JERZY DZIK

FEATURES OF THE FOSSIL RECORD OF EVOLUTION

DZIK, J.: Features of the fossil record of evolution. Acta Palaeont. Polonica, 36, 2, 91—113, 1991.

Neither allopatric speciations nor extinctions of lineages are directly observable in the fossil record. This significantly reduces the value of inferred durations of taxa as a basis for studies on patterns of evolution. The ranges of taxa detected in rock strata are inevitably shorter than the real durations of lineages. Rates of evolution estimated by counting reported ranges of taxa therefore appear higher than they really were. Biometric studies of gradually evolving lineages indicate that the durations of 'species' (morphologies) were actually many times longer. Therefore, the ancestor-descendant relationships along monospecific lineages remain the most important subjects of study in evolutionary paleontology. A way, in which an ancestor-descendant hypothesis can be falsified, is presented.

K e y   w o r d s: evolution, fossil record, methodology.

Jerzy Dzik, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 War-szawa, Poland.

INTRODUCTION

Paleontological data are used to reconstructions of both branching evolutionary trees (cladogenesis) and evolutionary transformations along lineages (phyletic evolution, 'anagenesis'). In the first approach the phenomenon of speciation, the ultimate cause of any branching of the tree, is involved. This introduces the factor of geographic space, as assumedly the most common, if not the only, way to split a lineage is by the means of allopatric speciation. To restore a complete picture of the phylogeny with its time-and-space dimensions paleontologists have cor-related particular evolutionary events identified in different sections. This, in turn, makes the inference on the phylogeny and the course of phyletic evolution quite different. The course of evolution is potentially observable in a single section, with application of the Steno's rule of superposition as the only guide to the time distribution of evolutionary events. The process of allopatric speciation cannot be recognized directly in any single section. It has to be inferred from data preserved in many

places and it is virtually impossible to precisely date due to methodological limitations of methods of rock correlation.

The purpose of the present paper is to discuss the limitations and advantages of these two ways of inference in evolutionary paleontology. It will be attempted to show that there is no contradiction between the Simpsonian approach to fossils and the Popperian methodology of science. A few examples of results of application of this approach to fossil organisms are inserted in the text.

GEOLOGICAL LIMITATIONS OF EVOLUTIONARY INFERENCE

It is tempting to extend the generalization that the fossil record is incomplete until it is assumed that no reliable data on microevolutionary processes can be provided by paleontology. Nevertheless, on a closer inspection the incompleteness of the fossil evidence of evolution appears not as great as it is usually assumed. Different criteria have to be used to characterize reliability of the fossil record. Much depends on whether a segment of an evolutionary lineage has to be reconstructed or a population sampled for paleoecological studies. The same section may provide an excellent record of population dynamics and structure in particular rock layers and very poor record of the evolution hidden somewhere between the layers. This can be deduced from the basically intermittent nature of sedimentation. Generally, with increase in stratigraphic condensation of sections a content of time in hiatuses increases.

It is now clear that different sedimentary environments are characterized by different regression curves for completeness of the record plotted against section thickness (McKinney 1985). Environments where erosion often dominated over sedimentation (like savannah analyzed by Behrensmeyer 1982) locally preserved rock sequences which abound in time gaps. They tend to be composed of rock beds deposited during very short time spans separated by hiatuses of extremely long duration. At the opposite end of the spectrum there are deep-water sedimentary environments with steadily low sedimentation rates and relatively rare and brief stages of non-deposition. This general pattern is further strengthened by abundance of coarse clastics in continental and fine sediments in open marine environments, giving in effect quite different conditions of fossilization. For instance, in effect of bioerosion macrofossils tend to be missing in slowly accumulating, fine-grained sediments.

These generalizations cannot be authomatically applied to any section representing a particular sedimentary environment. Some continental basins with stable sediment supply from surrounding highlands (like the Bighorn Basin of Wyoming) may contain unexpectedly complete record of evolutionary processes (see Gingerich 1979; Rose and Bown 1984).

Similarly, fine biostratigraphic studies on many 'condensed' marine limestone sections have shown unexpectedly complete representation of time in sections showing numerous sedimentary discontinuities (figs. 2, 5, 6). The general unpredictability of the scale of breaks in a section (Dott 1983; Sadler and Strauss 1990) implies that stratigraphic ranges of species are an unreliable measure of evolutionary processes. The 'art' of bio-stratigraphy has been based on vertical ranges of particular kinds ('species') of fossils determined in rock sections. In order to substantiate the methodological foundations of the biostratigraphic method it has been assumed that 'the ranges of species are individually determined by stochastic factors' (Shaw 1964: 47). This, of course, does not mean that ranges of species in rock sections vary around the value of their real time durations. The duration of a species may only be represented com-pletely in a rock section when an arbitrarily defined chronospecies is considered. Rare occasions when the complete range of a chronospecies is established show that only a small fraction of its complete duration is recorded in most sections (Dzik 1990b). This means that a simplistic direct transformation of biostratigraphic data into 'time ranges of taxa' results in preparation of a systematically biased matrix of data. The actual durations of 'species' are, as a rule, several times longer. It follows that estimates of the rate of evolution based on counting of such data yield artificially high values.

Despite of these obstacles it becames widely assumed that the majority of determined ranges of species correspond to the intervals between speciation events and extinctions. Attempts to find biological, instead of geological, justification for apparent discontinuous distribution of fossils (Gould and Eldredge 1977; Stanley 1979) in a sense reflect this common belief.

A MODEL OF FOSSIL RECORD OF EVOLUTIONARY PROCESSES

Let us consider an ideal picture of gradual evolution within the geographic range of a panmictic population, recorded in a few geologic sections showing the usual sedimentary discontinuities and geographic isolation events (fig. 1). Each discontinuity joins segments of the lineage originally separated by a long time interval. This is the classic Darwinian explanation of the punctuated distribution of morphologies in geological sections.

A lithological discontinuity does not necessarily need to correspond to geologically instanteous environmental change, representing significant intervals of erosion or nondeposition. The environmental changes occurring during the nondeposition period do not need to be abrupt; they are simply not recorded in rocks. On the other hand some very apparent
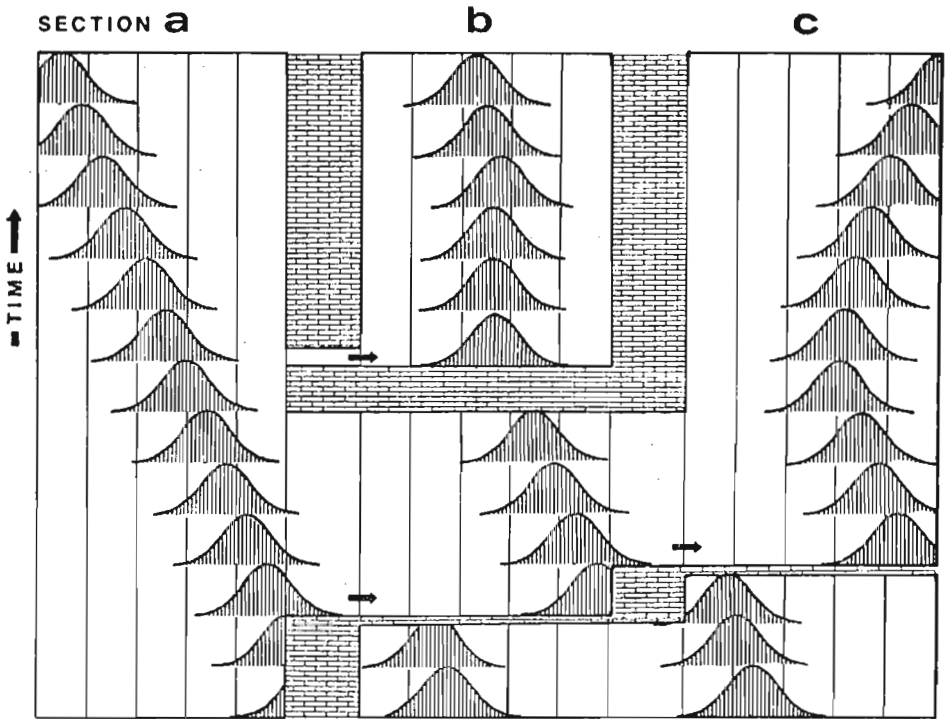
Fig. 1. An ideal pattern of distribution of paleontological data in sections which are complete (a) and punctuated by migration events and hiatuses in deposition (b, c). An effect of temporary isolation of particular areas (indicated by brick pattern) shown in the section c.

breaks in sedimentation (like 'hard grounds') appear to not be connected with any recognizable discontinuities in distribution of morphologic variability of fossils. They were evidently periods of local nondeposition having no long-term influence on the environment (fig. 2) and the record of evolutionary processes (fig. 5).

