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GRADUAL EVOLUTION OF CONODONTOPHORIDS IN THE POLISH TRIASSIC

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A monospecific continuum of populations of the conodont genus *Gondolella* occurs in a 23 m thick limestone set at the Anisian/Ladinian boundary in the southwest margin of the Holy Cross Mts, Poland. The change in distribution of morphological characteristics of the platform element is gradual and consists in an increase in contribution of morphologically juvenile stages to the fossil populations. Purely ecological interpretation of this trend as a continuous change in population dynamics is refuted. The trend reflects a true evolution. The other elements of the apparatus *Gondolella* do not undergo any significant changes, except possibly for the *pl* element ("*Enantiognathus*"). Time span separating fossil populations with non-overlapping standard-deviation ranges of diagnostic features sets actually the limit to recognition of temporal subspecies. This is also the limit to precision of biostratigraphic zonation based upon temporal taxa. It is here proposed to introduce a nomenclatorial difference between temporal and geographical (or biological) subspecies by insertion of a dash between specific and subspecific names.

Key words: Triassic, conodonts, evolution, biostratigraphy, taxonomy.

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INTRODUCTION

The Middle Triassic is represented by a conodont-rich carbonate facies in central and southern Poland. The carbonate facies passes both laterally and upwards into terrigenous and continental facies. The boundary between the facies is heterochronous, depending upon the paleogeographic situation. In the central part of the Polish basin, the Anisian and Lower Ladinian are represented by the carbonates (Trammer 1975; Zawidzka 1975). The beds with *Pecten discites* and the *Ceratites* beds (uppermost Anisian to Lower Ladinian) are especially rich in conodonts. This permits a detailed study of the termination of conodont evolution in the Central-European basin (Trammer 1974).

The uppermost Anisian to Lower Ladinian limestones are well exposed in the southwestern margin of the Holy Cross Mts. There are several sections in the vicinity of Lesica, Pierzchnica, and Stare Chęciny villages, the correlation of which can be reliably based upon a direct inference from lithology. These sections were also subject to detailed biostratigraphical and sedimentological investigations (Trammer 1971, 1975). The present paper is actually merely a reconsideration and further refinement of the inference from the previously studied material.

The conodontology has made much progress since the time the previous papers on the uppermost Anisian to Lower Ladinian conodonts of the Holy Cross Mts were published. The methodology of reconstruction of conodont apparatuses has been considerably refined (Marsal and Lindström 1972; Dzik 1976), and several reconstructions of conodont apparatuses of various geological age were presented (Klapper and Philip 1971; Baesemann 1973; Jeppson 1974, Sweet and Schönlaub 1975; Dzik 1976; Von Bitter 1976; Merrill and Von Bitter 1977; Nicoll 1977; Ramovš 1977; Barnes *et al.* 1979; Nowlan 1979; van den Boogaard and Kuhry 1979). Furthermore, one has become able to decipher the evolution of complete conodont apparatuses (McTavish 1973; Philip and McDonald 1975; Dzik 1976, 1978). The mode of conodont occurrence in the Polish Triassic does also permit a detailed study of the conodontophorid evolution.

METHODS FOR RECONSTRUCTION OF CONODONT APPARATUSES

Since the time the pioneer papers by Bergström and Sweet (1966) and Kohut (1969) appeared, inductive methods for reconstruction of conodont apparatuses have become widely used. In general, these methods consist in recognition of a statistically significant recurrence of various conodont elements with one another with use of a statistical analysis of large samples. Depending upon the power of a conodont-element association, apparatuses and ecological assemblages of apparatuses can be recognized. Marsal and Lindström (1972) introduced an additional method allowing to recognize the proportions of particular elements in an apparatus, assumed that there is no systematic bias introduced by taphonomic factors. Reconstructions achieved with application of the inductive methods are verified by the analysis of new samples and exceptionally, by findings of complete apparatuses.

Dzik (1976) proposed to introduce the falsification methodology of Popper (1977) to the study of conodont apparatuses. Instead of searching for more and more new data supporting a reconstruction of conodont apparatus, it is much more efficient to look only for data rejecting a reconstruction assumed previously inductively or even purely intuitively. Thousands of samples may fit well to a reconstruction but a single one may result in its refutation. The falsification procedure is very straightforward and its only requirement is a statistical significance of the sample permitting the ultimate rejection of a tested hypothesis. In fact, hypothesis that the elements A, B, C, ..., n make part of a single apparatus implies necessarily that all these elements have to occur in each statistically significant sample including some of them; absence of a single element from a sample falsifies the reconstruction claiming its constant recurrence with the other elements. An additional assumption of the continuity of organic evolution permits testing validity of a reconstruction with application of phylogenetic data (Dzik 1976). This makes a great help in separation of hardly discernible apparatuses representative of ecologically associated species.

One can fairly easily reconstruct Triassic conodont apparatuses because there are at most 2—3 co-occurring conodontophorid species in the Triassic, while often there is but a single one. Aside of a short time interval in the Late Anisian when the multielement species *Neospathodus kockeli* (Tadge, 1956) appeared, there is probably only a single phyletic lineage (genus *Gondolella*) in the Polish Middle Triassic. The available data (Trammer 1975, Zawidzka 1975) do not permit recognition of any other associated conodontophorid lineages.

APPARATUS TERMINOLOGY

The progressing specialization among conodontologists is probably responsible for different terminologies applied to conodont apparatuses depending upon their geological age. Following the previous attempts to unify terminology of conodont elements of various apparatuses (Von Bitter 1976), we propose here a complete homologization of the elements of *Gondolella* apparatus with the other Ozarkodinina. We agree with Von Bitter (1976) that the basic terminological framework for conodont apparatuses is that introduced by Jeppson (1971) for Silurian conodonts. Silurian conodont apparatuses were the first and most reliably reconstructed ones (see Mashkova 1972; Jeppson 1974). At the same time, they are far from overspecialization which considerably increases the feasibility of their homologization with apparatuses of the pre- and post-Silurian Ozarkodinina. One may claim that post-Silurian conodont apparatuses do not significantly differ in structure from the Silurian apparatus *Ozarkodina*, except for the genera *Neopanderodus* and *Icriodus* the ascendants of which were the Prioniodontina instead of the Ozarkodinina. However, the occurrence of five left *hi* elements (Ramovš 1978) in a single apparatus *Pseudofurnishius murcianus* van den Boogaard, 1966 appears to be indicative of a difference in number of at least some elements between the Silurian and Triassic conodont apparatuses. The Lower

Devonian *Ozarkodina steinhornensis* (Ziegler) shows only three couples of *hi* elements (Mashkova 1972).

Thus, the apparatus Gondolellidae includes the following elements:

1. *sp* element (spathognathodiform): platform element, supposedly a single couple; the left and right elements were not mirror images in *Pseudofurnishius* related closely to *Gondolella*, which permitted their tight occlusion (Ramovš 1977, 1978).

2. *oz* element (ozarkodiniform = pollognathiform, LD): supposedly a single couple, but a considerable intrapopulation variability in the Triassic apparatus *G. mombergensis* Tadge, 1956 may be suggestive of a greater number of these elements in an apparatus.

3. *pl* element (plethospathodiform = enantiognathiform, lonchodiniform, LC): supposedly a single couple; homology claimed by Dzik (1976) for enantiognathiform element with trichonodelliform element is a *lapsus linguae*.

4. *hi* element (hindeodelliform = LB): supposedly 5 couples with variable curvature of the anterior branch (see Ramovš 1978).

5. *ne* element (neoprioniodiform = synprioniodiniform, LA): a considerable morphological variability within a sample may reflect the occurrence of more than one couple of these elements in an apparatus; Von Bitter (1976) recognizes a distinct synprioniodiniform element within this wide range of variability, which resembles however so closely *ne* elements that respective conodont elements representative of different apparatuses can be easily misidentified; a single term is therefore to be used for the two element types insofar as their distinctness has not been proved.

6. *tr* element (trichonodelliform = U): supposedly odd element or a single couple.

EVOLUTION OF THE APPARATUS *GONDOLELLA*

The apparatus *Gondolella* is among those known for the longest (*Illinella typica* Rhodes, 1952) but nonetheless, its detailed reconstruction was presented only recently (Von Bitter 1976; see also Kozur and Mostler 1971: 10). The available data indicate that the Carboniferous, Permian, and Triassic representatives of the family Gondolellidae Lindström, 1970, show apparatuses very similar to each other in structure (fig. 1). These apparatuses include each a platform *sp* element ("*Gondolella*"), *oz* element ("*Pollognathus*", "*Xaniognathus*"), and a set of fragile branched elements assigned commonly to the "apparatus" *Ellisonia gradata* Sweet (by the way, *Ellisonia teicherti* Sweet and *E. triassica* Sweet make probably part of diverse multielement species of the genera *Anchignathodus* and *Neospathodus*). The elements "*Ellisonia*" and "*Pollognathus*" were already attributed to a single apparatus by Babcock (1976). The composition of gondolellid apparatuses has been recognized not only after reconstruction from isolated elements but also after the complete apparatuses *Gondolella sublanceolata* Gunnell, 1933 described by Von Bitter (1976) from the Upper Carboniferous and those assigned to *Pseudofurnishius murcianus*, a Triassic relative of *Gondolella* (see Ramovš 1977).

The oldest known apparatus of the genus *Gondolella* is *G. sublanceolata* Gunnell. 1933, from the Virgilian (uppermost Carboniferous) of Iowa (Von Bitter 1976). When compared to thus far known congeneric apparatuses, *G. sublanceolata* displays relatively robust branched elements.

