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THE CHRONOPHYLETIC APPROACH: STRATOPHENETICS FACING AN INCOMPLETE FOSSIL RECORD

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Abstract: Palaeontological evidence on the course of evolution is represented by fossil samples of ancient populations arranged according to their objective time-and-space coordinates. In the method of stratophenetics, morphological differences between successive samples that accumulate along a geological section are accepted as evolutionary in nature. Evolution is then reconstructed as a series of hypotheses of the ancestor–descendant relationship. Assuming a strict enough correspondence between morphological and molecular evolution, the lack of any statistically significant difference between samples neighbouring in time and taken from the same geographical location (a geological section) suggests a genetic continuity between the populations represented by them. With increasing time and space separating samples, the strength of such inference decreases, but the reasoning (referred to as chronophyletics) remains, in principle, the same. Different hypotheses of ancestry are in an unavoidable logical conflict because any lineage remains rooted in only one ancestral lineage although it may split into several descendant lineages. Testing phylogenetic trees with fossil evidence thus requires that a cladogram or phenogram is transformed into a set of hypotheses on the ancestor–descendant relationship (evolutionary scenario) and the inference has to proceed back in time (by retrodiction). The proposed methodology is illustrated with data on the Ordovician balognathid and Devonian palmatolepidid conodonts.

Key words: evolution, phylogeny, testing, methodology, conodont apparatuses.

THERE can be no doubt that the fossil record is awfully incomplete. Most organisms lack a mineralized skeleton and have little chance to be preserved as fossils; those that have such skeletons suffer from the incompleteness of time recorded in sedimentary strata. Time is missing from rocks because of either non-deposition or their subsequent removal by tectonics and erosion. What makes the situation even more painful to palaeontologists is that continental or shallow-water marine environments, which are taxonomically the most diverse, abound in sedimentary gaps. Although the record in deep oceanic sediments is more complete (McKinney 1985), it is continuously destroyed by subduction and so no deep ocean sediments older than Mesozoic are readily preserved. Nevertheless, despite all these shortcomings, in some regions and taxonomic groups the existing knowledge of ancient populations is good enough to be comparable in its completeness with data on Recent organisms. Finding a new species in a well-sampled rock succession may not be much easier than is enjoyed in invertebrate zoology or phycology.

In such extraordinary cases, the fossil evidence may be rich enough to dispense with speculation in deciphering the course of evolution. One has only to order the data stratigraphically to see the change. If at least simple biometric analyses are undertaken, such procedure is called 'stratophenetics', the term introduced by Gingerich (1979). Reliability of this inductive inference on the course of evolution suffers strongly from incompleteness of the record. It is no wonder that many neontologists go so far as to question the absolute significance of stratigraphic data and palaeontologically based reconstructions of evolution (e.g. Schaeffer *et al.* 1972; Patterson 1981). Only trees based solely on morphological data are considered by them to be of scientific value. Being so dependent on rarely achievable completeness of the fossil record, stratophenetics does not attract much interest even among palaeontologists. It is becoming completely superseded by cladistics. This is why it is rather difficult to compare efficiency of stratophenetics in approaching the real course of evolution with that of other attitudes to the fossil evidence.

The published cladistic analyses of fossils usually refer to high-rank taxa with a poor fossil record. Among rare cases of relatively complete fossil evidence used to such purpose is the work by Hengsbach (1990) on the evolution of ectocochliate cephalopods. He correctly noticed that conchs of the nautiloid *Aturia* and the ammonoid *Cymaclymania* are virtually identical in most aspects generally accepted to be of diagnostic value. The obvious conclusion, in terms of cladistics, is that the clymeniids (known only from the Famennian) and aturiids (known only from the Eocene–Miocene) are 'sister taxa' and thus had a common ancestor similar to Recent *Nautilus* (or, alternatively, to the early Ordovician *Lituites*). The only problem is that stratigraphically ordered findings document relatively well the evolutionary origin of both lineages and this hardly corresponds to the results of purely morphological analysis. The lineage of *Aturia* is rooted in generalized Cretaceous nautilids (e.g. Dzik and Gaździcki 2001) and *Cymaclymenia* belongs to a lineage initiated in the early Famennian from the tornoceratid goniatites (Korn 1992). Their common ancestor lived as early as in the early Ordovician and was morphologically distinct from either *Aturia* or *Cymaclymenia* (Dzik and Korn 1992). The methodologically interesting classical cladistic analysis by Hengsbach (1990) is thus a good case of *reductio ad absurdum*, showing the danger of neglecting stratigraphical order of fossils as the basic evidence. In the present review I use another opportunity to confront the efficiency of cladistic and stratophenetic approaches offered by the more sophisticated analysis of Donoghue (2001).

In fact, the problem of how not to lose stratigraphical information has been extensively discussed from the morphological (cladistic) point of view. Some solutions have been proposed to incorporate geological time into morphology-based phylogenetic trees as evidence additional to morphology (e.g. Harper 1976; Fisher 1994; Wagner 1998). Whenever an inconsistency between the resulting distribution of morphologies in the tree and their stratigraphical distribution emerges, this is considered to be a stratigraphical debt to be compensated for with morphological evidence of enough strength (e.g. Fox *et al.* 1999; Fisher *et al.* 2002). This attitude to palaeontological evidence, referred to as 'stratocladistics' (Fisher 1994), uses taxa defined exclusively on a morphological basis as the units of evolution. The stratigraphical extent of taxa is included subsequently (mostly because of technical reasons), at the stage when the cladogram is transformed into a phylogenetic tree with branching determined by assuming a bifurcating pattern of evolution (e.g. Benton *et al.* 1999; Benton 2001). In fact, the sister taxa relationship, i.e. the concentration of evolutionary change in speciation events, producing not necessarily an existing 'ghost range' in the introduced sister lineage, is plainly contradicted by palaeontological data (Dzik 1999). Thus, like any other variety of cladistic methodology, stratocladistics does not refer to evolution as a real world process with lineages composed of a continuity of specimens or populations sampled by palaeontologists as fossils or fossil assemblages. Instead, this is a rather abstract presentation of the pattern of distances in kinship (blood relationship) as a series of bifurcations creating 'sister taxa' (although there are attempts to make conclusions derived from cladistic analysis more realistic, e.g. Smith 1994).

All this makes the cladistic ways of reasoning involved in a rather complex interplay with the raw palaeontological data. If the method is to be used to infer the real course of past evolution from the morphology of organisms, the assumption that there is a correspondence between time and morphological difference is unavoidable. If so, fossil organisms, being geologically older and thus closer in time to the common ancestor than their Recent relatives, have a greater chance to be closer to the ancestor also morphologically, however imprecise the nature of correspondence between time and morphology. Circular reasoning, thus, emerges whenever data on organisms of different geological age are included in considerations (note that this has nothing to do with the circularity that is allegedly introduced by any use of stratigraphical evidence as claimed by Schaeffer *et al.* 1972, p. 39).

I am not ready to resolve this inherent difficulty with the method of stratocladistics. Instead of entering such methodological complexities, I propose rather to improve the opposite approach of Simpson (1976): to refer directly to the time, space and morphological dimensions of the process of evolution, i.e. to formulate hypotheses on the real course of evolutionary change ('vertical' ancestor–descendant hypotheses, instead of estimating distances in kinship-'horizontal' blood relationships) and confront them directly with the fossil evidence. This methodologically rather traditional attitude, with time and space considered the objective and definitive coordinates of palaeontological data, is discussed below. I attempt in particular to determine how much evolutionary palaeontology suffers from the incompleteness of the fossil record. Its influence on reliability of the methodology used is illustrated with examples. The fossil record of evolution of the palmatolepidid conodonts, the celebrated late Devonian guide fossils in the marginal area of the East European Platform, has been chosen for this purpose.

THE METHOD OF STRATOPHENETICS

The idea that fossils collected bed-by-bed from successive strata should allow restoration of the evolution of the lineage they represent was simple enough to grasp the attention of palaeontologists from almost the establishment of evolutionary theory (Reif 1983). Perhaps the oldest published case is the phylogeny of oppeliid Jurassic ammonites proposed by Waagen (1869). This approach immediately gained much popularity; one of the most stratigraphically strict evolutionary studies of those days is one on the early Palaeozoic hyoliths by Holm (1893). Although the use of biometrics soon followed, most of these early works have not survived close scrutiny; there are, however, a few exceptions, the famous Peterborough succession of the Jurassic ammonite *Kosmoceras* by Brinkmann (1929) being at the top of the list. Notably, such empirical studies actually pre-date the introduction of the genetically meaningful concept of biological populations. Measuring great numbers of fossil specimens, required by studies of this kind, is both time consuming and tedious and therefore in the majority of cases only rather limited numbers of characters are employed. Preferred characters are those that do not change during ontogeny, such as the size of mammalian teeth (e.g. Gingerich and Gunnell 1995), even if the information content in such traits is not especially impressive. In some cases, however, it has been possible to demonstrate profound changes in the dentition of mammals sufficient to distinguish genera (Rose and Bown 1984) or document the expansion of evolutionary novelties across the moulting stages in arthropods (Olempska 1989).

To be successfully applied, stratophenetics requires a rock section (1) that exhibits continuous sedimentation and, thus, offers a complete record of time (2) in which taphonomic conditions did not change significantly during its deposition, and (3) in which the environment was sufficiently stable that inhabiting populations were not forced to emigrate. Thus, the record has to be reliable from geological, ecological and taphonomic perspectives. This combination is rarely met in sedimentary strata, although not so rarely as is commonly assumed. Such studies are limited by patient collecting and fossil measurement and have to be undertaken in the context within which the data are to be analysed.

