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The concept of chronospecies in ammonites

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RIASSUNTO

Le sole unità tassonomiche direttamente identificabili in paleontologia sono i paleofena o gruppi di esemplari in un campione che presenta una distribuzione continua e unimodale della frequenza di tutti i caratteri. Paleofena coevi possono essere sistemati in biospecie mentre serie temporali di questo formano delle linee filetiche. I risultati di entrambi i procedimenti sono empiricamente comprovabili.

La ricostruzione delle linee è una condizione necessaria a priori per una definizione coscienziosa delle cronspecie, cioè segmenti arbitrariamente designati di una linea. Un esempio empirico dimostra che può non essere possibile riconoscere i paleofena senza la biometria.

Vengono discusse le prove per la presenza di due biospecie dimorfiche nel Calloviano di Łuków (Polonia) e per la natura dimorfica dei generi valanginiani Saynoceras e Valanginites.

ABSTRACT

The only directly identifiable taxonomic units in paleontology are paleophena, or groups of specimens within a sample that show continuous and unimodal frequency distribution of all characters. Coeval paleophena can be arranged into biospecies while time series of them may form lineages, the results of both these procedures being empirically testable. Lineage reconstruction is a necessary precondition for conscientious definition of chronospecies, i.e. arbitrarily designated segments of a lineage. An empirical example demonstrates that it may not be possible to recognize paleophena without biometrics. The evidence for presence of two dimorphic biospecies in the Callovian of Łuków, Poland, and for dimorphic nature of the Valanginian 'genera' Saynoceras *and* Valanginites *is discussed.*

KEY WORDS

Ammonites - Evolution Chronospecies - Dimorphism Callovian - Poland.

INTRODUCTION

Although it is not necessary to introduce any kind of taxonomic units of species rank for the sake of paleontologic evolutionary studies alone, this may be useful for scientific communication. One does not necessarily need species names to study evolution but one surely needs them to talk about the course of evolution. Since the introduction by Simpson (1944, 1953) of the basic concepts of population biology to theoretical paleontology, the methodology of empirical studies on evolution at the species level has been elaborated. The resulting standard taxonomic procedure can be summarized step by step in the following way:

(1) collecting samples of fossils,
(2) recognition of (paleo)phena in samples,
(3) assembling paleophena into biological populations within particular samples.
(4) delimitation of biospecies by identification of conspecific population in samples of the same geologic age (objective in principle),
(5) reconstruction of evolutionary lineages by assembling series of population from samples of different age, which are identified as being in close ancestor-descendant relationships,
(6) delimitation of chronospecies within the lineage (subjective in principle),
(7) naming the chronospecies.

Chronospecies is an evolutionary concept. Before any chronospecies can be precisely defined, the evolution of its lineage has to be determined. Even though the meaning of species in paleontology is so frequently vague, the gradualistic evolutionary nature of chronospecies is generally assumed as self-evident. Explicit presentation of a phylogenetic hypothesis of ancestor-successor relationship appears thus to be a necessary precondition of sound interpretation of a chronospecies, and the reliability of its identification depends on reliability of a time correlation of different paleontological data sets.

I shall discuss the methodological limitations at each of these steps and confront theoretical aspects of evolutionary studies with taxonomic practice by presenting the ways of identification of chronospecies in ammonites. To this end, four limestone concretions from the Callovian Łuków clays are chosen to show how paleontological samples can be processesed. The Łuków material can fulfill even the most severe requirements for paleobiologically meaningful sampling, concerning especially the geographic, lithologic and biostratigraphic homogeneity. To illustrate the method of identification of paleophena, the specimens of *Quenstedticeras* extracted from these samples are measured and the results are presented on plots showing ontogenetic changes in various features of their shell geometry and ribbing.

A series of populations occurring in stratigraphic order in the section of Volgian clays in Brzostówka, worked out by Kutek & Zeiss (1974), well exemplifies an empirically reconstructed evolutionary lineage. The effects of application of different modes of defining boundaries between chronospecies (vertical or horizontal) will be discussed in this context. It will be shown why the application of the vertical (typologic) approach to chronospecies results in false presentation of evolutionary processes and makes the ranges of biostratigraphic units sensitive to differences in sample size.

Another example represents the opposite extreme of reliability of sampling and availability of fossil materials. It concerns the olcostephanids from the Valanginian clays cropping out in Wąwał. In spite of the good preservation of fossils, this section is more typical of the usual working conditions in ammonite taxonomy and biostratigraphy in that the ammonite specimens are dispersed in unbedded clay lacking any marker horizons. Neither population variability nor evolutionary transformations can therefore be reliably identified on the basis of the available collections.

Finally, the results of the search of names appropriate for the chronospecies represented in Brzostówka, Łuków, and Wąwał will be discussed. The valid specific name for populationally understood chronospecies is the oldest one proposed for any member (holotype) of any population included in the chronospecies, irrespective of its morphology. This introduces some uncertainty when usual literature data, lacking any references to population variability, are to be used. Suggestions, how to proceed in such situations will be explained.

SAMPLING

There is no significant difference in requirements to be met by good sampling between different areas of paleontological studies. Whether samples are taken for paleobiological or evolutionary studies, they have to be homogenous in respect to the geographic space and environment (lithology). The time dimension represented in the part of the rock section from which the sample was collected should be as short as possible. Sampling for evolutionary purposes may require especially rigorous application of the criterion of geological time homogeneity. It would be unrealistic to expect that the time dimension of all samples used in such studies is insignificant. They must meet the precondition, however, that the time span involved in their accumulation was short enough to ensure that evolutionary transformations of the population do not interfere with its variability. When this condition is not fulfilled, the range of the morphologic population variability is artificially widened in effect of lumping together populations different in their evolutionary advancement (Westoll, 1956). The evolutionary transformation itself cannot be adequately recognized from data distorted in such a way.

It is widely assumed that only fossils collected from a single rock layer or even bedding plane can fullfill the basic requirements for properly performed sampling for evolutionary purposes. This unnecessarily severe precondition has appeared to be the most serious obstacle in application of macrofossils to studies on evolution. It is usually impossible to collect from a single bedding plane a sufficient number of specimens to allow for reliable biometrical study of sampled populations. One should not hesitate to blend together fossils from different beds, however, as long as there is no reason to believe that resulting sample is not homogenous in respect to space and geologic time.

It has to be noted that such procedure, as long as done consciously, does not necessarily diminish the scientific value of obtained results. Any estimate of the population variability is potentially falsifiable and can be tested by more extensive collecting of the same species from narrower parts of the section or by studying comparative materials from another section.

The most reliable material for population studies in paleontology can be obtained from single calcareous or sideritic concretions. Unless there is a special evidence of reworking one may safely assume that the whole content of a single concretion was assembled instantaneously in respect to the rate of evolution. It is well exemplified by concretions from the Łuków clays occurring as large drift blocks in eastern Poland (Kosmulska 1973). Ammonites in these concretions show excellently preserved aragonitic conchs (Kulicki 1979) with usually empty phragmocone chambers (Pl. 1: 1). They could not be redeposited or even exposed for a longer time before burial.

For the purpose of the present presentation I extracted all ammonite specimens from 4 concretions. Careful preparation with simultaneous glueing and measuring of specimens allowed to assemble a collection of 875 specimens. Ammonites occur in concretions in concentration of about one hundred specimens per kilogram of the rock. It is difficult to estimate number of specimens which were destroyed during preparation. It probably represented from 10 to 20 per cent of particular samples. No apparent correlation between the size of specimens and losses in preparation have been found, therefore I consider the samples statistically representative of original fossil assemblages. Almost all specimens have preserved at least a part of the living chamber and most of them have the chamber virtually complete. Ammonite shell fragments are practically absent in the rock matrix, which suggests that shell apertures were already broken before burial. In a few cases, there is evidence of breakage with some displacement of produced parts, which took part after burial but before diagenesis.

Particular samples significantly differ in the frequency distribution of specimen sizes. It is not clear whether this is a result of differences in population dynamics or rather of preferential segregation at the time of burial. These differences are of much importance when transformations of the morphology of shells are to be studied quantitatively. Changes in frequency distribution of morphologies from sample to sample may result from differences in quantitative contribution to the samples of the ontogenetic stage at which a particular character is best developed. Transformations of the population dynamics may then simulate evolutionary processes (Dzik & Trammer 1980).