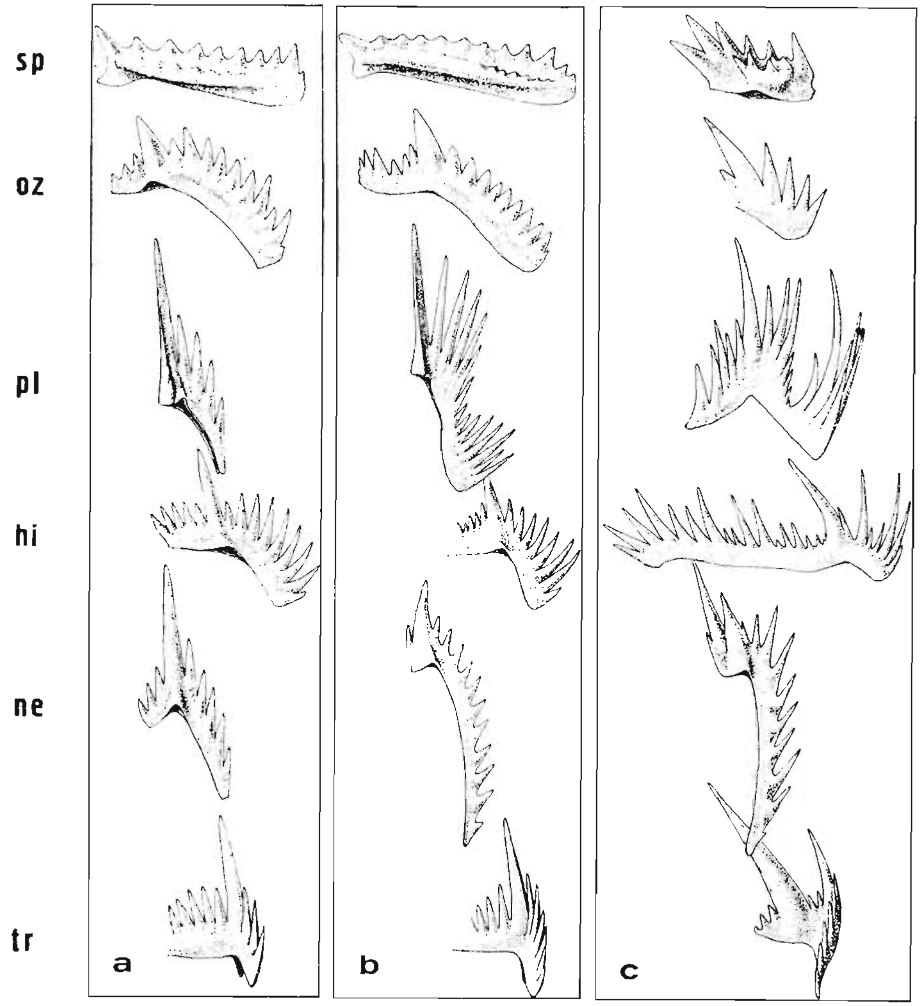


Fig. 1. Presumed homologies in apparatuses of Carboniferous (a), Permian (b), and Triassic (c) gondolellids. *a Gondolella sublanceolata* Gunnell, after Von Bitter (1976); *b Gondolella serrata-postserrata* Behnken (incl. *Ellisonia* sp. aff. *E. gradata* Sweet), after Babcock (1976); *c Pseudofurnishius murcianus* van der Boogaard, after Ramovš (1977).

Most branched elements illustrated by Von Bitter (1976) are considerably broken which makes any comparison to other multielement species rather difficult but nevertheless, their homologues can be recognized (fig. 1). The only problem is identification of the homologues of the highly variable *ne* and *syn* elements of *G. sublanceolata*. A similar variation in elements of this type appears also in the Triassic conodont assemblages from the Holy Cross Mts (fig. 2), but we can hardly say whether it does reflect merely an intrapopulation variability in a single couple of *ne* elements, or whether it is caused by co-occurrence of two couples of related but distinct *ne* and *syn* elements. The lonchodiniform element of *G. sublanceolata* is homologous to the element "*Enantiognathus*" of later representatives of *Gondolella*, and presumably to the plethospathodiform element of Silurian *Ozarkodina*.

Assemblages of the branched elements of the Permian apparatuses attributable to *Gondolella* have thus far been described under the name of *Ellisonia gradata* Sweet, 1970, separately from platform (*sp)* and *oz* elements. Babcock (1976) was right when he assigned the *oz* element described previously under the generic name *Xaniognathus* to the apparatus *E. gradata*. The Permian apparatus *Gondolella serrata-postserrata* Behnken (see the nomenclatorial remarks: chapter "Taxonomic implications") shows branched elements ("*Ellisonia* sp. aff. *E. gradata* Sweet"; see Babcock 1976) finer than those of *G. sublanceolata* but it does not significantly differ from the Triassic gondolellid apparatuses.

Reconstructions of Triassic apparatuses identical in structure to the Permian apparatus "*Ellisonia gradata*" were proposed by Kozur and Mostler (1971) under the names of *Enantiognathus ziegleri* and *E. incurvus*. A complete set of the elements (*sp* element including) is shown by the apparatus *Gladigondolella tethydis* as conceived by Kozur and Mostler (1971).

The only thus far well known Triassic conodont apparatus is *Pseudofurnishius murcianus* van den Boogaard (see Ramovš 1977, 1978). Its close resemblance in structure to the apparatus *Gondolella* points to a closer phylogenetic relationship of *Pseudofurnishius* to the *Gondolella* stock than to the *Neospathodus* one, even despite a greater affinity of the *sp* element to the latter than to the former genus. The branched elements of the Permian species *Anchignathodus typicalis* Sweet which is supposed ancestor of *Neospathodus* evolutionary line, described under the name of *Ellisonia teicherti* Sweet (see Sweet 1970, Babcock 1976), show a different from *Pseudofurnishius* denticulation of branches (close to the early Ozarkodinina), and the *pl* element is entirely different in outline. *Neospathodus divergens* (Bender and Stoppel, 1965), the elements of which were described from the Polish Permian as form species (Szaniawski 1969), also appears to be more closely related in apparatus structure to *Ozarkodina* than to *Gondolella*. This is indeed consistent with the position of *Anchignathodus* and *Neospathodus* intermediate in evolution between the Spathognathodontidae and Gondolellidae.

This review of the data on gondolellid apparatuses (fig. 1) shows that the branched elements underwent merely slight evolutionary modifications. The material investigated by us supports this claim. The greatest evolutionary change over the investigated part of the Early Ladinian was shown (fig. 2) by the *pl* element ("*Enantiognathus*" (Kozur 1968, Trammer 1974). There are *pl* elements with a long anterior branch and much shortened denticles in the middle ("*E. ziegleri*") in the lowermost part of the section; whereas *pl* elements with much shorter anterior

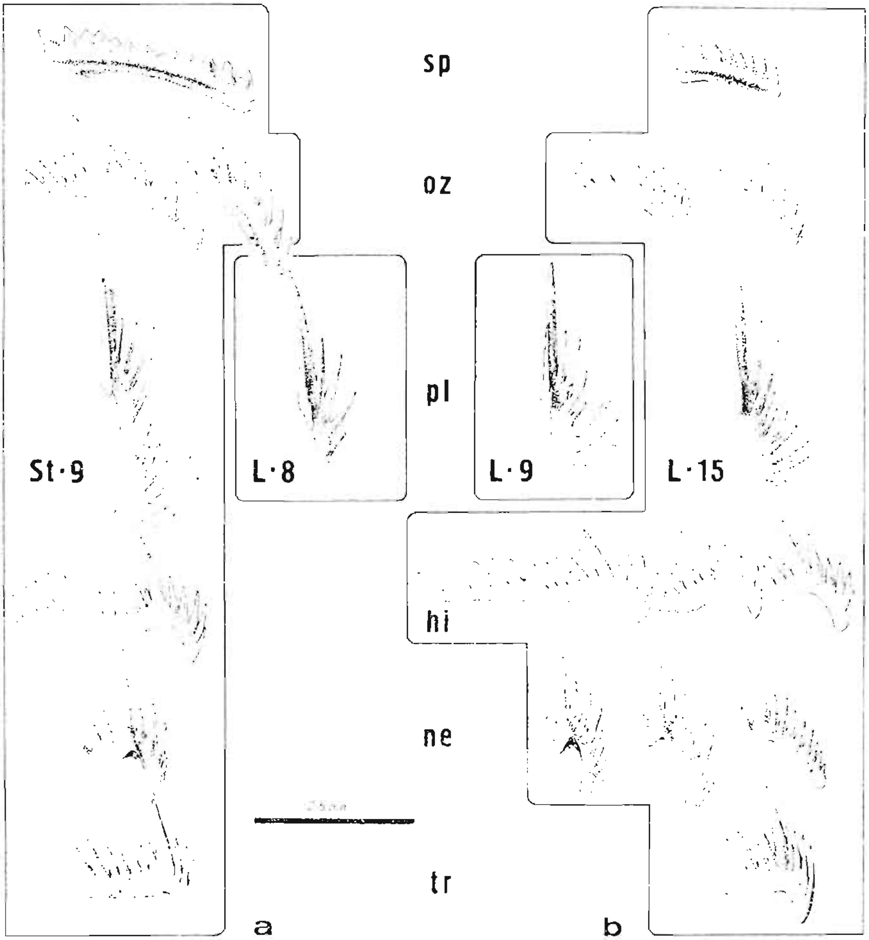


Fig. 2. Evolution in *Gondolella* apparatus in the uppermost Anisian to Lower Ladinian in the Holy Cross Mts; all the conodont elements (along with variation in some element types) are shown for samples representative of the lowermost (sample St-9) and uppermost (sample L-15) parts of the section, as well as the *pl* elements ("*Enantiognathus*") representative of the middle part of the section (samples L-8 and L-9). *a Gondolella mombergensis-mombergensis* Tadge, 1956; *b Gondolella mombergensis-haslachensis* Tadge, 1956.

branch and less distinctly shortened denticles in the middle ("*E. incurvus*") occur in the uppermost part of the section. The *pl* elements are among the most fragile ones in apparatuses attributable to *Gondolella*. The difference between the above recalled form species of "*Enantiognathus*" consists mostly in length of the anterior branch and hence, these morphotypes can be distinguished only in the case of very well preserved specimens. This considerably hampers any biometrical study of their variability and evolution. Elements of "*E. ziegleri*" type occur in the investigated section at least up to the sample L-8. The sample L-9 contains already elements of "*E. incurvus*" type. The distance inbetween is 4 m in the section. The evolutionary shortening of the branch must have happened during the respective time interval. The *pl* elements found in the sample L-10 located between the samples L-8 and L-9 are too poorly preserved to be doubtlessly identified. It is noteworthy that there are no significant differences in morphology of the other conodont elements among the samples L-8, L-10, and L-9. This fits well to the heterochroneity of evolutionary events that happen in particular elements of a conodont apparatus, as shown previously by Dzik (1976, 1978). It is however to be kept in mind that the *pl* element of *Gondolella* shows a large intrapopulation variability and a few investigated specimens may well be representative of the endmembers of the range of variation; the supposed acceleration of evolution in *pl* element would then be merely an artifact of statistically insignificant samples. In fact, there are *pl* elements with an elongate posterior branch in the uppermost part of the investigated section. Such conodont elements occur commonly in Late Ladinian populations reported from Thuringia (Kozur 1968, 1971). We are unable to trace this evolution in Poland because the Triassic marine sedimentation terminated earlier in the Polish basin (Trammer 1975).

Less significant but recognizable changes can be observed in the *oz* element ("*Ozarkodina*", "*Pollognathus*"). The posterior denticles of *oz* element are oriented more or less parallel to the main cusp in specimens from the lower part of the section (up to the sample L-8); in the sample L-10, *oz* elements with posterior denticles recurved considerably posteriorly appear for the first time (fig. 2). However, this feature is rather hardly discernible and highly variable in a population. Even the uppermost samples yield some *oz* elements resembling very closely those from the lower part of the section.

One may thus conclude that, judging from the investigated poor material, the branched elements of *Gondolella* underwent in the Early Ladinian evolutionary shortening of the anterior branch of *pl* element and recurving of the posterior denticle of *oz* element. The evolution in the two element types was heterochronous; supposedly, it started earlier and lasted longer in the *oz* element than in the other one. There is no significant change in size of any other branched element in the investigated samples from the Holy Cross Mts. It is however to be kept firmly in mind that the branched elements show very large intrapopulation variability and the above presented pattern of their evolution may well be an artifact of too small sample size; there is no sample with more than ten well preserved branched elements of particular type. The latter supposition may be indeed confirmed by the occurrence in the Upper Ladinian of Thuringia of *pl* and *oz* elements resembling those from the lower part of the investigated section (see Kozur 1971).