Unstable sedimentation

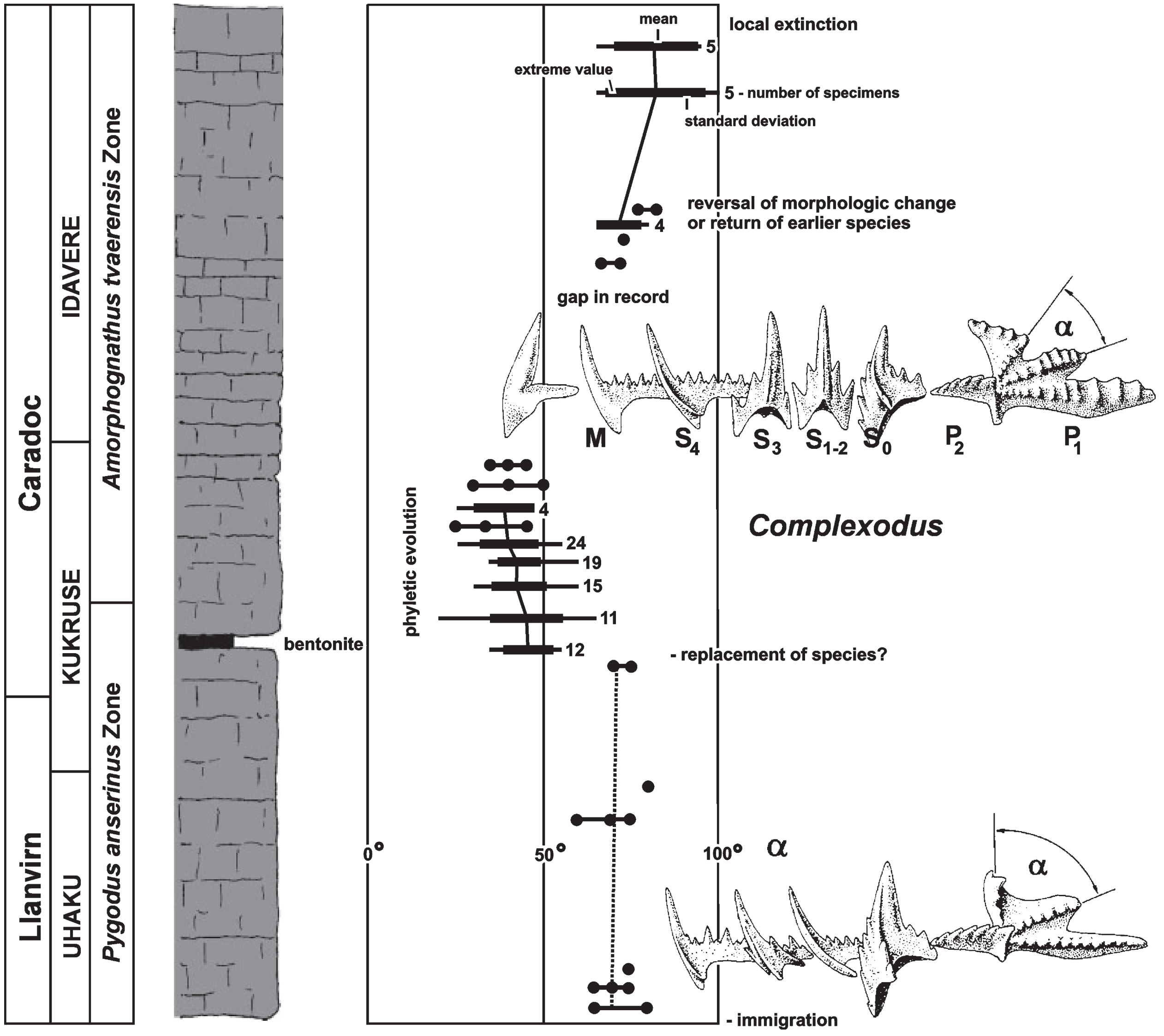
A complete record of geological time does not necessarily imply that the rate of sedimentation was uniform. Sedimentation rate variation may be dramatic in parallel with changes in primary productivity, when producers of rock-making calcareous skeletal remains (e.g. coccoliths) are replaced by those with organic skeletons (e.g. dinoflagellates). Decay of their remnants in the sediment increases its acidity, which dissolves calcareous grains (Ernst 1982; Ekdale and Bromley 1984). The effect is a misleading exaggeration of the rate of ecological or evolutionary change recorded in the rock. There are several cases of such distortion of the time record connected with black clay episodes within limestone successions (e.g. Dzik 1997). To some degree an increased density of sampling may help in coping with the unstable sedimentation rate if there is just stratigraphic condensation and not a complete lack of fossil sediment.

Taphonomic bias

The main difficulty with stratophenetics is that there is a significant difference between a complete record of geological time and a complete record of evolution. Taphonomy is the second obstacle. Only a small part of skeletal remains that were originally present on the sea bottom are fossilized. Of mineralogically different skeletons, those with the greatest potential to be fossilized are phosphatic teeth and bones that preserve well in carbonates but also in siliceous and clay-dominated sediments as long as the sedimentary environment was not too acidic. This makes vertebrates of much potential value in evolutionary studies. Unfortunately, with the exception of conodont and mammalian teeth, their dispersed skeletal elements are not sufficiently distinctive and numerous to allow the application of stratophenetics. Calcitic tests of foraminifers have been widely used in such studies (e.g. Grabert 1959; Berggren and Norris 1997) but aragonitic ammonite conchs, although restricted in their occurrence to specific facies, are somewhat more informative morphologically (e.g. Murphy and Springer 1989; Dzik 1990*a*). Well-preserved siliceous fossils are relatively rare; among them radiolarians are the most convenient subjects of stratophenetic studies (e.g. Kellogg 1975). Some uncertainty remains, however, regarding whether the biological species concept is applicable to them if interbreeding has not been documented in their Recent relatives. The same uncertainty exists for collagenous skeletons of pelagic graptolites (e.g. Lenz 1974; Springer and Murphy 1994), which are known to have lost sexual dimorphs (bithecae), probably representing males, early in their evolution.

Migrations

There are also sudden environmental changes that punctuate the distribution of organisms even in those parts of the stratigraphic column where neither apparent stratigraphical discontinuity nor taphonomic change is visible. This is because gaps in the fossil record of evolution may also result from ecologically controlled migrations (Text-fig. 1; Dzik 1990*b*). This aspect of incompleteness of the fossil record can be overcome to some degree by increasing sample sizes: unless the faunal change is drastic and truly instaneous, immigrants appear first as rare specimens contributing little to the fossil assemblage. Frequency distributions of lineages within the stratigraphic column tend to have a fusiform shape, with numbers of specimens gradually increasing with immigration and similarly



TEXT-FIG. 1. Record of evolution in a stratigraphically complete section discontinuous in effect of ecologically controlled migrations, as exemplified by the *Complexodus* lineage from Mójcza in the Holy Cross Mountains, Poland (from Dzik 1994, modified).

decreasing with migration of the habitat to another geographical location (Dzik 1984). In fact, distinguishing ecological change from evolution is not easy even in stratophenetic studies on fossil groups with an extremely good fossil record (e.g. Dzik and Trammer 1980).

Basic assumptions of stratophenetics

Whenever a section more or less complete in all aspects is available, a series of samples taken bed-by-bed of the rock offers the raw material for a stratophenetic study. Each of the ancient populations represented by fossils from neighbouring beds is in the same geographical place but separated by some distance of geological time. Although the method looks so obvious and simple, there is some implicit philosophy behind it. It has to refer to a series of assumptions, especially when sexual organisms are considered. Thinking in terms of population variability and its presentation in any possible way is then necessary. Stratophenetics requires not only stratigraphically dense sampling but also samples large enough to show a range of morphological variability in ancient populations arranged in lineages.

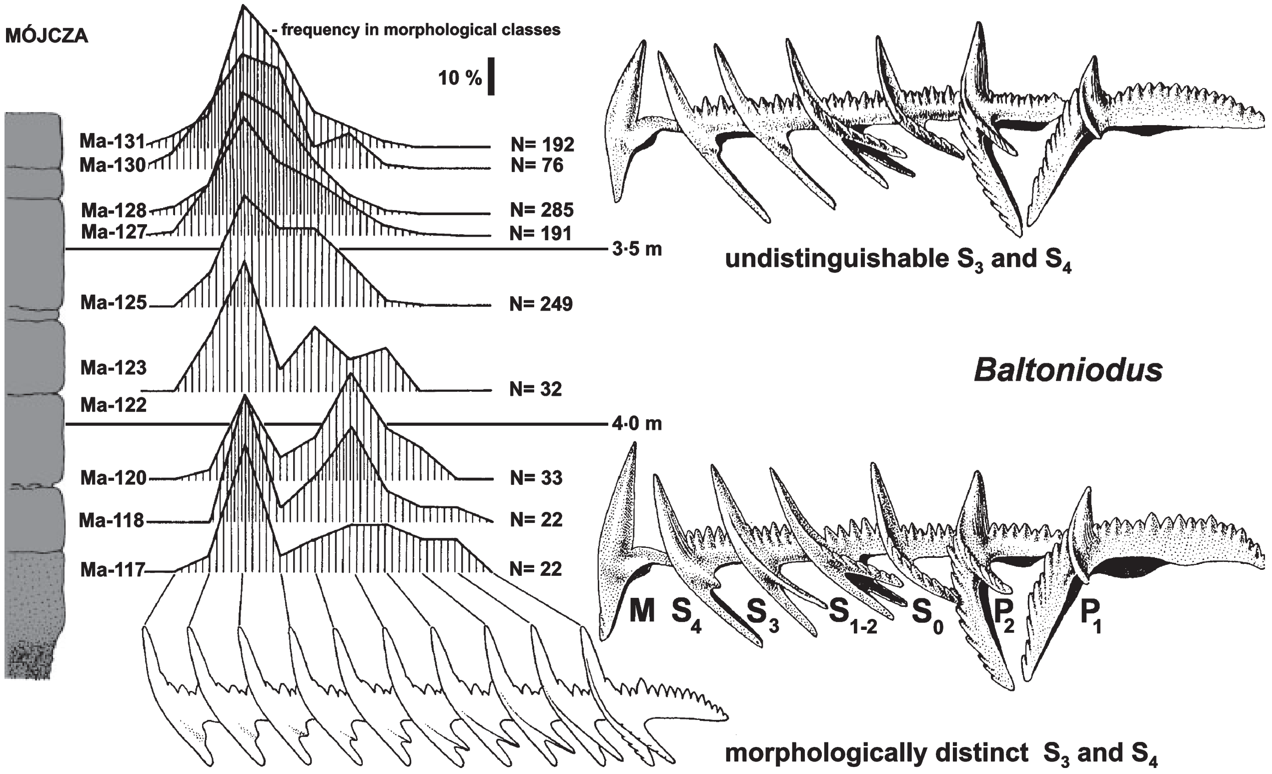
While interpreting the raw evidence it has to be assumed that (1) the unimodal distribution of all taxonomically significant characters proves a free interbreeding (panmixy) within the population represented by a sample; (2) a morphological similarity of samples close in time and space (neighbouring samples) results from a gene flow from the older one to the younger; and (3) a significant difference between the first and last samples of a stratigraphically ordered series is an expression of the evolution. This is based on an understanding of the population biology of Recent organisms and cannot be substantiated by palaeontological evidence alone. In fact, similar (if not the same) assumptions are necessary to undertake any taxonomic work based on morphology. In neontology, not unlike palaeontology, virtually all our knowledge of living populations is derived from studies of samples, not uncommonly taken at times different enough to introduce the problem of time averaging, or stored long ago in a museum. There is thus hardly any fundamental difference in methods of study of fossil and Recent organisms, although the fossil evidence has obvious limitations. As long as one accepts this as reasonable, if a series of insignificant differences between neighbouring samples accumulate along a geological section to result in a substantial difference between the basalmost and topmost populations, one is dealing with the process of evolution. This is how evolution can be observed from fossils.

