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TYPOLOGIC VERSUS POPULATION CONCEPTS OF  
CHRONOSPECIES: IMPLICATIONS FOR AMMONITE  
BIOSTRATIGRAPHY

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The effects of the application of horizontal (population) as opposed to vertical (typologic) taxonomy on precision of ammonite chronozonation are discussed and an example of stratigraphic inference that can be derived from the population method is presented. An almost complete macroconch from Świętoszewo, Pomerania, is compared with a standard, biometrically studied series of samples from the Early Volgian of Brzostówka, Central Poland. Specimens identical morphologically with that from Świętoszewo can be found among extreme end-members of the population variability much above and below the horizon of the best fit with the mean for the sample. Time correlation is thus a probabilistic kind of inference as the probable identity of time decreases with increasing distance from the horizon of the best fit. For this reason vertical (typologic) diagnoses of chronospecies cannot result in better and more reliable correlations than a horizontal (population) one. Because the typologic species concept leads to false representation in phylogenetics and biogeography it is proposed to abandon its use in biostratigraphy.

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INTRODUCTION

Our knowledge of evolutionary mechanisms has increased rapidly owing to recent, thorough studies of stratigraphically dense series of samples of fossil mammals (Gingerich 1979), conodonts (i.a. Dzik and Trammer 1980), foraminifers (i.a. Malgren and Kennett 1981), gastropods (Büttner 1982; Mensink *et al.* 1984), and radiolarians (Lazarus 1983). The ammonites have contributed little to this area of study despite the fact that they were

the first objects of empirical studies on phylogeny and strict methodology of phylogeny reconstruction was developed for ammonites by Brinkmann (1929; see also Raup and Crick 1981). This method, christened "stratophenetic approach" by Gingerich (1979), has been widely applied since its origination to many groups of fossils, with the notable exception of the ammonites. Despite great progress in understanding of the phylogeny of the Ammonoidea at higher taxonomic levels (Donovan *et al.* 1980), appropriate interpretation of detailed relationships of particular ammonite species seems to be hampered by ambiguity of the concept of chronospecies. In consideration of ammonite phylogeny the problem is especially well recognizable owing to great population variability and the long history of ammonite taxonomy, invented mostly by stratigraphers for stratigraphers with little attention paid to consistency with biological meaning of particular taxa.

The aim of the present paper is to show that there is no contradiction between biological and geological points of view on the basic problems of taxonomy at the species level. Moreover, I shall try to show that in ignoring the biological interpretation of fossils, stratigraphers lose much important information.

The case is worthy of attention also because the ammonites are unique among fossils in that they provide a commonly well preserved and easily accessible record of evolutionary modifications of the ontogeny. The group of ammonites on which the present study is based seems to be especially interesting in this respect, having a very complex and variable ontogeny.

#### THE PROBLEM

Let us consider an ideal transition series of samples representing a continuum of populations arbitrarily separated into two successive chronospecies, *a* and *b* (fig. 1). There are two basically different methods of delimitation of the boundary between related chronospecies.

According to the first method, currently in general use in ammonite studies, the boundary is defined on the appearance of a particular character or set of characters considered to be diagnostic for younger chronospecies. At the beginning of the time range of a chronospecies defined in this way such characters occur among extreme morphotypes of populations. Subsequently they spread out over the whole population being typical of most specimens until gradual suppression by newly appearing characters, typical of another, still younger species. This method of delimitation was named a vertical one (Sykes and Callomon 1979) as the line separating chronospecies is vertical (see fig. 1). In fact, it is an application of the typologic concept to chronospecies.

The second method, still rather rarely used, bases boundaries on particular features of whole samples of fossil populations. An exact beginning

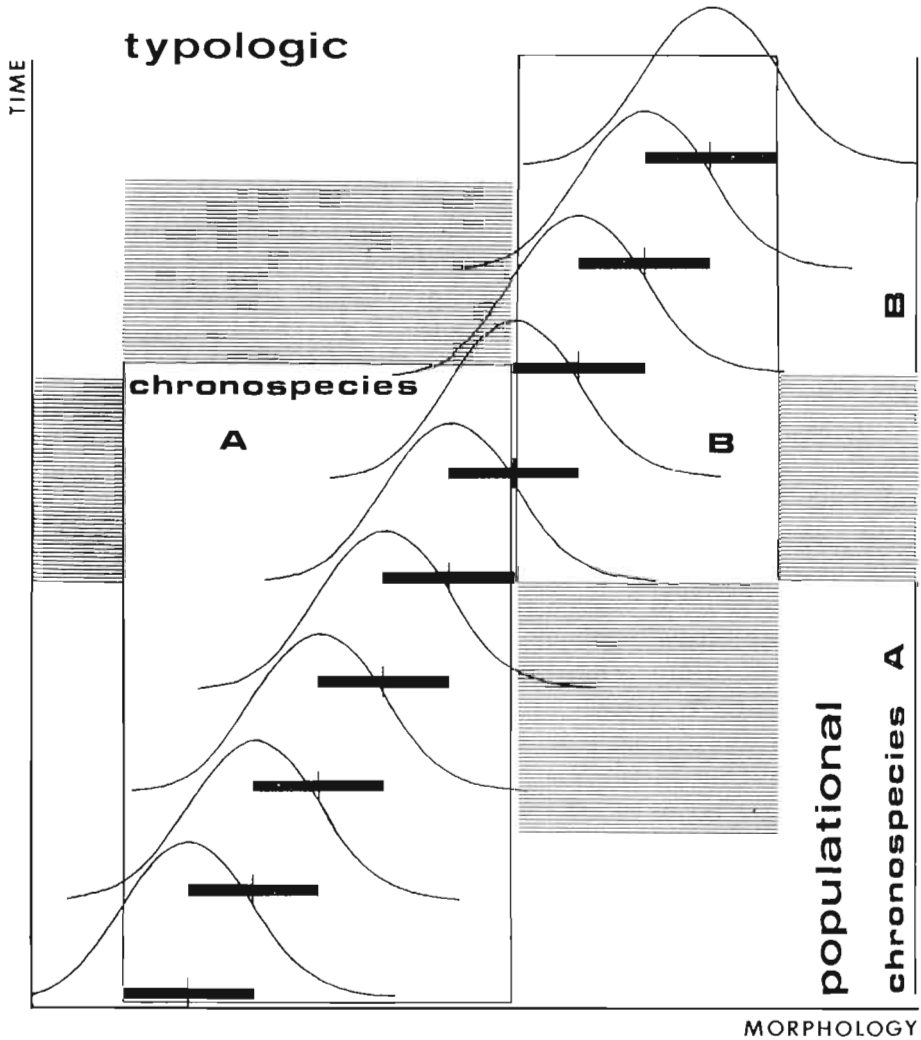


Fig. 1. Schematic presentation of relationship between vertical (typologic) and horizontal (population) concepts of chronospecies. Horizontal bars represent standard deviations from the mean of every sample; shaded parts of time ranges indicate limits of uncertainty in recognition of chronospecies (in case of population concept) or ranges of subordinate occurrence of the morphotype in samples (in case of typologic concept). Note that ranges of typologically defined chronospecies always overlap significantly.

of a chronospecies can be indicated only in its type section, where it was arbitrarily chosen. In any other locality samples can be identified as belonging to the chronospecies if they do not depart too much from the type sample in their morphologic features. Lack of any overlap in ranges of standard deviations was proposed as a minimum difference allowing recognition of chronospecies (Dzik and Trammer 1980); a maximum morphologic range of the species can be arbitrarily defined. There is thus a zone

at the boundary between succeeding chronospecies, corresponding to the morphologic shift in range of the standard deviation of the diagnostic feature, within which samples can be attributed either to older or to younger chronospecies (fig. 1). This is the horizontal or rather population method of chronospecies definition.