EVOLUTION OF THE PLATFORM ELEMENTS OF *GONDOLELLA* APPARATUS

The platform (*sp*) element of the multielement genus *Gondolella* Stauffer and Plummer, 1932, shows much morphological resemblance to its homologues found in the related genera *Anchignathodus* Sweet, 1970, *Neospathodus* Mosher, 1968, *Epigondolella* Mosher, 1968, and *Pseudofurnishius* van der Boogaard, 1966. The feature in common for all these genera is the extreme posterior position of the main cusp, which makes them different from all the other Ozarkodinina and hence, justifies their recognition for a distinct family Gondolellidae Lindström, 1970. The genus *Gondolella* is unique among the gondolellids in having a finely ornamented platform developed from widened lateral ribs of the *sp* element. The genus *Gondolella s.l.* is sometimes split into *Gondolella s.s.*, *Neogondolella* Bender, 1967. *Gladigondolella* Müller, 1962, and *Paragondolella* Mosher, 1968, because of a variation in development of the pitted ornamentation of *sp* elements (Von Bitter 1976, Von Bitter and Merrill 1977), supposed absence from the apparatus of any elements other than platform ones (Sweet 1970, Kozur 1976), and supposed polyphyletic origin (Mosher 1968). Von Bitter and Merrill (1977) suggested that the Permo-Triassic species of *Neogondolella* displayed apparatuses similar in structure to those of typical representatives of *Gondolella*, which is indeed confirmed by our results. A difference in platform ornamentation between species of *Gondolella s.s.* and *Neogondolella* is merely a quantitative one and it must not be indicative of any difference in phylogenetic relationships. The supposedly independent derivation of various Triassic gondolellid lineages from the genus *Neospathodus* (see Mosher 1968) follows from the interpretation of various ontogenetic stages as evolutionary grades. One may thus conclude that there is no reason to split the genus *Gondolella s.l.* into genera of a narrower taxonomic range (Kozur 1974).

Intrapopulation variability in morphology of the platform element of various species of *Gondolella* remains thusfar poorly understood (Von Bitter 1976). Tadge (1956) demonstrated a considerable intrapopulation variability in the Triassic form species *Gondolella mombergensis* Tadge and *G. haslachensis* Tadge, which is entirely consistent with our own results. Therefore, one can hardly say how many monospecific evolutionary continua occur at the same time within the range of the genus. One may however claim that the number of true evolutionary lineages was very small as a rule, and that in some time intervals the genus *Gondolella* was actually represented by a single biological species. Accordingly to the rules of zoological taxonomy (see Dzik 1976: 396), validity of the genera *Epigondolella* and *Pseudofurnishius*, both of them equally poor in isochronous species, appears to be questionable.

Some evolutionary changes in morphology of the platform element of the Early Ladinian *Gondolella* of the Germanic basin were claimed by Kozur (1968). According to Kozur (1968), the changes consist in an increase in teeth elongation and in predominance of the main cusp, paralleled by a decrease in denticle number and platform size. The concept of this evolutionary trend was applied for biostratigraphy of the German Triassic (Kozur 1968; Trammer 1972, 1975; Zawidzka 1975) and theoretically evaluated (Trammer 1974). The presumed evolutionary lineage of the Early Ladinian *Gondolella* was claimed to have included several species and subspecies with overlapping time ranges; these were (in ascending stratigraphic order): *G. mombergensis mombergensis* Tadge, *G. m. prava* Kozur, *G. m. media* Kozur, *G. haslachensis* Tadge, *G. watznaueri praecursor* Kozur, and *G. w. watznaueri* Kozur.

The biometrical study by Tadge (1956) demonstrated a considerable intrapopulation variability in *G. mombergensis* and *G. haslachensis* and a statistically significant difference between the respective fossil populations. This is indeed confirmed by our study of the conodonts from the Holy Cross Mts. None of the investigated samples shows a co-occurrence of distinct species of the genus *Gondolella*; the observed frequency distributions of the morphological characteristics are close to normal in all the samples (fig. 4). No doubt that all thus far recognized species are merely morphotypes. However, the taxonomic and evolutionary significance of between-population differences is far from unequivocal.

The observed frequency distributions of the morphological characteristics in particular fossil populations of the latest Anisian to Early Ladinian *Gondolella* from the Holy Cross Mts are indicative of a peculiar ontogeny of the *sp* element. Presumably, the *sp* element appeared in organogenesis as a single high denticle. Ontogenetic growth of the element consisted mainly in successive development of new denticles anteriorly to the main cusp, while the height of the older denticles was increasing only insignificantly. This pattern of growth is indicated by an almost linear relationship of denticle number to platform length (fig. 3*b*). The deviation from linear relationship apparent at the late ontogenetic stages reflects in part a growth allometry, and in part a fusion of denticles.

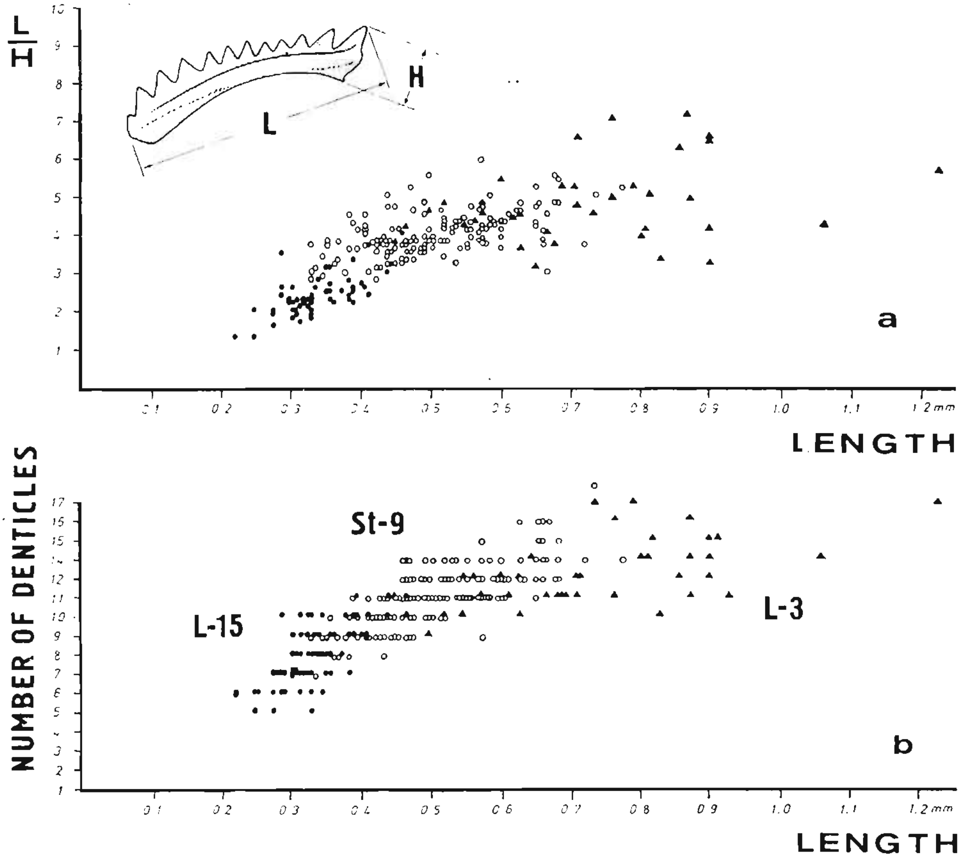


Fig. 3. Intrapopulation variability in some characteristics of the platform element recorded in the lowermost, intermediate, and uppermost samples. *a* conodont elongation (length/main cusp height) relative to the total length; *b* denticle number relative to conodont length. Dots — sample L-15 (uppermost), circles — sample St-9 (intermediate), triangles — sample L-3 (lowermost).

These are also the causes for the allometric growth of element elongation relative to the height of the main cusp (fig. 3*a*). In the latter case, non-linearity of the relative growth is also partly imposed by the facultative appearance of an additional denticle at the posterior edge of platform which takes sometimes the function of main cusp.

As shown by the above discussion, morphological characteristics of the platform element of *Gondolella* apparatus, those considered as diagnostic for species, are mutually interrelated and depending upon ontogeny. However, the interrelationship of these characteristics is far from strong, which permits the observed large intrapopulation variability. This is also the case with platform width and position relative to main cusp (fig. 5). Denticle number can be most easily studied in order to present the proportions of particular morphotypes in a sample (fig. 4). The plot of the frequency distribution of denticle number *versus* the geological time shows that in the investigated time interval the frequency distribution of denticle number in a population was changing continuously and gradually. The trend is clearly apparent. The standard-deviation ranges determined for the lowermost and uppermost samples do not overlap but there are several slight oscillations in trend direction inbetween. The above discussed correlation between denticle number and platform length is confirmed by the consistence in trends to decrease denticle number and conodont size in a fossil population (fig. 4).

ECOLOGICAL INTERPRETATION

The observed change in frequency distribution of the morphological characteristics of the platform element of *Gondolella* can be at first sight interpreted as reflecting a continuous change in population dynamics. The cumulative distributions recorded in the lowermost, intermediate, and uppermost samples can be regarded as resulting from allometric growth of the platform element. An increase in proportion of juvenile or adult individuals in a sample due to a change in mortality pattern causes a fundamental change in frequency distribution of morphological characteristics. Consequently, the prevailing morphotype does also change, which often cannot be recognized without use of biometrical methods.

There is no problem in pointing out a cause for a continuous change in mortality pattern at a single locality. The investigated geological section represents a regressive sequence. Terrigenous, continental deposits of the Keuper facies appear in the section above the sample P-24. This indicates that the investigated samples are representative each of a shallower-water and/or more nearshore marine environment than the preceding one. Some extant pelagic organisms show a clear variation in spatial distribution of particular developmental stages with respect to the water depth and distance from the shoreline. This has to be reflected in a variation in age distribution of dead organisms falling down to the bottom in various parts of the total area inhabited by a species. Juveniles of the Recent *Euphausia superba* Dana (Crustacea) live near seashore; the center of individual abundance shifts however offshore with individual growth and finally, sexually mature individuals live outside the shelf (see Jażdżewski *et al.* 1978). Migration with ontogenetic growth was also claimed by Jeppson (1977) for Silurian conodontophorids. Then, shallowing of a basin has to result in an increase in proportion of juvenile conodonts at a locality. Be the change in environmental conditions gradual, the change in age structure of a fossil population can also be expected to be gradual.