Extraction of the evolutionarily meaningful information from a continuous fossil record of evolution at the population level is relatively easy in principle. Despite all the preoccupation of evolutionary biology with taxa ('the taxic approach'; Levinton 2001) the course of evolution can be palaeontologically documented without reference to any discrete units. Taxonomic nomenclature is irrelevant to stratophenetics. Only samples are of importance: more precisely, the information they offer on unimodal units of variability that correspond either to ancient populations or to discrete polymorphs, for instance sexes (palaeophena; Dzik 1990*a*). Their identification and presentation technically can be made in quite an intuitive way, but also by counting frequencies in morphological classes (Text-fig. 2) or by applying more elaborate morphometrics (see literature data recently reviewed in, e.g. Dzik 1990*a*, Sheldon 1996 and Levinton 2001). Obviously the process remains the same irrespective of the approach to the raw data used in its reconstruction. The way of measuring and presenting results may only help in understanding what actually happened in the evolution of a lineage and to make the case more convincing.

To overcome limitations of the method of stratophenetics while choosing an object of study one has to look for fossils that occur in great numbers, in rocks possibly complete stratigraphically, being also possibly immune to local ecological changes and sedimentary regime controlling taphonomy. This is why pelagic marine organisms with well-mineralized skeletons generated interest from the beginning of evolutionary studies in palaeontology. Initially ammonites occupied the centre of this research (e.g. Waagen 1869; Brinkmann 1929; Dommergues 1990), but were subsequently replaced by microscopic foraminifers (e.g. Grabert 1959; Pearson 1996; Berggren and Norris 1997), radiolarians (Kellogg 1975) and finally conodonts (e.g. Murphy and Springer 1989), the last of which have appeared unbeatable as a source of evolutionarily meaningful information. These early chordates owe their special value to easy chemical extraction from the rock matrix, more than 300 myr duration in the fossil record (Sweet 1988), the almost cosmopolitan distribution of many species and the great morphological information content of their statistically reconstructed apparatuses. Stratophenetically studied temperate and cold-water conodont lineages from the Ordovician (Dzik 1990*b*, 1994) and tropical lineages from the Carboniferous (Dzik 1997) have provided valuable information on the pattern of evolution at the population level. No correspondence between changes in environment recorded by fossil associations and evolutionary change in particular lineages has been identified (Dzik 1990*b*). It does not appear that environment or climate had much influence on the pattern of evolution, although there are claims to the contrary (Sheldon 1990). Problems with completeness of the fossil record are especially apparent in the rock sections representative of the tropical Late Devonian (Dzik 2002). This is why they have been chosen here to illustrate various aspects of the fossil record.

APPLICATION OF STRATOPHENETICS TO FAMENNIAN PALMATOLEPIDID CONODONTS

The palmatolepidids show the most structurally complex apparatuses among all the post-Ordovician conodonts. They are convenient objects for evolutionary studies also because of their taxonomic diversity, being represented in the Famennian by several sympatric species. In traditional biostratigraphical studies only the posteriormost platform P_1 elements of the apparatus are used to determine species, all of them being classified in the single genus *Palmatolepis*. Ironically, it has been convincingly shown that the fastest evolving and taxonomically most sensitive are not the platform elements (Klapper and Foster 1993; Metzger 1994; Dzik 2002) but those technically most difficult to collect in reasonable numbers, the anteriormost M elements and the medial S_0 element. Nevertheless, complete apparatuses undoubtedly offer much more biologically significant information than single robust elements, even if the latter are easier to collect. In terms of the standard apparatus taxonomy, as used for the Ordovician or Triassic conodonts, the palmatolepidids deserve separation into at least a few genera (Dzik 1991*b*). Some of the non-platform elements in their apparatuses show a profound morphological difference in number and orientation of processes, as well as their denticulation



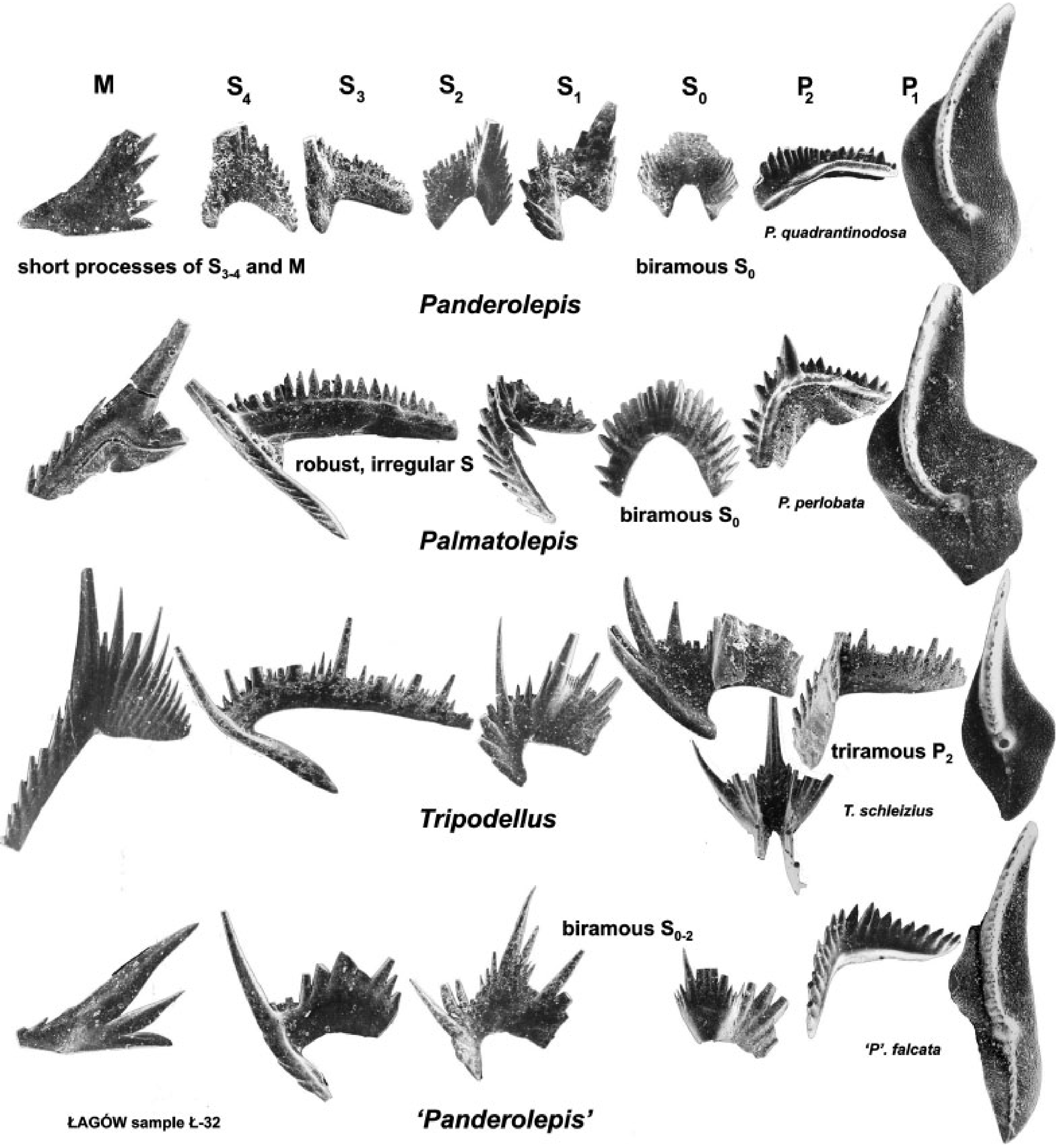
TEXT-FIG. 2. Gradual evolution of the conodont apparatus structure shown at the population level, without any metrics but by counting the frequency of particular classes within a morphological series, as exemplified by the early Ordovician (late Arenig) *Baltoniodus* lineage from Mójcza in the Holy Cross Mountains (from Dzik 1994, modified). Note that initially the frequency distribution is bimodal, with S_3 and S_4 locations morphologically distinct; in the course of evolution they became more and more alike, and in strata above this section are virtually undistinguishable.