PALEOPHENA

The only directly and objectively recognizable taxonomic unit in paleontology is a group of specimens within sample which shows continuous and unimodal frequency distribution of all characters. Mayr (1969) proposed for similar taxonomic units in neontology the term 'phenon'. Insofar as samples in paleontology usually have a significant time dimension, such a time extension is the immanent feature of phena recognized by paleontologists. Therefore it seems reasonable to accentuate their special nature by calling them 'paleophena'. Paleophena may represent sexual dimorphs, particular groups of discontinuously polymorphic populations, seasonal morphs, or even separately fossilized organs belonging to the same species (for instance, ammonite conchs and aptychi). In some cases, paleophena may quite well represent groups of sympatric species, which are undistinguishable on the basis of their skeletal structures which are used to define them (this is clearly the case when paleophena of aptychi are considered).

Although discreteness of particular paleophena in a sample usually is apparent even for a naked eye, it is not always so easy to decide how many paleophena one is dealing with. The Łuków samples well exemplify this problem. The morphologic variability of ammonites of the genus

Quenstedticeras, which occur there in abundance, followed by *Kosmoceras* which does not contribute more than 10% in number, presents a puzzle that used to be solved in quite different ways by different workers (see Makowski 1952, 1962; Reyment 1971; Matyja 1986). These *Quenstedticeras* conchs can be arranged into a completely continuous series of morphologies, from very flat to very wide in the cross section (Pl. 2). Callomon (1985), who noted the same phenomenon in other samples of ammonites of the family Cardioceratidae, concluded that it is practically always represented by a single, very variable species in any time horizon.

To test the idea of Callomon (1985), I measured specimens of *Quenstedticeras* from Łuków. Although it is generally believed (Makowski 1962; Kulicki 1979) that the number of shell whorls is the best measure of ontogenetic advancement of any ammonite, it appeared impractical to use this character when a great number of variously preserved specimens had to be studied. The mumber of whorls may differ between specimens of the same size due to their different whorl expansion rates. Then, however, also other dimensions of the shell would differ (relative whorl height and umbonal diameter, for instance). It does not seem that application of the shell diameter, instead of counting whorls (requiring time consuming preparation of umbones), drastically biased results of the study.

The measured characters of shell geometry and ribbing are here plotted against shell diameter, as an indicator of the ontogenetic advancement of specimens (Fig. 1, 3). Concerning whorl compression, most measurements form two clusters separated by an area of rather unnumerous records (Fig. 1) around whorl compression index close to 1.1. Conchs larger than 10 mm in diameter are virtually lacking in this field. The difference between the clusters seems to disappear when smaller and smaller specimens are considered, which may be partially due to an increase of the error when minute specimens are measured with the same calliper. Moreover, two distinct groups within each cluster can be recognized among larger specimens which show the morphologic features of microconchs; they are separated and bordered by fields occupied by juvenile macroconchs. This pattern strongly suggests the presence of four paleophena among representatives of *Quenstedticeras* in spite of continuous morphologic transitions between them.

Apart from apertural modifications the differences between macro- and microconchs in the cardioceratids are expressed mostly in involuteness. Microconchs are usually more evolute and show a decreasing whorl expansion rate at later stages of their ontogeny. To discriminate more precisely between the presumed paleophena in the Łuków samples, the indices of involuteness are plotted against whorl compression for the measured specimens (Fig. 2). For the clarity of presentation, the ontogenetic stage of particular individuals is indicated by dot size, with the juveniles below 15 mm in diameter being represented by smaller points and the adult specimens by larger ones

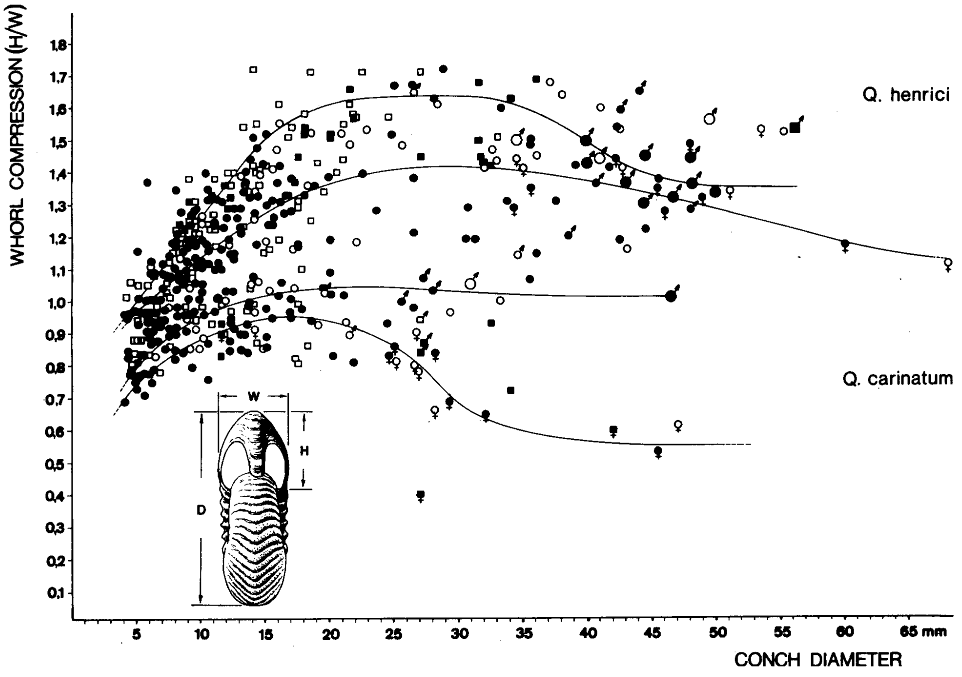

Fig. 1. Ontogenetic changes of whorl compression in samples of ammonites of the genus *Quenstedticeras* from the Callovian of Łuków, Poland. The largest dots represent adult males. Circles = sample 210-D, black points = 210-C, black squares = 210-B, and white squares = 210-A. Note that the male conchs form two separate clusters with juvenile females inbetween.