The ecological interpretation of the recorded changes in morphology

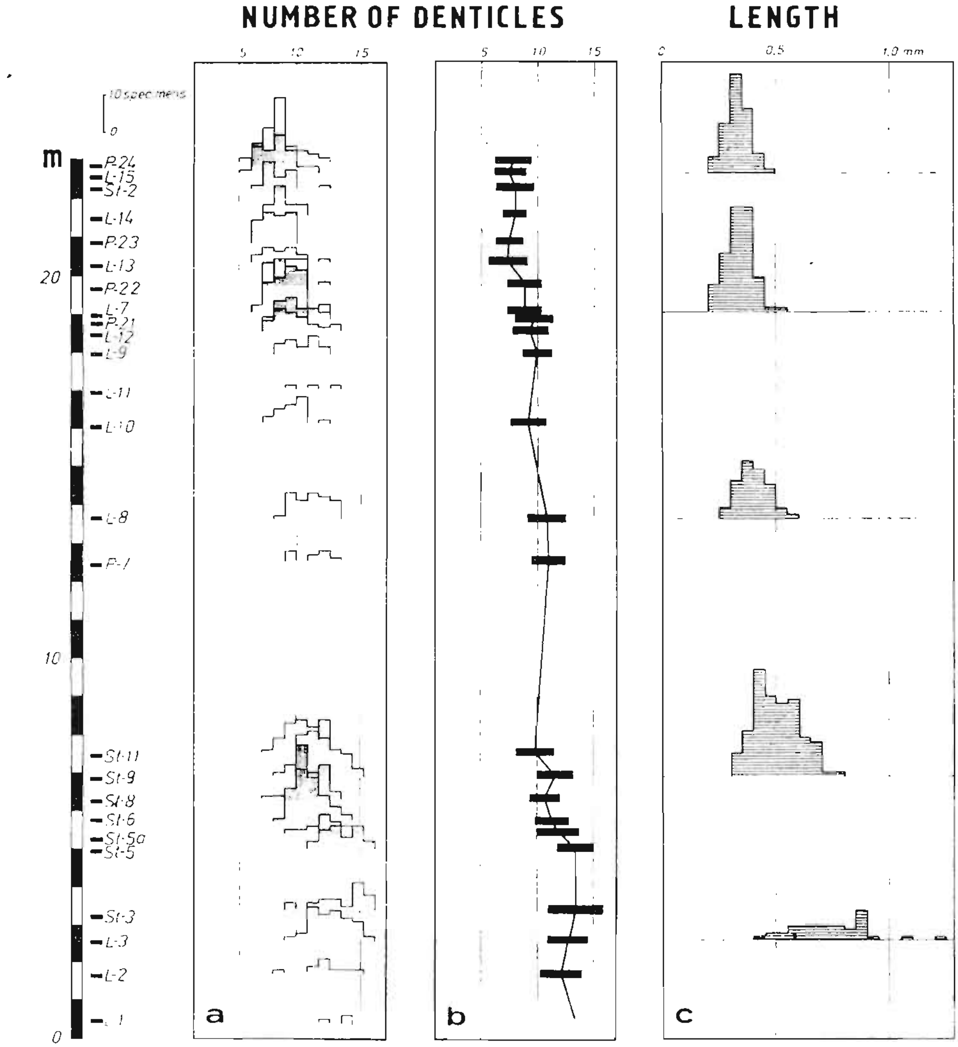


Fig. 4. Changes in frequency distribution of some morphological characteristics of the platform element of *Gondolella* in the uppermost Anisian to Lower Ladinian in the Holy Cross Mts. *a* histograms of denticle number; *b* standard-deviation ranges of denticle number; *c* histograms of conodont length for some samples.

of the platform element of *Gondolella* apparatus may appear plausible but there are some data permitting its refutation even though they are impossible to be studied biometrically. These are: (*i*) the branched elements do not show any significant change in size in the investigated section; (*ii*) the branched elements show some changes in morphology in the investigated section, as it was demonstrated above; and (*iii*) changes in population structure of *Gondolella* happened simultaneously over a large area (fig. 6) even though there was a heterochroneity in facies development among particular parts of that area (Trammer 1975).

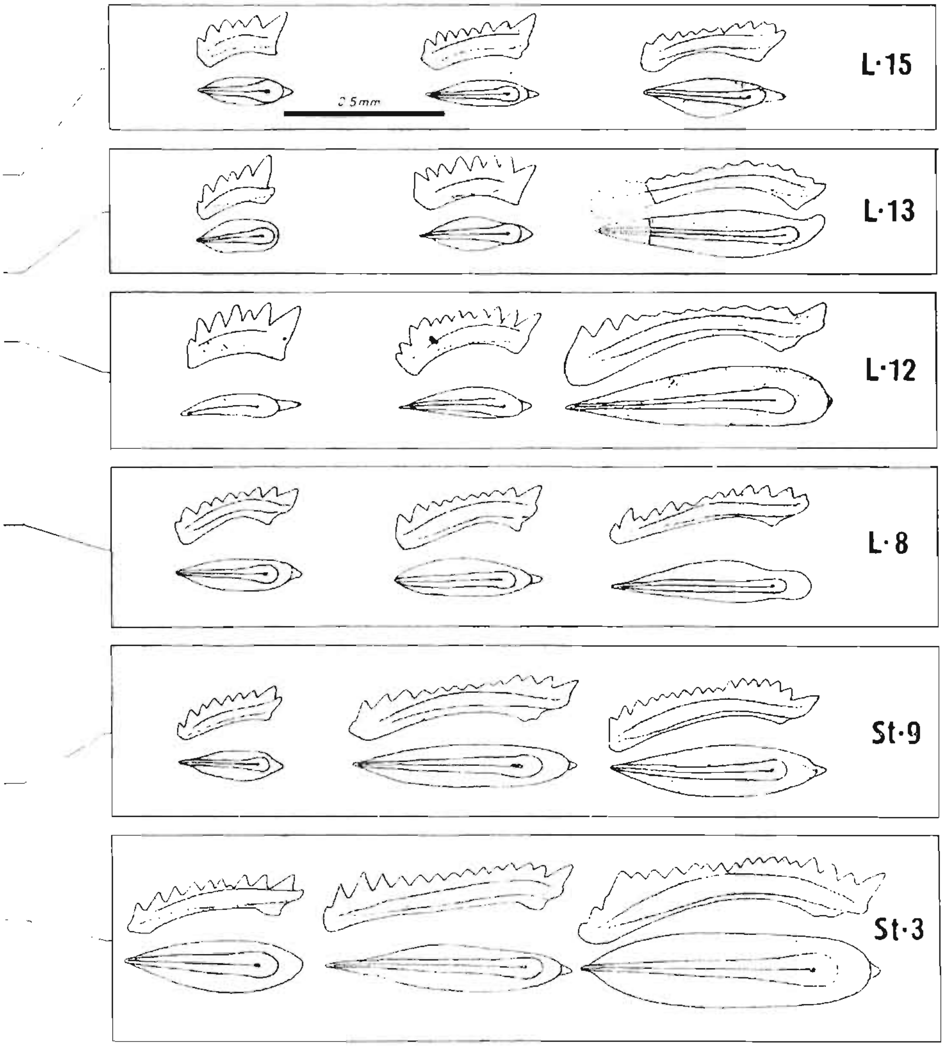


Fig. 5. Variation in outline of the platform element of *Gondolella* in some samples from the uppermost Anisian to Lower Ladinian of the Holy Cross Mts. At the center — morphotype typical of a sample, at both the sides — endmember morphotypes.

EVOLUTIONARY INTERPRETATION

The first two lines of argument in support of the evolutionary nature of the recorded morphological changes in *Gondolella* were already discussed above. After all, these are not crucial points. Much more important is the claim that the changes are of more than local significance, going on simultaneously over a considerable area. Fortunately, one is able to consider some indices of the geological time more precise than conodonts

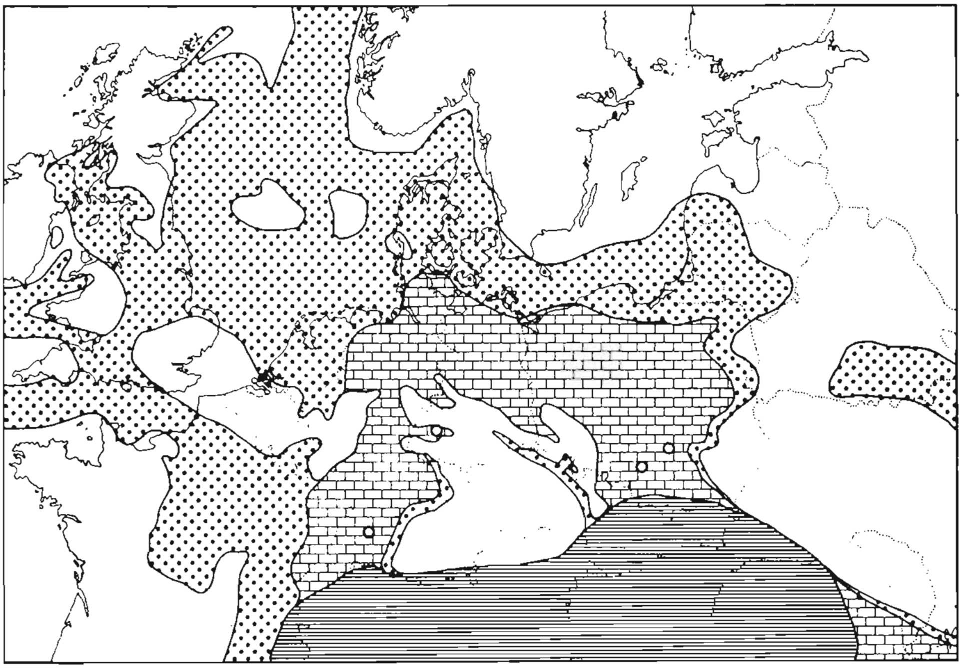


Fig. 6. Lower Ladinian paleogeography in Central Europe; shown are the localities (circles) where the evolutionary continuum *Gondolella mombergensis-mombergensis* → *G. mombergensis-haslachensis* → *G. mombergensis-watznaueri* has been recorded. Dotted — terrigenous marine and continental facies, brick-like — carbonate facies, hachured — Alpine realm. After Głazek *et al.* (1973), Ljutkevitch *et al.* (1973), and Ziegler (1978).

in the investigated time interval. These are the ceratitid ammonoids. There is little doubt that the taxonomy of the Germanic ceratitids is typological and oversplitted. Therefore, precision of the ceratitid-based biostratigraphic zonation seems to be far from reliable. There is nevertheless a confidence interval of the ceratitid zonation as a reference point for time correlation of conodont faunas. The genus *Ceratites* represents probably a monospecific (with regard to the concept of biological species) evolutionary continuum of populations with unrecognized but supposedly weakly developed sexual dimorphism. The characteristics of this evolutionary continuum is a distinct increase in size of adult shell with time, which contrasts to the change in size of the platform element of *Gondolella* (fig. 7, see Trammer 1972: 227). In the case of ammonoids, one is however able to achieve certainty that a change in specimen size with geological time reflects something more than merely a change in ecological conditions inducing changes in mortality pattern. Adult ammonoid shells can be quite easily distinguished from equally large juvenile shells; increase in suture density, smoothening of the surface of final chamber, aperture modifications, etc. may serve here as the criteria (fig. 7). As judged from the time distribution of ceratitids, the Keuper facies ap-