(Text-fig. 3), far exceeding that observed in other Late Devonian genera, even those most widely defined.

The small area of the Holy Cross Mountains in central Poland, about 20 km wide, is one of many places where the complex evolution of the Palmatolepididae is well recorded (Text-fig. 4). This marginal part of the East European Platform was tectonically quiet in the late Devonian and its limestone strata are rich in conodonts, relatively little altered thermally and well preserved. Some of the sections there are thick enough to rely exclusively on the principle of superposition in stratigraphy. They represent various sedimentary environments and therefore may differ strongly from each other in composition of conodont assemblages because of the ecological sensitivity of many species. This makes homotaxy unreliable even over short distances, although this method of correlation may otherwise allow a high time resolution. The age correlation has to be based on probable phyletic transitions in lineages of index fossils, a type of reasoning which is reliable but of low resolution (Dzik 1995).

The stratigraphical condensation and punctuation of the record by numerous gaps in sedimentation limit evolutionary studies in the Famennian of the Holy Cross Mountains. The record is complete in the deeper parts of the local basin but fossils of conodonts are not common enough there to allow apparatus studies, probably both a result of a higher sedimentation rate and lower biological productivity of the environment. Immigration of new lineages and terminations of others, possibly replaced as a result of ecological competition or simply by random lateral environmental shifts, is a feature of the succession of assemblages (Dzik 2002).

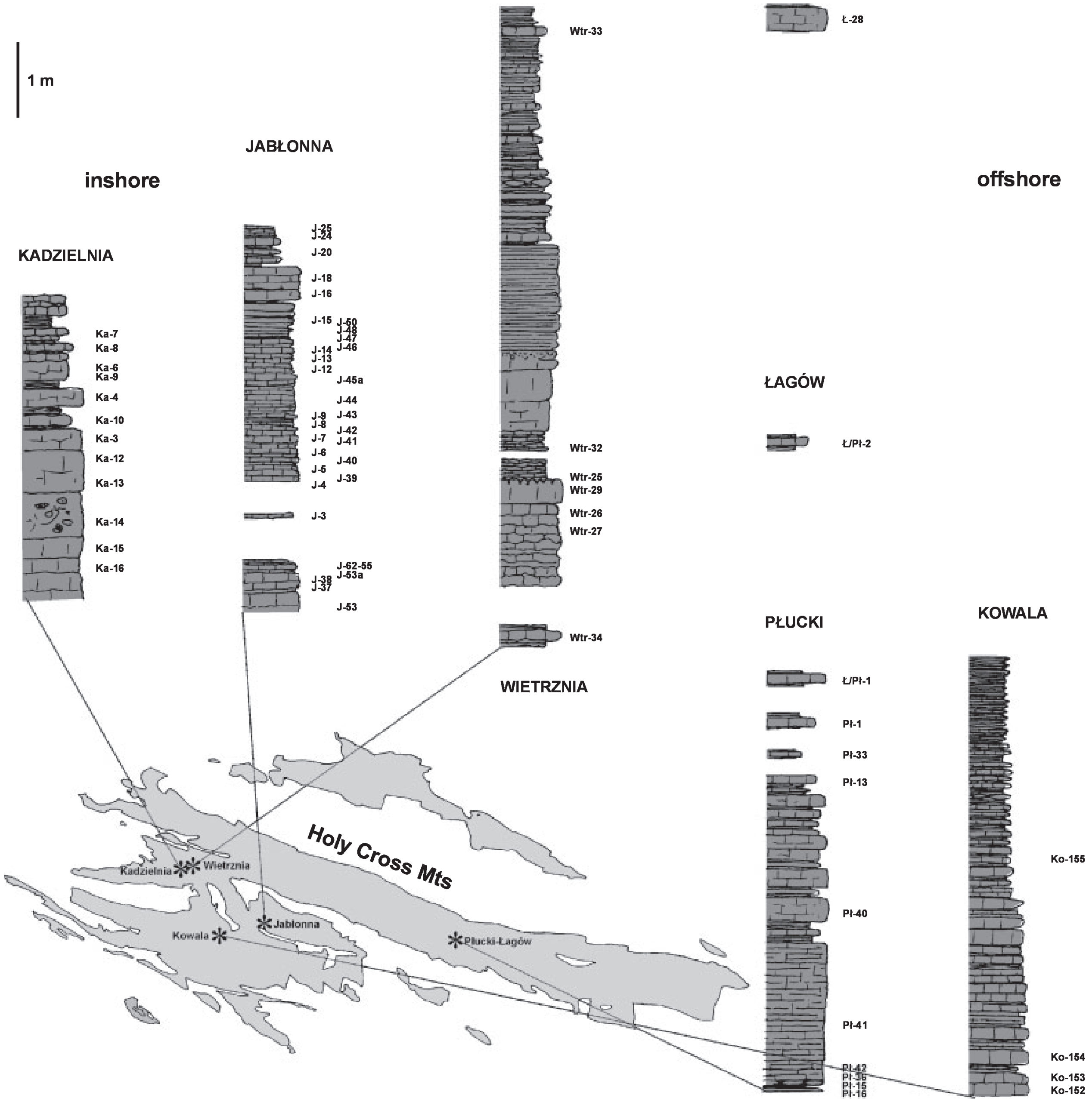
Despite all the shortcomings of the empirical evidence on evolution, some examples of a successful application of stratophenetics to the Famennian conodonts of the Holy Cross Mountains can be offered. Among the lineages most persistent and well represented by numerous specimens is that of the early *Tripodellus* (Text-fig. 5), at the stage of evolution prior to the development of its diagnostic triramous P_2 elements (the generic affiliation of these populations thus remains arbitrary). Some measuring has been done on the platform P_1 elements from a section at Jabłonna. The strata there are poorly exposed, being deeply weathered and overgrown with forest vegetation. As a result, only sets of samples separated by gaps are available. Noteworthy within each of the sets is that



TEXT-FIG. 3. Apparatuses of the Famennian genera of the Palmatolepididae; statistical reconstructions based on material from the Holy Cross Mountains.

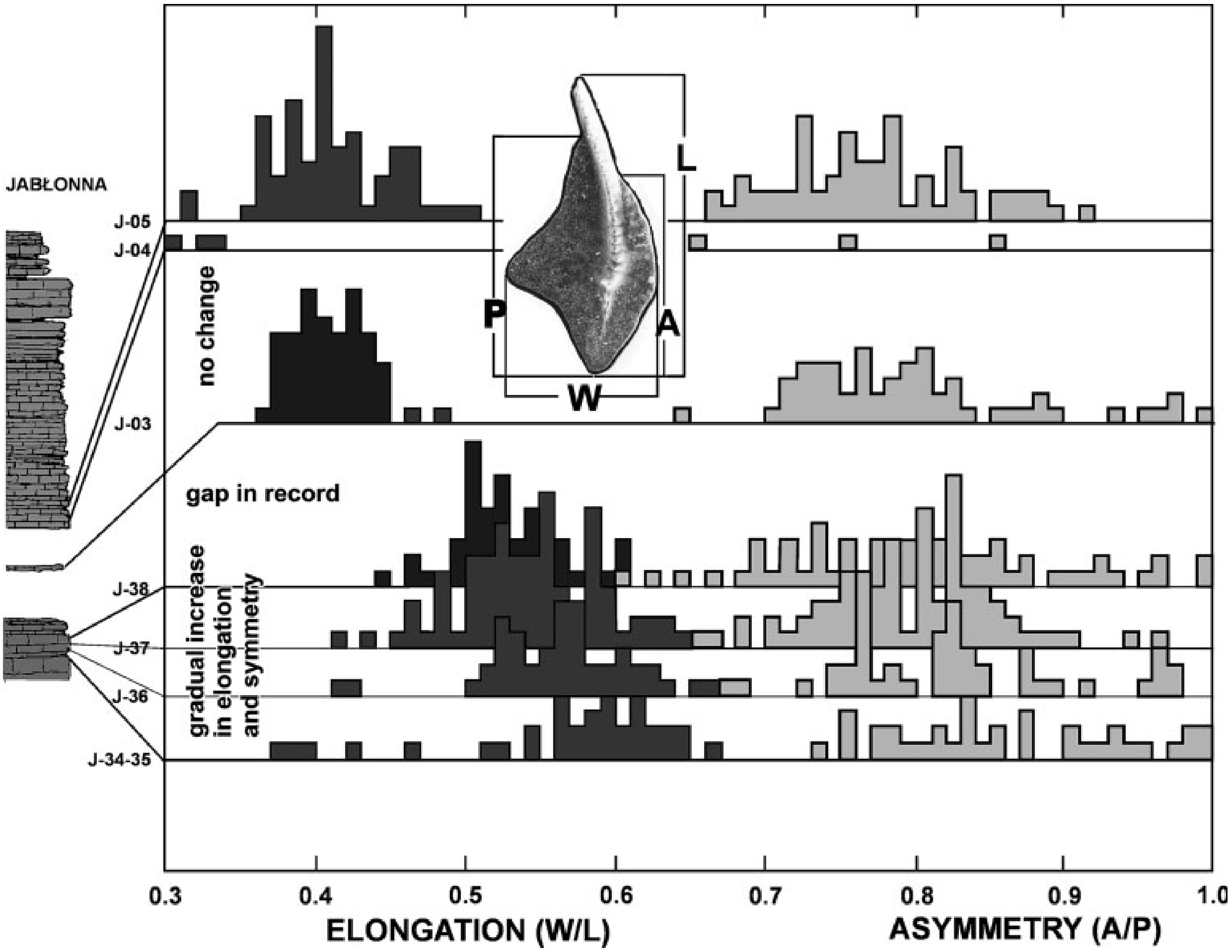
the change in the distribution of platform width is continuous. All sets together show the apparent general trend: an increase in elongation, which continues well above the segment of the lineage represented at Jabłonna.