Superficially, the first method looks like the stricter and more convenient one. It enables definitions of chronospecies (and zones corresponding to them) on appearances of particular, easily and unequivocally recognizable characters. This is perhaps why the majority of ammonite students prefer the use of typologic species over the population method.

It can easily be noted that the vertical definition of chronospecies makes time ranges of succeeding chronospecies significantly overlapping even if they represent a single continuum of populations and that never more than a single biospecies of the group existed simultaneously (see Gingerich 1979). The use of the method results thus in presenting non-existing sympatric speciations in evolutionary trees, artifacts which are, in fact, indistinguishable from real speciation events included in the same tree. The method leads unavoidably to artificial splitting of objective biospecies into subjective typologic units. When ammonite assemblages from different localities are compared, one is then unable to say how many biospecies occurred in each of them, whether species (not necessarily identical with morphologic) diversity was similar or not, and so on. Biogeography built on such a poor basis makes little sense. There is more than enough reason to reject the vertical method as a tool for paleobiological studies.

Is the vertical method so much superior over the horizontal one in biostratigraphical applications to counterbalance its biological deficiencies? Let us analyze an example of age determination based on a Volgian ammonite from Pomerania.

#### REFERENCE STANDARD

*Material.* — The best known and most complete section of fossiliferous Early Volgian is that at Brzostówka near Tomaszów Mazowiecki in central Poland. Ammonites from this classic section are relatively well known owing to works of Michalski (1890), Lewiński (1923), and Kutek and Zeiss (1974).

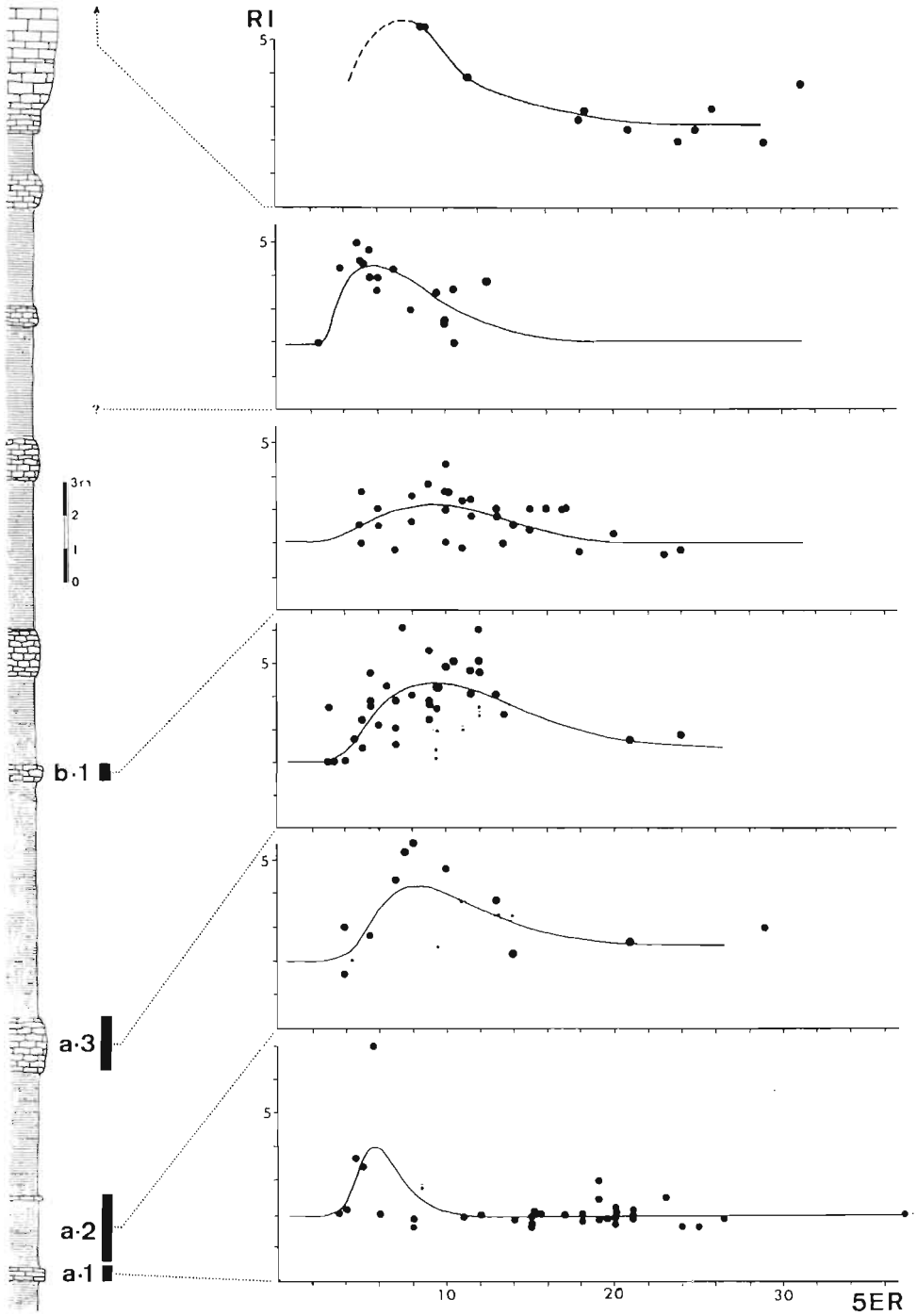
Kutek and Zeiss (1974) described ammonites collected in an abandoned clay-pit at Brzostówka, where about 15 meters of marly shales and marls were exposed. They subdivided it into six units, five of them containing rich ammonite assemblages. A few years later, on the occasion of construction in the area, an additional sample of flattened ammonites was collected in black shales situated about ten meters above the top of the clay-pit exposure. A few specimens have been collected also from the

overlying limestone series during many years of investigations of the area by Professor Jan Kutek. Together with specimens illustrated by Lewiński (1923) they form the youngest sample.

Modes of preservation of these materials are rather diverse. Specimens from limestones and limy concretions are preserved three-dimensionally, most of the specimens from the clay-pit section are partially flattened, whereas specimens from the overlying black shales are completely flat. This surely introduces significant biases into measurements, but strict estimation of degree of deformation for particular specimens would be too complex to be attempted in this study. Nevertheless, specimens from the same sample are generally deformed in the same way, so the introduced systematic error seems to be insignificant in view of the purpose of the study.

Kutek and Zeiss (1974), applying the vertical concept of chronospecies, identified fifteen species and subspecies of ammonites, belonging to five genera of two subfamilies, in the fauna from the clay-pit. They noted (Kutek and Zeiss 1974: 529) that: "on the strength of the existence of transitional forms, all the existing species of *Zaraiskites* could possibly be referred to but one or two large species. It seems better, however, to retain the hitherto established formal species of *Zaraiskites* which differing in their stratigraphic range, enable the *scythicus* Zone to be subdivided stratigraphically". These comments obviously concern both vertical transitions between populations and horizontal transitions between morphotypes. In the present study all ammonite specimens from each unit are analyzed as a single sample. Previous taxonomic identifications have not been taken into account.

