Paläont. Z.	61	3/4	223–227	–	Stuttgart, Dezember 1987

Population variability of Paleozoic nautiloids: a reply to TUREK & MAREK (1986)

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Kurzfassung: Die methodologischen Grundlagen der monographischen Übersicht von DZIK (1984) über die Evolution von Nautiloidea werden präsentiert und den kritischen Bemerkungen von TUREK & MAREK (1986) gegenübergestellt.

Abstract: Methodological foundations of the monographic review of the evolution of the Nautiloidea by DZIK (1984) are presented and confronted with critical comments made by TUREK & MAREK (1986).

Immediately after the modern formulation of the biological species concept had been presented at the beginning of the forties (MAYR 1940), the concept of its fossil counterpart, chronospecies, was introduced. It was extensively discussed during a symposium of the Systematic Association in 1954 (SYLVESTER-BRADLEY 1956). Since that time, the population approach to the fossil record of evolution has become more and more widely accepted, although there still are many areas of study where the typologic approach is preferred by most paleontologists. This is well exemplified by the methods of research on the Paleozoic Nautiloidea, vigorously defended by TUREK & MAREK (1986).

A multidimensional chronospecies is represented by biospecies in every time slice within its range of occurrence. There is no serious objection against applications of the biological population concepts to fossil assemblages. The only condition to be met is the homogeneity of a sample, which has to be collected from a single lithological unit, covering a time span short enough to ensure that evolutionary processes do not interfere with intrapopulation variability (i. e. HOWARTH 1973).

Identification of a phyletic lineage from its fossil record requires several standard steps:

(1) Each sample has to meet the condition of temporal and spatial homogeneity.
(2) Groups of specimens, characterized by continuous and unimodal frequency distributions of morphology (phena of MAYR 1969), have to be identified in each sample.
(3) Phena representing sexual dimorphs or different body parts of the same organisms have to be assembled into populations.
(4) Morphologically similar populations represented in coeval samples have to be clustered into biospecies.
(5) Biospecies of different geological ages are then arranged in lineages, which may or may not be cut into named chronospecies.

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0031-0220/87/0061-0223 $ 1.25

I attempted to follow this concept while preparing my monographic review of the evolution of the Nautiloidea (DZIK 1984). The reference standards for the range of population variability in particular nautiloid groups were provided by samples from several Upper Devonian localities in the Holy Cross Mountains, Poland. Biometrical studies of these Devonian cephalopods revealed surprisingly wide ranges of variability in some fossil populations. Conspecific adult specimens with constricted aperture of the shell may differ in diameter by factor of 2.5 in a single sample! Similar variability was found in the curvature and cross-section of shells, as well as in the distribution and concavity of septa. I identified similar ranges of variability in large samples of Devonian and Silurian breviconic nautiloids from Timan, the Urals, and Gotland, examined in several museum collections. Just after the publication of my monograph, the results of biometric studies on some Silurian oncoceratids (STRIDSBERG 1985) have fully confirmed my observations on their population variability.

It would not make much sense to put together these data on species defined by populations and literature data on species defined typologically. Such a procedure would result in an artificial phylogenetic tree presenting non-existing lineages within ranges of species variability. Thus I had to accomodate literature data to my own empirical material. It was certainly not my intention to discredit the morphologic and stratigraphic data presented by various authors following different taxonomic methodologies. I was, however, of the opinion that it was highly undesirable to continue the typologic approach to fossil cephalopods. I knew of a growing concern about disparity between the classification and the biological reality also among students of Mesozoic ammonites (i. a. CALLOMON 1985), which resemble Paleozoic brevicones in this respect.