Even if the sparsely distributed single examples of *Tripodellus* or their sets are considered, the differences between neighbouring samples do not appear to be especially significant, but the extreme samples are quite dissimilar. In many cases it is enough to arrange them in a stratigraphical order to see this (Text-fig. 6). Sometimes, despite the stratigraphical distance between samples, the variability of some characters overlaps. For instance, rare triramous P_2 elements occur significantly below the level of their exclusive occurrence.



TEXT-FIG. 4. The sampled sections of early Famennian deposits in the Holy Cross Mountains, with their relative position indicated on a map showing the extent of Devonian exposures. Lithological columns are arranged according to their time relationship; no formal zonation is attempted. Note a profound facies differentiation over short distances; condensed sections in the centre of the area show the geological time record punctuated with gaps; in more complete sections to the south fossils are generally rare, probably because of low biological productivity and/or a high sedimenation rate.

The evolution within particular lineages of *Tripodellus* or any other Famennian conodont genus can thus be represented as a series of ancestor–descendant hypotheses concerning pairs of samples possibly close in time and space. Any such hypothesis can be tested by increasing the density and size of samples if the ancient populations are represented in rocks with fossils (frequently they are). It is possible to increase resolution to the level at which stratophenetics can be applied. Of course, this requires a lot of work, and so does not seem practical, but potential testability of an ancestor–descendant hypothesis is obvious in this particular case.



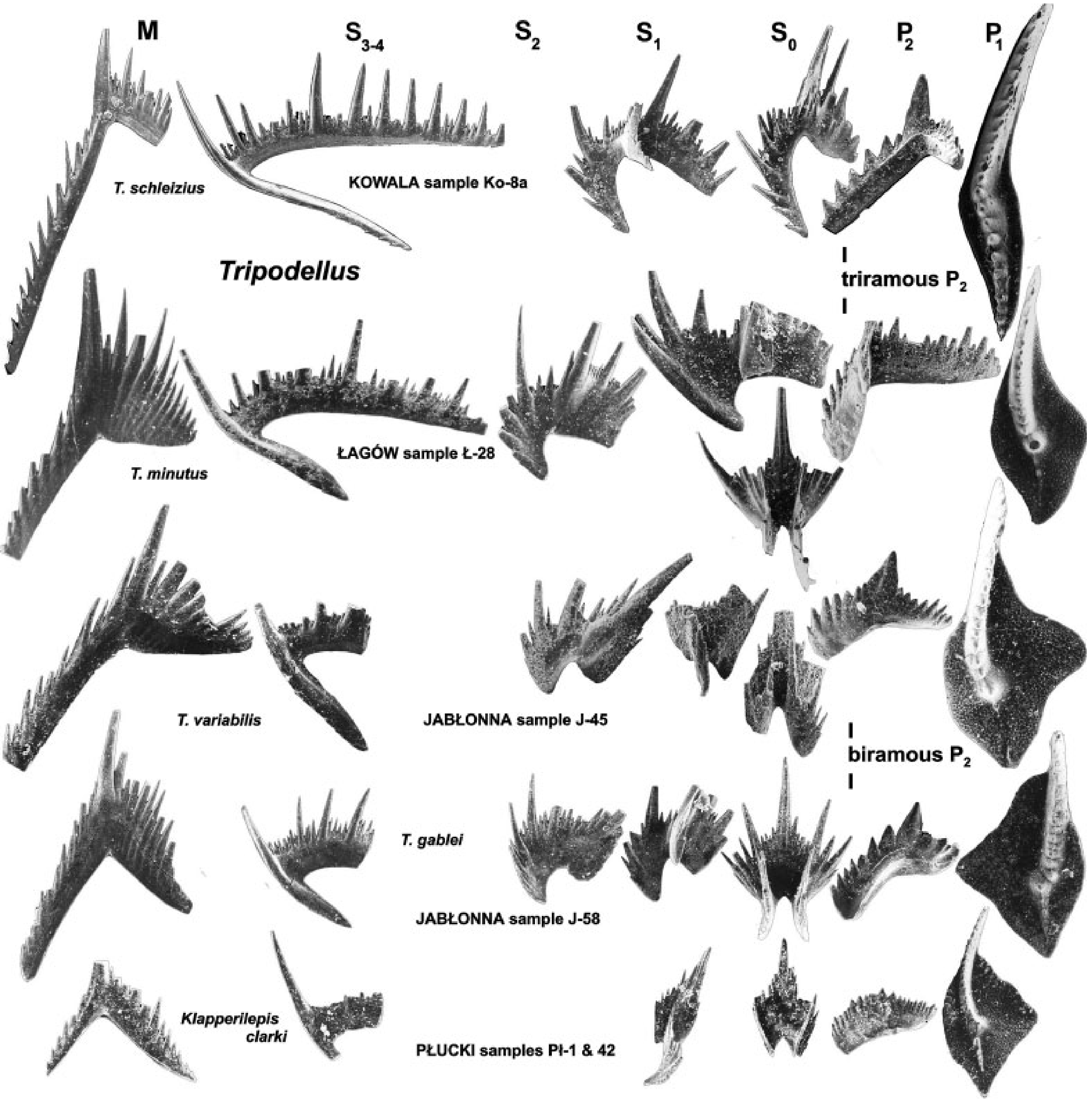
TEXT-FIG. 5. Stratophenetics of a segment of the early *Tripodellus* lineage in the Jabłonna section, Holy Cross Mountains. Note that the sampling is generally incomplete and only isolated sets of samples separated by gaps (mostly a result of poor exposure) are available; continuous changes are documented within particular sets and they seem to be consistent with the apparent general trend.

The conclusion most important to the subject of this review from cases such as Jabłonna or Mójcza (Text-figs 1, 5) is that there is no methodological difference between methods of reconstructing evolution based on complete and incomplete fossil evidence. It is just a matter of limitations in the availability of data. Stratophenetics appears to have a more general application to the extreme case.

Wide temporal gaps in the record may hide reversals and changes in the direction of evolution. However, there is no reason to restrict evolutionary studies to single geological sections and the missing evidence can be recovered potentially by additional sampling in other locations. At the very least, data from exposures in proximity have to be assembled. However, this introduces a spatial dimension to considerations, which forces the limits of stratophenetics to be crossed.

GEOGRAPHICAL DIMENSION OF EVOLUTION

The most obvious aspect of the geographical dimension of evolution is the phenomenon of migration of lineages. In any single section this produces a record that looks as if a cloud of organisms passed overhead, dropping to the sediment a rain of skeletal remnants that give the quantitatively presented stratigraphical range of a lineage its fusiform aspect (Dzik 1990*b*). Migrations thus influence the record in any place, but their documentation requires data from several localities. This aspect of the spatial distribution of organisms is of particular importance in the evolution of sexual organisms. Expansions and contractions of the geographical range of an originally panmictic population may result in its spatial split into daughter lineages that separately evolve within their own habitats. This may



TEXT-FIG. 6. Succession of the *Tripodellus* lineage apparatuses arranged according to their stratigraphical order in the Holy Cross Mountains. Although in places the phylogeny of this clade is rather complex, with up to three sympatric species represented in the area, a general pattern of the main chronomorphocline is apparent. Usually in the populations their variability overlaps between neighbouring pairs of samples, suggesting genetic continuity.

be temporal, followed by subsequent homogenization of the populations through hybridization, but may also continue for long enough to allow a genetic barrier to develop, making reunification impossible. This is actually a description of the classic model of allopatric speciation (e.g. White 1968). Other ways to develop genetic isolation are a possibility but the available evidence (e.g. Bush 1994) remains controversial; however, there can be little doubt that in the real world of highly differentiated environments, the process of evolution of sexual organisms is very complicated in its geographical dimension (e.g. Avise *et al.* 1998).

Stratophenetics is a method of studying the phyletic evolution of lineages; their splitting is not accessible as long as only geological time and morphology are considered, not geographical space. An allopatric speciation cannot be observed in any single section. The final effect of a speciation can be noticed only when the newly established lineage immigrates. It has to be borne in mind, however, that the replacement of one population by another may as well occur before as after the allopatric speciation event they were subjected to. This distinction does not need to be expressed in morphology. If the populations can interbreed despite already developed morphological differences (but not genetic isolation), this smooths the change, but a sudden change in morphology may take place within the lineage, a change having nothing to do with speciation. The opposite occurs when one of the sibling species is replaced by another; no morphological change exists to be detected, although speciation has already taken place. In fact, the process of speciation is thus out of reach of not only stratophenetics but also palaeontology as a whole (Dzik 1991*a*).

Are species (and speciation) really of so great a significance in attempts to understand the phylogeny? This depends on what one actually wants to know. It could be argued that it is most important to see the process of anatomical and physiological transformations, mostly expressed in the morphology of organisms, not just count units of interbreeding.

The choice of one of these attitudes may depend on what material is dealt with. The biological species concept offers in principle the objective unit of diversity for students of Recent organisms. In palaeontology species have a dual, objective/arbitrary nature being 'objective evolutionary units on a time plane and at the same time arbitrary units crossing time planes' (Gingerich 1985, p. 29), which means that as long as one is studying fossil organisms from the same sample, same locality or from different sites not significantly different in geological age (thus, essentially on the same time plane) the concept of species may be used in its objective sense. Procedures of applying population and species rank taxonomy for palaeontological purposes are widely used (e.g. Dzik 1990*a*). However, this can be done only when obvious morphological differences developed between species, which tends to be the case when sympatric species assemblages are considered (e.g. Brown and Wilson 1956). If one wants to classify allopatric populations at the species level, numerous difficulties have to be faced. To overcome this, the precise age correlation of sections is necessary and a series of transitional localities available to show that morphologically different and geographically distant populations represent either end-members of a morphocline or spatially uniform separate species. This can be proven if their ranges overlap and both species occur sympatrically in marginal localities (Dzik 1979).