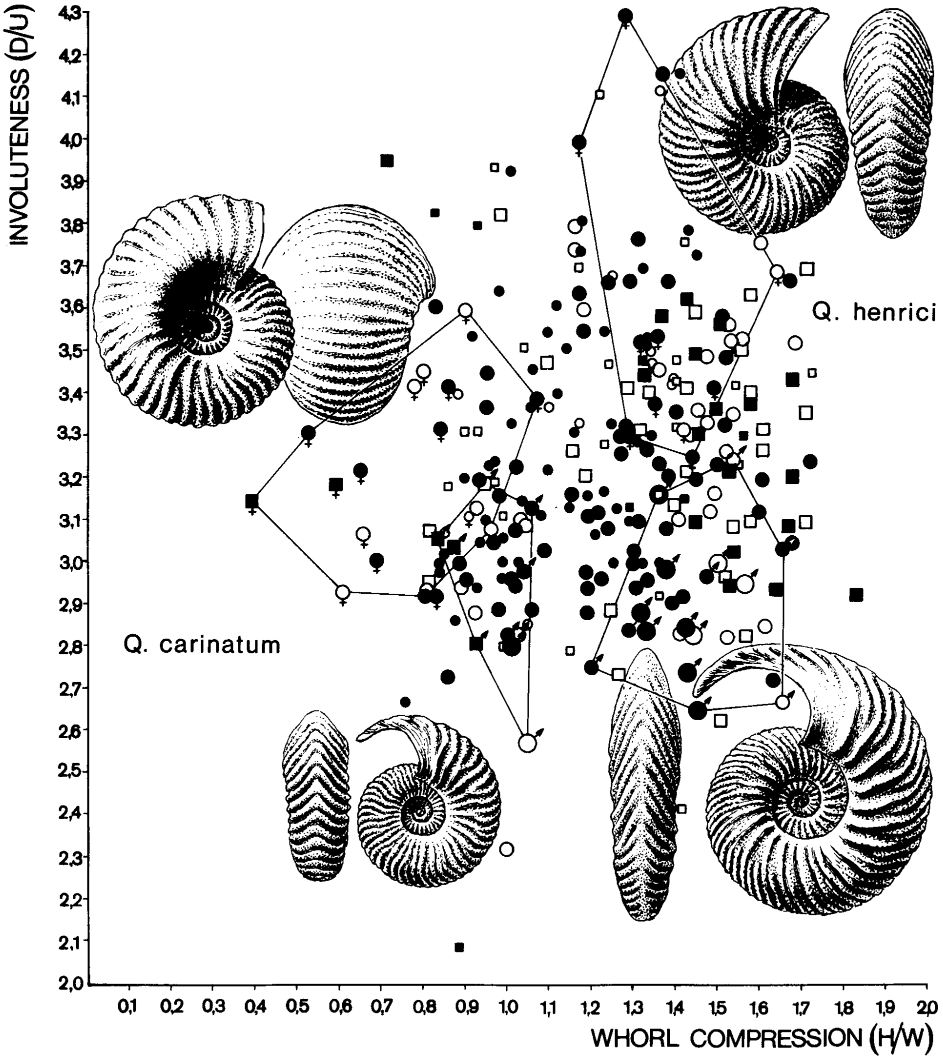

Fig. 2. Recognition of paleophena in samples of the ammonite *Quenstedticeras* from Łuków, Poland. A plot of conch involuteness against the whorl compression reveals four groups among specimens with determinable sex. The smallest dots represent specimens with size ranging from 10 to 15 mm in diameter (smaller specimens were not considered because of too high measurement error). The largest dots represent adult males. Circles = sample 210-D, black points = 210-C, black squares = 210-B, and white squares = 210-A. Note the juvenile specimens concentrated in vertical belts in the center of the plot; with increasing size they tend to occur closer to the area of respective paleophena recognizable only at the adult stage of development.

The fields of identifiable macro- and microconchs are delimited by lines connecting extreme records. The resulting picture (Fig. 2) shows two vertically elongated clusters of juveniles in the center, with rare records inbetween, and four clearly separated fields of micro- and macroconchs. The presence of four separate paleophena in each of the Łuków samples appears evident. One may thus move to the second point of the standard of paleontological taxonomic studies: recognition of populations in samples.

FOSSIL POPULATIONS

Since the classic reviews of the problem of sexual dimorphism in ammonites by Makowski (1962) and Callomon (1963, 1969) appeared it has been generally accepted that the dimorphism is profoundly expressed in Mesozoic ammonites in the size and morphology of their conchs (i.a. Westermann 1966; Lehmann 1966; Palframan 1966, 1969; Riccardi *et al.* 1971; Ziegler 1974; Riegraf *et al.* 1984). Particular macro- and microconchs in the Łuków materials were already identified as sexual dimorphs in species of *Quenstedticeras* and *Kosmoceras* by Makowski (1962). In the case of the investigated samples, it seems reasonable to consider flat macro- and microconch phena as representing one species and the wide ones as belonging to another. No evidence for the presence of the third phenon within the range of *Quenstedticeras* species proposed by Matyja (1986) has been found.

The above interpretation is supported by the observed course of ontogeny (Fig. 1). Specimens representing each of the two major clusters are initially undistinguishable but diverge later on in their development, thus producing two pairs of subordinate clusters representing the particular paleophena. It is remarkable that the pattern of ontogenetic differentiation of sexes differed in the two identified dimorphic pairs. In the population of flat conchs, the males show more profound ontogenetic transformations in the conch morphology. while females seem to preserve more juvenile features of the shell geometry at the subadult stage. The whorl compression had increased strongly during growth of a subadult male conch and finally reduced to the value typical for females, which corresponds to the reduction of the whorl expansion rate at the attainment of adult stage. Among robust wide conchs it was the male, which preserved more of juvenile features in its shell geometry. Its female mate underwent a profound change in parameters of the whorl expansion rate. Almost suddenly, at some stage of ontogeny, it began to increase much more in the lateral diameter, giving in effect a *Cadoceras*-like adult shell morphology quite dissimilar to that of the juveniles and males (Pl. 2: 5). Interestingly, this change may occur at quite variable stage of the ontogeny. In a few specimens it has been recognized at the conch diameter of only 2 mm; usually it occurs at the diameter of about 25 mm, but there are also specimens in which this change in the shell geometry evidently did not took place at all (Pl. 2: 2-3; Makowski 1962, Pl. 13: 1). They are rather subordinate in the

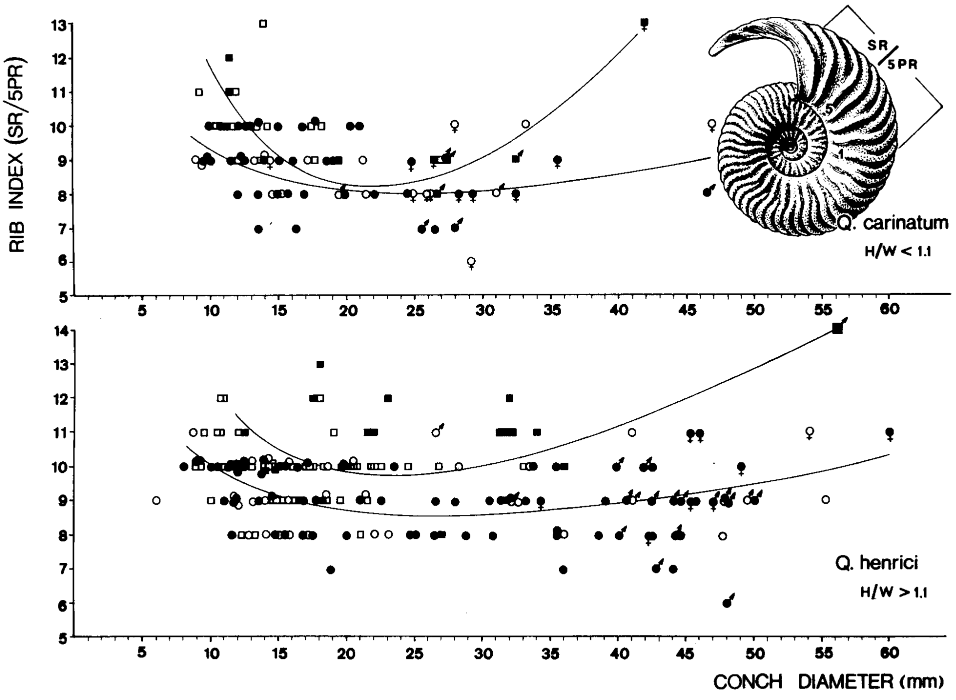

Fig. 3. Ontogenetic change in development of intercalatory ribs in different samples of *Quenstedticeras carinatum* and *Q. henrici* from the Callovian of Łuków, Poland. Rib index refers to the number of secondary ribs corresponding to 5 primary ribs (RI = 10 means thus that divisions are strictly dichotomous). Note that idealized regression line is U-shaped in every case but in both species specimens from the sample 210-B (black squares) tent to arrange along much deeper curve than specimens of other samples. Circles = sample 210-D, black points = 210-C, and white squares = 210-A.

Łuków material, and because of the relative rarity they cannot be collected from any single concretion in a number sufficient to establish their relation to the other forms of *Quenstedticeras*. A use of museum specimens might result in lumping together specimens from quite different time horizons. Therefore the biological significance of these relatively rare occurrences of robust shells lacking abrupt changes in shell geometry remains unclear. Makowski (1962) considered them to represent separate population (biospecies) of *Quenstedticeras*. They might, however, originate by imprecise physiologic controls on ontogenetic development in these ammonites.

A similar feature was already reported regarding shell ornamentation of Volgian virgatitds (Dzik 1986), where an abrupt change in rib division took place, from densely packed bifid ribs to polygyrate ones. This change is correlated with a corresponding change in shell involuteness (Dzik 1986). The exact ontogenetic timing of the change in ribbing, although subject to directional evolution which suggests influence of directional selective pressure, was a matter of profound intrapopulation variability (Fig. 3). In effect of this unprecise control of the course of ontogeny, the changes, which are apparent when particular specimens are studied, appear almost unrecognizable on plots of large samples. Asynchrony in development makes its record virtually unreadable at the population level.

Some ontogenetic and evolutionary transformations of the ribbing patterns occur also in the cardioceratids. This is of much importance regarding the methods of recognition which populations from different samples may belong to the same biospecies.