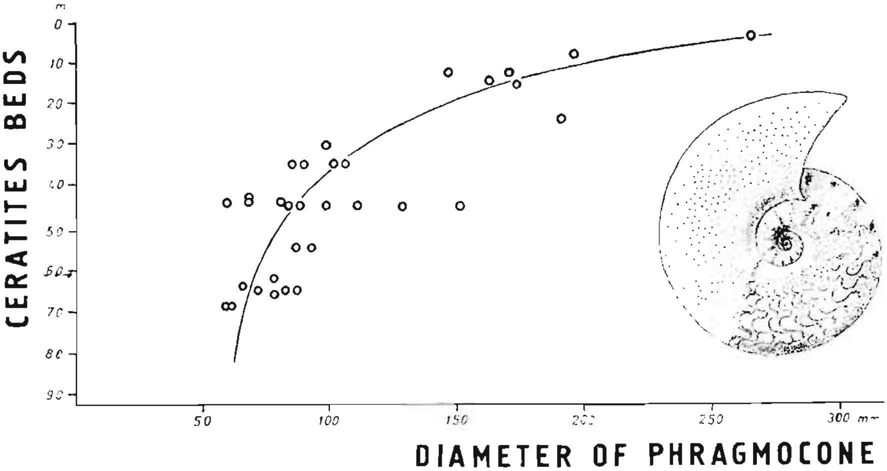


Fig. 7. Changes in adult phragmocone diameter in the species of the genus *Ceratites* in the Ceratite beds in Swabia and Frankonia. After Wenger (1957).

peared in Poland prior to the *C. nodosus* Zone, whereas the carbonate facies persisted in Germany two ammonoid zones more (Trammer 1975: 205).

Were the population structure in *Gondolella* dependent exclusively upon paleogeographic relationships, samples from the uppermost part of the Polish Muschelkalk could be expected to show a frequency distribution of morphological characteristics entirely consistent with that found in samples from the uppermost part of the German Muschelkalk. This is not the case. The platform conodonts recorded in the uppermost Muschelkalk of Germany represent in morphology a progress along the trend direction recognized in the conodonts from the Holy Cross Mts. They show less numerous and much more elongate denticles than the Polish specimens do. As judged from the sample illustrated by Kozur (1971: pl. 4), they show only 5 denticles in average. The other elements of *Gondolella* apparatus do not show any significant difference in size from those from the Holy Cross Mts. A minor evolutionary advancement is only displayed by the *pl* and *oz* elements. One may thus conclude that the population of *Gondolella* inhabiting the Central-European basin was evolving simultaneously and regardless of local facies changes. Various portions of the considered evolutionary continuum have been reported (fig. 6) from Swabia and Hesse (Tadge 1956), Thuringia (Kozur 1968, 1971), Upper Silesia (Zawidzka 1975), and the Holy Cross Mts (Trammer 1972, 1975).

The considered evolutionary continuum can be most plausibly interpreted as a gradual shortening of the organogeny (Trammer 1974). Further evaluation of this hypothesis is hampered by the lack of any unequivocal morphological indices of conodont maturity. The absence of ontogenetic-age criteria makes impossible deciphering of the actual relationship of the recorded evolutionary changes to selection factors. One is indeed unable to say whether the changes in mortality pattern reflect an evolution induced by some other factors, or whether these changes themselves induced a selection for earlier termination of the ontogeny. The latter hypothesis requires as a necessary prerequisite that the mortality peak occurs at an immature developmental stage. Selection pressure is effective in evolution only when it acts upon developmental stages earlier than those following the termination of sexual activity. When a juvenile fitness is higher than the adult one, which is to be reflected in mortality rate increasing with age, shortening of the ontogeny is preferable. When such a selection presure evolves towards an increase in fitness of the earlier and earlier ontogenetic stages, an effect like that observed in the investigated Middle Triassic section can be to occur. One cannot however reject a hypothesis that the mortality peak occurred at the gerontic stage of the sampled populations of *Gondolella*; then the actual cause for the observed evolutionary decrease in conodont size remains unrecognizable. The occurrence of conodonts with considerably developed platform provided with a few denticles in the upper part of the section may support the hypothesis that there was indeed a selection for shortening of the ontogeny because the platform thickness may be indicative of ontogenetic age. However, platform thickness is so variable and so hardly treated with biometrical methods that it cannot be regarded as an index more reliable than, e.g., denticle number.

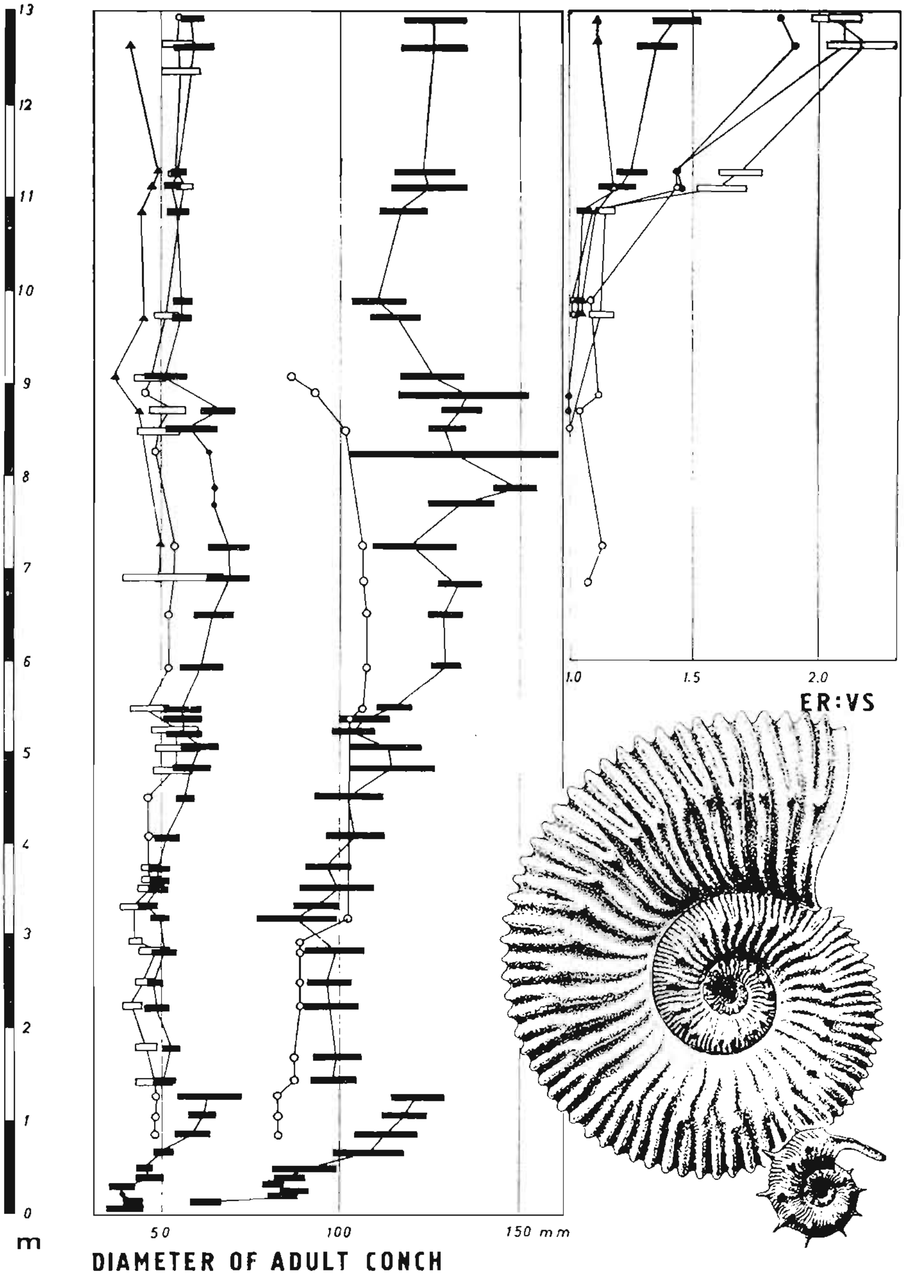
THEORETICAL IMPLICATIONS

The above presented gradual evolutionary changes in the Triassic conodonts have some bearing on the dispute on gradual *versus* punctuated mode of organic evolution. The concept of punctuated equilibria, postulating that "most evolutionary change is concentrated in rapid events of speciation in small, peripherally isolated populations", was recently presented by Eldredge and Gould (1972; Gould and Eldredge 1977). In its original, radical version (Eldredge and Gould 1972), the concept of punctuated equilibria referred to the totality of evolutionary processes and hence, it was falsifiable. Actually, it had been falsified long before it was proposed by data documenting a gradual evolutionary transition in various organic groups. When discussing the evidence for a gradual nature of evolutionary changes presented by modern authors in response to that paper, Gould and Eldredge (1977) weakened their concept and claimed only that the punctuationism is the dominant mode of biotic evolution. When it is conceived in the latter sense, the concept of punctuated equilibria is non-falsifiable and hence, the whole discussion may become long and tedious but unfruitful. The immense complexity of the biosphere makes impossible taking any random sample which would be the only way allowing to test whether or not discontinuous evolutionary phenomena occur indeed more commonly than the continuous ones. The way that Gould and Eldredge (1977) discuss the evidence for evolutionary gradualism does also appear methodologically questionable. The method that Gould and Eldredge (1977 : 127 and 131) apply to demostrate discontinuity of evolutionary changes consists in ommission of samples representative of an acceleration of the evolution and in statistical testing of the remaining samples. This method may actually allow to prove any hypothesis one wishes to prove. The paleontological raw material can be arbitrarily manipulated because of the inconsistent use of the notion of temporal species. Organic evolution does not need display a linear relations to the geological time (or sampled sediments) (see Boucot 1978) and hence, an evolutionary continuum can always be split into intervals sufficiently small to show no statistically significant changes in morphology.