Temporal isolation of part of the originally uniform habitat of a species may result in a divergent evolution of the previously panmictic population (sections a and c). The only sign of an independent evolution would be a lack of synchrony in phases of the evolutionary development (if one is able to synchronize records from different sections) and/or divergent morphologic transformations. In order to recognize these features one needs a precise and independent dating of the sections. This means that these allopatric speciation events are not directly visible in the fossil record and their recognition has to be based on an unreliable chain of inferences (Hallam 1982; Ager 1983; Johnson and Lennon 1990).

The problem is even more complicated because of frequent misuse of the term 'sympatric speciation', which is commonly applied to describe evolutionary transformations within a monospecific lineage, in which

successive chronospecies are defined. The creation of separate species then takes place only in a mind of a taxonomist. The typologic (vertical) definition of chronospecies results in reconstruction of artificial 'sympatric' speciation which, by definition, precludes identification of any significant microevolutionary processes in paleontological material (Gingerich 1979; Dzik 1986). Since the time limits of chronospecies depend on rather arbitrary choice of a diagnostic character, they hardly have anything to do with the biological reality. The durations of such defined species (and especially higher taxa) can perhaps be used to study the population of paleontologists but are useless as objective features of the evolution. The old dream that the Linnean concept of a discontinuous variability of the living world can be extended to paleontology is deeply rooted in our cultural tradition (Rieppel 1984) and it is also matter of convenience to use arbitrarily defined taxonomic units (Haldane 1949; Culver *et al.* 1987) instead of referring only to samples and populations. Nevertheless, paleontological species names may help us to talk about the evolution but not to analyse it.

There is no reason to accept *a priori* assumptions regarding the distribution of rates of the evolution within lineages. Empirical paleontological evidence therefore remains decisive. The traditional model of speciation stressing importance of complete or partial reproductive isolation of populations, irrespective of their sizes (Barton and Charlesworth 1984), can safely be applied to extinct sexual organisms. Geographic distance and the patchiness of the environment are the most important factors resulting in the isolation. This means that speciation depends mostly on geographic factors limiting the distribution and dispersal of organisms, rather than on the rate of evolution itself. No direct relationship between the speciation rate and the rate of morphological change is necessary. It is easy to imagine a varied environment, in which numerous slowly evolving lineages develop and, to the contrary, an uniform environment inhabited by a few quickly evolving lineages. Rates of speciation and extinction are therefore quite unreliable measures of the rate of biological evolution. They mostly reflect features of the physical environment and its evolution. Whenever the geographic dimension or patchiness of an ecosystem increased, an increase in the rate of speciation also occurred. Any reduction in the area inhabited by a community, in accordance with the model of Mac Arthur and Wilson (1963), must result in an increase of the extinction rate. This perhaps may be a good measure of the evolution of complexity in ecosystems and/or effectiveness of their biocoenoses in exploiting resources. Such an analysis can be very profitable at the level of particular geographically limited ecosystem with a good fossil record. At global level it can hardly be substantiated because available data are strongly biased in effect of sociologically controlled differences in interests to different groups of fossils (Teichert *et*

al. 1987) and highly limited stratigraphic reliability of data ('bag stratigraphy' of Jaanusson 1976).

After the isolating factor had disappeared the populations represented in our ideal sections either joined by hybridisation or one of them was locally replaced by another in effect of competition (basal parts of sections *b* and *c*). Lateral displacements of populations therefore represent the second most important factor causing the punctuational vertical distribution of fossil species ('faunal shift' of Jaanusson 1976). Actually it is not the incompleteness of sections but rather frequency of horizontal shifts of populations that makes the fossil record of evolution so unreadable.

It therefore appears that even if all the evolutionary transformations were gradual (as it was assumed in the discussed model) their record in rock sections would still look punctuated. There wolud be no way to separate real discontinuities in evolutionary processes from discontinuities caused by trivial breaks in sedimentation and lateral displacements of populations. This is an inherent methodological limitation of paleontology and authors of repeated attempts to prove discontinuity of evolution on paleontological grounds seem to forget about it. The assumption that some discontinuous lineages exist is not falsifiable and does not help in any paleontological research. It is thus fruitless (Gingerich 1984) and would endanger all methodology of inference on the evolution in paleontology.

PATTERNS OF LINEAGE DISTRIBUTION IN ROCKS

The best way to study patterns of introduction and disappearance of species in sections are logs of changes in percent contribution of particular species to assemblages along a section, a routine method of data presentation in palynology and many areas of micropaleontology. The species dynamics of organisms having an especially good fossil record, for instance the conodonts (fig. 2), show differences between environments, with 'noise' disturbing general patterns in shallow equatorial environments and smooth patterns of distribution characterizing cool-water open-sea environments.

The most striking feature of distribution of particular species is a more or less fusiform shape of the logs, irrespective of analyzed groups of organisms (see *i.a.* Cisne and Rabe 1978; Sweet 1979; Jeppson 1979; Cherns 1988; Dzik 1990*b*). This fusiform pattern shows that the contribution of an invading species to the total productivity of the assemblage was initially quite small. It increased and after some time of stability gradually disappeared. Single specimens 'contaminate' assemblages far below and above the easily detectable occurrence of the species (see Dzik
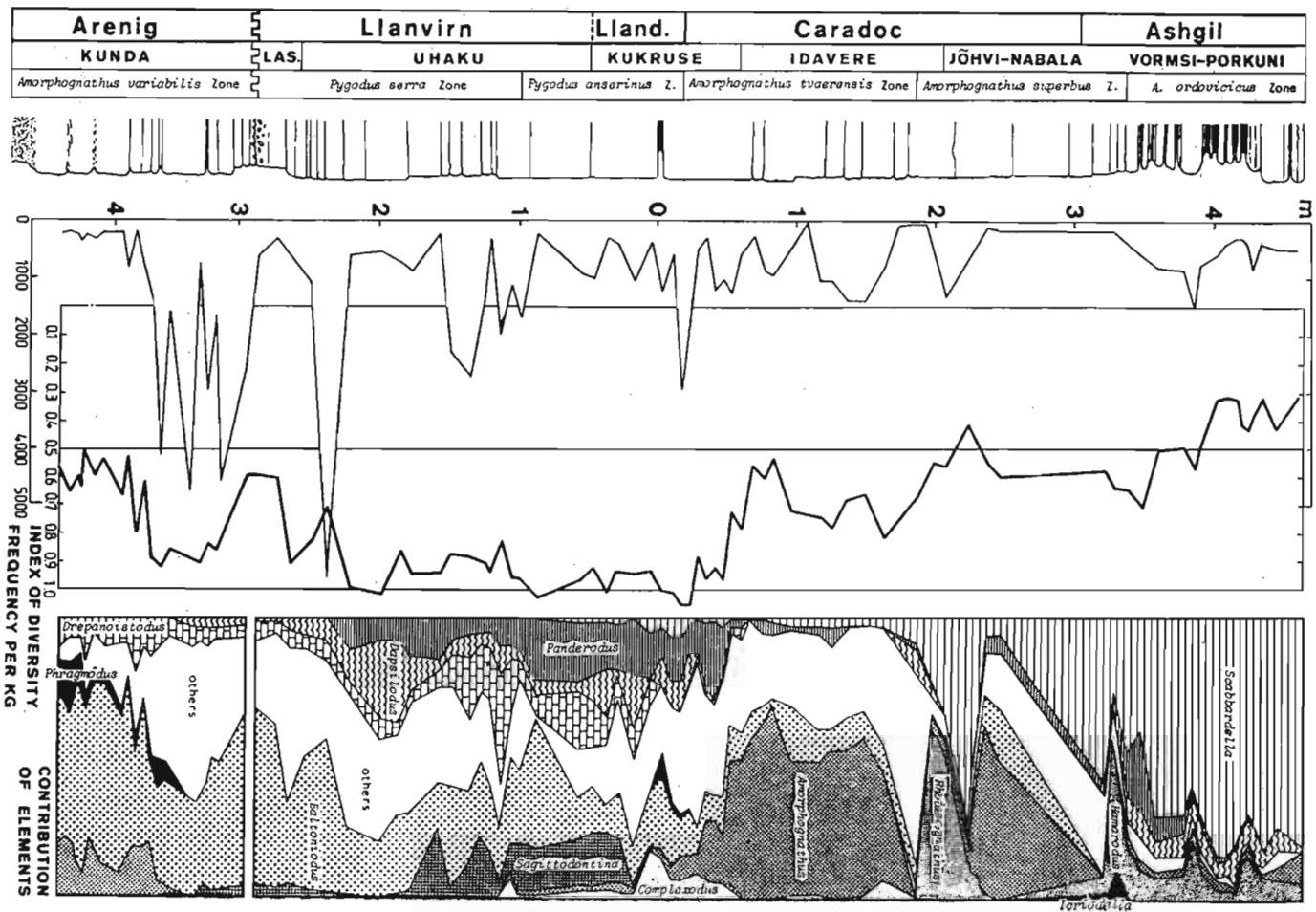
Arenig	Llanvirn	Lland.	Caradoc	Ashgil