FOSSIL BIOSPECIES

The most important evolutionary transformation known to occur in the *Quenstedticeras* lineage is the change from basically dichotomous ribbing to ribbing with secondary ribs many times more numerous than the primary ones (see Callomon 1985). The pattern of ribbing underwent deep modifications also in ontogeny. Generally, just after the ribbing appears in juvenile conchs, the ratio of secondary to primary ribs is significantly higher than in later stages prior to development of the dimorphic features. At the stage of recognizable sexual dimorphism the ratio increases again (this feature does not seem to be a subject of otherwise profound dimorphism) to be lowered in adult male conchs just before the development of terminal aperture. In female conchs the ribbing gradually dissapears (Pl. 1 & 2).

In the case of the Łuków material it appears that samples from different concretions differ significantly in conspicuousness of the change in ribbing at the middle stages of the ontogeny (Fig. 4). In specimens from the sample 210-A and perhaps also 210-B the change is apparently much deeper and the rib ratio is much higher than in the remaining samples 210-C and 210-D. Particular samples of ammonites differ too much in the population dynamics to allow recognition of the pattern with adequate precision (for instance, juveniles dominate in the sample 210-A, while they are much less numerous in the sample 210-B). This precludes also a precise quantitative between-sample comparison of variability at particular stages of ontogeny.

The most surprising feature of the data is that the disparity between the two pairs of samples concerns both the biological populations recognized in each of them. Although, as noted above, the patterns of ontogeny are different, the higher ratio of secondary to primary ribs at the middle of the ontogeny characterized both flat and wide conchs of *Quenstedticeras* in the samples 210-A and B. This apparently synchroneous expression of the same trend in populations of different sympatric species is suggestive of a transfer of genetic information between them. It can hardly be explained by a residual transfer across the genetic barrier between species, however, and an influence of non-Mendelian ways of exchange of the genetic information (Jeppson 1985) are even less likely. Another possible explanation, that the synchroneous change in ribbing reflects a response to environmental factors, would undermine the usefulness of the ribbing features for time correlation. The interpretation most appealing to me is that this superficially sophisticated parallelism in evolution of the ribbing pattern is a by-product of a much simpler trend shared by the whole branch of early cardioceratids. The pattern of ribbing depends on the involuteness of ammonite conchs (Dzik 1986), which is known to change in the evolution of *Quenstedticeras*. It may thus be that *Q. carinatum* followed the same as *Q. henrici* trend in increase of involuteness, even if it is not apparent from the analysis of available data.

Whatever is the reason of the differences, it has to be concluded that the same two biospecies are represented in the samples 210-A and B, while the populations from the samples 210-C and D represent another pair of biospecies, probably from a different time horizon. What remains to be elucidated is the relationship between these pairs of conspecific populations.

LINEAGES

The four biospecies recognized in the studied Łuków samples almost certainly represent two evolutionary lineages. This is indicated by the significant overlap in character frequency distribution between equivalent populations and by the obvious time proximity of these samples. If one assumes that the evolution of ribbing in *Quenstedticeras* was strictly directional, then the populations from the samples 210-A and B are slightly younger. Reliability of such an assumption, however, is far from obvious, and the differences may just be caused by temporal oscillations in direction of the evolution or may even represent environmentally controlled features, insignificant from the evolutionary point of view. For a more lucid presentation of the ways of reasoning in lineage reconstruction it seems therefore better to refer to another example, namely to the series of samples from the Volgian of Brzostówka near Tomaszów Mazowiecki, Poland. Several populations, representing both macro- and microconchs of early virgatitids, were identified in samples collected by Professor Jan Kutek in an abandoned clay pit at this locality (Dzik 1986). Although, due to poor preservation of the specimens, some uncertainty remains whether they all are strictly monospecific or not, this does not seem to undermine validity of the general evolutionary trends recognized there by Kutek & Zeiss (1974). According to their evolutionary interpretation the stage of polygyrate ribbing, initially restricted to a narrow zone

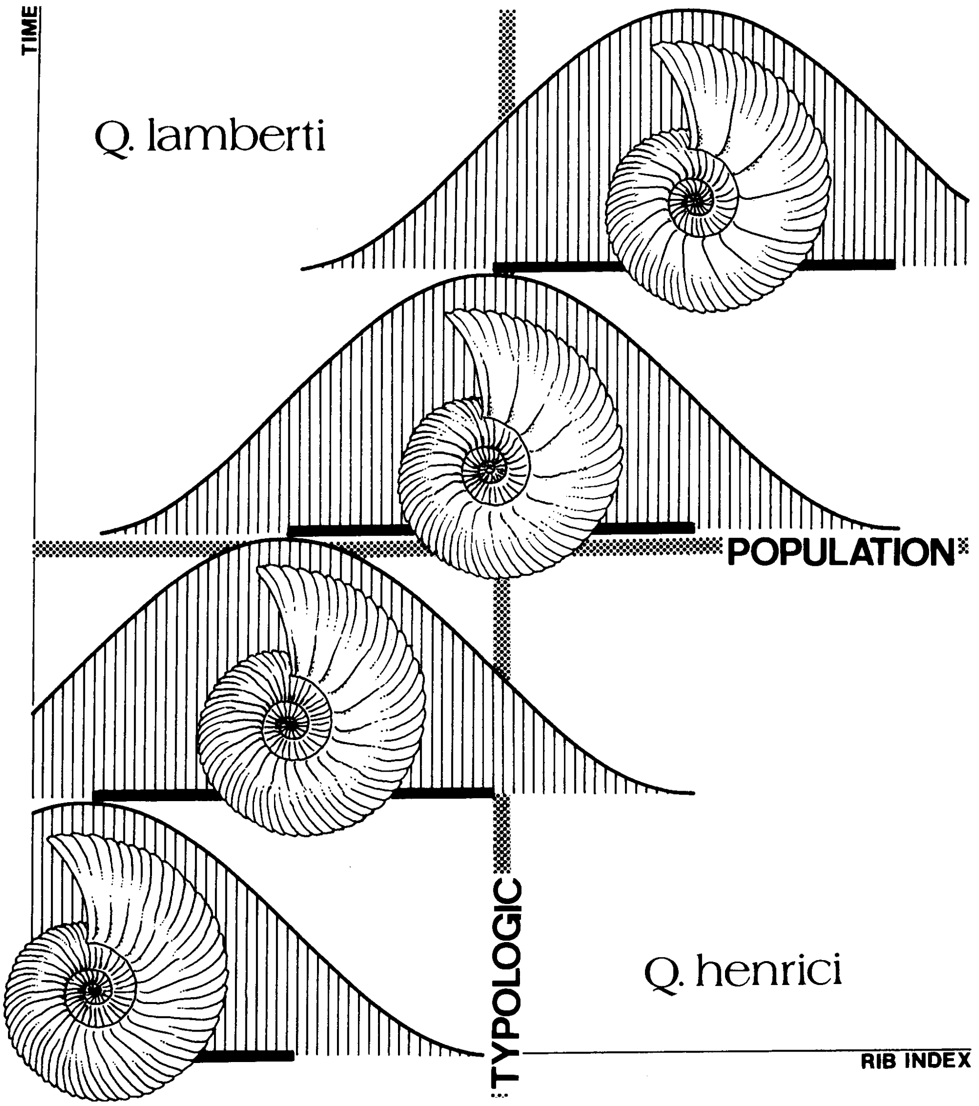

Fig. 4. Distinction between typologic and population concepts of chronospecies as exemplified by the problem of demarcation of the boundary between *Quenstedticeras henrici* and *Q. lamberti*. According to the typologic approach all specimens having more than three secondary ribs per a primary rib (rib index 30) belong to *Q. lamberti*, if the population approach is followed all populations showing modal values of the rib index exceeding 30 at the size class 50-60 mm are to be included in this species.

in some juvenile conchs, expands both back and forth in the ontogeny being expressed in more and more juvenile stages (Fig. 5). At the same time, ontogenetic changes concerning the ribbing pattern and the conch involuteness became dumped, producing in effect a uniformly polygyrate ribbing of microconchs and juvenile macroconchs, which slowly disappears in larger macroconchs. Completely gradual evolutionary transformations were quite far-reaching, although the particular morphologies show rather long durations due to very wide population variability.