The important limitation on the usefulness of the biological species concept is that it refers to reproductive isolation, not morphology, as the defining aspect. In the case of allopatric units, speciation events and species distinction do not need to have anything to do with ecological adaptations or any morphological difference (de Vargas and Pawlowski 1998). The very existence of allopatric sibling species is thus of little importance to the evolution of ecosystems and the impact of 'new taxonomy' based on genetic instead of morphological distinctions may not be so great as is frequently claimed (e.g. Knowlton and Jackson 1994). Only after the species meet does niche partitioning becomes a must if more than one species is to survive. Although this may sound too radical, identification of speciation events in palaeontology is not only impossible technically but also of limited importance to the evolution of communities and their ecosystems.

In fact, speciation events are not necessary for evolution to occur. Fossil evidence convincingly shows that there is no connection between speciation events and evolution, although obviously no speciation is possible without evolutionary change. This is self-evident also on the basis of neontological observations: there is no correspondence between the number of species in a taxonomic group and the rate of its evolution. Our own monospecific lineage of *Homo* demonstrates this well.

There is no reason to assume that migrations occur immediately after speciation is completed. To determine the appearances and disappearances of taxa in rock sections is thus a waste of time from the evolutionary point of view. Both events are ecologically controlled and have nothing to do with evolution (Dzik 1994). At best they allow the correlation of ecological events in different sections. They definitely do not indicate the time and location of the speciation events. To see what happened in the evolution of a lineage before its immigration one has to look for a geological section in the geographical area of its origin. Obviously, to do this one has to determine their phyletic evolution stratophenetically.

Typically, any long-enough segment of the evolution of a fossil community appears to be a mixture of evolution in place and immigrations of allopatrically originating lineages (Text-fig. 1). Such is the Famennian evolution of the palmatolepidid conodonts in the Holy Cross Mountains. An interesting aspect of this interplay of local change and immigration is its influence on the population variability of morphological characters. This has been documented biometrically in the earliest Famennian, when the initial stage in the diversification of these conodonts took place.

SPECIATION AND MIGRATION OF FAMENNIAN PALMATOLEPIDIDS

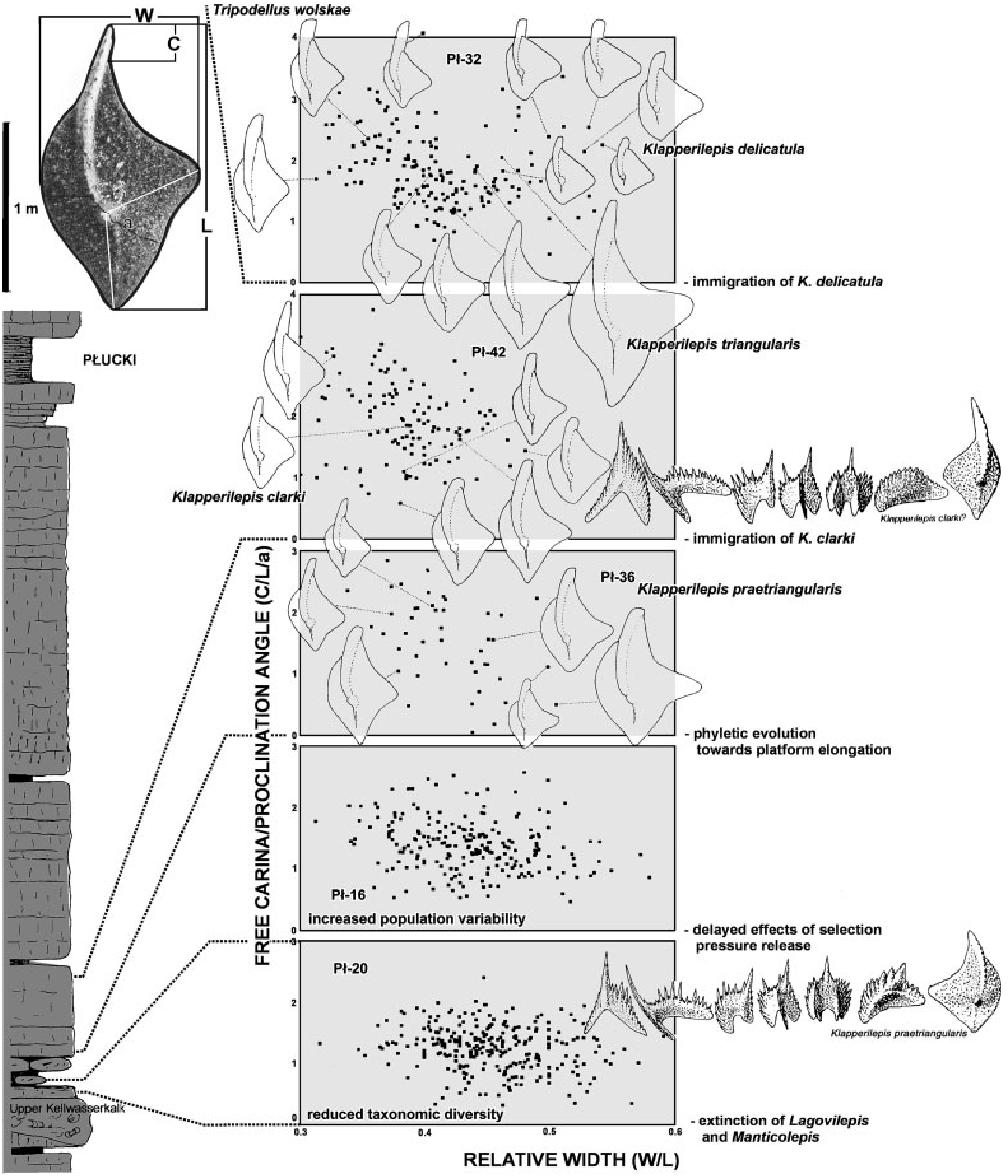
Unlike their chronologically preceding relatives, the earliest Famennian palmatolepidid faunas, as shown by their apparatuses reconstructed by Schülke (1999), were of a rather low morphological diversity. Their diversification probably started from the three lineages documented in the upper part of the most complete section transitional from the Frasnian to Famennian at Płucki (Text-fig. 7, sample Pł-32). The extreme variability of platform elements in the early palmatolepidids makes biometric discrimination of species difficult. Some important characters, like the raising upward of element tips and more or less horizontal disposition of the platform margin are difficult to measure. Anyway, even an imperfect presentation allows an estimate of the extent of population variability in particular samples (Text-fig. 7). The morphology of the platform in P_1 elements ranges there from relatively narrow and planar (typical of later members of the lineage of *Tripodellus*), through sinuous and extended up to the dorsal end of the element (typical of the *Palmatolepis* lineage), to wide but short (*Klapperilepis delicatula*).

Below in the Płucki section, only two lineages are represented, documented unequivocally by the associated M elements of two kinds (Dzik 2002). One of them is of a generalized morphology possibly inherited from the Frasnian *Klapperilepis praetriangularis*, the other shows a fan-like arrangement of denticles on the external process, similar to those attributed to '*P.*' *arcuata* by Schülke (1999; the type population of the species is of significantly younger age). Although there is no doubt that two species are represented, there is a completely smooth transition in the morphology of platform P_1 elements. Specimens with a relatively narrow platform and transverse orientation of the angular platform lobe seem to form a separate cluster. Close to the base of the Famennian, where only one type of M element occurs, the frequency distribution of their shapes is clearly unimodal. The modal morphology is the same as in the related populations from higher samples. Nevertheless, the range of variability is much wider, encompassing not only most of the range occupied by the younger species with narrower platforms but also morphs with a very wide platform, which also occur in the latest Frasnian. In fact, the earliest Famennian and latest Frasnian populations of the *Klapperilepis* lineage do not differ from each other in their apparatus morphology (Dzik 2002).

