumping should delay progress biologically". That is true, no excessive

lumping should take place in our work. However, excessive splitting is much more dangerous for our science.

Fortunately, not all foraminiferologists have used such narrow limits for species and subspecies definitions and some have provided valuable documentations of the great variability of foraminifers (see review in Boltovskoy 1965, and Boltovskoy and Wright 1976, and references therein).

In the seventies and eighties many more studies appeared in which the high variability of foraminifers was shown. In this context a most interesting study was done by Schnitker (1974), who studied cloned cultures of *Ammonia beccarii* and concluded that six foraminifers, described in the literature as distinct species, are really synonyms of *Ammonia beccarii*. Smith (1973), Bhalla and Abbas (1975), Medioli and Scott (1978), Poag (1978), Miller *et al.* (1982), Kaminski (1984), Grünig (1984), among many others, also demonstrated examples of highly variable species with a proliferation of synonyms (up to 11!), which is mainly the result of a too narrow interpretation of the species concept by previous authors. There have been many other similar studies, but I believe that the above will suffice for illustrating that foraminifers are indeed very variable organisms.

So far this discussion has concerned mainly benthic foraminifers. Observations with respect to the variability of planktonic forms are less numerous and they have been carried out mostly on Recent species. This relates to the fact that planktonic taxa are several times fewer, and that their milieu is more uniform, than, for example, the environmental conditions of the shelf. In addition, they have been used much more intensively by stratigraphers, who are "splitters" by nature.

In reality, however, the planktonic foraminiferal species are also highly variable. Many of these variations, concerning practically all characters of the test, have been recognized by many authors, beginning with Brady (1984). Kennett (1976) gave an excellent review of all the studies in which variations in size, coiling direction, wall thickness, aperture, and some other characters of planktonic forms are discussed. Bé (1969) indicated that the extreme representatives of this variability spectra, often assigned to different species and even genera are interconnected by clines. Numerous other authors have also recognized considerable intraspecific morphological variations in planktonic species (Parker 1962; Hecht 1974; Emiliani 1974).

EVOLUTIONARY TRENDS

Many evolutionary trends (so called lineages) have been established in planktonic foraminifers during the last few decades (Blow 1956, 1969; Bolli 1957, 1986; Banner and Blow 1959, 1965; Kennett 1966; Berggren

and Poore 1974; Rögl 1974; Scott 1980; Malmgren and Kennett 1981, among many others). Not all of the lineages are thoroughly documented; some are based on speculative data; some contradict others, and inappropriate taxonomic categories have been used in some cases. Examples illustrating the last problem are discussed below.

Let us consider the situation with the *Globorotalia merotumida* Blow et Banner — *G. plesiotumida* Banner et Blow — *G. tumida* (Brady) lineage (Blow 1969; Malmgren *et al.* 1983). In this lineage the transformation from *G. merotumida* to *G. plesiotumida* reportedly took place at the base of zone N17 (late Miocene) and that from *G. plesiotumida* to *G. tumida* at the base of zone N18 (Miocene/Pliocene boundary). The morphological differences among these foraminifers involve an increase of size, elongation, and whorl height, and a thickening of the encrustation. All these differences, even to a much greater degree, can be observed within a single population of many species and they most probably are valuable only in infraspecific nomenclature (Boltovskoy and Wright 1976: 214—221). In particular the size increase, as mentioned earlier, represents tendency of most foraminiferal species; the known increase in many cases is much greater than in the lineage discussed. I am inclined to think that the foraminifers described as *G. merotumida* and *G. plesiotumida* cannot be interpreted as separate species; instead they should be considered as *formae* of *G. tumida*.

Next, the *Globorotalia margaritae primitiva* Cita — *G. margaritae margaritae* Cita — *G. margaritae evoluta* Cita lineage (Cita 1973). *G. margaritae primitiva* is typical of the lower Pliocene where it co-occurs (in most of its range) with *G. margaritae margaritae*. *G. margaritae margaritae* was originally described by Bolli and Bermúdez from upper Miocene deposits, although somewhat later the same authors (Bolli and Bermúdez 1978) stated that the age of the type level should be changed to the early Pliocene. *G. margaritae evoluta* was described from the Pliocene.

First, assigning a subspecies rank to these planktonic forms is not correct, because they co-existed for a long period of time in the same area; subspecies must have disjunct distributions. Incidentally, Rögl (1974), in defining his *Globorotalia truncatulinoides* (d'Orbigny) and *G. tosaensis* Takayanagi et Saito lineage makes a similar mistake. At the same time, morphological differences among the forms described by Cita are too small (some insignificant changes in the equatorial outline, in the height of the chambers, and in the axial profile) for the recognition of independent species. Probably the most notorious change is in size, which increased gradually from *G. margaritae primitiva* toward *G. margaritae evoluta*. Yet, it is precisely this trait which is the least important from the taxonomic viewpoint. It seems to me that it would be more correct

to consider *G. margaritae primitiva* and *G. margaritae evoluta* as *formae* rather than as subspecies.