The picture of ammonite evolution in the Brzostówka section was obtained by a simple ordination of data on particular populations according to their position in the rock column. This populational methodology, introduced for the first time in perfect form to evolutionary paleon-

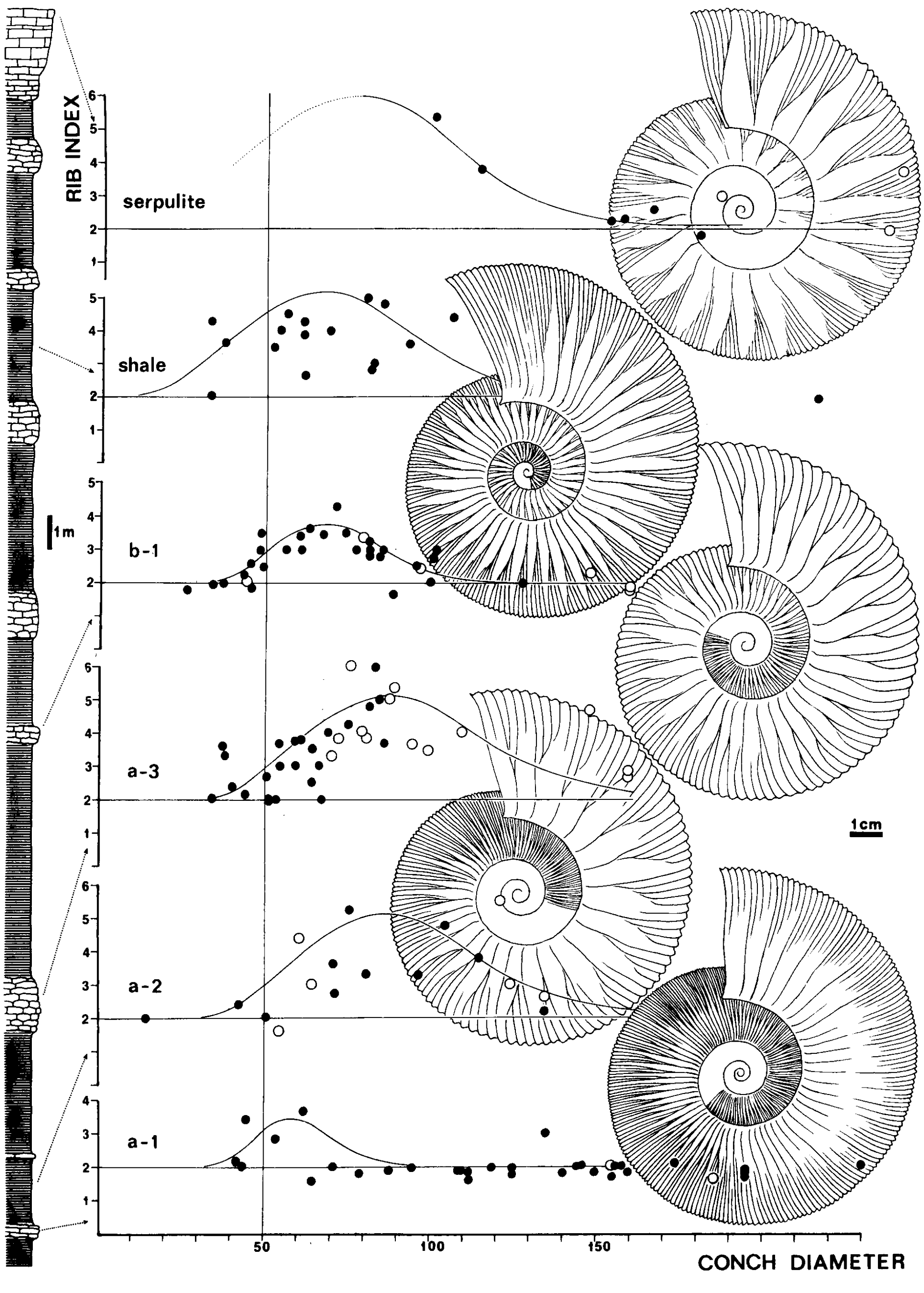

Fig. 5. Transformations of the ontogeny in the *Zarajskites scythicus* (Michalski 1884) lineage, the Volgian of Brzostowka near Tomaszow Mazowiecki, Poland.

tology by Brinkmann (1929), was named the stratophenetic approach by Gingerich (1979). It has turned out to be a powerful tool of phylogenetics in every group of fossils, to which it was applied.

As long as samples consist of numerous specimens collected from single beds or concretions, there is no serious objection to reliability of results achieved by stratophenetic approach. The paleontological practice is rarely so appealing. Usually one has to base his evolutionary conclusions on a few poorly preserved specimens having bad or inadequate stratigraphic control, just opposite to the situation in Brzostówka. This is well exemplified by problems connected with studies on Valanginian ammonites at the locality Wąwał, not far from Brzostówka.

Ammonites are preserved in Wąwał with aragonitic shell walls, pyritized phragmocones, and living chambers filled with phosphorite. Any lithologic marker horizons are practically lacking in the main portion of the section, and the frequency of well preserved ammonites is insufficiently high to allow for collection of representative samples just by digging the clay bed by bed. Several large collections, however, were assembled during many years of work by many students of the locality.

Of special interest are the 'olcostephanids', which are represented in collections by numerous specimens with complete terminal aperture. Some of them represent typical minute microconchs with long lappets (*Saynoceras*), while other, somewhat larger specimens have their aperture armed with a thick roll and may represent macroconchs (*Valanginites* and *Dobrodgeiceras*) (Pl. 3). Both the macro-and microconchs collected in the lower part of the section are generally smaller than those from higher levels. A single phosphorite concretion in the middle of the section provides a small sample in which moderately ribbed proposed macroconchs are associated with rather small microconchs. Although few in number, these specimens show a range of variability which clearly indicates that, except for the mean size change, no evolutionary transformation of the microconch morphology occurs in the Wąwał material (Fig. 6). This is not so clear with respect to the morphology of the macroconchs. The small macroconchs occurring in lower strata are prominently and densely ribbed, with prominent ventral tubercles (Pl. 3: 9.), while the large specimens occurring in higher strata are more or less smooth throughout their ontogeny. There is a complete gradation between forms having prominent lateral tubercles associated with low ventral ribbing (*Dobrodgeiceras* morphotype) and those which are completely smooth (*Valanginites* morphotype). Whether this is expression of evolutionary transformations or rather intrapopulation variability cannot be determined with the available data.

The *Dobrodgeiceras* and *Valanginites* type conchs are the only ones which can be matched as macroconchs with the microconch *Saynoceras* in the Wąwał section. Such a relationship was already proposed by Thieuloy (1965: 841), although he subsequently changed his mind (Kemper *et al.* 1981: 277). It can be supported by the similarity in patterns of lateral tuberculation and the identity of the early stages of ontogeny between the proposed dimorphs. All these ammonites have smooth conchs at the early stages of ontogeny (Fig. 6A), and their ornamentation, however different between macro- and microconchs, developed at similar conch diameter. The hypothesis is therefore proposed that a lineage represented by paleophena of micro- (*Saynoceras*) and macroconchs (*Dobrodgeiceras* and/or *Valanginites*) occurred in the section of Wąwał and evolved toward larger size and smooth appearance of female conchs. Additional collections from Wąwał as well as from other localities of similar age can be used to test this hypothesis.

All the preceding steps of the discussed taxonomic procedure were oriented toward recognition of objective biological processes. The two remaining steps, definition of chronospecies and its naming, are just matters of convenience in scientific communication. It does not mean that there is complete freedom of decision in paleontological taxonomy. To be useful, even subjective taxonomic definitions must observe strict and generally accepted rules.