*Biometrics.* — The most remarkable evolutionary change revealed by biometric investigation of the studied series of samples is a gradual modification of the shell ontogeny, already noted by Michalski (1890) and described in detail by Kutek and Zeiss (1974). The course of ontogeny is extremely variable among specimens in all samples. Obviously, physiologic control of the shell ontogeny was not strict, especially in older populations. This hampers taxonomic studies because the usual sample size appears to be too small to allow strict discrimination of biospecies. Comparison of different samples is also difficult because of different population dynamics. Some samples are dominated by juveniles (for example a-3), others by adults (a-1). I am thus unable to say whether evolute specimens, prominently ribbed, with dichotomous rib branching, which were included in the genus *Isterites* by Kutek and Zeiss (1974), represent really a separate evolutionary lineage or are rather end members in the range of variability (figs. 2, 3). The same concerns a group of specimens attributed previously to *Ilowaiskya*, represented only by adult macroconchs (?) difficult to compare with co-occurring specimens attributed to *Pseudo-virgatites*. In the case of so much doubt I consider provisional treatment



of the whole sample as monospecific a proper application of Occam's Razor.

Features that undergo the most profound modifications in ontogeny and phylogeny are patterns of rib divisions and the shell involuteness. The oldest studied sample a-1 contains specimens with shells evolute throughout ontogeny, ornamented with dichotomously branching ribs which are densely distributed at early ontogenetic stages (up to the shell diameter ranging from 45 to 60 mm). Some specimens show trichotomous rib branching close to the end of this stage of development (at a diameter about 50 mm). Rarely this kind of ribbing reaches a diameter of 135 mm; in a single specimen (Kutek and Zeiss 1974: pl. 11: 4) the ratio between secondary and primary ribs reaches 7.0. These extreme members of the sample, exhibiting *Ataxioceras*-like ribbing of mid-whorls, were attributed by Kutek and Zeiss (1974) to *Pseudovirgatites*, while forms lacking polygyrate ribbing were identified as belonging to the genus *Ilowaiskya*. A single juvenile specimen departs slightly from the others in having more sparsely distributed ribs and was identified as a member of the genus *Isterites* by them. The poor state of preservation of ammonites and the small number of specimens do not allow a definite decision as to whether there are many biospecies or only a single one. Subjectively I am inclined to the second interpretation.

In the subsequent sample a-2 most of the specimens still show dense primary ribbing with dichotomous divisions up to the diameter of about 50 mm. Distribution of high ratios between secondary and primary ribs extends to later stages of ontogeny exceeding a diameter of 100 mm in almost all specimens. The same pattern of ontogeny is typical of the next sample a-3 but in this sample specimens with ribbing disappearing on the flanks (of the *Pseudovirgatites* morphotypes) become rare. In the sample b-1 the ratio between secondary and primary ribs (rib index RI) at mid-whorls decreases to the mean of 3.0, instead of about 4.0 in older samples. Transformation of the ribbing pattern, as well as involuteness, become more smoothly arranged, without sudden changes typical of shells from older units (figs. 2, 3).

The evolution of the lineage beginning from the sample b-1 involves somewhat different features than before. Namely, instead of expanding

Fig. 2. Rib index (RI; mean ratio between secondary and primary ribs for approximately one-fifth portion of the whorl) plotted against distance separating each fifth rib (5ER) as a measure of ontogenetic stage for each of the ammonite samples collected from the section at Brzostówka near Tomaszów Mazowiecki. Based on data of Lewiński (1923), Kutek (1967) and Kutek and Zeiss (1974), and unpublished materials of Professor Jan Kutek. Position of samples indicated on the stratigraphic column (after Kutek 1980 and Kubiatowicz 1983) by letters and vertical bars. Each dot represent single measurement for portion of the whorl, more complete specimens are thus represented by few dots; asterisks indicate specimens identified by Kutek and Zeiss (1974) as belonging to the genus *Isterites*. Thick lines represent roughly estimated curves of ontogenetic changes.

toward later ontogenetic stages, the polygyrate ribbing (meanwhile appearing less prominent) expanded toward progressively earlier ontogenetic stages. Here the ratio of secondary to primary ribs reaches its peak, decreasing in the course of ontogeny. In the sample taken from about ten meters above the clay-pit section, disappearance of dichotomous, dense branching can be noted at a diameter of about 30 mm or even earlier (only two specimens preserved early growth stages well enough to enable identification of the ribbing pattern). Still in samples b-1 and the succeeding one, specimens with permanently dichotomous sparse ribbing throughout the whole ontogeny and evolute shells occur. It seems that they are connected by transitions with typical forms. Their ontogeny seems to pass over the middle ontogenetic stage present in other forms. There is no clear evidence for multimodal distribution of ribbing patterns and an occurrence of more than a single lineage seems rather unlikely.

In the sample from black shales above the clay-pit section another unusual feature of ribbing began to develop. In a few specimens bunches of secondary ribs are separated by depressions slightly wider than distances between regular secondary ribs. Such a feature is clearly recognizable in almost all specimens from the limestone series above the marls and shales in the Brzostówka section. This is, in fact, the feature typical of all later species of virgatitids in Poland and Russia. In this youngest sample evolute specimens with rather sparse ribbing occur together with less numerous specimens exhibiting involute, densely ribbed mid-whorls (Kutek 1967).

The general pattern of evolutionary transformation in the discussed lineage is intuitively easy to recognize. It is, however, not so easy to present objectively in plots. I have tried to present these transformations in a series of two- and three-dimensional plots. The pattern of intrapopulation variability is multivariate. The ontogenetic transformations are non-linear in respect to the shell size and they are organized in a different way at every stage of the phylogeny. I failed to find any single index that would allow description of particular specimens and that can be used for clear presentation of changes of its frequency distribution. Such analysis appears possible only for particular, selected stages of ontogeny (see fig. 7).

*Sexual dimorphism.* — Proper interpretation of dimorphic pairs necessarily requires knowledge of the monospecific population extent for the discussed ammonites. Otherwise it may happen that artificial dimorphic species are proposed (as already has been done) which lack any biological sense — with fat males and females grouped into one species and tall males into another. On the other hand neglection of sexual dimorphism may also result in false taxonomic and evolutionary judgements.

Little is known, unfortunately, on sexual dimorphism in virgatitids. It has been suggested by Makowski (*in*: Kutek and Zeiss 1974: 529) that sexual dimorphism is expressed in this group of ammonites only in size