KUNDA	LAS.	UHAKU	KUKRUSE	IDAVERE	JÕHVI–NABALA	VORMSI–PORKUNI

Amorphognathus variabilis Zone	*Pygodus serra* Zone	*Pygodus anserinus* Z.	*Amorphognathus tvaerensis* Zone	*Amorphognathus superbus* Z.	*A. ordovicicus* Zone

INDEX OF DIVERSITY

FREQUENCY PER KG

CONTRIBUTION OF ELEMENTS

Drepanoistodus

Phragmodus

others

others

Drepanodus

Panderodus

Baltoniodus

Sagittodontina

Complexodus

Amorphognathus

Rhodesognathus

Icriodella

Tortodus

Scabbardella

Fig. 2. Actual pattern of distribution of lineages of conodonts in the section of the Ordovician in Mójcza, Holy Cross Mountains, Poland (From Dzik 1990b). Note stability and gradual changes in contribution of representatives of most lineages and sudden appearance and disappearance of some of them in the log of percent contribution of specimens (for instance *Rhodesognathus*).

97

1990b). One has a feeling that their spatial distribution resembles a cloud, with particle densities highest in the center and gradually decreasing toward margins. The 'cloud' seems to move across the locality giving the increase in contribution of the species and, after a period of relative stability, it gradually disappears. In some assemblages a single species may dominate over all the others during its acme.

It is not my intention to argue that all species follow the fusiform pattern of distribution. In almost every section some species can be detected, which appear and disappear instanteously. Perhaps these were the most ecologically sensitive members of communities and useful indicators of subtle changes in environment (fig. 2: levels 3.0 and 3.4 m high in the section).

The pattern presented above may be partly a by-product of bioturbation and reworking. Bioturbation may result in artificially earlier gradual introduction of a species, which in fact appeared suddenly in a large amount of specimens. Reworking may smooth out patterns of disappearance, even if it was actually sharply cut. One has to be aware of these factors. Paradoxically, sometimes a presence of a species with discontinuous distribution may serve as an appropriate control of reliability of the record in a section.

However striking it may sound, despite of general incompleteness of the fossil record, some ecologic groups of animals in certain time spans are well enough documented in the fossil record to be comparable in any time plane with the degree of knowledge of equivalent Recent groups. There are many islets of such an unexpectedly good record of evolution. This concerns, i.a., the conodonts in the Ordovician and Silurian of the North America and Europe, the ammonites in the Jurassic of the central Europe or planktonic foraminifers of the Cretaceous and Tertiary. If still so little of available information can be used in studies on evolution is due mainly to inadequate methods of collecting, processing, and presentation of data (for discussion see i.a. Gingerich 1979; Dzik and Trammer 1980; Dzik 1986, 1990a; Bown and Rose 1987).

THE BASIC UNIT OF PHYLOGENETIC STUDIES

Species is the only taxonomic unit, which can be defined in Popperian terms, that is, as an empirically testable statement. The most widely accepted biological definition of species is that of Mayr (1986: 26), which states that 'species are groups of interbreeding natural populations that are reproductively isolated from other such groups'. The concept of a species may thus be formulated as a non-existence statement: interbreeding between different species and lack of breeding within the species are prohibited. Potentially, any particular species concept within frames

of neontology can be refuted by a negative test of breeding. Separation of two populations to different species may be shown to be false in a similar way (by positive test).

The standard theoretical concept of biological studies is a population: 'the community of potentially interbreeding individuals at a given locality' (Mayr 1969: 401). That different sympatric populations belong to different species can be recognized by tests of breeding. Boundaries separating populations within the same species are drawn along more or less discontinuous boundaries in distribution of environmental factors and cannot be defined on strictly biological grounds. Both species and populations are theoretical concepts but what is really studied by taxonomists are morphological groups which may or may not form a biological population. Such a group, characterized by possibly continuous and close to normal distribution of morphologic characters, was named a 'phenon' by Mayr (1969). Any study on a population or a species starts from recognition and grouping of phena (fig 3; Dzik 1990a; Hoffman and Reif 1990). It is assumed that there is a direct relation between reproductive isolation and morphologic differences among specimens. Presence or lack of continuity in distribution of morphologic characters between and within groups may then be used to test particular taxonomic concepts.

The methodological distinctions between the neontological and paleontological taxonomies are not great when units of the phenon rank are studied (see Reif 1984; Gingerich 1986). Paleontologists also identify groups of specimens in fossil assemblages characterized by continuous and close to normal distribution of morphologic characters. They may represent distinct species, sexual dimorphs, parts of a polymorphic population, or particular parts of a skeleton. However, paleontological samples have an additional time dimension which can not always be ignored. To be useful in taxonomic and phylogenetic considerations, paleontological phena must fulfill a few important requirements. First of all they must be properly separated from other phena of the same fossil assemblage. This can usually be performed with a high degree of confidence by application of simple biometric methods.