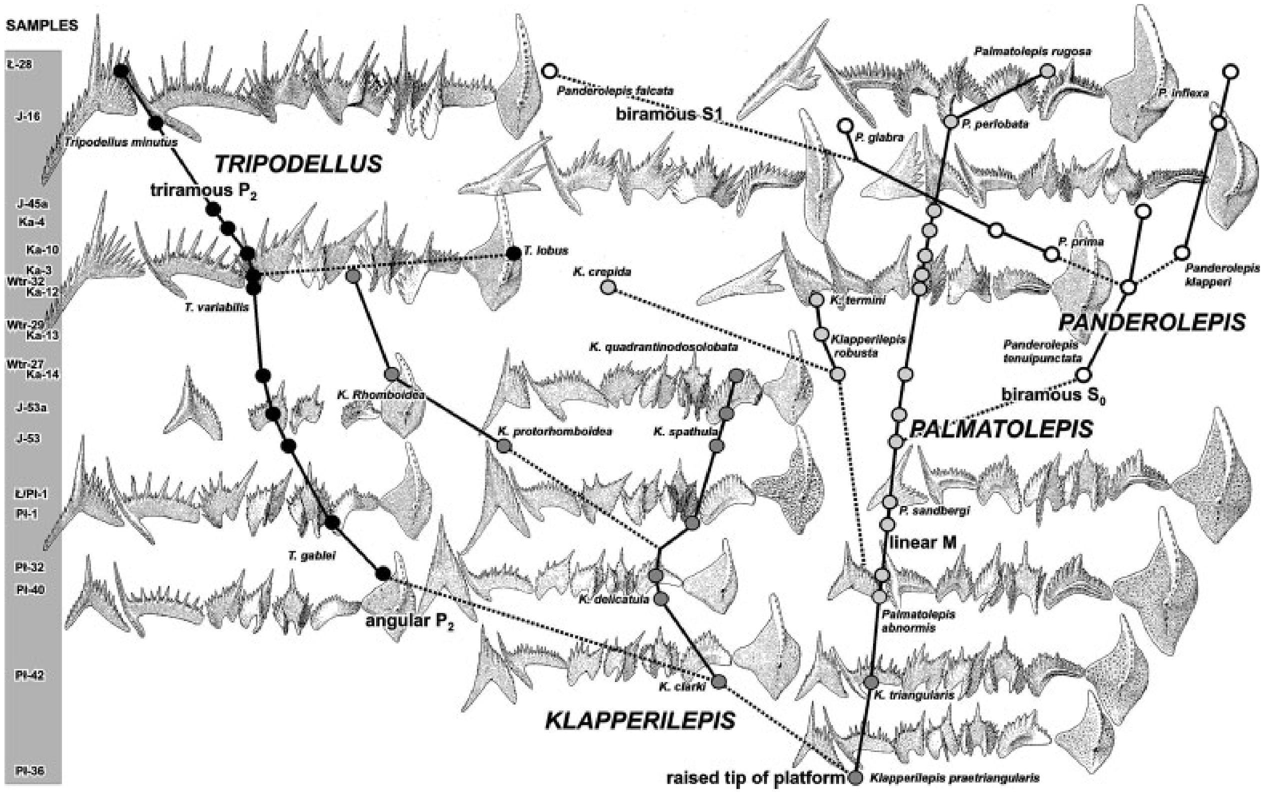
Two aspects of this succession are of interest from an evolutionary point of view: the continuity across the Frasnian/Famennian boundary and the decrease in population variability within the same lineage after additional species appeared in the assemblage. The *Klapperilepis* population from the earliest Famennian, where it occurs alone without any other palmatolepidids, is morphologically identical to that of the latest Frasnian Upper Kellwasserkalk. The rather profound environmentally controlled faunal changes marked by the disappearance of the typically Frasnian lineages of *Lagovilepis* and *Manticolepis* had, thus, no influence on the phyletic evolution of the *Klapperilepis* lineage except for a somewhat delayed increase in its population variability. The latter may possibly be an effect of relief from competitive influence of other palmatolepidid species. They were rather distantly related and this is probably why their extinction from the assemblage had rather minor consequences. When the earliest Famennian assemblage was enriched in closely related species by immigration from the areas of their allopatric origin, the decrease in population variability of *K. praetriangularis* became more apparent. The platform elements of the species new in the area covered the range of shapes not much different from that represented originally by just the single ancestral species. The local population of *K. praetriangularis* was probably forced to adapt to the new conditions of partially overlapping ecological niches. The ecological phenomenon of character displacement (Brown and Wilson 1956) has already been invoked to interpret similarly profound changes in the population variability of Carboniferous conodonts (Dzik 1997, p. 70). Perhaps also in this case the competition between sympatric species reduced their variability.

Thus, in the evolution of Famennian palmatolepidids in the Holy Cross Mountains only one local lineage was represented at the beginning of the Famennian and new lineages emerged sequentially by immigration from their places of origination. Almost certainly they evolved there in a similar way as the lineage that shows a complete record in the Polish sections, that is by gradual morphological change and under competitive pressure from immigrants. This offers support for the traditional view of the evolution of the palmatolepidids: earliest Famennian recovery after extinction.

The evolution of the palmatolepidids was a process of ramification of their phylogenetic tree but the points of bifurcation invariably appear to be out of reach of the palaeontological method (Text-fig. 8). The method allows much confidence while tracing particular lineages but the origination of lineages remains obscure. To identify their origin one has to propose a hypothesis on their origin and look for ancestry in geographically distant places. If such a record is found, stratophenetics can be used. The inference on identity of the ancestor has to be based not only on its morphology but also on geological age (older than the base of the lineage documented elsewhere) and geographical location (close enough to make physical continuity between lineages likely). The inference proceeds back in time. This is one of the basic aspects of the method. The second is that tested hypotheses do not refer to taxa but to ancient populations. This general approach is specific for palaeontology in that it refers directly to ancestor–descendant hypotheses and uses geological time as the basic evidence. It is here referred to as 'chronophyletics'.



TEXT-FIG. 7. Populations of the earliest Famennian Palmatolepididae in the Holy Cross Mountains (from Dzik 2002, modified). The latest Frasnian and earliest Famennian populations of *Klapperilepis praetriangularis* did not differ in the morphology of their apparatuses and the lineage evolved subsequently in place. Immigration of allopatrically originating, closely related new species influenced the population variability (character displacement). The assemblage became richer in species although the complete range of morphologies initially did not increase very much. Eventually, as a result of subsequent divergent evolution generic rank differences emerged.



TEXT-FIG. 8. Famennian phylogeny of the Palmatolepididae based on fossil evidence from the Holy Cross Mountains. Reference populations (circles) with statistically well-documented apparatus structures are connected by hypothetical ancestor–descendant relationships (lines); hypothesized allopatric speciation and subsequent immigration events are indicated by broken lines. Note that only phyletic evolution can be potentially proven by increasing the density of sampling; speciation events are speculative irrespective of the quality of the record as they almost certainly occurred allopatrically in all cases. Their first appearances in geological sections are invariably the result of ecologically controlled immigration and have nothing to do with their evolutionary origin.

CHRONOPHYLETIC APPROACH TO THE FOSSIL RECORD

Stratophenetics may potentially offer definite evidence on the course of evolution at the population level. However, to be sure that one is dealing with evolution, a complete fossil record is required, from geological, ecological and taphonomic points of view. The normal situation in palaeontology is far from that. The evidence is frequently limited to single specimens, sparsely distributed in time and space and does not offer characters that are truly diagnostic. How to proceed then with such data to keep presentation of hypotheses on the course of evolution testable, despite the incompleteness of the record?

The answer offered here derives from the observation that there is no fundamental difference between complete sampling, sets of samples separated by gaps and quite isolated pieces of the record. In principle the hiatuses in time and space can be filled in future. Obviously, it would be unrealistic to expect that the assembled evidence will ever be complete enough to allow definite tests of hypotheses even on the phylogeny of the most privileged pelagic organisms equipped with mineralized skeletons. Only a small fraction of all those billions of individuals that lived in the geological past were fossilized and we do not have enough technical facilities even to document evolution of those that have a relatively complete fossil record. Evolutionary inference unavoidably has to be based on less abundant material, and commonly just on single crucial findings. Most of the description of the course of evolution will remain hypothetical or even conjectural. This should not result in any discomfort as long as the potential remains to test hypotheses on the ancestor–descendant relationship with the fossil evidence. Moreover, such hypotheses are not only testable but can even be refuted by evidence. They are falsifiable and this makes evolutionary studies in palaeontology truly scientific.

Falsifiability of ancestor–descendant hypotheses

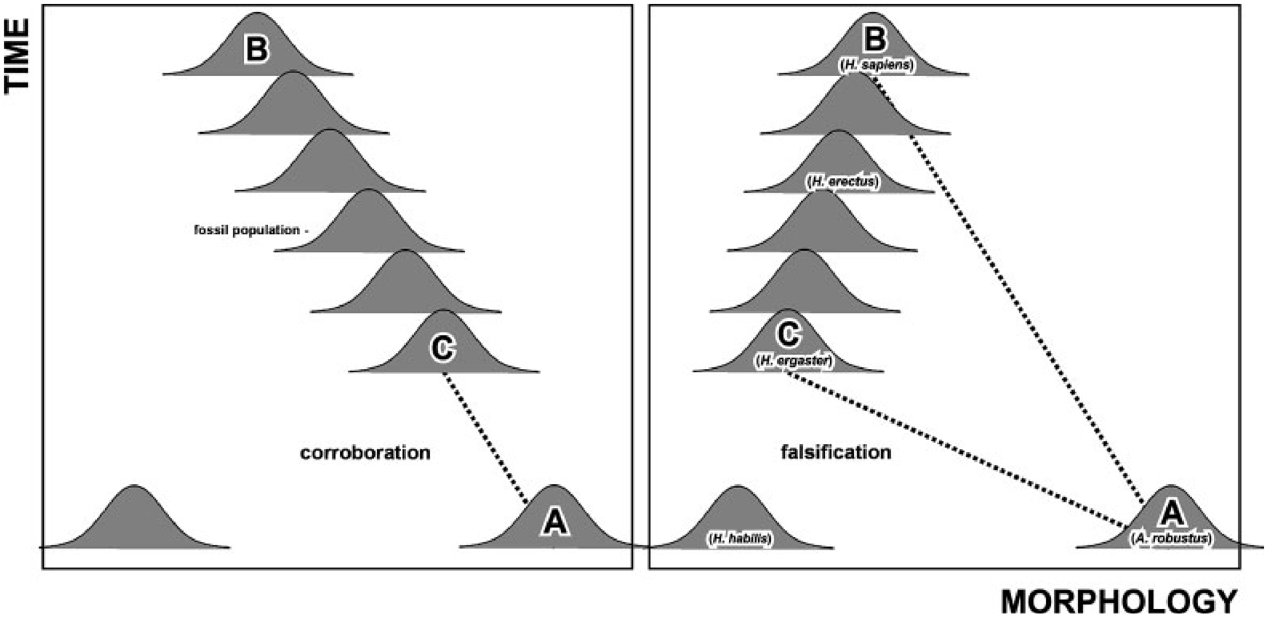
To test an ancestor–descendant hypothesis the reasoning has to proceed back in time. This is because any organism may have uncountable successors and there is no way of deciding with which of those numerous lineages we deal while studying a particular fossil. However, only one hypothesis of ancestry is true, as any asexual organism may have only one ancestor and any sexual species only one ancestral species. The true course of evolution is being approached by increasing time, space and morphological proximity of data sets. Any new piece of evidence extending the lineage backward supports the hypothesis or contradicts it with power proportional to the dimensions of its departure from the expected. A hypothesis can be finally refuted if the restored succession of populations reaches the time horizon of the earlier proposed ancestor (Text-fig. 9). Such definite falsification is rarely reached but its possibility makes the method scientific (Dzik 1991*a*; see Engelman and Wiley 1977 for discussion from a cladistic point of view).