The single most important literature source of data on Silurian and Devonian nautiloids is the monograph of BARRANDE (1865–1877). The species concept employed in this monumental work was typical of its times and, despite the enthusiastic opinion of TUREK & MAREK (1986: 245), BARRANDE's data cannot be applied to any serious evolutionary study without reinterpretation. Because of the structural complexity of the Lower Paleozoic rocks in Bohemia and of the generally similar lithologies in horizons of different geological age, the original material of BARRANDE, with for present requirements inadequate field references, cannot be used for population studies (DZIK 1984: 7, 9). Examination of BARRANDE's specimens during three weeks at the Narodní Muzeum, Prague ("cursory" in the opinion of TUREK & MAREK), led me to the conclusion that the ranges of population variability in the majority of BARRANDE's localities did not differ from those recognized in the Polish, Swedish, and Russian collections. Hence, I attempted to group provisionally the morphotypes described by BARRANDE into what might be at least tentatively regarded as biological species. It has to be stressed that the effects of this grouping are falsifiable and can easily be tested by population studies of the Bohemian materials. Unfortunately, this is the only way to either prove or disprove TUREK & MAREK's (1986) or my views on the morphologic ranges of various species of *Peismoceras, Kosovoceras, Digenuoceras,* etc.

Three matters of dispute have been supplemented by TUREK & MAREK (1986) with new illustrations and hence deserve special attention. Thus, TUREK & MAREK (1986: 248) indicate that in *Bathmoceras* "the connecting rings never intrude in the body chamber, because adapically they grow steadily larger and are fully developed by about the seventh or eighth camera from the body chamber". They do not present evidence that each particular connecting ring changed the shape in its ontogeny in this way, but it is at least apparent that the connecting rings did not protrude into the adult living chamber. I assumed, apparently wrongly, that in *Bathmoceras,* similarly as in other well known ellesmeroceratids (see MUTVEI & STUMBUR 1971), connecting rings did not change in ontogeny. This possible misinterpretation, however, does not have any bearing on the phylogenetic reconstructions presented in my monograph. TUREK & MAREK (1986: 248) failed to show data, which could indeed contradict a derivation of *B. complexum* from older forms usually attributed to the separate genus *Eothinoceras.*

TUREK & MAREK (1986: 248) also contest my alleged transfer of the genus *Ptenoceras* from the order Oncoceratida to the Nautilida. Actually, however, I left the problem of relationships of the *Ptenoceras* group unresolved. I listed (with question marks) these genera together with the morphologically and stratigraphically closest family Trochoceratidae, but their possible relationships were discussed within the chapter on the Oncoceratida (DZIK 1984: 57) and alternative interpretations of phylogeny of the group were presented in Fig. 17 (as oncoceratids) and 59 (as early Nautilida). I explicitly wrote (DZIK 1984: 57) that "the oncoceratid affinities of *Ptenoceras* are suggested by the muscle scar pattern recorded from *Doleroceras*" which closely resembles *Ptenoceras.* I thus predicted discovery of the muscle pattern in *Ptenoceras* which is now considered by TUREK & MAREK (1986: 248) as the evidence against my interpretations.

TUREK & MAREK (1986: fig. 3) illustrate variability in size of the apical part in *Sphooceras,* treating it as a decisive evidence for truncation. The range of this variability, when restricted to a sample taken from a single locality (Zadní Kopanina) falls in the typical size range of adult living chambers of oncoceratid nautiloids (the factor of 2.5; see DZIK 1984: figs. 19–25; STRIDSBERG 1985: figs. 7–12). TUREK & MAREK dismiss my "curious interpretation" because it allegedly proposes that "this nautiloid's egg capsule would have varied from millimetre values to the size of an ostrich's egg" (TUREK & MAREK 1986: 252). They do not mention, however, that I explicidly rejected any possibility that the apical part of *Sphooceras* conch represents the embryonic shell (DZIK 1984: 135).

The paper by TUREK & MAREK (1986) abounds in expressions like "any possibility of admitting that this species may be conspecific with one of the other species mentioned by DZIK is out of question" (p. 247), "completely unfounded" (p. 248), "completely unjustified" (p. 248), "this curious interpretation" (p. 252), which indicate much emotional involvement. These emotions, however, cannot be an excuse for unfairness in the way they present my work. For instance, TUREK & MAREK (1986: 248) write that *Systrophoceras arietinum* "is actually compared by DZIK with the goniatite species *Anetoceras (A.) fritschi*", while I only mentioned that "some shell fragments similar to *S. arietinum* were also recorded from the Siegenian (. . .) and Eifelian (*Gyroceras fritschi* BARRANDE 1877, pl. 517)". The latter fragmentary specimen lacking preserved siphuncle, was identified as a member of the *Anetoceras solitarium* population after my monograph had been printed.