The second requirement is the time homogeneity of phena. A phenon should be a product of a temporally continuous single population, and the time span covered by the sample should be as short as possible. Numerical studies on densely sampled geological sections (fig. 2; see also Sweet 1979; Jeppson 1979; Dzik 1990b; Cherns 1988) show that the composition of fossil assemblages of pelagic organisms is generally rather stable in geological time. It is quite rare to find a succession of completely unrelated briefly occurring populations in a section that is continuous lithically. Unless there is a reason to believe that the continuum of populations was broken, even a phenon with extended time dimension remains a homogenous sample from the lineage.
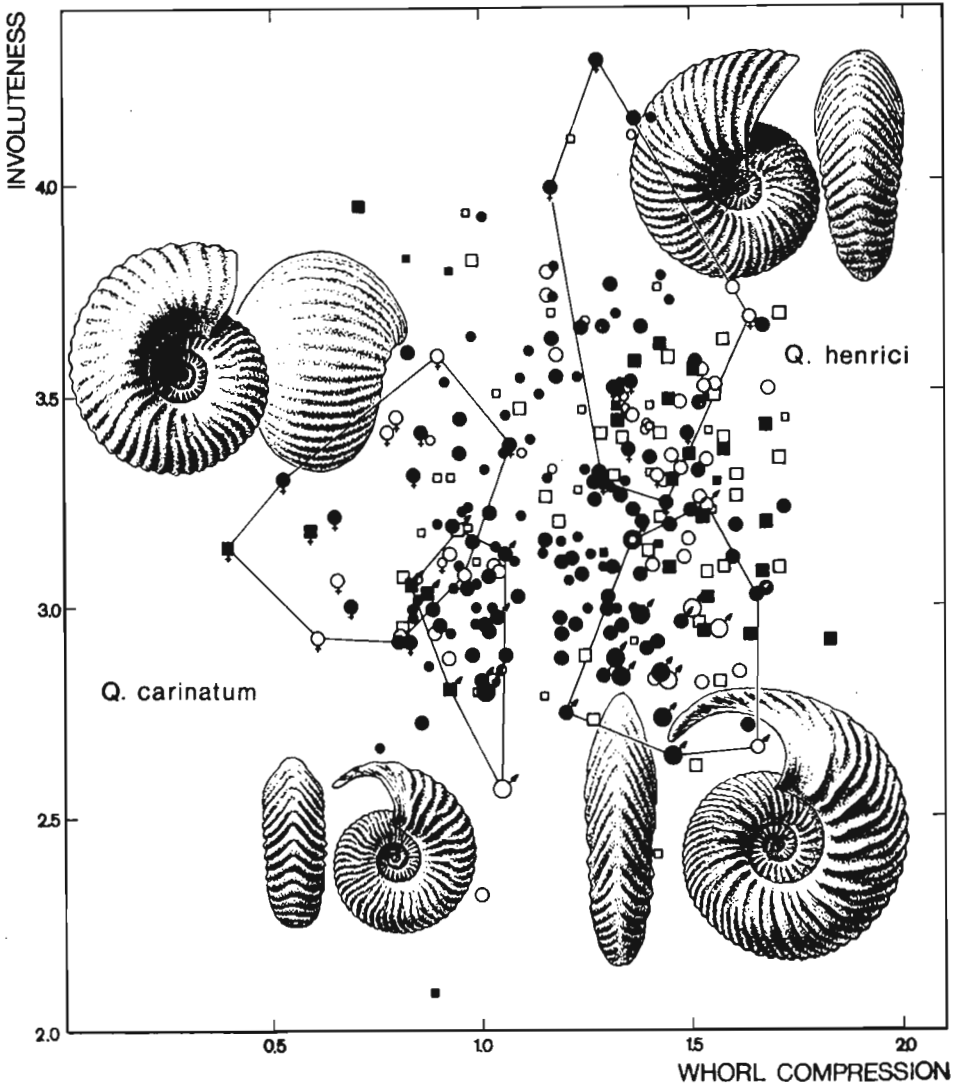
Fig. 3. An example of recognition of phena in a sample of fossils. Four limestone concretions (corresponding to black and white circles and squares in the plot) from the Callovian of Łuków, Poland contained conchs of ammonites *Quenstedticeras* of different, ontogenetic stages (three sizes of points correspond to juveniles, subadults, and adults). In the scattergram of involuteness (expressed by a ratio between conch and umbo diameters) against whorl compression (whorl height to width), adult and subadult conchs cluster in four fields corresponding to males and juvenile females of two species (after Dzik 1990a).

The third requirement to be fulfilled is that evolutionary processes do not interfere with the population variability expressed by the phenon (*i.a.* Howarth 1973: 247). Perhaps the safest way to avoid such interference is to keep the time segment covered by a single sample brief enough in relation to the expected rate of evolution in the studied lineage.

Phena are the only objective taxonomic units in paleontology. Accepting an assumption that fossils are remnants of extinct organisms basically similar to Recent ones one can apply neontological theories of species and population to interpret paleophena and paleontological phylogenetic trees. Another reasonable assumption is that morphologic gaps express genetic barriers between sympatric populations. This allows one to treat those phena which do not represent morphs or organs within the same sample as representatives of separate evolutionary lineages, which are discrete in space but continuous in time. A strict application of the neontological concept of species to paleontological data is therefore only possible in phena collected from the same time horizon. Although in paleontological practice rarely anything more than the morphologic features and geographic distribution of phena can be considered during identification of ranges of species, it is exactly the way in which neontological taxonomy works. In this respect there seems to be no real methodological difference between these two areas of study.

PALEONTOLOGICAL PHYLOGENETIC TREES

Any paleontological phenon has its own properties of morphology and space-and-time coordinates. Fossil phena are thus objectively ordered *a priori*, according to their geographic distribution and positions on the geological time scale. These coordinates do not depend on subsequent taxonomic or phylogenetic operations with the matrix of phena. The original geographic order is provided by tectonic reconstructions proposed by geologists with application of evidence not necessarily related to paleontology. The time order is given by the rule of superposition and the age correlation based on geological records of global climatic and/or diastrophic events, on physical methods of age estimation, and on the evolution of fossils. The last method does not need to be necessarily involved in a circular reasoning when used to phylogenetic studies: the dating has just to be based on another lineage than that studied for the phylogeny.

Paleontological phena with their time-and-space coordinates and morphologic features form a multidimensional matrix of data, which can be used in the reconstruction of phylogenetic trees. To transform the matrix, with paleophena plotted against time and space, into a phylogenetic tree it is enough to connect particular paleophena by hypothetical links of ancestor-descendant relationships (fig. 4—6). It is not especially important what would be a basis for choice of particular connections among possible ones and for proposal of particular phylogenetic hypotheses. All inductive methods of phenetics and/or cladistics can be used to recognize patterns of the blood relationships among coeval phena, which may suggest par-

ticular ancestor-descendant relationships to older phena (see Charig 1982 for comments on methodology). The more important debate seems to be whether or not there is any objective method of selection of better hypotheses from several possible and whether they are falsifiable.

The concept of paleontological phylogenetic trees is rooted in the Agassiz (1844; reviewed by Patterson 1981) presentation of relationships among fossil and Recent fishes, with a clear indication of the time distribution of particular groups and with morphologically continuous sequences (morphoclines) shown to be polarly extended in time (forming thus chronoclines). His diagram preceded public presentation of the Darwinian theory and because of this anachronism, as well as of its author's philosophy, it has been treated as an evidence for the lack of any correspondence between concepts of evolution and multidimensional presentations of relationships (Patterson 1981: 180). Whatever is the background philosophy behind the Agassiz's tree they are exactly what is expected to be a result of evolutionary studies in paleontology. Conscious studies of evolutionary transformations recorded in rock sections date from Waagen (1969) studies of ammonites, and the Hilgendorf (1863; reviewed by Reif 1986; see Mensink et al. 1984) and Neumayr and Paul (1975; see also Büttner 1982) studies on the evolution of fresh-water snails inhabiting ancient lakes (Gorthnauer and Meier-Brooks 1985). A good example of early exact indication of positions of particular samples on the geological time scale in the analysis of ancestor-descendant relationship is also the diagram of the pedigree of Early Paleozoic hyoliths published by Holm (1893). The next step was taken by Brinkmann (1929), who applied biometrics to description of phena of some Jurassic ammonites, later recognized as sexual dimorphs.

The most important feature of this method of phylogeny reconstruction is the population approach. All considerations start from a recognition of phena. A picture of the population variability, inferred from a sample, when put on the geological time scale (or a lithologic sequence), starts to be an element of the reconstructed evolutionary lineage. This approach was theoretically strengthened by Simpson (1953, 1961). Because it is methodologically related to his 'evolutionary systematics' I shall apply the term 'evolutionary method' to it. Although the best examples of its application are microevolutionary studies (i.a. Grabert 1959; Rose and Bown 1984; Baarli 1986; Olempska 1989) this does not imply that it necessarily requires dense sampling or sophisticated biometrics.