We are free from illusion that our data can eventually solve the problem in gradual *versus* punctuated mode of organic evolution, at least in its version presented by Gould and Eldredge (1977). Because of methodological reasons, one is obviously unable to demonstrate that all or even most species have been undergoing a gradual evolution. We also do not intend to discuss here all questions connected with theories of punctuated or gradualistic nature of evolution. (comp. Boucot 1978). No doubt however that the actual number of well known and documented gradualistic cases has been underestimated by Gould and Eldredge. The data are indeed hardly available because they are scattered over the paleontological literature and obscured by taxonomical oversplitting. It is to be noted that the concept of punctuated equilibria, claiming that species originate stochastically and are the subject of selection, (Stanley 1979) is rooted just in a taxonomical oversplitting and typological notion of species. This reminds more than enough the idea of a species-group as the basic unit of phylogenetic trees (cf. Enay 1966; Kutek and Zeiss 1974). In fact, the latter concept is concerned with morphotypes instead of biological species, while a group of species conceived at a single time place corresponds more of less exactly to a biological species. A nice example of gradual evolution well documented, but described in terms of species-groups, is offered by the evolution of the ammonite genus *Zarajskietes* in the uppermost Jurassic of Poland (Kutek and Zeiss 1974). The ammonites collected bed-by-bed show a large intrapopulations variability in each bed. The ranges of variability overlap but nonetheless, a trend towards increased complexity of shell ornamentation appears very clearly; it is followed by a change in distribution of particular ornamentation types throughout the ontogeny. The authors are aware of monospecificity of every single sample (Kutek and Zeiss 1974: 536) but nevertheless, they follow the tradition of typological taxonomy and split their fossil populations each one into several species and co-occurring (!) subspecies. Consequently, the samples are entirely incompatible in their taxonomic composition and discovery of the true nature of evolutionary change requires much patience in analysis of the text and the material. One can recall lots of similar examples to show that the nature of evolution is commonly obscured by taxonomical oversplitting. This is especially the case with ammonite evolution because the ammonites display an enormous intrapopulation variability (see Kennedy and Cobban 1976). Without undertaking the task of revision of the original paleontological material, one can hardly transform a typological phylogenetic tree into the respective biological one. However, multispecific branches shown by Wenger (1957), Kemper (1961), Ziegler (1962), Rieber (1963), Gygi (1977), Cope (1978), and others are most probably examples of monospecific evolutionary continua.

The actual course of the evolution is also considerably obscured by a common graphical manner permitting an overlap of stratigraphic ranges of various temporal taxa within a single phylogenetic tree. This is often aimed to increase intelligibility of a graph. When one is concerned with data derived from a single section, this implies however sympatric origination of the species and co-occurrence (over a recognizable time interval) of the declining ascendant with its descendant species (see e.g. Klapper and Johnson 1975). To prove such a co-occurrence, one needs obviously a biometrical study of the samples. Actually, it is merely the artifact of an arbitrary assignment of some individuals found in a sample intermediate in age to either the ascendant, or the descendant species. This graphical manner is therefore indicative of typological approach to species and makes questionable validity of the claimed phylogenetic relationships.

To extract the evidence for gradual evolution from the body of typological paleontology is an uphill work. It permits however finding of unexpectedly large material. In addition to the papers mentioned by Gould and Eldredge (1977), one may also refer to some older works documenting gradualistic cases (e.g. Brinkmann 1929; fig. 8 in this paper) and several studies on conodont evolution. Examples of conodont evolution recorded in a single section but confirmed by data from the whole bioprovinces are given by Bergström (1971), McTavish (1973), and Dzik (1976, 1978). Those data have not been studied biometrically but the cited authors took into account intrapopulation variability and applied the biological concept of species. In this context, the condensed sequence exposed at Mójcza, Holy Cross Mts, is remarkable because it can be easily correlated with Baltoscandian sections and shows (within 8 m thick limestone set) generally gradual evolutionary transitions between the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conodont faunas of Lanvirnian, Llandeillian, and Caradocian age. Aside of sympatric gradual evolution in monospecific lineages, one can also recognize allopatric speciation and migration of new lineages in the Baltoscandian Ordovician basin (Dzik 1976, 1978). There is no reason to claim that allopatric speciations were enormously rapid.

The role of taxonomic oversplitting in obscuring phylogenetic relationships among fossil organisms can be exemplified by a recent monograph of the Silurian tentaculites of the Baltic region (Larsson 1979). Four families, nine genera, and 44 typological species (41 of them new to the science) recognized by Larsson can be interpreted as representatives of two monospecific lineages (one of them very short-lasting) each one with very large intraspecific variability. It is noteworthy that the 180-page monograph lacks any comment on the method of setting the limits of tentaculite species range in time as well as in a single fossil assemblage.

Geological sections constant in facies but as long-lasting (in time terms) as those available in the Baltoscandia and Holy Cross Mts are among the rarities, which hampers looking for evidence for evolution at a supraspecific level (let alone the equivocality of the latter term; see below). Nevertheless, one can find out much more examples of this sort than it is commonly assumed. The nice evolutionary continuum recorded in the Neogene freshwater gastropods from Kos Island (Willmann 1978; Boger *et al.* 1979) is still awaiting for a biometrical investigation.

The above presented evolution of the conodont genus *Gondolella* in the Early Ladinian in Central Europe represents merely a small interval of the evolution of the genus. There is however no reason to claim that this interval shows anything unique when compared to other evolutionary episodes in the history of this particular genus or other conodont genera. It can therefore be considered as an exemplification of taxonomic and biostratigraphic problems arising with increasing precision of paleontological research.

←

Fig. 8. Evolution in the ammonites *Kosmoceras* in the Callovian of Peterborough, England (after Brinkmann 1929). The changes in diameter of adult conches can be eventually explained as non controlled genetically ones but influenced by changing environmental factors. Changes in distribution of external ribs (*ER*) in relation to the ventral spines (*VS*) indicate, however, that these lines evolved directionally, though with some fluctuations. Above the described bimetrically by Brinkmann part of the Peterborough section this direction of evolution is continued — dimorphic pair of conches of *Kosmoceras spinosum* is drawn as an example of advanced species of the genus. Almost complete evolutionary history of *Kosmoceras* can be also observed in Popielany section in Lithuania (Brinkmann 1929) on the other side of Callovian epicontinental sea of northern Europe. Black — *K. jason* (Reinecke) line, white — *K. aculeatum* (Eichwald) line, triangles — *K. ornatum* (Schlotheim) line (each line represented by micro- and macroconches). *K. ornatum* redrawn from Makowski (1963).

TAXONOMIC IMPLICATIONS

Whether the range of evolutionary change in the genus *Gondolella* as recorded in the investigated 23 m long section of the Middle Triassic of the Holy Cross Mts (fig. 4), is large enough to recognize it for a difference between two species, depends upon a convention. This is however not to say that in paleontology, every taxonomic decision is arbitrary by its very nature. Recognition of species in a paleontological sample or in a set of samples isochronous in evolutionary time (let alone the problem in recognition of such an isochroneity) is almost as objective as it is in the case of extant organisms.

The observed frequency distributions of the biometrically studied conodont characteristics do not allow to recognize more than a single biological species in any of the investigated samples. Those morphological characteristics of the conodonts that cannot be measured (e.g. platforms outline, denticle distribution and mode of fusion) do also show gradual transitions in a sample. Hence, the taxonomic names applied thus far to these conodonts refer actually to morphotypes instead of species. This is also the cause for the apparent overlap in their stratigraphic ranges (Trammer 1972, 1975). One may conclude that a single monospecific evolutionary continuum occurs in the investigated section.

Acceptance of the biological concept of species does not facilitates recognition of the stratigraphic range of a species; the problem seems to be even more difficult to be objectively solved. The stratigraphic range can be determined only arbitrarily. A considerable intrapopulation variability in each sample introduces additional problems. One would like to have temporal species and subspecies distinguishable even without detailed biometrical studies. Therefore, it would be unsound to erect temporal taxa with overlapping standard-deviation ranges of diagnostic morphological features. In the investigated Middle Triassic section, the only doubtlessly distinguishable conodont populations are those yielded by the two extreme samples. It is therefore unreasonable to recognize more than two temporal subspecies in the sampled interval (fig. 2). The frequency distribution of platform length and elongation recorded in the extreme samples are identical to those found in the topotype samples of *G. mombergensis* and *G. haslachensis* (see Tadge 1956). Hence, we propose to apply the name *Gondolella mombergensis-mombergensis* Tadge, 1956, for the populations found in the lowermost samples from the investigated section of the Holy Cross Mts, and *Gondolella mombergensis-haslachensis* Tadge, 1956, for those found in the uppermost sample (see p. 78). The third temporal subspecies, *Gondolella mombergensis-watznaueri* Kozur, 1968, occurs in its typical form in strata above the investigated section. Before saying that it is indeed reasonable to recognize *G. m.-watznaueri* for a distinct subspecies, one should however look at the biometry of its topotype population.

Boundaries separating the temporal subspecies cannot be precisely traced, at least after the morphology of the platform element. A more precise and biometrically supported determination of the time-stratigraphic position of those boundaries requires some comments exceeding the Linnean terminological framework. We hope that the uncertainty inherent in recognition of the three subspecies may be diminished with application of the knowledge of heterochroneity in evolution of particular elements of the conodont apparatus *Gondolella*. The phenomenon of evolutionary heterochroneity was already used in taxonomy of Ordovician conodonts (Dzik 1976, 1978). Assumed that the supposed shortening of the anterior branch of the *pl* element ("*Enantiognathus*") is not an artifact, it may permit setting a more precise boundary between the subspecies *G. m.-mombergensis* and *G. m.-haslachensis*, namely between the samples L-8 and L-9. The former subspecies would then be defined by its considerably elongate *sp* element with low and fused denticles located in the middle of the platform, and its *pl* element with a long anterior branch; in turn, short platform element with high denticles, and *pl* element with a short anterior branch would be diagnostic of *G. m.-haslachensis*. To trace a boundary between *G. m.-haslachensis* and *G. m.-watznaueri* seems to be much more difficult. Possibly, a recognition of intrapopulation variability in *pl* element and of its change in evolutionary time may increase the taxonomic precision in the latter case, too. The problem in tracing the lower boundary of the temporal subspecies *G. m.-mombergensis* remains still to be solved. Actually, it exceeds considerably the range of the investigated section. One may only note that the conodont population recorded in the Smithian of Spitsbergen (represented by the typological species *Neogondolella jubata* Sweet, *N. planata* (Clark), and *N. nevadensis* (Clark); Weitschat and Lehmann 1979) preceding in time the Anisian *G. mombergensis* can hardly be distinguished from the latter without use of biometrical methods.

When paleontologists accepted the rules of neontological taxonomy, they expressed implicitly their hope that evolutionary transitions from a taxon to another one are discontinuous in nature. The apparent collision of taxonomical rules and paleontological data is rather rarely perceived. It is so mostly because of the "fortunate" incompleteness of the fossil record. To overcome this problem, paleontologists accepted also the principle of arbitrariness in setting the limits to a species and by this way, renounced *de facto* all the achievements of biological taxonomy aimed to make objective the concept of species. Finally, the natural variation in evolution rate permits sometimes tracing the boundary between temporal species at either an acceleration of evolutionary process, or a decrease in sedimentation rate an consequent stratigraphic condensation. However, one can only exceptionally achieve certainty that a newly erected paleontological species is separated from its ascendant and descendant species by a distinct acceleration in the rate of evolution. To assume that evolutionary transition from one species to another one is discontinuous, as it is claimed by Gould and Eldredge (1977), seems to be promising to traditional paleontological taxonomy but at the same time methodologically dangerous. Were this assumption valid, every discontinuity in the fossil record would be indicative of a discontinuous transition from one species into another one, as it was pointed out by Gingerich (1978); and every discontinuity in morphology between heterochronous populations would be indicative of their specific distinctness. We propose to follow Simpson (1961) in considering a paleontological species as a unit persistent in time (which contrasts to biological species), delimited objectively at every moment in geological time (in this context it is identical to biological species), with time limits set only arbitrarily. To set the time limits of a species at an acceleration in the rate of evolution is a postulate, not an attribute of temporal species as such. In fact, this concept of species has been for long applied by various paleontologists (e.g. Bergström 1971, 1978).