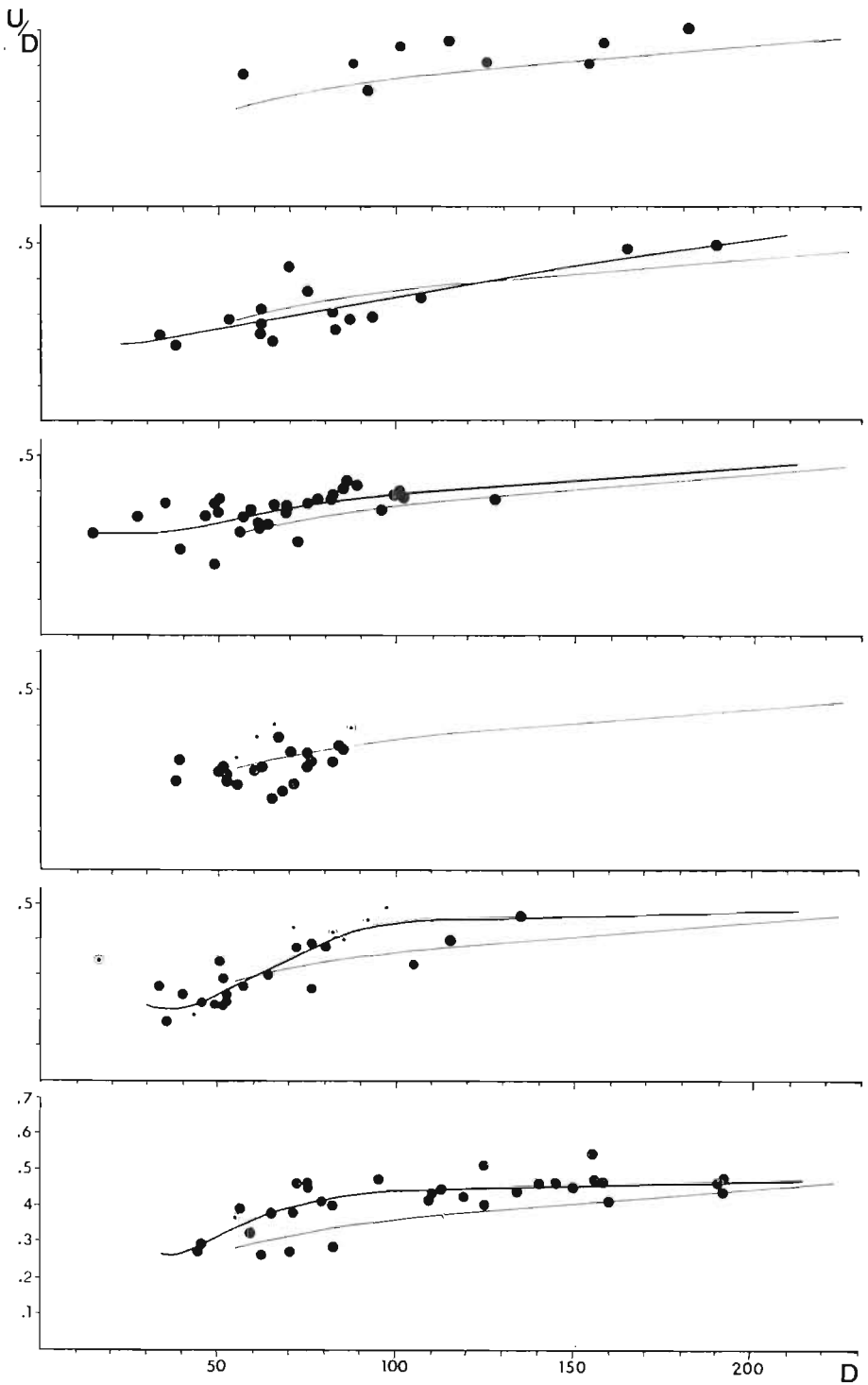


Fig. 3. Index of involuteness of the shell (diameter of umbilicus to the shell diameter;  $U/D$ ) plotted against diameter of the shell for the same samples as in fig. 2. Thick lines represent estimated curves of ontogenetic changes for each sample, whereas a thin line is the curve for the complete specimen from Świętoszewo.

differences between sexes. This opinion is consistent with size distribution of supposedly adult specimens from the clay-pit section (Kutek and Zeiss 1974). Also the sample collected above the highest unit of the clay-pit contains a few possibly adult specimens having slightly modified ornamentation in proximity of the aperture. One of these specimens is 107 mm, another about 217 mm in diameter. It seems that virgatitid microconchs lacked lappets, similar to their British distant relative *Pectinatites*, which developed, however, a ventral horn (Cope 1978; Donovan *et al.* 1980).

One may conclude that features of sexual dimorphism probably do not introduce significant distortion into biometrically recognizable evolutionary patterns of the lineage of virgatitids from Brzostówka.

*Taxonomic nomenclature.* — The problem of choice between horizontal and vertical classifications of ammonites has been briefly discussed by Sykes and Callomon (1979: 858). The main objection against the horizontal classification that was raised by them concerns supposed inclusion of an age criterion into horizontal definitions. This may introduce circular reasoning when species are identified away from their type sections. According to these authors, vertical definitions lack this deficiency being based exclusively on morphologic criteria. Such representation of the problem is not free from oversimplification. Vertically defined chronospecies of ammonites have their objective time-and-space coordinates which allow recognition of homeomorphs and they do not differ in this respect from horizontally defined chronospecies. A postulate of removal of everything but morphologic criteria from taxonomy does not seem realistic. The difference between vertical (typologic) and horizontal (population) definitions, both based generally on morphologic criteria, consists rather in understanding of the function of a holotype and a type series. In the typologic concept of chronospecies a holotype (or a whole type series) is a standard of a mean value of arbitrarily defined range of morphologic variability allowed to occur within a species. In the population concept a holotype is nothing more than a member of the type population, an indicator of its exact time-and-space coordinates. Any population-taxonomic identification refers thus to the type population (not to the holotype) as the reference standard.

Before nomenclatorial problems connected with the discussed virgatitid lineage are solved, one needs to know populations (samples) to which holotypes of already designated species belong. This is a difficult task. As has been noted above, morphologically identical specimens can potentially be found in quite different populations just as quite different specimens may belong to the same population. For example, a specimen with ribbing of its mid-whorls of the *Ataxioceras*-type (thus belonging to the vertically-defined early species *Pseudovirgatites puschi* Kutek et Zeiss, 1974) was found by Lewiński (1923: pl. 7: 8) as high as in the limestone series containing evolutionarily advanced species of the lineage. The oldest

available specific names of virgatitids are those based on materials from the vicinity of Moscow, Russia. The Russian section of the Early Volgian is extremely condensed and incomplete. Ammonites that can be compared with those from Brzostówka occur in a few layers of sand and are preserved usually as phosphoritic casts (Michajlov 1957). Most of the outcrops are not now accessible. Until a proper revision of existing materials is done it is impossible thus to say whether the holotypes of *Zaraiskites quenstedti* (Rouillier, 1849), *Z. scythicus* (Vischniakoff, 1882), and *Z. zarajskensis* (Michalski, 1890) represent typical or extreme members of their populations.

Whatever is the true position of holotypes of enumerated species, their names are now in general use applied to populations having typical morphotypes identical morphologically with these holotypes. At least *Z. scythicus* and *Z. zarajskensis* are understood as chronospecies diagnostic for biozones of their own. It would be irrational to oppose the prevailing opinion in this case. The name *Z. zarajskensis*, can be applied safely to the population from the limestone series of Brzostówka, sample b-1 and probably b-2 can be attributed to *Z. scythicus*, whereas sample a-3 may represent *Z. quenstedti*. Morphologic features of the sample collected above the clay-pit section surely substantiate erection of a new chrono-(sub)species for it. For the oldest populations, a-1 and a-2, several specific names proposed by Lewiński (1923) and Kutek and Zeiss (1974) may apply. Because of some uncertainty in attribution of Lewiński's materials to particular layers, it seems reasonable to select the name *Pseudovirgatites puschi* Kutek et Zeiss, 1974 for this species.

The type population of the Tethyan species *Pseudovirgatites scruposus* (Oppel, 1865) differs from the population of *P. puschi* in the wider distribution of the densely ribbed stage of development of the shell (Kutek and Zeiss 1974; Zeiss 1977). If the stable reduction in extent of this stage, observed in the Brzostówka section, was a stable trend the population of *P. scruposus* from the Klentnice beds may form the oldest known link in this evolutionary lineage. This may mean that the epicontinental Middle to East European virgatitids had their roots in the Tethyan realm (Kutek and Zeiss 1974). There is also evidence that at least at somewhat later stages of evolutionary development the lineage was still present in the Tethys (Nowak 1971).