Finally, the *Globorotalia puncticulata sphericomiozea* Walters — *G. puncticulata puncticulata* (Deshayes) — *G. inflata* (d'Orbigny) lineage (Scott 1980). This lineage was described in detail by Scott (1980) from the uppermost Miocene-lower Pliocene deposits of New Zealand. His paper included numerous excellent photographs of the foraminifers studied, but an analysis of these illustrations suggests that the discrimination of the forms involved is extremely difficult and in many cases too speculative. According to the text, the most important differences consist of the change in the outline (the test becomes less crescentiform and more symmetrical), the change of the axial shape of the chambers, the reduction of the number of chambers in the last coil and the disappearance of the keel. However, all these changes are insignificant and can easily be encompassed by the range of normal species variability. Even such traits as the keel and the number of chambers are unimportant, because in the original description of *G. puncticulata sphericomiozea* (described by Walters as *G. miozea sphericomiozea* and cited by Scott as *G. puncticulata sphericomiozea*) the keel is not mentioned and only the last chamber is reported to be more "angular". Furthermore, Scott pointed out that the keel is present only in a small percentage of the tests and, in addition, it is usually weak and difficult to determine. The illustrations of this species show several specimens without any clear angularity. As for the number of chambers in the last whorl, typical specimens of Recent *G. inflata* have four chambers in the adult and five in young individuals. The number of chambers in *G. puncticulata sphericomiozea* is usually four, although occasionally four and a half. In addition, Scott pointed out that some specimens of *G. inflata* are indistinguishable from the typical form of *G. puncticulata puncticulata* and that "no simple rule for discrimination of *Globorotalia inflata* from *G. puncticulata puncticulata* has been found" (Scott 1980: 673).

Thus, in the case of this lineage we have a notorious example in which members of the proposed evolutionary sequence are morphologically too similar to be interpreted as separate subspecies. Apparently they should be considered as *formae* of *G. inflata*.

Benthic foraminifers are not so suitable for the recognition of phyletic trends because they are considerably less abundant and their evolutionary rates are much slower. However, some authors, after thoroughly studying ample material and using statistical methods have adequately documented phylogenetic lineages in some species of *Gaudryina*, *Spiroplectammina*, *Vaginulina*, *Marsonella*, *Spiroplectinata* and *Gavelinella* (e.g. Grabert 1959; Bettenstaedt 1962; Michael 1966). Some lineages have also been proposed with incorrect use of the subspecies nomenclature. An example of this is the *Aubignyna mariei primitiva* Margerel — *Aubign-*

nyna mariei praemariei Margerel — *Aubignyna mariei mariei* Margerel lineage (Margerel 1988). This lineage was described by Margerel (1988) from Cenozoic deposits of western Europe. The differences between the subspecies named are minimal and consist mainly of a size increase from the older taxon (*A. mariei primitiva*) to the younger (*A. mariei mariei*) and small changes of the shape and ornamentation (development of granulosity of the umbilical side). In the abundant population of *Buccella peruviana*, which lives on the Patagonian shelf (the genus *Aubignyna* is very close to *Buccella*), morphological differences among specimens are considerably greater; these specimens inhabit the same area and have all kinds of transitional forms (Boltovskoy *et al.* 1980). I do not think that the foraminifers described by Margerel should be considered as subspecies. It seems to me that the lineage described represents the morphological spectrum of variability of a single species (*A. mariei mariei*) divided into three groups (*formae*) for the sake of biostratigraphy.

In this context it would be interesting to cite a statistical study of *Bolivina argentea* by Lutze (1974) based on abundant material collected from different localities. This author concluded that several so called phylogenetic lineages should really be interpreted as lineages of phenotypic modifications.

DANGER OF MASSIVE CREATION OF POTENTIALLY INVALID NAMES AND A SUGGESTION TO USE THE "FORMA" CATEGORY

It is true that splitting of taxa helps to achieve finer stratigraphic resolution and, as Miller *et al.* (1982) emphasized, is very valuable also in paleoecological studies. For these reasons the preservation of the lineages cited is desirable and useful. However, I think that we, foraminiferologists, should follow more closely the rules of the International Code of Zoological Nomenclature and make proper use of the taxonomic categories. It is also a mistake to ignore the rules of theoretical biology for the sake of convenience of practical activity, i.e., to assign specific and subspecific names to ecophenotypes.