A detrimental inconsistency in paleontological terminology has arisen from the common use of the term subspecies meant as both a geographic race and a subspecific unit of biological evolution. In practice, the term subspecies has become equivalent to the term variety ruled out of the modern taxonomy. Several new subspecies are commonly erected after a single sample, which shows clearly the misuse of the term. The difference in meaning between the terms temporal subspecies and subspecies as a geographic race (see Mayr 1969) consists in that a temporal subspecies appears in time section as a biological species, whereas a biological subspecies (geographic race) extended in time can be transformed into a series of arbitrarily recognized temporal subspecies. A temporal subspecies may thus include several biological subspecies (geographic races). For the sake of clarity we propose a slight modification on nomenclature of temporal subspecies; namely we propose to insert a dash between specific and subspecific names. Within this terminological framework, temporal subspecies may make a basis for recognition of isochronous biological subspecies (geographic races). For example, the name *Gondolella mombergensis-haslachensis santacrŭcensis* would designate a geographic race, that is a group of population living in the Holy Cross Mts coevally with the Swabian populations assigned to the subspecies *Gondolella mombergensis-haslachensis haslachensis*. Geographic races can be recognized in the fossil record only exceptionally.

BIOSTRATIGRAPHIC IMPLICATIONS

Precision and reliability of biostratigraphic zonation depend directly upon precision and reliability of the recognition of temporal taxa. Methodological limitations inherent in taxonomy set also the limits to a biostratigraphic inference.

Most biostratigraphers are of the opinion that an application of either biological, or typological concept of species does not affect to any significant extent the validity of biostratigraphic zonation. The above presented evolution in some conodonts important for biostratigraphy demonstrates clearly the erroneousness of this common wisdom. Close to the limits of its stratigraphic range, a morphotype species is represented by end-members of intrapopulation variability of the biological species. The larger is sample size, the greater is the probability of finding such an end-member morphotype. Paradoxically then, the range of a biozone defined after a morphotype species depends upon the size of the uppermost and lowermost samples. The larger are the samples, the longer-ranging is the biozone.

From the gradualistic point of view, there is no doubt that, so far as the samples are not treated quantitatively, the confidence intervals of zonal boundaries cannot be smaller than a distance in section sufficient to permit non-overlap of the standard-deviation ranges of diagnostic morphological features. In the investigated Middle Triassic section in the Holy Cross Mts, only the lowermost and uppermost samples yield easily distinguishable conodont populations. Tracing a precise boundary between the two samples, which would also be a precise zonal boundary, is impossible even in spite of biometrical study because there are oscillations in evolutionary trend direction. The supposed acceleration in evolution of the *pl* element in the middle of the section may appear promising but nevertheless, it is for the moment unsound to recognize three distinct zones, as claimed by Kozur (1968), in the investigated time interval.

That the concept of punctuated equilibrium has attracted as much attention as it did is in part the effect of a dream, in common for biostratigraphers, of unequivocal and precise biostratigraphic indices. Rapid appearances of new species (i.e. speciation in zoological sense) have been expected to provide such ideal indices. The increasing evidence of evolution at the populations level demonstrates more and more clearly that this is merely a wishful thinking. Sharp zonal boundaries can only be delimited by gaps in the fossil record (e.g. sedimentary discontinuities) or faunal migrations. Correlation value of such boundaries seems to be doubtful because one can hardly assume their isochroneity over a large area. To the contrary, it is much more probable that changes in distribution of both facies and the associated organisms happen heterochronously in a basin (cf. Cisne and Rabe 1978; Johnson 1979). It is therefore more reasonable to base upon the natural variation in the rate of evolution, and to trace zonal boundaries at the acceleration of evolution. In order to recognize a zonal boundary for approximately discrete in nature, one has to prove that there happened indeed an acceleration in evolution of the diagnostic organisms. This condition is only rarely met in the fossil record. One should therefore expect that a zonal boundary is equally extended in time as are the zones themselves. The above presented conodont evolution may serve as an exemplification.

FUNCTIONAL INTERPRETATION

Any undisputable remains of conodontophorid soft body have not thus far been recognized but nevertheless, the understanding of the biological nature of the conodonts increases constantly even though slowly. A relationship of conodonts to feeding process is widely assumed. Conodont apparatuses are most commonly claimed to have been just a filter apparatus (Lindström 1973; Conway Morris 1976; Hitchings and Ramsay 1978), which hypothesis is refuted by some authors (Bengtson 1976; Dzik 1976; Carls 1977; Jeppson 1979). In fact, the above hypothesis is incompatible with morphology of the platform elements lacking any adaptations to perform a filter function but nonetheles, evolving at the highest rate in conodont apparatuses (Dzik 1976). One can also hardly point to any reasonable interpretation of the hard denticles as a lophophore skeleton. It is more plausible to suppose that the platform elements performed a chewing or crushing function, while the function differed among various elements having ranged up to a straining one in especially fragile elements (Dzik 1976). The latter interpretation is indeed consistent with the model of conodont-apparatus formation presented by Dzik (1976) after the deformation of element arrangement in "natural assemblages" caused by fossilization processes. The model claims that the conodont elements were originally arranged parallel one to its equivalent one, working under the condition of occlusion.

Carls (1977) put forth a hypothesis of periodical replacement of platform elements, intended to account for disproportionately large amounts of platform elements in most conodont samples. The hypothesis was refuted by Jeppson (1977). In fact, a prediction follows from the hypothesis that some "natural assemblages" should include platform elements much smaller in size than the associated conodont elements. Such a prediction would be reasonable so more that an increase in mortality rate should coincide in time with teeth replacement. The lack of such findings falsifies the Carls (1977) hypothesis. Different contributions of various element types to a sample can be most easily explained by reference to their different hydrodynamic properties and resistances to the breakage. The correlation between these features of conodont elements and their frequency in samples is indeed striking. Predominance of platform elements over the associated branched ones is actually a good index of the environmental energy.

When the conodonts are interpreted as teeth, a considerable trouble arises in seeking an explanation for regeneration of broken conodont denticles. The explanation consists in the mode of secretion of the conodont tissue. The tissue was secreted by epithelium inwards, just as it is in the case of the enamel of vertebrate teeth with which it was supposedly homologous (see Dzik 1976). In turn, the tissue of the basal filling, supposedly homologous with the vertebrate dentine, was secreted from the inside. Mechanical function of the phosphatic conodont tissue induces removements of the epithelium, which makes in turn impossible any regeneration. Thus far, the only coherent solution to this seemingly antinomian problem has been presented by Bengtson (1976) with reference to a difference in growth between the conodonts and the Cambrian "paraconodonts". Accordingly to Bengtson (1976), the conodonts were growing within epithelial pockets, getting out of them only when functioning. The "paraconodonts" are built up by an organic-phosphatic tissue (phosphate may be a secondary matter) growing inwards to the basal cavity. The mode of growth contrasting to that shown by the conodonts, and the structure of "paraconodont" apparatuses (Müller 1976; Landing 1977) are suggestive of a relationship to the Chaetognatha (Szaniawski in preparation). Carls (1977) further evaluated the model presented by Bengtson (1976) and referred it also to the branched conodonts. The reasonability of this model is supported by denticle morphology of both the branched and platform conodonts The denticles show medial ribs in places of supposed fusion of the epithelium folds (Carls 1977; fig. 2). It is however to be noted that similar ribs occur in shark teeth which decreases significance of the latter argument.

Accordingly to the above compiled functional interpretation of conodont apparatuses, the evolution of *Gondolella* apparatus in the Polish Triassic is to be regarded as reflecting a change in conodontophorid diet. The observed decrease in platform robustness and increase in denticle elongation at the mature developmental stages are suggestive of a transition to feeding upon less mechanically resistant organisms, digestable without use of crushing, resembling those eaten by the juveniles of the ascendant forms. It is noteworthy that the evolution in *Gondolella* resulted at the investigated moment of geological time in a considerable convergence to the genus *Neospathodus* (fig. 9). Gracile apparatuses of *Neospathodus* co-occur with massive apparatuses of *Gondolella* in strata below the investigated section. Unfortunately, a gap in the fossil record makes impossible recognition of the extinction pattern of *Neospathodus.* Did the extinction of *Neospathodus* result in a change in evolutionary trend shown by *Gondolella*? One may suppose that *Neospathodus* and *Gondolella* occupied two adjacent ecological niches. The extinction of *Neospathodus* could then induce an increase in intrapopulation variability in *Gondolella* towards the morphotype typical of *Neospathodus* (such

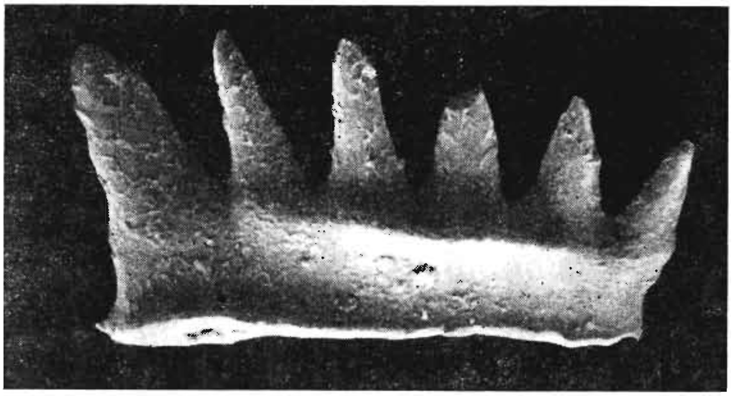

Fig. 9. Outline of the platform element of *Gondolella mombergensis-haslachensis* Tadge from the uppermost part of the Ladinian of the Holy Cross Mts (sample P-24). Note a resemblance to the platform element of *Neospathodus*, ×300.

morphotypes of *Gondolella* must had competed with *Neospathodus* before) and thereafter, a shift of the peak of variability towards the center of the two niches. It seems improbable that *Neospathodus* was actually outcompeted by *Gondolella*. There are no data to argue for a competition between the two lineages (i.e. biological species). One may claim that either some other organic groups outcompeted *Neospathodus*, or some environmental changes excluded it from the habitat. It is however impossible for the moment to recognize the true nature of the extinction cause.

CONCLUSIONS

We have presented example of continuous gradual evolutionary changes of conodontophorid population occupying the Mid-European epicontinental sea during the Upper Anisian and the Lower Ladinian. Similar continuum of evolving conodontophorid populations has been previously described in Ordovician epicontinental sea of Baltic region (Dzik 1976, 1978). Jurassic kosmoceratid (Brinkmann 1929) and virgatitid (Kutek and Zeiss 1974) ammonites evolved in the same way. Analysis of literature data leads to conclusion that at least majority of ammonites and conodontophorids, the groups of animals with the best paleontological evidence of their evolution, evolved phyletically in the large populations. This mode of evolution is therefore much more common than it has been postulated by Gould and Eldredge (1977). There is no reason to believe that parts of populations isolated geographically or ecologically were evolving in any different manner. Therefore allopatric speciation does not need to be caused by faster evolutionary processes than phyletic evolution.