*Biogeography.* — Geographic distribution of virgatitids is considered as evidence for biogeographic distinction of Polish and Russian epicontinental seas at a provincial rank. If really all the virgatitids represent a single evolutionary lineage, not worthy of separation into distinct genera, such an interpretation may appear to be somewhat exaggerated. There is no evidence for direct connection between Russian and Polish populations — they seem to represent rather parts of a wider area of distribution of the lineage covering also the Carpathian part of the Tethys. The Polish sea

was separated from the British sedimentary basin of the Upper Kimmeridge clay and identifications of *Pectinatites* in the Polish lowland (Dembowska 1973) are probably erroneous, being based on unidentifiable juveniles probably representing the virgatitid lineage. The Polish sea, seemingly lacking any other ammonite lineages, with belemnites also absent, extended up to Western Pomerania, where shallow carbonate facies with significant amounts of coarse quartz grains indicate proximity of the shore. Volgian ammonites occurring in this area are thus unlikely to belong to different populations from those of Brzostówka. Thus, they can safely be compared with the described reference standard.

#### THE EXAMPLE

A fortunate occasion to emphasize methodological problems connected with the taxonomic identification of single ammonite specimens belonging to a well known lineage is provided by the recent find of well preserved ammonites in Volgian rocks of Pomerania. The Volgian strata crop out in Western Pomerania in two quarries of a cement plant in Czarnogłowy near Kamień Pomorski (Zarnglaff of German authors), not working since 1962. Not infrequent, fragmentary virgatitid shells were found in the southern of the two quarries, near the village Świątoszewo (Schwanteschagen in German literature) by Schmidt (1905) and Wilczyński (1962). Both quarries are now abandoned and completely filled with water, but by chance in 1980 an almost complete specimen of an ammonite was found by Dr. Michał Gruszczynski, in one of the top layers approximately in the middle of the eastern wall of the quarry. The limestone layer contains numerous nuclei of *Iotrigonia hauchecornei* (Schmidt, 1905), *Laevitrigonia micheloti* (Loriol, 1875), and *Isognomon subplanum* (Etallon, 1862). Most probably it corresponds to layers 18—19 of Wilczyński (1962) and Dmoch (1970), although exact identification is not possible considering the present state of the outcrop. It is also not possible to say whether two whorl fragments illustrated by Schmidt (1905) and a single one by Wilczyński (1962) occurred in the same layers or somewhat below, as suggested by Wilczyński (1962). These specimens do not differ from comparably sized parts of the complete shell but, in fact, are unidentifiable at the species level if taken alone.

*Morphology.* — When complete, the shell was probably more than 240 mm in diameter, perhaps up to 300 mm. Only a small part of the living chamber has been found, which is difficult to fit its proper place on the phragmocone. Diameter of the phragmocone is 198 mm; initial whorls up to the diameter of 32 mm are not preserved (pl. 9, 10; fig. 4, 5).

The shell changed its shape during ontogeny from significantly involute to almost evolute (ratio of the diameter of umbilicus to the total diameter changes from 0.30 to 0.46). Involuteness appears to be rather strictly correlated with the pattern of ribbing (fig. 6), at least at diameters of more than 50 mm. The earliest preserved whorls, unfortunately lacking their

adumbonal parts, show dichotomous branching of ribs which subsequently changes into triplicate divisions. At mid-whorls (diameter 45 to 120 mm) four secondary ribs correspond to each primary rib. Up to the diameter of 150 mm transition back to dichotomies occur with gradually disappearing trichotomies. Density of secondary ribs changes rather smoothly in ontogeny (fig. 6), although the regression is not linear. Initial whorls show primary ribs more densely packed than could be extrapolated from subsequent changes in rib density. This is easily visible on a plasticine cast illustrated by Schmidt (1905: pl. 10: 13) where the change from densely distributed and dichotomously divided primary ribs to polygyrate ones occurs at a diameter of about 25 mm.

The shell is almost surely a macroconch.

*Age correlation.*—The stratigraphic distribution of the population variability of ammonites from Brzostówka and geographic distribution of other known virgatitids strongly support the view that the Pomeranian population of virgatitids represents a part of the same evolving species which is represented by the continuum of populations in the Brzostówka section. It thus seems reasonable to look for the place in the Brzostówka section in which the degree of evolutionary advancement of the lineage corresponds to that of the Pomeranian population.

The population from Świętoszewo is surely older than the population of *Z. zarajskensis* from the limestone series of Brzostówka, because none of the known Pomeranian specimens shows separation of rib bunches typical of almost all known specimens from that part of the Volgian at Brzostówka. It is also surely younger than populations from the clay-pit section, because there is significant reduction in extent of the developmental stage with densely packed, dichotomous ribs, much beyond the range of variability observed in samples a-1 and a-2. There is only a span of the section above sample a-3 that can be considered as a possible place for the population isochronous with that from Pomerania.

In fact, the smooth pattern of the ontogeny shown by the complete specimen from Świętoszewo fits best with means for sample b-1 and for the sample from black shales above the clay-pit section (fig. 2). In this part of the section the most significant evolutionary transformations concern the pattern of ribbing at a diameter approximately between 30 and 80 mm. For the purpose of identification of relationships of the specimen from Świętoszewo, it will be most convenient to restrict discussion to features of ribbing at this particular stage. Because many specimens are incompletely preserved and the diameter of the shell is then hard to measure, instead of diameter I used density of ribbing as an indicator of ontogenetic advancement. Density of secondary ribs increases almost linearly in development and use of this factor permits inclusion into consideration of many more specimens than if only complete coiled shells are analyzed.