CHRONOSPECIES

The first problem to be invoked is how the time dimen-

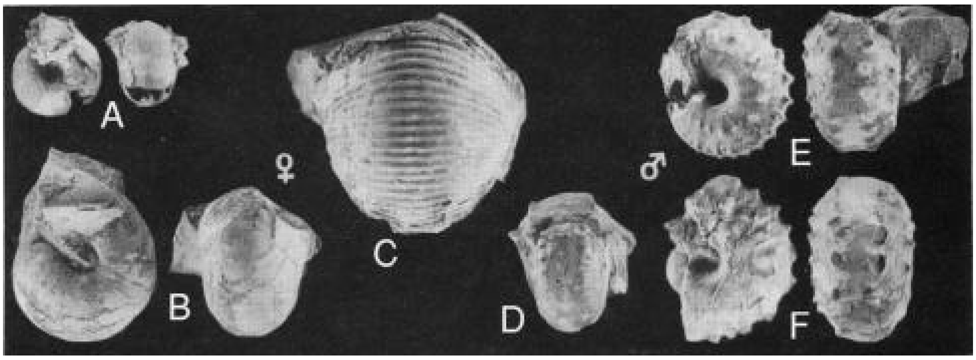

Fig. 6. Ammonite shells extracted from a sigle dark phosphorite concretion collected in the middle of the section at Wawal and proposed to represent the single species *Saynoceras verrucosum* (d'Orbigny 1841). A. Juvenile ZPAL Am IX/22. B. Juvenile female ZPAL Am IX/11. C. Somewhat older juvenile female ZPAL Am IX/20. D. Juvenile male ZPAL Am UX/15. E-F. Adult males ZPAL Am IX/17, 16. All. × 2.

sion of a species should be defined to allow for its identification solely on the basis of its morphological features. Any lineage can be subdivided into chronospecies in two basically different ways. Either it is assumed that particular morphologic features of a specimen determine its attribution to a species, or the taxonomic decision is based on features of a whole population. The first approach results in that the line cutting the lineage into species separates different morphologies. It is thus vertical according to the standard presentation of evolutionary processes with the time scale on the abscissa. When the second approach is in use, the line separates different populations (biospecies); it is thus horizontal.

The vertical (typologic) definition results in a false representation of the process of evolution. The ranges of chronospecies defined in such a way always overlap. The range of the overlap as well as the range of the whole chronospecies defined typologically strongly depend on size of the samples used in studies, especially in the marginal parts of the stratigraphical range of chronospecies. Because of this feature of the method, I proposed to abandon it, in spite of its still wide usage (Dzik 1986).

The populational definition of chronospecies, like any other known definition, allows for identification of the time limits of a chronospecies in sections other than locus typicus only with a limited resolution. A zone of uncertainty always remains, within which it is impossible to decide objectively to which of two successive chronospecies populations are to be classified. These limitations result from natural oscillations in direction of the evolution and they cannot be removed by additional sampling or by increasing the sample size.

Decision regarding the time range of a chronospecies should be taken in a specified section, possibly the type section of the nominal biospecies, that is the section, in which the holotype was found. There are already cases of such formal indication of the boundaries of a proposed chronospecies in a rock section (i.a. Bergström 1971).

Although decisions concerning the ranges of proposed chronospecies are always subjective, it is convenient to follow some standards of morphologic ranges for species (Culver *et al.* 1987). This prevents creation of either too narrowly (which would hamper identification in other sections) ot too widely defined chronospecies (which would leave unexploited correlation potentials of the species). Standardized morphologic dimensions of chronospecies may also potentially appear a useful unit of evolution, allowing for quantification of its progress and rate.

While discussing possible measures of the rate of evolution, Haldane (1949) suggested to employ the lenght of time necessary to change the population mean by one standard deviation. Commenting upon this proposal, Simpson (1953: 6-7) explained that, "the variation in a population constitutes the raw material for evolution (insofar as this is controlled by natural selection) and that the standard deviation measures the (absolute, not relative) variation, so that a rate in terms of standard deviation measures utilization of the raw material. Rate of change in standard deviations also tends to measure rate of reduction of overlap in two related populations". Following this line a reasoning Dzik & Trammer (1980: 76) proposed that succeeding chrono(sub)species should not have overlapping ranges of one standard deviations from the mean in any diagnostic character. Within the range of singular standard deviations from the mean, 68% of specimens are represented, therefore taxa which do not show overlap at one standard deviation from the mean are easily distinguishable even without biometric population studies.

The usage of temporal subspecies (chronosubspecies) in paleontology was criticized by Gingerich (1986), because they are usually confused with true geographic subspecies. Subspecies are recognizable only within geographically widespread biospecies; thus they can occur only in geographically distant localities. With increasing geographic distance, the reliability of time correlation decreases, however, which makes the recognition of biosubspecies in paleontology rather vague methodologically. It is hard to disagree with this opinion, especially since proposals to introduce nomenclatorial distinctions between chronosubspecies and biosubspecies (i.a. Dzik & Trammer 1980 proposed to put a dash between sub- and specific names) have not found support among paleontologists.

It has thus to be concluded that the basic taxonomic unit in paleontology should be chronospecies defined in such a way that the distance between mean values of diagnostic characters for its extreme populations should not be smaller than one standard deviation mesured in the center of the time range of the chronospecies.

In paleontological practice it is rarely possible to quantify the variability of diagnostic characters so precisely as to allow for calculation of standard deviation, particularly because many definitions of chronospecies are polythetic. Therefore, the procedure of defining chronospecies is usually qualitative rather than quantitative. With a statistically significant sample in hand one is easily able to estimate the real range of variability even without biometrics. Such procedure had also to be followed in the case of subdividing the lineage of *Zarajskites* from Brzostówka into chronospecies (Dzik 1986). Measurements are necessary only if there is a suspicion that the variability is not unimodal.

TAXONOMIC NOMENCLATURE OF CHRONOSPECIES

To serve properly as a means of scientific communication, a defined chronospecies has to be named according to precise and unequivocal rules. The rules which are used to name chronospecies should also be consistent with the regulations proposed for biospecies by the International Code of Zoological Nomenclature.

To identify the proper name which should be used for a chronospecies, among existing names of fossils, it is not enough to find a holotype which fits the mean morphologic features of the chronospecies. The holotype may turn out to be an endmember of variability range of a biospecies, which is actually distantly related to the studied segment of the lineage or not related to it at all. The holotype morphology has thus little to do with both identification of chronospecies and its naming. Rather, it is important whether a particular holotype (irrespective of its morphology) is representative of a population included in the chronospecies or not. It may happen that a specimen designated to be the type of a species is an aberrant form quite dissimilar to typical representatives of its own population. In fact, this is quite common a case because curiosity in form always attracts the attention of students, while the most common morphology may remain for long unnoticed, being regarded as too trivial. To make proper choice of the name for the chronospecies, it is thus necessary to complete the list of all, ever proposed holotypes which are believed to belong to populations of the considered chronospecies. The first introduced holotype is the holotype of the chronospecies, irrespective of the relationship of its morphology to the morphology proposed to be typical of the chronospecies. It gives the name for the whole chronospecies.

Practical application of these simple nomenclatorial rules may be quite complicated. In many cases it is not possible to identify with certainty the population to which a particular holotype belonged. Sometimes the problem may be solved by additional collecting at the type locality, but there are many examples where the locality is unknown or no longer existing (i.a. Dzik 1979). In other cases identification of population is impossible. This concerns especially species established in reworked materials from condensed sections. When such situation is met, it is recommended, for the sake of nomenclatorial stability, to base decisions on the assumption that holotypes represent the modal values of variability of their populations unless there is any evidence to the contrary (Dzik 1986).

Complications of similar kind arise when a single specimen is to be identified taxonomically and named. It is then tempting to assume that the specimen is representative of the mode of its population. It has to be kept in mind, however, that, although very likely, this is nothing more than an assumption. With an increasing number of morphologically similar specimens collected, the likelihood that the assumption was correct increases, but it may well be that the first specimen was an endmember of variability range of its own population. The same morphology which is typical of a population can be found much above and below its horizon as an extreme representative of different populations. The probability that such an extreme morphotype is found depends on sample size. When only a few specimens are collected it is most likely that they are representative of the modal morphology (though there is always a chance to collect the most unusual specimen as the first one). This is why the ranges of typologically defined chronospecies are so sensitive to sample size. Identification of chronospecies in small samples is thus probabilistic by its very nature, and this fact should find its expression in nomenclature. Traditional ways of indicating uncertainty, like cf., aff., or sp. should be in common use. Regardless of whether or not this indicated formally, one has always to remember that not every fossil specimen of ammonite or any other group of organisms is specifically identifiable even if it is very well preserved. This is a trivial truism for any biologically oriented taxonomist but there are many geologists using fossils to determine the age of rocks who seem to be unaware of it.