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JERZY DZIK i JERZY TRAMMER

CIĄGŁA EWOLUCJA KONODONTÓW W TRIASIE POLSKI

Streszczenie

W 23 metrach miąższości wapieni pogranicza anizyku i ladynu na SW obrzeżeniu Gór Świętokrzyskich, występuje nieprzerwany monospecyficzny ciąg populacji konodontów rodzaju *Gondolella*. Zmiany rozkładu cech morfologicznych elementu platformowego mają ciągły charakter i polegają na zwiększaniu udziału w populacji kopalnej stadiów morfologicznie młodocianych (fig. 2, 4, 5). Przedyskutowano i wykluczono czysto ekologiczną interpretację tych zmian jako ciągłych zmian dynamiki populacji. Mają one ewolucyjny charakter.

Przedstawiony tutaj ciąg ewolucyjny rodzaju *Gondolella* w dolnym ladynie środkowej Europy stanowi niewielki wycinek, niezbyt zresztą burzliwej ewolucji tego rodzaju (fig. 1). Nie ma jednak powodów sądzić, że odcinek ten wyróżnia się jakimiś szczególnymi cechami od pozostałych epizodów w ewolucji tego i innych rodzajów konodontów. Można go więc potraktować jako przykład modelowy, ilustrujący problemy taksonomiczne i biostratygraficzne pojawiające się przy zwiększaniu precyzji badań paleontologicznych.

To, czy zakres zmian ewolucyjnych rodzaju *Gondolella* w obrębie naszego 23-metrowego profilu (fig. 4), uznamy za przekraczający różnice gatunkowe pomiędzy gatunkami temporalnymi, czy nie, jest sprawą umowy. Nie oznacza to jednak, że wszelkie wydzielenia taksonomiczne w paleontologii mają arbitralny charakter. Wydzielenia gatunków w obrębie jednej próby, czy synchronicznych z ewolucyjnego punktu widzenia prób (pomijamy tu problem możliwości przeprowadzenia takiej synchronizacji), mają charakter obiektywny niemal w tym samym stopniu co wydzielane dzisiaj gatunki współcześnie żyjących organizmów.

Przyjęcie biologicznego ujęcia gatunku nie zmniejsza trudności z wyznaczeniem pionowego zasięgu, a nawet pozornie je zwiększa. Jest ono ciągle arbitralne. Znaczna wewnątrzpopulacyjna zmienność w obrębie każdej z prób wprowadza dodatkowe utrudnienia. Chciałoby się, żeby wydzielane w czasie temporalne gatunki i podgatunki były od siebie odróżnialne bez konieczności badań biometrycznych. Niecelowe byłoby więc wydzielanie temporalnych taksonów różniących się tak niewiele, że standartowe odchylenia diagnostycznych cech zachodziłyby na siebie. W badanym profilu jednoznacznie odróżnialne są tylko próby skrajne. Nie wydaje się zatem uzasadnione wydzielanie na tym odcinku czasowym więcej niż dwu temporalnych podgatunków (fig. 2).

Już w samym przejęciu przez paleontologię zasad taksonomii neontologicznej zawiera się *implicite* nadzieja, że przejścia ewolucyjne między taksonami mają nieciągły charakter. Stosunkowo rzadkie dostrzeganie przez autorów konfliktu między zasadami taksonomii a charakterem dokumentacji paleontologicznej ma swoją główną przyczynę w niekompletności dokumentacji paleontologicznej. Ominięciem tych trudności jest też przyjęcie zasady arbitralności wydzieleń na poziomie gatunkowym, czyli faktyczna rezygnacja z korzystania z osiągnięć taksonomii biologicznej w obiektywizacji pojęcia gatunku. Wreszcie, naturalna nieregularność przebiegu przemian ewolucyjnych pozwala niekiedy na postawienie granicy między gatunkami w odcinkach przyspieszenia ewolucji albo kondensacji stratygraficznej (zwolnienia sedymentacji). Wydzielając nowy gatunek paleontologiczny wyjątkowo rzadko mamy jednak pewność, że jest on od sąsiednich czasowo gatunków oddzielony wyraźnym przyspieszeniem tempa ewolucji. Przyjmowanie *a priori* nieciągłości przemian ewolucyjnych pomiędzy gatunkami temporalnymi, jak chcą Gould i Eldredge (1977), aczkolwiek atrakcyjne dla tradycyjnej taksonomii, wydaje się metodologicznie niebezpieczne. Każda nieciągłość w dokumentacji będzie wówczas traktowana jako dowód nieciągłego przejścia pomiędzy gatunkami, jak to wskazał Gingerich (1978), a każda nieciągła różnica pomiędzy różnowiekowymi populacjami jako dowód odrębności gatunkowej. Postulujemy zgodnie z Simpsonem (1961) traktowanie gatunku paleontologicznego jako jednostki rozciągłej czasowo (w przeciwieństwie do gatunku biologicznego), która oprócz obiektywnych granic w każdym przedziale czasowym (równoznaczność z gatunkiem biologicznym) ma subiektywnie wyznaczone granice czasowe. Postawienie tych granic na przyspieszeniu tempa ewolucji jest postulatem a nie atrybutem wynikającym z samej natury gatunku temporalnego. Takie ujęcie gatunku jest w praktyce stosowane od dawna przez wielu autorów (np. Bergström 1971, 1978 etc.).

Do niebezpiecznego bałaganu terminologicznego doprowadziło w paleontologii stosowanie pojęcia podgatunku zamiennie w stosunku do rasy geograficznej i jako mniejszej od gatunku jednostki przemian ewolucyjnych. W praktyce termin ten przejął funkcje wyrugowanej z taksonomii odmiany. Skutkiem kompletnego pomieszania pojęć jest częste opisywanie nowych podgatunków w obrębie pojedynczych prób. Różnica w znaczeniu pojęcia podgatunku jako rasy geograficznej i podgatunku temporalnego (patrz Mayr 1969) zawiera się w tym, że przekrojem czasowym podgatunku temporalnego jest gatunek biologiczny, zaś wydłużony w czasie podgatunek biologiczny przekształcony być może w serię arbitralnie wydzielanych podgatunków temporalnych. Podgatunek temporalny może się składać zatem z licznych ras geograficznych (podgatunków biologicznych). Dla uniknięcia nieporozumień proponujemy drobną modyfikację sposobu zapisu nazw podgatunków temporalnych. Proponujemy mianowicie połączenie nazw szczebla gatunkowego i podgatunkowego podgatunku temporalnego myślnikiem. Przy takim ujęciu terminologicznym podgatunki temporalne mogą stanowić podstawę do tworzenia równoczasowych podgatunków geograficznych, np. nazwa *Gondolella mombergensis-haslachensis santacrucensis* oznaczałaby geograficzną rasę czyli grupę populacji żyjących na obszarze Gór Świętokrzyskich w tym samym czasie, co populacje podgatunku *Gondolella mombergensis-haslachensis* ze Szwabii. Użycie podgatunku rozumianego jako rasa geograficzna jest w paleontologii możliwe tylko w wyjątkowych przypadkach.

Precyzja i wiarygodność wyznaczeń biostratygraficznych bezpośrednio zależą od precyzji i wiarygodności wydzielania temporalnych jednostek taksonomicznych, na których wyznaczenie jest oparte. Metodologiczne ograniczenia taksonomii są równocześnie ograniczeniami biostratygrafii.

Wśród biostratygrafów rozpowszechnione jest przekonanie, że biologiczny czy formalny sposób ujęcia gatunku nie ma większego wpływu na wartość wydzieleń biostratygraficznych. Zapoznanie się z przedstawionym tutaj przebiegiem ewolucji ważnych biostratygraficznie konodontów wykazuje błędność takiego mniemania. Każdy morfotypowy gatunek na krańcach czasowego rozprzestrzenienia jest reprezentowany przez skraje zmienności wewnątrzpopulacyjnej gatunku biologicznego. Im większa próba, tym większe prawdopodobieństwo znalezienia takiego skrajnego morfotypu. Prowadzi to do paradoksalnego wniosku, że zakres opartej na morfotypowym gatunku biozony zależy od liczebności skrajnych prób. Im większe próby, tym dłuższa biozona.

Z punktu widzenia „gradualizmu ewolucyjnego" jest oczywiste, że precyzja określenia granic zon nie może być (bez ilościowych analiz prób) większa od odcinka ewolucji, w trakcie którego zmienności diagnostycznych cech skrajnych populacji oddalą się przynajmniej w tym stopniu, że ich standartowe odchylenia nie będą na siebie zachodziły. W badanym przez nas profilu tylko skrajne próby zawierają populacje, które można bez trudu od siebie odróżnić. Postawienie precyzyjnej granicy pomiędzy nimi, która mogłaby wyznaczyć precyzyjne granice poziomów, jest niemożliwe, nawet przy pomocy badań biometrycznych, ze względu na oscylację kierunku przemian ewolucyjnych. Na obecnym etapie badań wyodrębnienie na badanym odcinku trzech poziomów, postulowane przez Kozura (1968) jest nierealistycznie dokładne.

Żywe przyjęcie koncepcji *punctuated equilibrium* jest w pewnym stopniu wyrazem marzeń biostratygrafów o znalezieniu jednoznacznych i precyzyjnych wyznaczników poziomów biostratygraficznych. Granice takie miałyby wyznaczać gwałtowne pojawianie się gatunków (momenty specjacji w rozumieniu zoologicznym). Powiększająca się dokumentacja wydarzeń ewolucyjnych na poziomie populacyjnym coraz wyraźniej wykazuje, że jest to tylko pobożne życzenie. Ostre granice poziomów wyznaczać mogą jedynie luki w dokumentacji paleontologicznej (np. powierzchnie nieciągłości sedymentacyjnej), lub migracje fauny. Wartość korelacyjna takich granic jest jednak problematyczna, nie można bowiem *a priori* zakładać ich równoczesności na dużych obszarach. Wręcz przeciwnie, bardziej prawdopodobne jest, że tak zmiany układu rodzajów osadu jak i rozprzestrzenienie związanych z nim organizmów są niesynchroniczne w różnych częściach zbiornika (por. Cisne and Rabe 1978, Johnson 1979). Słusznie jest do wyznaczania granic poziomów wykorzystać naturalną nierównomierność tempa ewolucji i stawiać je w okresach przyspieszenia przemian ewolucyjnych. Stwierdzenie, że granica między zonami ma nieciągły charakter wymaga jednak wpierw udowodnienia, że wystąpiło przyspieszenie ewolucji diagnostycznych form. Warunek ten spełniony jest jednak rzadko. Wówczas liczyć się należy z tym, że granica między poziomami jest równie rozciągła w czasie co same poziomy. Ewolucja konodontów przedstawiona tutaj jest tego przykładem.