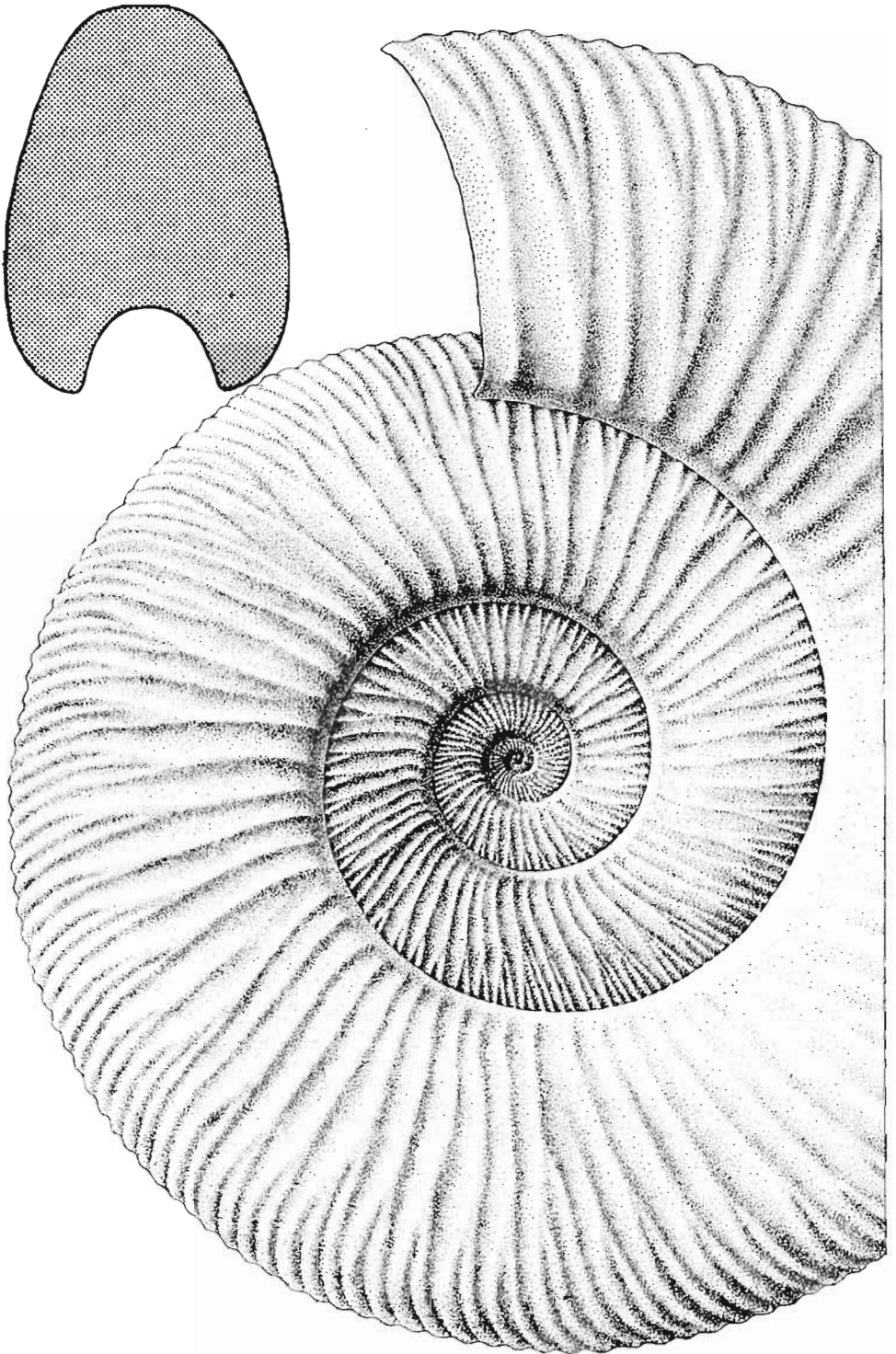


Fig. 4. Reconstructed shell of a virgatitid ammonite from Świętoszewo (specimen ZPAL Am.VI/1; see also pl. 9, 10); youngest whorls after specimen illustrated by Schmidt (1905: pl. 10: 13).

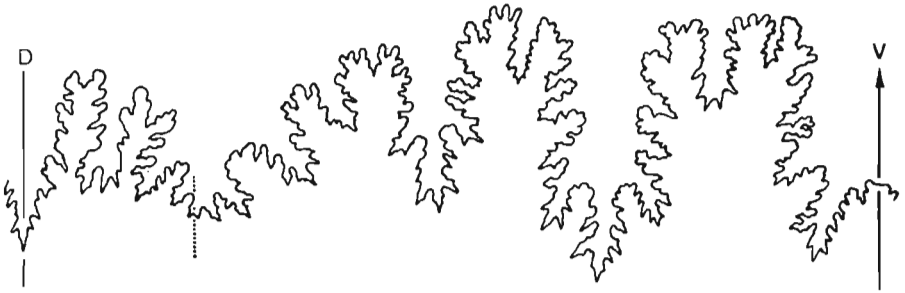


Fig. 5. Composite drawing of the suture line of the specimen ZPAL Am.VI/1.

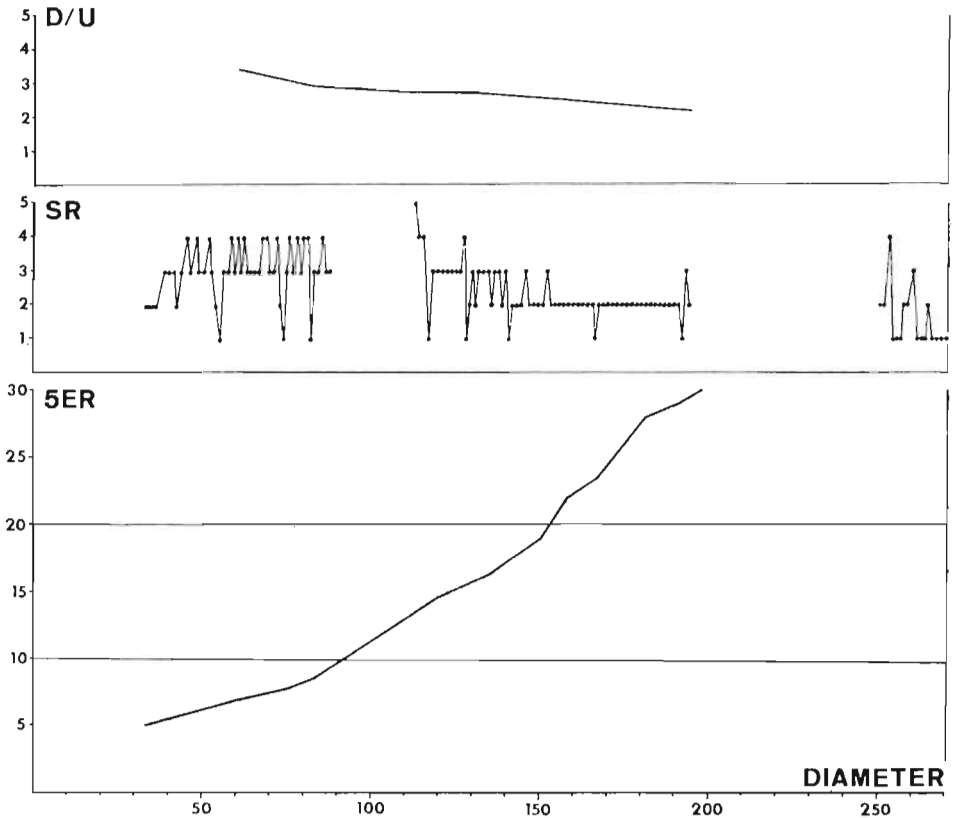


Fig. 6. Measurements of the specimen ZPAL Am.VI/1 of a virgatitid ammonite from Świętoszewo (see also fig. 4; pl. 9, 10). Values of the index of involuteness (diameter of the shell to diameter of the umbilicus; D/U), number of secondary ribs per each primary rib (SR), and distance between each fifth secondary rib (5ER) are plotted against the shell diameter.