Coming back to the discussed empirical data, it may be suggested that the Łuków population characterized by flat conchs represent the same biospecies as the population from the beds H. 1-3 of Villers-sur-Mer, France, from where the type specimen of *Quenstedticeras henrici* was selected by Douvillé (1912). A population of robust *Quenstedticeras* close to that of Łuków is also present in this French locality, interpreted by Douvillé (1912) to be conspecific with Russian *Q. carinatum* (Eichwald 1865). Makowski (1962) chose for the Łuków population the name *Q. vertumnum* (Leckenby 1859), which is based on a microconch holotype from England. Microconchs of this morphology occur in strata of different age, associated with significantly different robust macroconchs. It is not clear what was the exact age of the type horizon of *Q. vertumnum*. Its association with *Q. lamberti* (J. Sowerby 1819) sensu Douvillé 1912, a chronospecies more advanced than *Q. henrici*, is not unlikely. Therefore, the name *Q. carinatum* (Eichwald 1865) is used here, following its interpretation by Douvillé (1912). Unfortunately, the exact type horizon is unknown also in the case of the holotype of *Q. carinatum*. In central Russia, the species is reported to occur throughout the ranges of both *Q. henrici* and *Q. lamberti* (Sazonova & Sazonov 1967), though the latter species is understood by Russian studens in a different way than by Douvillé (1912) and it may be conspecific with advanced *Q. henrici*.

In the case of the Wąwał material, nomenclatorial problems are even more complicated, in accordance with the uncertain status of the recognized chronospecies. The proposed dimorphism of *Saynoceras* is quite unlike that known in the Olcostephanidae (see Riccardi *et al.* 1974; also here Pl. 3: 16-17), and it seems doubtful if *Saynoceras* is really a member of this family. Anyway, chronospecies within the lineage represented in Wąwał are best defined on the basis of macroconch morphology. Most unfortunately, the oldest species name used for these ammonites is *Ammonites verrucosus* d'Orbigny 1841, based on a microconch holotype. I was not able to identify from the literature data which macroconch paleophenon was associated with the holotype in the type locality. Also the kind of relationships between the macroconch morphotypes of *Dobrodgeiceras* and *Valanginites* is hard to determine because of the scarcity of materials from the type locality. The valid generic name for all these forms is undoubtedly *Saynoceras*, and it is highly probable that the species names *A. verrucosus* and *A. nucleus* Roemer 1840 non Phillips 1829 can also be synonimized within the proposed range of the chronospecies. The latter species name, as understood now, is a younger homonym (see Kemper 1981: 274), it seems therefore reasonable to name the considered chronospecies *Saynoceras verrucosum*.

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Plate 1

1. Limestone concretion from the Callovian Łuków clays with assemblage of juvenile *Quenstedticeras* conchs. 8h = *Q. henrici* Douville 1912. Qc = *Q. carinatum* (Eichwald 1965).
2-3. Adult macroconch of *Q. henrici* Douville 1912 from the Callovian of Łuków; ZPAL Am VIII/1.
All natural size.

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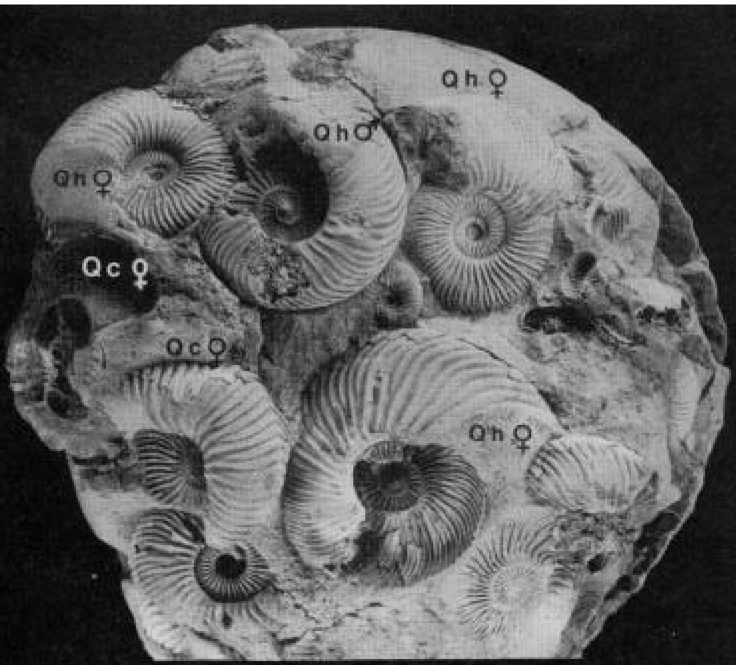

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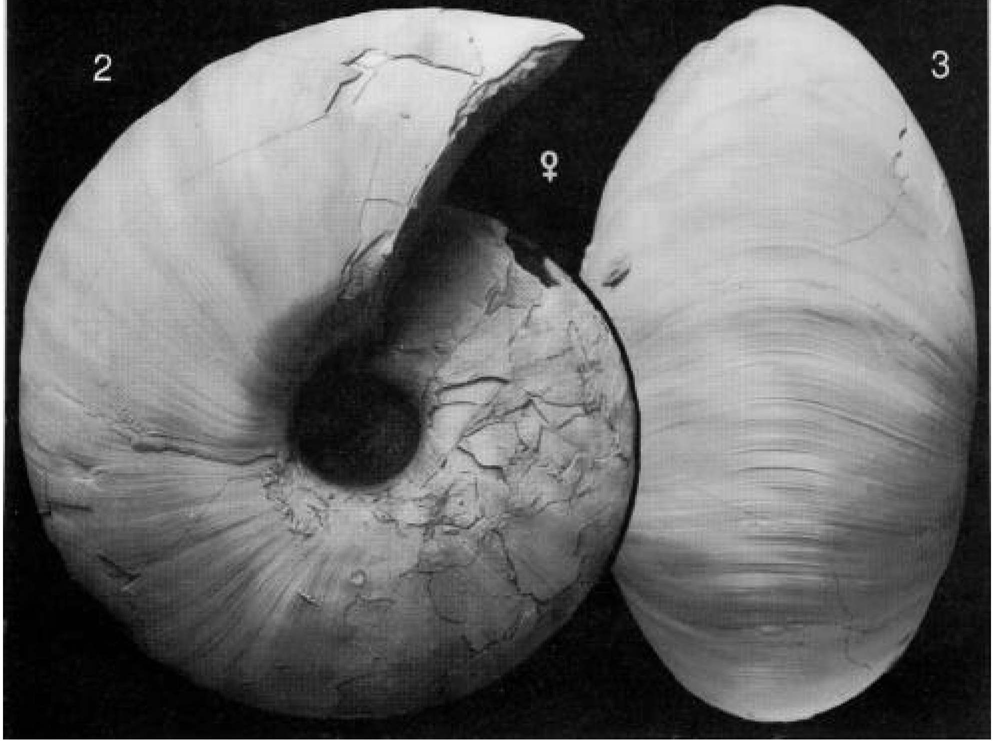

Plate 2

Quenstedticeras henrici Douville 1912 from the Callovian of Łuków, Poland.
1. Juvenile female ZPAL Am VIII/2.
6-8. Adult males ZPAL Am VIII/9, 4, 8, respectively.

Quenstedticeras carinatum (Eichwald 1865) from the Callovian of Łuków, Poland.
2-5. Juvenile females ZPAL Am VIII/3, 5, 10, 11.
9-10. Adult males ZPAL AM VIII/6, 7.
All natural size.