Objections of two kinds are usually invoked against the evolutionary method. The first is that the fossil record is too incomplete to provide a sufficient basis for reliable reconstructions of the phylogeny. This is surely true for groups of organisms characterized by a low fossilization potential, but nobody has yet shown any profitable alternative to cur-

rently used ways of inference (Paul 1982). Phylogenetics is a historical science and one cannot reject usefullness of an ancient document only because it contains less information than an evening newspaper! Moreover, there is no contradiction between the evolutionary method and other, indirect ways of inference on the phylogeny.

The second objection refers to supposed low resolution power of the morphologic criteria, which does not ensure a proper separation of cryptic species in paleontological samples. This questions the reliability of practically all methods of inference in paleontology and represents 'a defeatist attitude' (Jeppson 1986). The impact of this deficiency in the methodology of paleontology on reliability of phylogenetic trees is not dramatic. The worst which may happen is that a bifurcation of a lineage may be recognized somewhat higher in the rock column than it really occurred. It is true that obvious morphologic differences in fossils may only develop in populations already widely separated genetically. They are usually wide enough to allow a sympatric cooccurrence without interbreeding (i.a. Jeppson 1986). Perhaps this is the reason why apparently sympatric speciations are so commonly reported in the fossil record (see i.a. Grabert 1959; Gingerich 1979; Mensink et al. 1984).

Despite of these obvious deficiencies of the method and the rather more intuitive than formal recognition of its rules, paleontological data have been effectively used in testing of phylogenetic trees (Van Dongen and Vossen 1984; Campbell and Barwick 1988). Several attempts to improve methods of inference have been proposed (i.a. Ghiselin 1972; Kitts 1974; Harper 1976). They suggest more extensive applications of the Occam's Razor rule to phylogenetic reconstructions, especially in their time dimensions. The rule of parsimony, despite of many objections regarding its biological reliability, is widely used to the morphological dimension of phylogenetic trees (see Panchen 1982).

TESTABILITY OF PHYLOGENETIC HYPOTHESES

Can a phylogenetic hypothesis be refuted by empirical evidence? It depends what the term 'phylogenetic hypothesis' means. For cladists it is a cladogram presenting, in the most parsimonious way, distribution of characters among taxa. It has been convincingly shown by Panchen (1982) that the supposed falsification procedures of cladistics actually represent an application of the criterion of parsimony and hardly anything more. Both cladistics and evolutionary science are not easily justified by the Popperian methodology of science. This was already shown by Popper (1979), who applied the Darwinian theory of evolution to explain features of his World 3, in which the processes controlling the historical development of human knowledge have the same properties as the process of

biological evolution. His criticism to historicism in social sciences concerns thus the historical concept of phylogeny as well.

Is there any possibility to overcome these methodological constraints? The future course of the evolution cannot be predicted and there is no reason to believe that such predictions are possible in paleontology at all. However, in historical sciences along with prediction another way of reasoning in also possible, namely postdiction (retrodiction), directed back in time, toward the past. One may wonder whether the methodology of falsificationism can be applied to postdictions of the course of evolution based on extrapolations of observed trends or interpolations between the final and the supposed initial states. It is rather the job of logicians than paleontologists to analyze this problem but some features of evolutionary applications of the method of postdiction are apparent.

Thus, owing to the dichotomous pattern of branching of the evolutionary tree, the number of real ancestors is always smaller than the corresponding number of successors. Moreover, any species may have several successors but only the single ancestor. This means that an indication of the ancestry is contradictory to all other possible indications of ancestry for the same species, while no such contradiction occurs when a successor is indicated.

Another basic feature of the evolution, namely the generally unimodal distribution of evolutionary rates (at least in paleontologically detectable transformations, Simpson 1944), with extremely low and high values being rare, has some bearing on the value of fossil data in testing evolutionary trees. Thus, in the case of any older representative of a monophyletic taxon the probability that it is close morphologically to the common ancestor of the whole group is much higher than in the case of its younger relatives. One cannot be sure, of course, that this particular fossil is actually closer but it is enough to expect that results of any phylogenetic analysis based on a sample of older species should result in a more reliable indication of the common ancestor than in the case of a younger sample being analyzed (see Campbell and Barwick 1988 for example).

The traditional search for ancestors can therefore be substantiated due to the privileged position of our time plane in the phylogenetic tree of organisms and the methodological implications of the above observations. No doubt paleontological evidence is crucial in stimulating progress in our understanding of the phylogeny. It is apparent that at least some degree of falsifiability is connected with phylogenetic hypotheses presented in this way. To examine this let us consider a simple example. Thus, any phylogenetic tree can be reduced to a set of elementary hypotheses (fig. 4) of the type: A → B, where A and B are populations (or phena) of different geological age, B being younger than A. Let us assume that a population (phenon) C, which is intermediate in age between

the A and B, is ancestral to B. If the elementary hypothesis A → B is true, the A must be ancestral also for C because only a single evolutionary lineage can lead to the B: A → C → B. When the time distance between the A and B is small enough (in respect to the rate of evolution in the lineage), it may be deduced that the C should be morphologically intermediate between A and B. If it is the case, the hypothesis would be
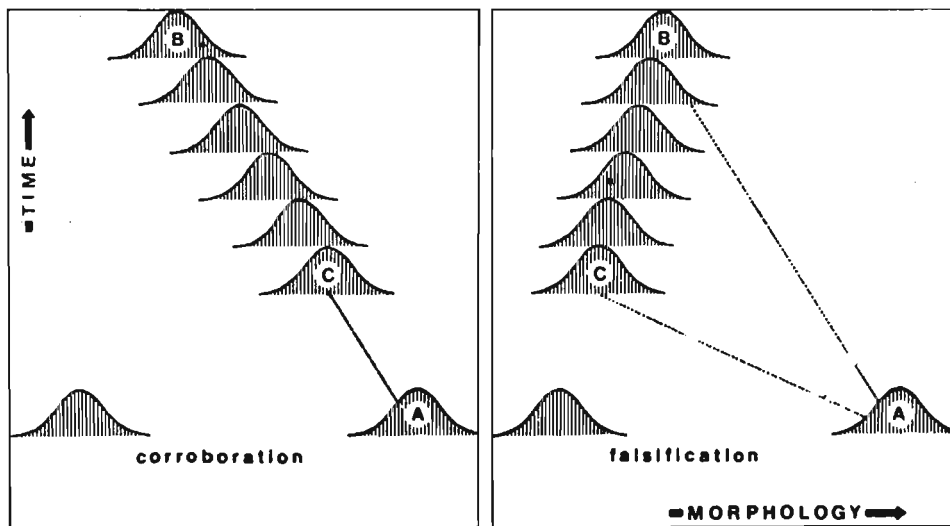

Fig. 4. A diagrammatic presentation of the procedure of testing an ancestor-descendant hypothesis A → B by identifying a transitional form C known to be ancestral for B. The 'power of falsification' increases with increasing morphologic and decreasing time distance between A and C. When A and C occur in the same time horizon the hypothesis A → B is definitely rejected.

corroborated. However, if the C is significantly away of supposed direction of a morphologic transformation between the A and B a contradiction between the empirical evidence and the hypothesis would appear. The strenght of contradiction depends, of course, on a morphological, time, as well as geographic distance between A and C. Actually, the hypothesis A → B could be definitely rejected if C reaches the time horizon of A (as in the case A being *Australopithecus robustus*, B representing *Homo erectus*, and C *H. habilis*). The assumption that C → B can be tested in the same way: by introducing of another population intermediate in age between the C and B and assumed to be ancestral for the B. This procedure does not lead *ad infinitum.* It ends when the time and morphologic distances between B and its proposed ancestor are no longer significant, that is when the phylogenetic analysis becames identical with stratophenetics.

As everywhere in paleontology the application of an operational morphologic species concept seems unavoidable in this case. A statement

that two morphologically undistinguishable phena, close to each other in time and space, belonged to the same continuum of populations is untestable (this would require tests of breeding between populations living in different times) but still reasonable.