The distribution of the index of rib divisions (RI) at the stage of development corresponding to distances between each fifth rib ranging from 3 to 7 mm changes significantly through the Brzostówka section (fig. 7). It is of interest to note that sample b-1 and that from above the clay-pit differ significantly in this respect. As standard deviations do not

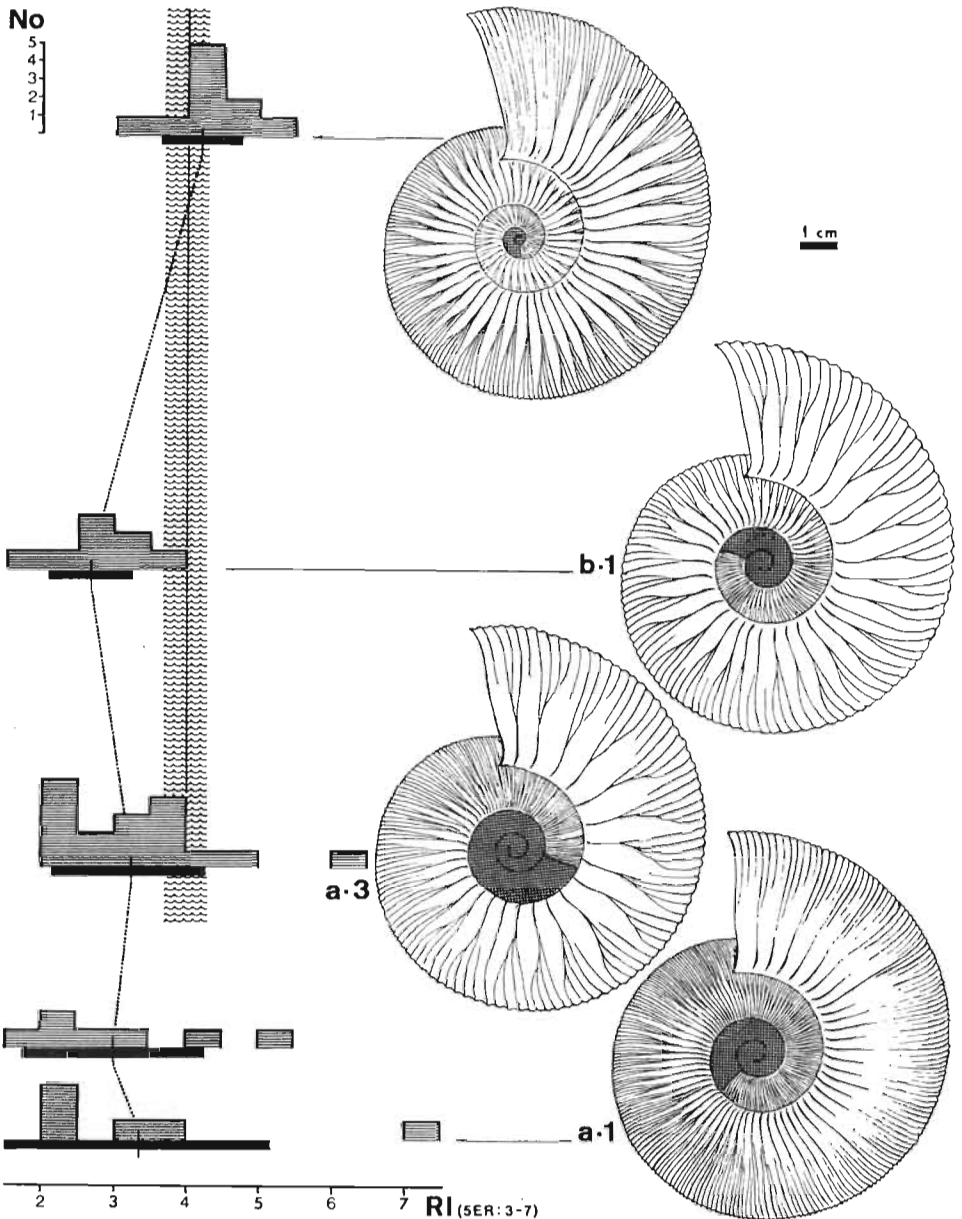


Fig. 7. Frequency distribution of the rib index (RI) at the most significantly evolving ontogenetic stage delimited by values of the distance separating each fifth rib between 3 and 7 mm shown for samples from Brzostówka (the highest one is omitted). The mean value of the index in corresponding stage of ontogeny of the specimen ZPAL Am.VI/1 from Świętoszewo (see pl. 9: 1a) indicated by vertical line, range of the values by hachured area. Note that above these samples the evolution of the virgatitid lineage is expressed mostly in development of transverse furrows separating bunches of secondary ribs.



overlap, separation of these samples into two chronospecies is thus well substantiated (see Dzik and Trammer 1980).

It is perhaps noteworthy that standard deviations of the rib division index decreases significantly from the bottom to the top of the Brzostówka section (fig. 7). Several interpretations of this feature can be proposed. It may be interpreted as an evolutionary improvement of mechanisms controlling the course of the ontogeny, which gradually became more and more efficient. Also, an increasingly more straightforward, instead of a sinuous, pattern of development may have been of some importance in producing such an effect. Also heterogeneity of older samples cannot be excluded.

All variation of the rib division index in the specimen from Świętoszewo in the considered ontogenetic stage falls within ranges of population variability for both Brzostówka samples under discussion. The fit is much closer in the case of the sample from the black shales. Here the mean for the specimen is only slightly smaller than the mode for the sample, and well within the standard deviation.

If we thus assume that the specimen from Świętoszewo exactly represents the modal features of its own population, then this population was only slightly older than that represented by the sample from the black shales. This specimen may quite well be an end member of the range of variability of its population, however. Then it could correlate with a population from the layer b-1, a-3, or even from the limestone series. It is most probable, however, that the Pomeranian specimen corresponds to a population slightly older than that from the black shales. A probability of correlation decreases with increasing stratigraphic distance from the latter population. To restrict possibilities one needs more specimens from the Pomeranian population. The cast of an umbilicus illustrated by Schmidt (1905), the only other specimen from Świętoszewo with preserved diagnostic stages of development, agrees very well with features of the specimen under discussion. This significantly increases the probability that the proposed correlation is correct. A statistically significant sample size permitting description of features of the population would provide the best basis for correlation. The inference of correlation is always probabilistic, however, independent of the sample size. It is also probabilistic, independent of which method of chronospecies definition is used.

#### CONCLUSIONS

It follows from the preceding considerations that the probability of finding a particular morphotype in a sample is related to two factors: a time distance from the horizon in which the morphotype is typical of the population and the sample size. Thus, definitions of time correlation units (chronozones) by the first known occurrence of a morphotype do not

provide a completely reliable basis for study. The first known occurrence of a morphotype depends not only on the geologic age of the sampled strata but also on the sample size. Biostratigraphic units can be defined in this way but not a chronozone. If chrozones are to be based on vertical taxonomy, additional data characterizing distribution of the species have to be included into the definition, namely an expected probability of finding a morphotype at the boundary of the chronozone on which it is based. Improvements of this kind would make definitions of chronospecies too complex and inconvenient to use. Moreover, they cannot offer a higher degree of stratigraphic resolution than definitions based on horizontal taxonomy. Considering the recent stage of development of taxonomy of ammonite species, which is split far below biologically justified levels, the assumed resolution of ammonite biostratigraphy is much finer than the real possibilities of the method. Our efforts should not be directed towards increasing resolution, but rather toward making time correlation procedures more reliable, as well as testable. This may be achieved through population studies.

Instead of creating dimorphic pairs, biogeographic provinces, and evolutionary trees of an inevitably artificial nature, I would suggest that we abandon the typologic concept of chronospecies, and that improved methods of stratigraphic inference can be based on the population concept of chronospecies.