Attempts are frequently made to base the systematic classification of organisms in general, and foraminifers in particular, on phylogenetic grounds. However, the foraminiferal systematic frameworks, overloaded with invalid names, is becoming more and more artificial. The enormous, chaotic increase of new taxa, as well as inattention to the laws of theoretical biology, are two principal handicaps that hinder the normal progress of our science. "The proliferation of generic names, as observed in recent years... has made ... the use of such a modern classification difficult and, in many cases, impractical" (Herb 1971: 253). Many examples from recent literature attest to the fact that the mas-

sive creation of new names based on insufficient material and observation are still in full progress. One such example is a detailed study of Holocene/Recent unilocular calcareous foraminifers by Jones (1984). Using excellent photographs, Jones described 14 new genera, 22 new species and 19 new subspecies, leaving 27 foraminifers in the open nomenclature. Unfortunately, many of his species are based on only two specimens, the subspecies on only one. Moreover, the creation of *Solenina lagenoides hibernica* subsp. n. was based on only one broken (!) specimen. When describing a new taxon, it is important to include observations with respect to its variation. How can this be done on the basis of only one broken specimen? For the description of a new genus (*Buchnerina*) the author used only four individuals. The differences between his new taxa and those established by previous authors are apparently insufficient in several cases.

More than three decades ago, Hiltermann (1954) published ten "rules" which should be followed when a new taxon is established. These are really very good "rules" and many colleagues have followed them while describing new species. One of these "rules" is that at least ten well preserved specimens are needed to ensure that the prospective new taxon is not a phenotypic variant. I will not cite these "rules" here; they can be found in Hiltermann (1954) and Boltovskoy and Wright (1976). Lutze (1974), in his excellent statistical study of the variability of *Bolivina argentea*, also emphasized great importance of the adequate material in establishing a new taxon, because only then the ecophenotypes and transitional forms can be distinguished. It is a pity that these suggestions are ignored by many modern foraminiferologists.

Certainly, I do not suggest that no new taxa established by Jones (1984) has any zoological value. It is quite probable that many of them are indeed valid, but I insist that they should be based on much more material.

Let us consider a little more the nomenclature of unilocular benthic foraminifers. At the beginning of this decade, the number of calcareous monothalamous benthic genera accepted in manuals and monographs was between four and six (Furssenko 1981; Haynes 1981; Boltovskoy and Giussani de Kahn 1982). In the past 6—7 years this number increased up to nearly 40 (Loeblich and Tappan 1988). How many genera will we have for the unilocular calcareous foraminifers at the end of this century considering the fact that this group now is apparently "in fashion"? Do not be scandalized, please, by the expression "in fashion". I am convinced that this phenomenon (to be in fashion) takes place not only in ordinary life, but in science too.

An illustrative example of the chaotic situation in foraminiferological nomenclature is described by Brolsma (1978). Four foraminiferologists (all of them experienced scientists, well familiar with benthic foraminifers)

identified the same set of 200 specimens. Only two (!) species names were used by all four specialists. At the generic level agreement was somewhat better, namely ten genera were shared by all four.

I may be reproached for contradicting myself: insisting that we follow closely the International Code of Zoological Nomenclature, and at the same time suggesting to use the category "forma" which is not accepted by this Code. That is right, but remember that the use of *forma* (the lowest taxonomic category with so called "directed variability") is harmless, insofar as it does not have official validity and thus is not in conflict with the ICZN. It does not increase our nomenclatural "household", while at the same time it allows a more precise definition of morphological traits and their changes. Since "forma" does not belong to the group of "legal" names, it should be separated from the trivial name by a comma and typed unitalicized. Unfortunately, however, in spite of great convenience of this category, relatively few authors (e.g., Buchner 1940; Friese 1951; Boltovskiy 1959; Closs 1962; Poag 1978; Boltovskoy *et al.* 1980, among some others) have used it so far.

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ZMIENNOŚĆ OTWORNIC, NIEKTÓRE TRENDY EWOLUCYJNE I WARTOŚĆ KATEGORII TAKSONOMICZNYCH

Streszczenie

Poważnym brakiem literatury dotyczącej otwornic jest bardzo wąska interpretacja gatunków oraz ignorowanie praw biologicznych. Podgatunki kopalnych otwornic w niektórych liniach filetycznych są często tworzone na niedostatecznym materiale lub bez uwzględniania zmienności wewnętrzgatunkowej. Prowadzi to do powiększania ilości nieważnych nazw. Autor uważa za użyteczne stosowanie zamiast kategorii „subspecies”, kategorii „forma”, która nie jest akceptowana przez Międzynarodowy Kodeks Nomenklatury Zoologicznej. W celu zaznaczenia nieoficjalnego charakteru tej kategorii, autor proponuje oddzielenie nazwy formy od nazwy gatunkowej przecinkiem oraz niedrukowanie jej kursywą.