My expression "the supposedly bactritid affinities of the genus *Bactroceras* (= *Eobactrites*) are disputable" (DZIK 1984: 18) is presented by TUREK & MAREK (1986: 248) in a rather surprising way: "DZIK compares the lower Ordovician genus *Eobactrites* with the Devonian genus *Bactrites* on the basis of the single aperture, although, as he himself writes, the form of the body chamber is unknown". Actually, my observation that "*Bactroceras* (= *Eobactrites*) is homeomorphic with the Devonian *Bactrites;* it differs from the latter in its simple aperture" was based on the Baltic specimens of *Bactroceras,* while the earlier statement that "the form of the body chamber is unknown" referred only to *B. sandbergeri,* the Bohemian type species of *Eobactrites.*

A similar misrepresentation of my views concerns the relationship between the genera *Cyrtocycloceras* and *Ctenoceras.* With reference to p. 121 of my work, the relationship is claimed to be "doubtful, to say the least" (TUREK & MAREK 1986: 249). This was also my opinion. Actually, I included the Llanvirnian *Ctenoceras* in the family Orthoceratidae (p. 97, also fig. 39a); while discussing (p. 121) the evolution of the family Cycloceratidae I only wrote: "it seems to me very likely that the late Silurian species of *Cyrtocycloceras* are descendant of so-called [Caradocian] »*Ctenoceras schmidti*«". Elsewhere, TUREK & MAREK (1986: 249) state that "DZIK demonstrates the considerable intrapopulation variability (. . .) by referring to illustrations of what, by DZIK own determination, are two different species" although there is a clear indication in the appropriate place (DZIK 1984: pl. 6: 2–3) that the photographs represent the extreme morphotypes of *Trocholites orbis.*

TUREK & MAREK (1986: 252) write that "many of technically excellent reconstructions are based on fragmental and very poorly preserved material, a fact which detracts in general from the credibility of the drawings" and indicate, as examples, my reconstructions of *Orthoceras regulare* and *O. bifoveatum.* These are the two most common species in the Baltic Ordovician, studied by many authors and illustrated even in textbooks. They are represented by hundreds of specimens in museum collections (including Narodní Muzeum, Prague). The photographs published show fragments of body chambers with preserved shell wall and thus present a supportive evidence for my interpretation of depressions on the body chamber; the respective areas are clearly indicated on the drawings.

It is not quite clear to me what TUREK & MAREK (1986: 250) mean by stating that, "DZIK's concept on the genus strongly resembles that held at the end of the last century", but their subsequent remarks that my interpretations are "solely on the basis of outer morphology, completely ignoring stratigraphic differences" is amazing. The main and explicit criterion for arranging taxonomic data in the phylogenetic trees presented in my monograph was "continuity of all morphologic transformations along the time axis" (DZIK 1984: 11). The methodology of microstratigraphic dense sampling and biometric analysis of large populations is the one I have followed since many years (DZIK & TRAMMER 1980; DZIK 1985).

In conclusion, I suggest that instead of continuing this fruitless discussion of problems which are either already resolved or cannot be resolved without additional empirical evidence, we should rather study the population variability of Silurian and Devonian nautiloids. They still are very inadequately known in this respect, and the beautiful Bohemian material provides extraordinary opportunities to this end. The need is growing: since the publication of my critical review, dozens of papers on fossil nautiloids have been published, in which hundreds of new taxa are proposed on the basis of specifically undeterminable phragmocone fragments, while totally neglecting not only intrapopulation but even developmental variability. There are, fortunately, some good news, too. New attitudes are exemplified by the monograph of STRIDSBERG (1985), presenting the population variability and sexual dimorphism in some Silurian breviconic nautiloids, and by the excellent work of MUNDLOS & ULRICHS (1984) showing convincingly, with application of biometrics, that the Carnian *Thuringionautilus* is an end member of the gradually evolving *Germanonautilus* lineage.

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Eingang des Manuskripts bei der Schriftleitung am 18. 4. 1987.