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KONSEKWENCJE STOSOWANIA TYPOLOGICZNEJ LUB POPULACYJNEJ  
KONCEPCJI GATUNKU TEMPORALNEGO DLA BIOSTRATYGRAFII  
AMONITOWEJ*Streszczenie*

Gatunek w paleontologii obok obiektywnych wymiarów morfologicznych i geograficznych w każdym momencie czasu swojego występowania ma również, nieznaną neontologii, subiektywny wymiar czasowy. Pozostawmy na uboczu nierozstrzygalny na gruncie paleontologii problem czy granice gatunków mogą być obiektywnie nieciągłe w czasie ograniczając rozważania do dziedziny udowodnionej ciągłości przemian ewolucyjnych w obrębie znanych ciągów filogenetycznych. W każdym z licznych tego rodzaju przypadków znanych badaczom konodontów, graptolitów czy amonitów wyznaczanie granic gatunku w obrębie ciągu jest arbitralną decyzją taksonoma. Ze względu na konieczność identyfikacji przedstawicieli gatunku w różnych stanowiskach wyznaczenie takie musi być oparte na cechach morfologicznych podlegających ewolucji w obrębie ciągu i przez to umożliwiającą odróżnienie gatunku od jego przodków i potomków bez potrzeby odwoływania się do datowań.

Stosowane bywają dwie zasadniczo odmienne metody wyznaczania granic gatunku temporalnego (chronospecies). Zgodnie z najczęściej używaną z nich, granicę gatunku definiuje się jako powstanie diagnostycznej cechy lub grupy cech. Początkowo cechy te właściwe są skrajnym morfotypom w populacji. Stopniowo w toku ewolucji ich udział w populacji wzrasta, stają się typowe dla jej wszystkich osobników, póki wreszcie nie zostaną wyparte przez nowe cechy, które mogą posłużyć do zdefiniowania kolejnego gatunku temporalnego. Ponieważ linia rozdzielająca gatunki na standartowym diagramie (fig. 1) jest pionowa, metodę tę nazywa się metodą wertykalną. W istocie jest to zastosowanie typologicznej koncepcji gatunku.

Druga z metod, nieczęsto stosowana, opiera granice gatunku temporalnego na własnościach całej populacji (czy raczej próby) kopalnej. Początek gatunku może być wskazany ściśle jedynie w topotypowym profilu geologicznym, tam gdzie został arbitralnie wyznaczony. We wszystkich innych stanowiskach próba może być zidentyfikowana jako należąca do danego gatunku jeśli jej cechy nie odbiegają istotnie od cech morfologicznych populacji typowej dla tego gatunku. Przyjmuje się milcząco, że podobieństwo morfologiczne odpowiada genetycznej bliskości i brak istotnych różnic morfologicznych wskazuje na potencjalną możliwość krzyżowania pomiędzy populacjami współwystępującymi czasowo. Rozumowania tego nie można jednak odnieść do różnowiekowych populacji stanowiących części ciągu ewolucyjnego. Identyfikacja prób z różnych stanowisk jako należących do jednego gatunku, nawet jeśli jest oparta na czysto morfologicznych podstawach, wymaga powzięcia pewnego wyobrażenia o czasowych stosunkach pomiędzy populacjami. Populacje przejściowe pomiędzy

typowymi populacjami kolejnych gatunków temporalnych należących do jednego ciągu nie mogą być zazwyczaj jednoznacznie zidentyfikowane z którymkolwiek z tych gatunków. Granica pomiędzy tymi gatunkami jest więc rozmyta. Ponieważ jednak strefa rozdzielająca gatunki jest pozioma (fig. 1) metodę tę nazwano horyzontalną lub populacyjną.

Na pierwszy rzut oka pierwsza metoda sprawia wrażenie bardziej precyzyjnej i wygodniejszej w użyciu. Byłoby tak, gdyby nie komplikacje występujące na styku dwu kolejnych temporalnych gatunków wydzielonych przy pomocy metody wertykalnej. Nietrudno zauważyć, że samo użycie tej metody wprowadza efekt zażębiania się zasięgów wiekowych kolejnych gatunków temporalnych. Reprezentują one wszak z założenia przyjętego na początku jednorodną linię ewolucyjną i w żadnym momencie nie występował więcej niż jeden obiektywnie wyróżnialny biologiczny gatunek. Tymczasem w wyniku zastosowania metody wertykalnej uzyskujemy drzewo rodowe, w którym przez pewien czas współwystępują ze sobą obydwa gatunki. Jest to obraz fałszywy. Niezgodne z rzeczywistością jest wyznaczanie specjacji (rozdzielania się dróg ewolucji poszczególnych części populacji) na początku zasięgu czasowego tak zdefiniowanego gatunku. Co gorsza, tego rodzaju pozorne specjacje są nieodróżnialne od specjacji prawdziwych, rzeczywistych rozdzieleni dróg ewolucji, skoro zostaną wprowadzone do drzewa rodowego.

Metoda wertykalna prowadzi zatem nieuchronnie do rozdzielania obiektywnych gatunków biologicznych (rozróżnialnych w każdym horyzoncie czasowym) na subiektywne gatunki typologiczne. Skutki tego bywają opłakane. Nie sposób porównywać ze sobą zróżnicowania zespołów organizmów z różnych stanowisk, jeśli do ich opisu użyto typologicznej koncepcji gatunku, bowiem z zasady nie próbuje się wówczas określić rzeczywistej liczby występujących w nich gatunków biologicznych. Cóż zaś warta jest biogeografia bez możliwości obiektywnych porównań stopnia zróżnicowania zespołów i ścisłej identyfikacji gatunku? Te same morfotypy mogą przecież występować w populacjach nader różnych gatunków, tak jak i różne morfotypy mogą w istocie należeć do tego samego gatunku. Nie lepiej muszą przedstawiać się rekonstrukcje par dymorficznych, polegające raczej na dobieraniu podobnych do siebie samców niż na zasadnej analizie stosunków biologicznych.

Z nomenklatorycznego punktu widzenia podstawowa różnica pomiędzy wertykalną (typologiczną) a horyzontalną (populacyjną) koncepcją gatunku temporalnego polega na odmiennym rozumieniu funkcji holotypu i serii typowej. W koncepcji typologicznej holotyp (lub cała seria typowa wybrana przez autora gatunku) jest standartem średniej wartości cech morfologicznych właściwych dla gatunku zgodnie z jego definicją. W koncepcji populacyjnej holotyp jest niczym więcej niż przedstawicielem typowej populacji. Jest dogodnym wskaźnikiem czasowoprzestrzennych koordynat tej populacji. Nie musi być wcale typowym przedstawicielem populacji typowej ani gatunku. Wszelkie identyfikacje taksonomiczne zgodne z metodą horyzontalną odwołują się do populacji typowej a nie holotypu.

W angielskojęzycznej części artykułu wykazuję, na przykładzie identyfikacji okazu amonita ze Świętoszewa na Pomorzu zachodnim z odpowiednią częścią standartowego ciągu ewolucyjnego opisanego na podstawie profilu w Brzostówce koło

Tomaszowa Mazowieckiego, że zastosowanie koncepcji populacyjnej nie zmniejsza precyzji datowania warstw skalnych w oparciu o skamieniałości. Czyni natomiast wnioskowanie bardziej przejrzystym odsłaniając słabości metody biostratygraficznej zazwyczaj ukryte za pozornie ścisłą nomenklaturą taksonomiczną.

#### EXPLANATION OF THE PLATES 9 AND 10

##### Plate 9

*Virgatites* ("Zaraiskites") sp. n., Świętoszewo, Pomerania; complete specimen ZPAL Am.VI/1, natural size.

##### Plate 10

*Virgatites* ("Zaraiskites") sp. n. (transitional between *Z. scythicus* and *Z. zarajskensis*), Świętoszewo quarry, top of the eastern wall, Pomerania; specimen ZPAL Am.VI/1, natural size.

1. Internal whorls, lateral (a) and ventral (b) views.
  2. Fragment of the living chamber.
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