It may be concluded from the above discussion that the pattern of evolutionary relationships presented by the mean of a phylogenetic tree can be potentially tested by comparing the directions of evolutionary transformations inferred from the tree with the course of (phyletic) evolution observed in the fossil record. The reliability of inference on the course of evolution is thus crucial for a testability power of paleontological data. Reasoning of this kind reaches its greatest power when stratigraphically dense sampling is used. With increasing time distances between phena possible deviations from the interpolated directions of the evolution are of less and less value in testing an ancestor-descendant relationship.

RECONSTRUCTION OF THE COURSE OF EVOLUTION

The simplest way to recognize evolutionary processes in a geological sections is to put the biometric characteristics of all identified phena on a chart with the rock thickness scaled on the vertical axis and morphological parameter scaled on the horizontal axis (fig. 5). Although only the morphology of some organs can be studied in fossils, one can safely assume that phena, which are almost identical morphologically in every neighbouring pair of samples and belonging to unbroken morphologic continua described along the section, were members of a single ancestor--descendant continuum of populations. Any significant deviation from the initial frequency distribution of morphology in the continuum represents thus the evolution.

The method, applied to different groups of organisms by Brinkmann (1929), Grabert (1959), and many others, has been christened by Gingerich (1979) the 'stratophenetic approach'. The term 'stratophenetics' (by analogy also 'stratocladistics' has been introduced: Doyle et al. 1982) unfortunately suggests a relationship to the methodology of phenetics, which is not the case. It is, however, a useful descriptive for special applications of the evolutionary method to densely sampled geological sections.

It was indicated already above that geological sections complete and fossiliferous enough to be subjects of quantitative studies on evolution are not so rare as it is generally assumed (see Dzik and Trammer 1980 for a review of potential fields of research). It is usually a refusal to use appropriate methodology which hampers wider application of paleontological data to biometric studies of evolutionary processes. Especially destructive for evolutionary paleontology is general application of the
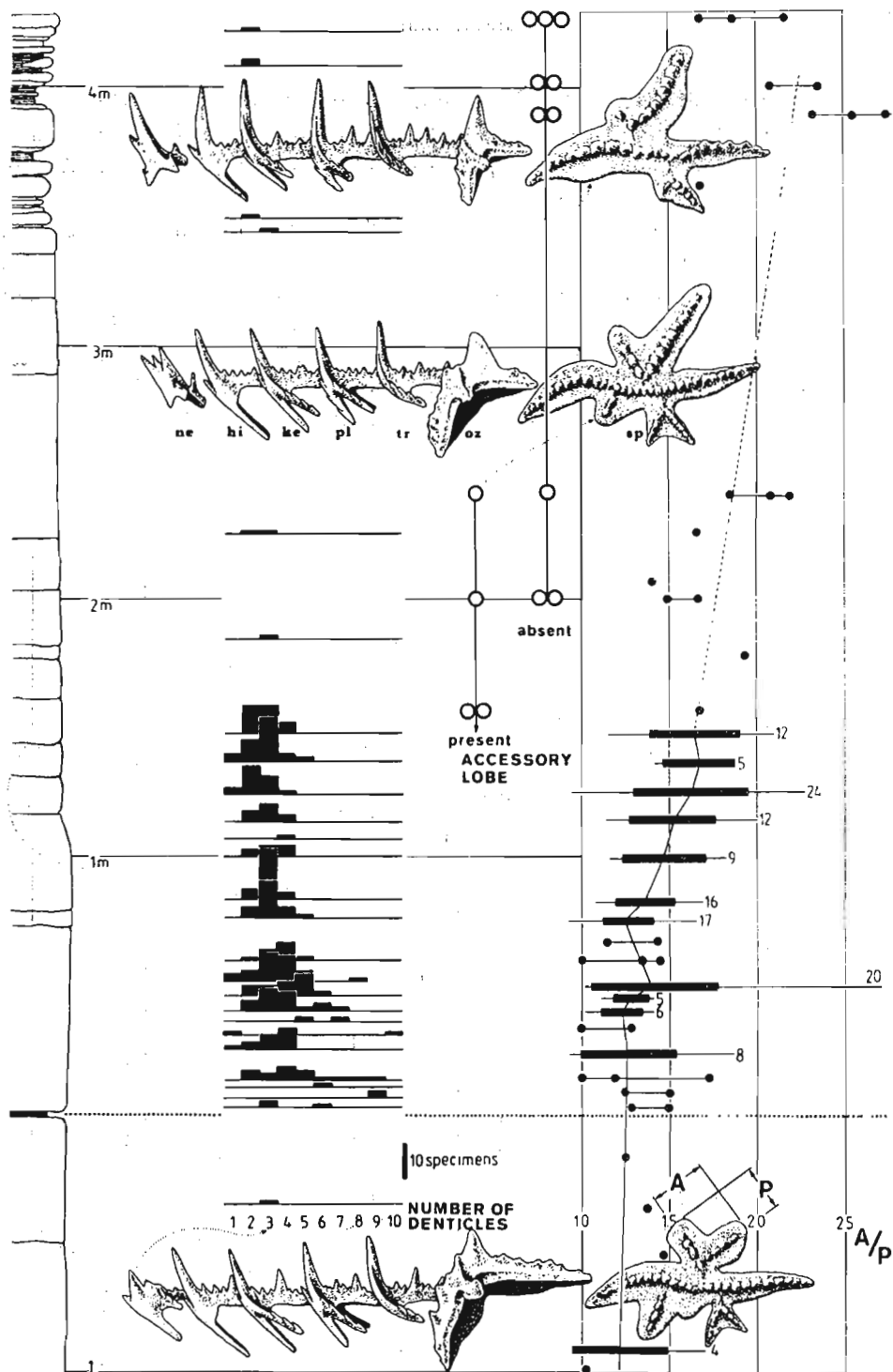
Fig. 5. An example of application of the stratophenetic method to conodont lineages represented in the Mójcza section; horizontal bars indicate range of standard deviation, thin lines total ranges of variability of particular characters (from Dzik 1990b).

vertical (typologic) method to defining chronospiecies (Dzik 1986). The use of such a tool in evolutionary studies almost precludes the recognition of evolutionary process recorded in a rock section (compare, for instance, Adamczak 1958 and Olempska 1989).

Chronomorphoclines identified in a rock section in this way do not necessarily need to represent true biological evolution. Migrating species showing clinal geographic variation may produce similar effects (Joysey 1956). Sometimes it appears also virtually impossible to distinguish ecologically controlled changes in the population dynamics from genetically stabilized transformations of the ontogeny (Dzik and Trammer 1980). Most of the evolutionary transformations are connected with partial
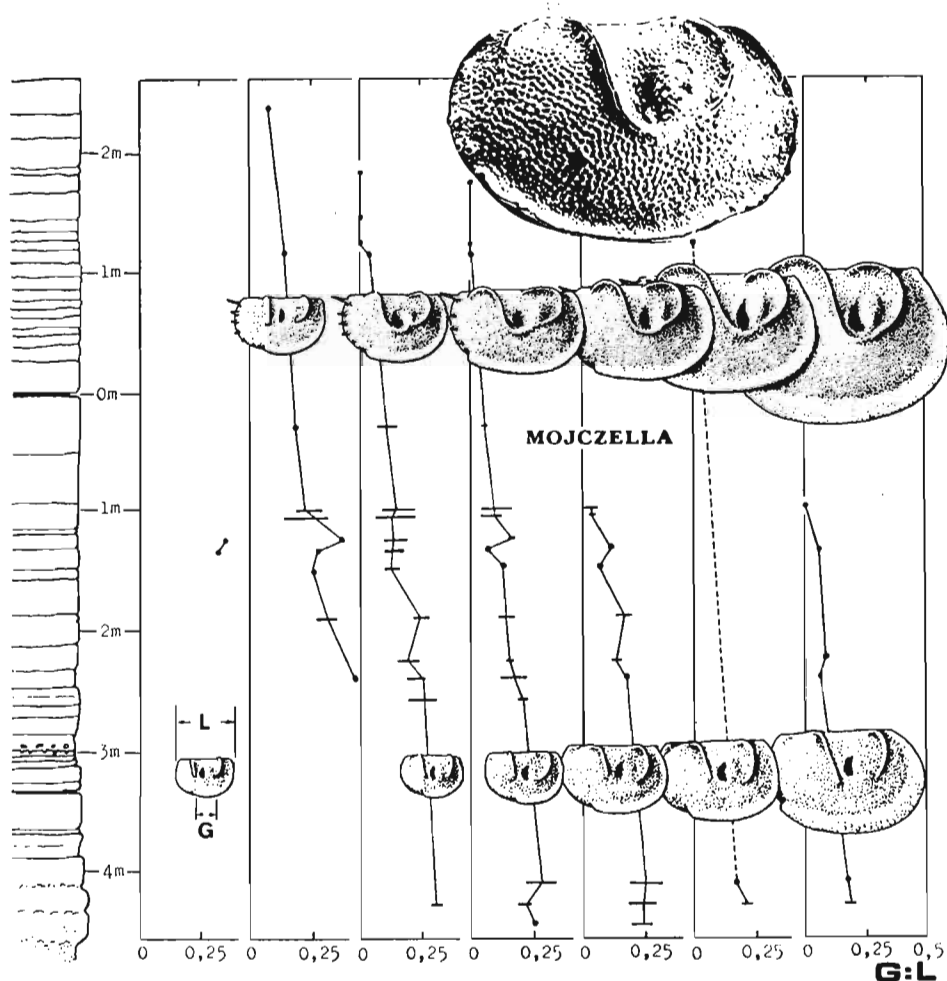