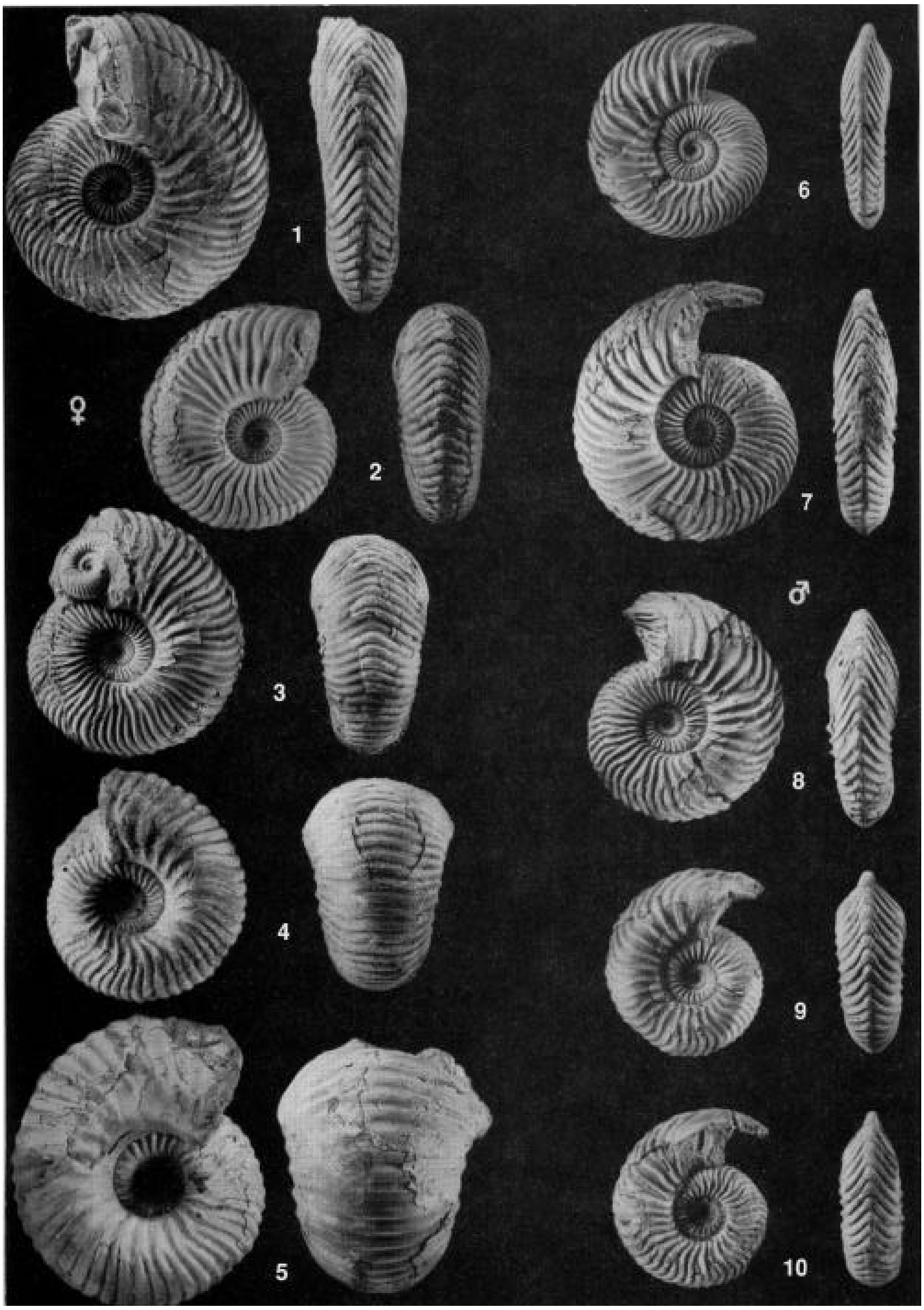
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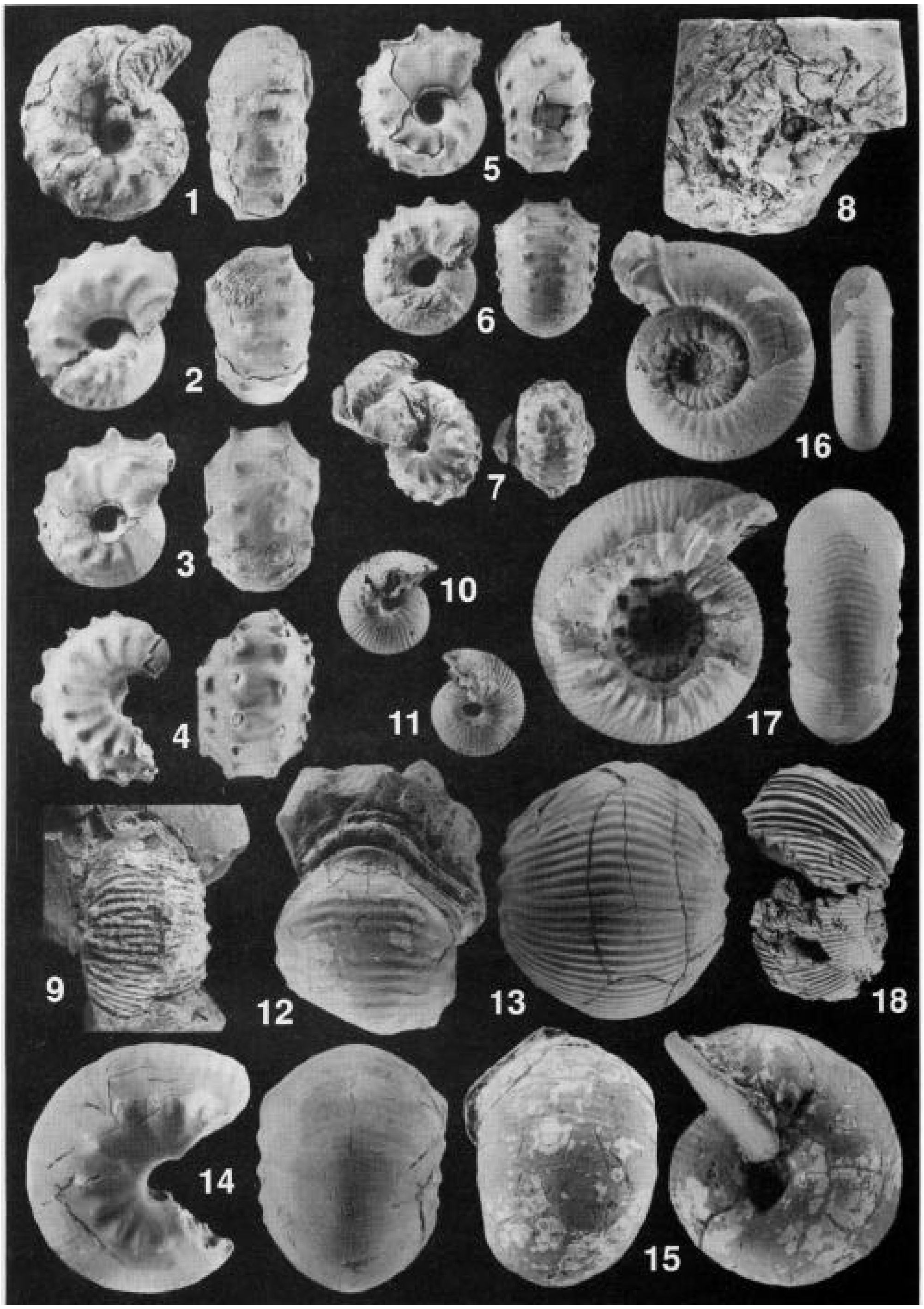
Plate 3

Saynoceras verrucosum (d'Orbigny 1841) from the Valanginian of Wąwał near Tomaszów Mazowiecki, Poland.
1. Complete adult male ZPAL Am IX/13; preserved in soft yellow phosphorite concretion collected in the upper part of the section.
2-6. Incomplete pyritized shells of adult males from the middle of the section; ZPAL Am IX/10, 5, 14, 19, 18, respectively.
7. Adult male ZPAL AM IX/12; in dark phosphorite collected in lower part of the section.
8. Crushed male shell in clay with complete lappets; ZPAL Am IX/9.
9. Unusually small adult female ZPAL Am IX/2 with ventral tuberculation; in dark phosphorite collected in lower part of the section.
10-11. Pyritized phragmocones of females ZPAL Am IX/4, 3.
12-15. Adult female shells from the upper part of the section; ZPAL Am IX/6, 1, 8, 7.

Spiticeras sp. from the Berriasian of Rogoźnik, Pieniny Klippen Belt, Polish Carpathians.
16. Adult male with lappets ZPAL Am X/2.
17. Juvenile female ZPAL Am X/1; both specimens from a single block of light micritic limestone.

Olcostephanus sp. from the Valanginian of Wąwał.
18. Fragment of pyritized phragmocone ZPAL Am IX/21.
Natural size except for Figs. 1-9 which are × 2.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