The concept of chronospecies in ammonites

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RIASSUNTO
Le sole unità taxonomiche direttamente identificabili in paleontologia sono i paleopera a gruppi di esemplari in un campione che presentano una distribuzione continua e unimodal della frequenza di tutti i caratteri. Paleopera conosciuti possono essere individuati in biospecifiche mentre serie temporali di questo formato delle linee filometriche. I risultati di estremi procedimenti sono empiricamente comprovabili.

La ricostruzione delle linee è una condizione necessaria a priori per una definizione concisa della chronospecies, cioè segmenti aritmatamente designati di una linea. Un esempio empirico dimostra che può essere possibile riconoscere i paleopera senza la biometrica.

Vengono discusse le prove per la presenza di due biospecifiche dimorfe nel Calloviano di Kuców (Polonia) e per la natura dimorfa dei geneti valangiani Saynoceras e Valanginites.

ABSTRACT
The only directly identifiable taxonomic units in palaeontology are paleopera, or groups of specimens within a sample that show continuous and unimodal frequency distribution of all characters. Correlate paleopera can be arranged into biospecifics 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 paleopera without biometrics. The evidence for presence of two dimorphy biospecifics in the Callonian of Kuców, Poland, and for dimorphic nature of the Valangian 'genera' Saynoceras and Valanginites is discussed.

KEY WORDS
Ammonites - Evolution Chronospecies - Dimorphism Callonian - 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)phora in samples,
(3) assembling paleopera into biological populations within particular samples,
(4) delimitation of biospecifics by identification of common specific 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 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 Callonian Kuców clays are chosen to show how paleontological samples can be processed. The Łośów 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 paleopera, 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 Brzótkówka, 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 material. It concerns the oncostephanids from the Valangian clays cropping out in Węgorz. 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 evidence.

Finally, the results of the search for names appropriate for the chronospecies represented in Březnoštěka, Łuków, and Wiżaw 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 morphological structure. 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 preconditions, 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 distored in such a way.

It is widely assumed that only fossils collected from a single rock layer or even bedded plane can fulfill 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 bedded 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 (Kozulska 1973). Ammonites in these concretions show excellently preserved aragonitic conchs (Kulicki 1979) with usually empty phragmocone chambers (Pl. 1, 1h). 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 gluing 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 such magnitude that the 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 & Tramer 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 'pheno'. 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 dimorphism, particular groups of discontinuously polymorphic populations, seasonal morphs, or even separately fossilized organs belonging to the same species (for instance, ammonite conchs and apytchi). In some cases, paleophena may quite well represent groups of sympatric species, which are indistinguishable on the basis of their skeletal structures which are used to define them (this is clearly the case when paleophena of apytchi are considered).

Although discreetness 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...
**CHRONOSPECIES IN AMMONITES**

*Quenstedtoceras*, which occur there in abundance, followed by *Koumoceras* 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 *Quenstedtoceras* 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 *Quenstedtoceras* from Ełkow. 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 number 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 paleophora among representatives of *Quenstedtoceras* 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 involutions. 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 paleophora in the *Ełkow* samples, the indices of involutness 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 *Quenstedtoceras* from the Cullonian of Ełkow, Poland. The largest dots represent adult males. Circles = sample 210-D, black points = 210-B, black squares = 210-C, and white squares = 210-A. Note that the male conchs form two separate clusters with juvenile males inbetween.
Fig. 2. Recognition of paleoforms in samples of the ammonite *Quenstedtoceras* from Łuków, Poland. A plot of coiled 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 paleoforms recognizable only at the adult stage of development.

The fields of identifiable macro- and micrococonchs 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 macrococonchs. The presence of four separate paleoforms 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 Callovian (1963, 1969) appeared it has been generally accep-
ted that the dimorphism is profusely expressed in
Mesozoic ammonites in the size and morphology of their
conchs (i.e., Westermann 1966; Lehmann 1966; Pulfrach-
man 1966, 1969; Riccardi et al. 1971; Ziegler 1974;
Riegraf et al. 1984). Particular macro- and microconchs
in the Echker materials were already identified as sexual
dimorph in species of Quenstedtia and Kosmoceras by
Makowski (1962). In the case of the investigated sam-
ple, 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 phena within the range of Quen-
stedtia 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 indistinguishable
but diverge later on in their development, thus produc-
ing two pairs of subordinate clusters representing the par-
ticular 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 trans-
formations in the conch morphology, while females seem
to preserve more juvenile features of the shell geometry
at the subadult stage. The whorl compression had in-
creased 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 be-
gan to increase much more in the lateral diameter, giv-
ing 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 recog-
nized at the conch diameter of only 2 mm; usually it oc-
curs at the diameter of about 25 mm, but there are also
specimens in which this change in the shell geometry evi-
dently did not take place at all (Pl. 2, 3, Makowski
1962, Pl. 13: 1). They are rather subordinate in the