Fig. 6. Expansion of an evolutionary novelty (connection between crests) in the lineage of the ostracode *Mojczella* in the section of the Ordovician Mojcza Limestone (same as at figs. 2 and 5) (modified after Olempska 1989).

modifications of the ontogeny. The most important obstacle in studies of such modifications in the evolution of organisms with skeletons preserving complete record of their development (like molluscs or brachiopods) is the lack of exact indications of ontogenetic stage. The size alone is insufficient to be a guide in comparing ontogenies of different individuals. In effect of the lack of strict synchroneity between growth in size and morphologic transformations the fossil record of introduction of evolutionary novelties may appear practically unreadable at population level (Dzik 1986; Dommergues 1987). The best way to overcome these obstacles is to base research on arthropod exuvia (Olempska 1989) or structures which do not change in ontogeny, like mammalian teeth (Gingerich 1979; Bown and Rose 1984).

CONCLUSIONS

The above presented review of the ways of inference in evolutionary paleontology may sound awfully traditional and it is such actually. Today this basically Simpsonian approach seems to be quite unfashionable among paleobiologists. There is much more interest in theoretical considerations about supposed mode of evolution at and above the species level and about strict methods of inference on the course of evolution from purely morphological data. Nevertheless, the time-and-space order in distribution of morphologies shown by fossils remains the most objective basic evidence for the polarity of evolutionary change and this is the most significant advantage of studying the fossil record of evolution. Decades of biostratigraphically oriented paleontological research have resulted in presentation of a great amount of new data on evolutionary transformations. It is the duty of paleobiologists now to analyse and interpret this empirical evidence.

REFERENCES

ADAMCZAK, F. 1958. The ontogeny and evolution of *Kozlowskiella* (Přibyl) (Ostracoda). — *Acta Palaeont. Polonica*, 3, 75—116.

AGER, D. V. 1983. Allopatric speciation — an example from the Mesozoic Brachiopoda. — *Palaeontology*, 26, 555—565.

BAARLI, B. G. 1986. A biometric re-evaluation of the Silurian brachiopod lineage *Stricklandia lens/S. laevis.* — *Palaeontology*, 29, 187—205.

BARTON, N. H. and CHARLESWORTH, B. 1984. Genetic revolutions, founder effect, and speciation. — *Ann. Rev. Ecol. Syst.* **15**, 133—164.

BEHRENSMEYER, A. K. 1982. Time resolution in fluvial vertebrate assemblages. — *Paleobiology*, **8**, 211—227.

BOWN, T. M. and ROSE, K. D. 1987. Patterns of dental evolution in Early Eocene anaptomorphine Primates (Omomyidae) from the Bighorn Basin, Wyoming. — *J. Paleont.* **61**, Suppl., **5**, 1—162.

BRINKMANN, R. 1929. Statistisch-biostratigraphische Untersuchungen an mittel-jurassischen Ammoniten ber Artbegriff und Stammenentwicklung. — *Abh. Ges. Wiss. Göttingen, Math.-Naturwiss.* Kl. N.F. **1**, 3, 1—249.

BÜTTNER, D. 1982. Biometrie und Evolution der *Viviparus*-Arten (Mollusca, Gastropoda) aus der Plio-Pleistozän von Ost-Kos (Dodekanes, Griechenland). — *Berliner Geowiss. Abh.*, **42A**, 1—63.

CAMPBELL, K. S. W. and BARWICK, R. E. 1988. Geological and palaeontological information and phylogenetic hypotheses. — *Geol. Mag.*, **125**, 207—227.

CHARIG, A. J. 1982. Systematics in biology: a fundamental comparison of some major schools of thought. — *In*: K. A. Joysey and A. E. Friday (eds.), Problems of Phylogenetic Reconstruction. 363—440. Academic Press, London.

CHERNS, L. 1988. Faunal and facies dynamics in the Upper Silurian of the Anglo--Welsh Basin. — *Palaeontology*, **31**, 451—502.

CISNE, J. L. and RABE, B. D. 1978. Coenocorrelation: gradient analysis of fossil communities and its applications in stratigraphy. — *Lethaia*, **11**, 341—364.

CULVER, S. J., BUZASA, M. A. and COLLINS, L. S. 1987. On the value of taxonomic standardisation in evolutionary studies. — *Paleobiology*, **13**, 169—176.

DOMMERQUES, J. L. 1987. L'evolution chez les Ammonitina du Lias Moyen (Carixien, Domerien basal) en Europe occidentale. — *Doc. Lab. Geol. Lyon*, **98**, 1—297.

DOTT, R. H. 1983. 1982 SEPM Presidential Address: Episodic sedimentation. How normal is average? How rare? Does it matter? — *Jour. Sedim. Petrol.*, **53**, 5—24.

DOYLE, J. A., JARDINE, S. and DOERENKAMP, A. 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of northern Gondwana. — *Bull. Cent. Rech. Explor.--Product. Elf Aquitaine*, **6**, 39—117.

DZIK, J. 1986. Typologic *versus* population concepts of chronospecies: implications for ammonite biostratigraphy. — *Acta Palaeont. Polonica*, **30**, 71—92.

DZIK, J. 1990a. The concept of chronospecies in ammonites. — *In*: G. Pallini *et al.* (ed.), Atti del secondo Convegno internazionale Fossili, Evoluzione, Ambiente, Pergola 25—30 ottobre 1987, 273—289.

DZIK, J. 1990b. Conodont evolution in high latitudes of the Ordovician. — *Cour. Forsch. Inst.*, Senckenberg, **117**, 1—28.

DZIK, J. and TRAMMER, J. 1980. Gradual evolution of conodontophorids in the Polish Triassic. — *Acta Palaeont. Polonica*, **25**, 55—89.

GHISELIN, M. I. 1972. Models in phylogeny. — *In*: T. J. M. Schopf (ed.), Models in Paleobiology, 130—145. Freeman, Cooper and Co., San Francisco.

GINGERICH, P. D. 1979. The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. — *In*: J. Cracraft N. and Eldredge (eds), Phylogenetic Analysis and Paleontology. 41—76. Columbia University Press, Irvington.

GINGERICH, P. D. 1984. Punctuated equilibria — where is the evidence? — *Syst. Zool.* **33**, 335—338.