Fig. 3. Ontogenetic change in development of intercalary ribs in different samples of Quenstedtia carinatum and Q. henrici from the Callovian of Ecklow, Poland. Rib index refers to the number of secondary ribs corresponding to 3 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) tend to arrange along much deeper curve than specimens of other samples. Circles = sample 210-D, black points = 210-C, and white squares = 210-A.
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 *Quenstedtia* in the samples 210-A and B. This apparently synchronous 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 synchronous change in ribbing reflects a response to environmental factors, would undermine the usefulness of the ribbing features for time correlation. The integration most appealing to me is that this superficially observed trend in the 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 involute- ness of ammonite conchs (Dzik 1986), which is known to change in the evolution of *Quenstedtia*. It may thus be that *Q. carinatum* followed the same as *Q. bennici* trend in increase of involutiveness, 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 *Quenstedtia* 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 Brażostówka near Tomaszów Mazowiecki, Poland. Several populations, representing both macro- and microconchs of early virgatids, 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...
in some juvenile conchs, expands both back and forth in the ontogeny being expressed in more and more juvenile stages (Fig. 3). 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 paleo-
Fig. 5. Transformations of the ornament in the Zamajsterzynt (Michalski 1884) lineage, the Volgian of Brounowka near Tomaszow Mazowiecki, Poland.
tology by Brinklmann (1929), was named the stratigraphic 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 stratigraphic 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 Waława, not far from Brzostówka.

Ammonites are preserved in Waława 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 'oosteanphalids', which are represented in collections by numerous specimens with complete terminal aperture. Some of them represent typical minute microconchs with long lappets (Sayanoceras), while others, somewhat larger specimens have their aperture armed with a thick roll and may represent microconchs (Valanginites and Dolomijiceras) (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 microconchs 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 Waława material (Fig. 6). This is not so clear with respect to the morphology of the macroconch. 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 (Dolomijiceras 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 Dolomijiceras and Valanginites type conchs are the only ones which can be matched as macroconchs with the microconch Sayanoceras in the Waława section. Such a relationship was already proposed by Thienoloy (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 paleoconchs of micro- (Sayanoceras) and macroconchs (Dolomijiceras and/or Valanginites) occurred in the section of Waława and evolved toward larger size and smooth appearance of female conchs. Additional collections from Waława 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 solved is how the time dimer-
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 abcissa. When the second approach is in use, the line separates different populations (biotypes); 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 sample 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 based on the sections of the stratigraphical range 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.e. 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) or 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 length of time necessary to change the population mean by one standard deviation. Commenting upon this proposal, Simpson (1953: 67) 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 deviation also tends to measure the rate of reduction of overlap in two related populations”. Following this line a reasoning Dzik & Trammer (1980: 76) proposed that subspecies 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 biospecies in paleontology rather vague methodologically. It is hard to disagree with this opinion, especially since proposals to introduce always overlap. The range of the overlap as well as the range of the whole chronospecies defined typologically strongly depend on size of the sample 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).

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 measured 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 Zanuckites from Brassocitida 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 morphospecies 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 (c.f. Dzik 1979). In other cases, the type specimen of the holotype 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 morphotype 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 the horizon is exposed it is most likely that they are representative of the modal morphotype (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 sensitive to sample size. Identification of chronospecies in small specimens is thus probabilistic by its very nature, and this fact should find its expression in nomenclature. Traditional ways of indicating uncertainty, life 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 Łękow 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 beneci was selected by Douville (1912). A population of robust Quenstedticeras close to that of Łękow is also present in this French locality, interpreted by Douville (1912) to be conspecific with Russian Q. carinatum (Eichwald 1865). Makowski (1962) chose for the Łękow population the name Q. serratum (Leckebusch 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. serratum. Its association with Q. lamberti (J. Sowerby 1819) seems Douville 1912, a chronospecies more advanced than Q. beneci, is not unlikely. Therefore, the name Q. carinatum (Eichwald 1865) is used here, following its interpretation by Douville (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. beneci and Q. lamberti (Sazonov & Sazonov 1967), though the latter species is understood by Russian students in a different way than by Dzik (1912) and it may be conspecific with advanced Q. beneci.

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

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REFERENCES


BRINKMANN, R., 1929 - Statistisch-biostatigraphische Untersuchungen an mitteljurassischen Ammoniten über Arbegriff.


Plate 1


2-3. Adult macroconch of Q. breviss. Douville 1912 from the Callovian of Kuków; ZPAL Am VIII/1. All natural size.
Plate 2

*Quenstedtoceras bernici* Douville 1912 from the Callovian of Łuków, Poland.
2-8. Adult males ZPAL Am VIII/9, 4, 8, respectively.

*Quenstedtoceras carinatum* (Eichwald 1865) from the Callovian of Łuków, Poland.
9-10. Adult males ZPAL AM VIII/6, 7.
All natural size.
Plate 3

Samoscena verrucosa (d'Orbigny 1841) from the Valanginian of Wąwął 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.
12-15. Adult female shells from the upper part of the section; ZPAL Am IX/6, 1, 8, 7.

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

Olcostephanus sp. from the Valanginian of Wąwął.
Natural size except for Figs. 1-9 which are × 2.