GINGERICH, P. D. 1986. Species in the fossil record: concepts, trends, and transitions. — *Paleobiology*, **11**, 27—41.

GORTHNER, A. and MEIER-BROOKS, C. 1985. The Steinheim basin as a paleo-ancient lake. In: U. Bayer and A. Seilacher (eds.), Sedimentary and Evolutionary Cycles. 322—334. Springer Verlag, Heidelberg.

GOULD, S. J. and ELDREDGE, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. — Paleobiology, 3, 115—151.

GRABERT, B. 1959. Phylogenetische Untersuchungen an Gaudryina und Spiroplectammina (Foram.) besonders aus dem nordwestdeutsche Apt und Alb. — Abh. Senck. Naturf. Ges., 498, 1—71.

HALDANE, J. B. S. 1949. Suggestions as to quantitative measurements of rates of evolution. — Evolution, 3, 51—56.

HALLAM, A. 1982. Patterns of speciation in Jurassic Gryphaea. — Paleobiology, 8, 354—366.

HARPER, C. W. jr 1976. Phylogenetic inference in paleontology. — J. Paleont., 50, 180—193.

HOFFMAN, A. and REIF, W.-E. 1990. On the study of evolution in species-level lineages in the fossil record: Controlled methodological sloppiness. — Palänt. Z., 64, 5—14.

HOLM, G., 1983. Sveriges kambrisk-siluriska Hyolithidae och Conulariidae. — Sveriges Geol. Und., C112, 1—170.

HOWARTH, M. K. 1973. The stratigraphy and ammonite fauna of the Upper Liassic Grey Shales of the Yorkshire coast. — Bull. Brit. Mus. (Nat. Hist.), Geology, 24, 237—277.

JAANUSSON, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia. — In: M. G. Bassett (ed.), The Ordovician system: Proceedings of a Palaeontological Association Symposium, Birmingham, Sept. 1974. 301—326. University of Wales Press, Cardiff.

JEPPSON, L. 1979. Conodonts. In: V. Jaanusson, S. Laufeld and R. Skoglunt (eds.), Lower Wenlock Faunal and Floral Dynamics — Vattenfallet Section, Gotland. — Sveriges Geol. Und. C762, 225—248.

JEPPSON, L. 1986. A possible mechanism in convergent evolution. — Paleobiology, 12, 80—88.

JOHNSON, A. L. A. and LENNON, C. D. 1990. Evolution of grypheate oysters in the Mid-Jurassic of western Europe. — Palaeontology, 33, 453—485.

JOYSEY, K. A. 1956. The nomenclature and comparison of fossil communities. — In: P. C. Sylvester-Bradley (ed.), The Species Concept in Palaeontology, 89—96. Systematic Association, London.

KITTS, D. B. 1974. Paleontology and evolutionary theory. — Evolution, 28, 458—472.

MAYR, E. 1969. Principles of Systematic Zoology. 428 pp. McGraw-Hill Book Co., New York.

MENSINK, H., BAHRIG, B. and MERGELSBERG, W. 1984. Die Entwicklung der Gastropoden in Miozäner See des Steinheimer Beckens (Süddeutschland). — Palaeontographica, 183A, 1—63.

MACARTHUR, R. and WILSON, E. D. 1967. The Theory of Island Biogeography. 203 pp. Princeton University Press, Princeton.

MCKINNEY, M. 1985. Distinguishing patterns of evolution from patterns of deposition. — J. Paleont., 59, 561—567.

NEUMAYR, M. and PAUL, C. 1875. Die Congerien- und Paludinenschichten Slavoniens und deren Faunen. — Abh. kk. geol. Reichsanst., 7, 1—111.

OLEMPSKA, E. 1989. Gradual evolutionary transformations of ontogeny in an Ordovician ostracod lineage. — Lethaia, 22, 159—167.

PANCHEN, A. L. 1982. The use of parsimony in testing phylogentic hypotheses. —
    Zool. J. Linn. Soc. London, 74, 305—328.
PATTERSON, C. 1981. Significance of fossils in determining evolutionary relation-
    ships. — Ann. Rev. Ecol. Syst., 12, 195—223.
PAUL, C. R. C. 1982. The adequacy of the fossil record. — In: K. A. Joysey and
    A. E. Friday (eds.), Problems of Phylogenetic Reconstruction. — Systematic
    Association, Spec. Vol. 21, 75—117.
POPPER, K. R. 1979. Objective Knowledge: An Evolutionary Approach. 380 pp.
    Clarendon Press. Oxford.
REIF, W.-E. 1983. Hilgendorf's (1863) dissertation on the Steinheim planorbids (Gas-
    tropoda; Miocene): The development of phylogenetic research program for
    paleontology. — Paläont. Z., 57, 7—20.
REIF, E.-W. 1984. Artbegrenzung und das Konzept der evolutionaren Art in der
    Paläontologie. — Z. zool. Syst. Evol., 23, 263—286.
RIEPPEL, O. 1984. Atomism, transformism and the fossil record. — Zool. J. Linn.
    Soc., London, 82, 17—32.
ROSE, K. D. and BOWN, T. M. 1984. Gradual phyletic evolution on the generic level
    in Early Eocene omomyid primates. — Nature, 309, 250—252.
SHAW, A. B. 1964. Time in Stratigraphy, 365 pp. Mc-Graw-Hill, New York.
SADLER, P. M. and STRAUSS, D. J. 1990. Estimation of completeness of strati-
    graphical sections using empirical data and theoretical models. — J. Geol. Soc.,
    London, 147, 471—485.
SIMPSON, G. G. 1944. Tempo and Mode of Evolution. 237 pp. Columbia University
    Press, New York.
SIMPSON, G. G. 1953. The Major Features of Evolution. 434 pp. Columbia University
    Press, New York.
SIMPSON, G. G. 1961. Principles of Animal Taxonomy. 247 pp. Columbia University
    Press, New York.
STANLEY, S. M. 1979. Macroevolution: Pattern and Process. 332 pp. W. H. Freeman
    and C., San Francisco.
SWEET, W. C. 1979. Late Ordovician conodonts and biostratigraphy of the western
    Midcontinent province. — Brigham Young Univ. Geol. Stud., 26, 45—74.
TEICHERT, C., SWEET, W. C. and BOUCOT, A. J. 1987. The unpublished fossil
    record: implications. — Senckenbergiana lethaea, 68, 5—19.
VAN DONGEN, P. A. M. and VOSSEN, J. M. H. 1984. Can the theory of evolution
    be falsified? — Acta Biotheoretica 33, 35—50.
WAAGEN, W. 1869. Die Formenreiche des Ammonites subradiatus; Versuch einer
    paläontologische Monographie. — Benecke's Paläont. Beitr., 2, 181—256.

JERZY DZIK

WŁAŚCIWOŚCI KOPALNEGO ZAPISU EWOLUCJI

Testowalność rekonstrukcji przebiegu ewolucji jest jednym z najważniejszych
zagadnień paleontologii ewolucyjnej. Wiąże się bezpośrednio z fundamentalnym
problemem, czy drzewo rodowe spełnia wymagania stawiane teoriom naukowym.

Jego rozstrzygnięcie wymaga precyzyjnego i jednoznacznego sformułowania zasad tworzenia hipotez o powiązaniach ewolucyjnych. Nie wystarcza konstruowanie ich przy użyciu obciążonych subiektywizmem pojęć taksonu i pokrewieństwa krwi. Obiektywnie wyróżnialne są natomiast zespoły skamieniałości w obrębie prób paleontologicznych wykazujące ciągły i jednomodalny rozkład zmienności morfologicznej (odpowiadające neontologicznym fenonom Mayra), które obejmują na tyle krótki odcinek czasu geologicznego, że przemiany ewolucyjne nie deformują w nich rozkładu zmienności. Hipotezy o stosunku pokrewieństwa przodek-potomek dotyczące co najmniej dwu takich jednostek o różnym wieku geologicznym są możliwe do obalenia (sfalsyfikowania) na gruncie paleontologii.