The straight line connecting populations of different age in a hypothesis on the ancestor–descendant relationship does not imply a linear course of evolution. This is just an application of Occam's Razor to the time and morphological dimensions of evolution. There is no need to violate the principle of parsimony by presenting the evidence in terms of hypothetical sister taxa. This would introduce an unnecessary ghost range, a succession of nonexisting populations of the 'sister lineage'. Only empirical evidence obtained later may force us to make the theory more complex.

The inferences by retrodiction, that is by proposing hypotheses on ancestry and potential testability of ancestor–descendant hypotheses, are thus crucial aspects of the chronophyletic approach to the fossil record of evolution. Evolution is therefore understood as an objective physical process with samples (populations) of different age connected to a series of hypothetical descent. To show how this can be done in practice a few examples from the Frasnian history of the palmatolepidids are discussed below.

CHRONOPHYLETICS OF THE PALMATOLEPIDID CONODONTS

Chronophyletics overcomes the methodological limitations of stratophenetics by introducing the geographical space and retrodiction to evolutionary considerations. This provides the basis for representing the course of evolution as a phylogenetic tree, here exemplified by the Famennian phylogeny of the Palmatolepididae (Text-fig. 8). As long

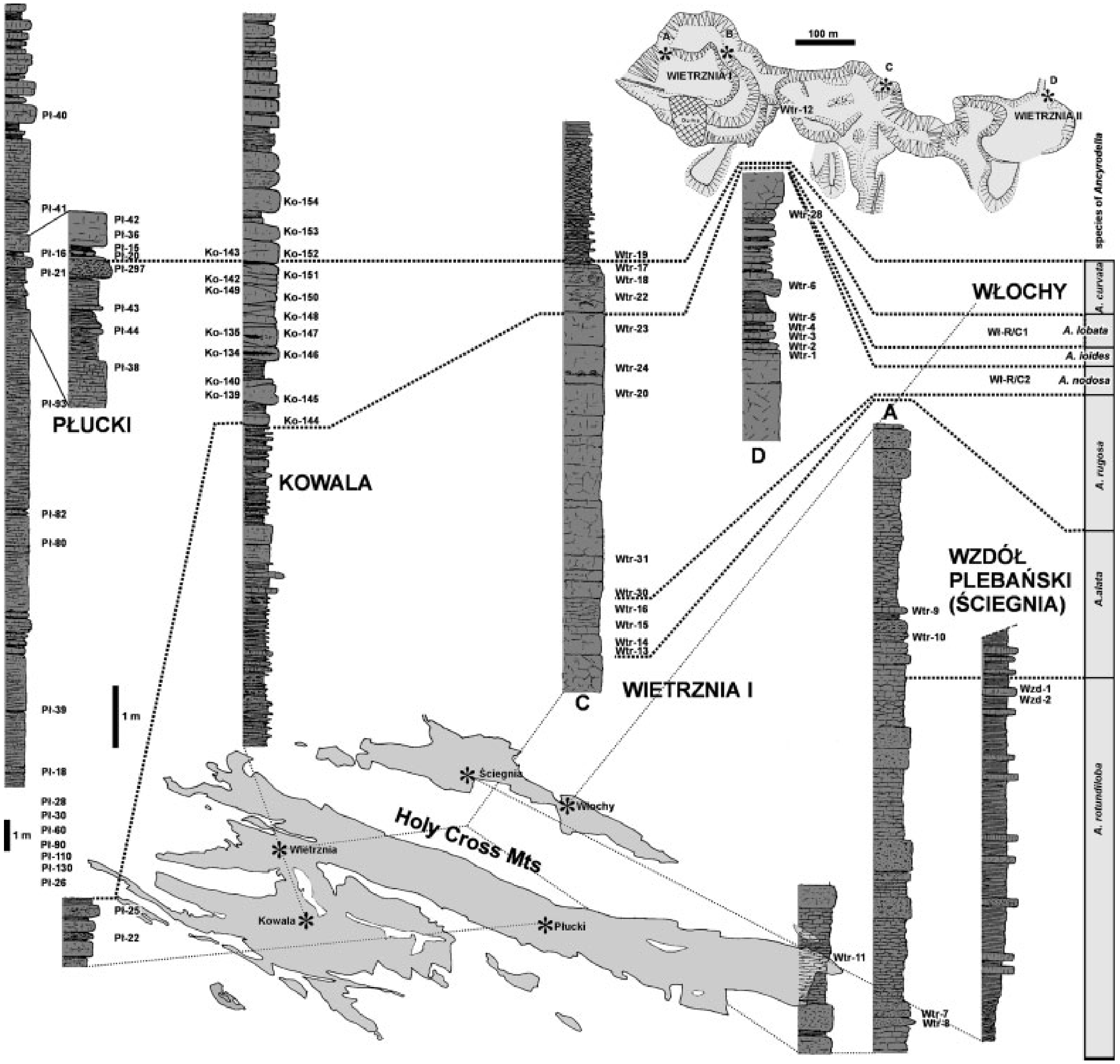


TEXT-FIG. 9. Testability of chronophyletic hypotheses based on the assumption that a species may have many successors but only one ancestor: hypotheses on ancestry are thus contradictory. The conclusive dismissal of a hypothesis can be achieved when retrodiction reaches an ancestor coeval to that originally proposed. Note that a departure of stratigraphically transitional new evidence from expectations may offer an estimate of the power of falsification. The evolution of hominids may serve as a simple explanation of the proposed way of reasoning: the claims that the Asian population of *Homo erectus* was derived from the African population of *Homo habilis* or, alternatively, *Australopithecus robustus*, are contradictory. The finding of a population ancestral to *H. erectus* (i.e. the population classified as *H. ergaster*), which is closer in morphology to *H. habilis* than to *A. robustus*, makes the second possibility weaker and its power is proportional to the time, space and morphological distance between the populations. After a continuous succession between *H. erectus* and *H. habilis* has been assembled, the *A. robustus/H. erectus* hypothesis is definitely refuted.

as it is based on materials from the restricted area of the Holy Cross Mountains, only the phyletic evolution of Polish populations can be potentially proven stratophenetically. The spatially disjunct speciation events have to remain speculative, as by definition they took place elsewhere. Even if the place of origin of those species in any single section can be identified, the process of speciation would be represented just by a phyletic change.

Going back in geological time, one can see an apparent decrease in the taxonomic diversity of the palmatolepidids and reduction of morphological differences separating sets of sympatric species. This aspect of the phylogeny is shown by the pattern of recovery after their terminal Frasnian decrease in diversity. Close to the base of the Famennian, the sympatric species differ almost exclusively in details of denticulation of the anteriormost element in the apparatus. Their lineages appear so similar to each other that proximity to the first split is apparent there, even if this cannot be documented in the area (Text-fig. 8).

The Frasnian in the Holy Cross Mountains (Text-fig. 10) is even less suitable for stratophenetic studies than the Famennian. The facies distribution is rather complex and



TEXT-FIG. 10. Frasnian sections in the Holy Cross Mountains productive enough to restore statistically conodont apparatuses but extremely condensed stratigraphically. This makes the fossil record of evolution strongly punctuated and only general morphological trends are recognizable. An independent age correlation is based on changes in the lineage of *Ancyrodella*.

no doubt the region was ecologically highly diverse. Homotaxy in this case is also of little use in the precise age correlation. Different palmatolepidid lineages may be restricted in their occurrences to sections less than 20 km apart. Those that are productive enough to offer material to evolutionary apparatus studies are extremely condensed stratigraphically. To base correlation on evidence independent of the evolution of palmatolepidids, the succesion of the polygnathid conodont *Ancyrodella* is chosen. This appears evolutionary in nature and as such seems a rather reliable basis for age correlation (Klapper 1990).

The fossil record of evolution of Frasnian palmatolepidids thus remains strongly punctuated. In such a situation only general morphological trends can be recognized. Series of samples arranged according to their geological age show a sequential introduction of evolutionary novelties, which subsequently marked major clades. It is most apparent in the symmetrical element of their apparatuses, originally having a median process that gradually disappeared to be replaced by the bifurcation of lateral processes.

Most interestingly, immediately below the Frasnian/Famennian boundary palmatolepidid diversity was closely similar to that in the middle Famennian (Text-fig. 11). The differences were expressed mostly in the morphology of the anteriormost M and symmetrical S_0 elements in the apparatus. The only systematic distinction of the Famennian lineages is bending of the tip of P_1 element platform: in the Frasnian it was bent upward except for a single species of *Klapperilepis*. In addition, in morphology of non-platform elements of the apparatus each of the geologically oldest members of the early Famennian palmatolepidid lineages resemble *Klapperilepis*, but not other late Frasnian conodonts. It appears thus to be the only lineage that survived to the Famennian and gave rise to all later palmatolepidids. Its roots are probably in an early *Manticolepis*, as suggested by its rather primitive M and generalized S_0 element morphology with bifurcation of lateral processes developing relatively late in ontogeny. Transitional populations were polymorphic. This kind of ramification of processes was initiated in the neighbouring, laterally located S_1 element before it expanded to the medial S_0. Apparently, the biramous S_0 of another latest Frasnian lineage, *Lagovilepis bogartensis*, represents a reversal to the ancestral status as its S_1 element is normally bifurcated. This species is thus unlikely to be ancestral to *K. praetriangularis*. Also, in the more anterior S_2 and S_{3-4} locations some temporally ordered changes can be identified, which were followed by a phylogenetic split into lineages that differ from each other mostly in the morphology of the M element (Text-fig. 11). The typical palmatolepidids possess highly arched M elements with straight processes. This trait had already developed in the early Frasnian *Mesotaxis* (Dzik 1991*b*) well before the medial process in the S_0 element disappeared (Text-fig. 12).

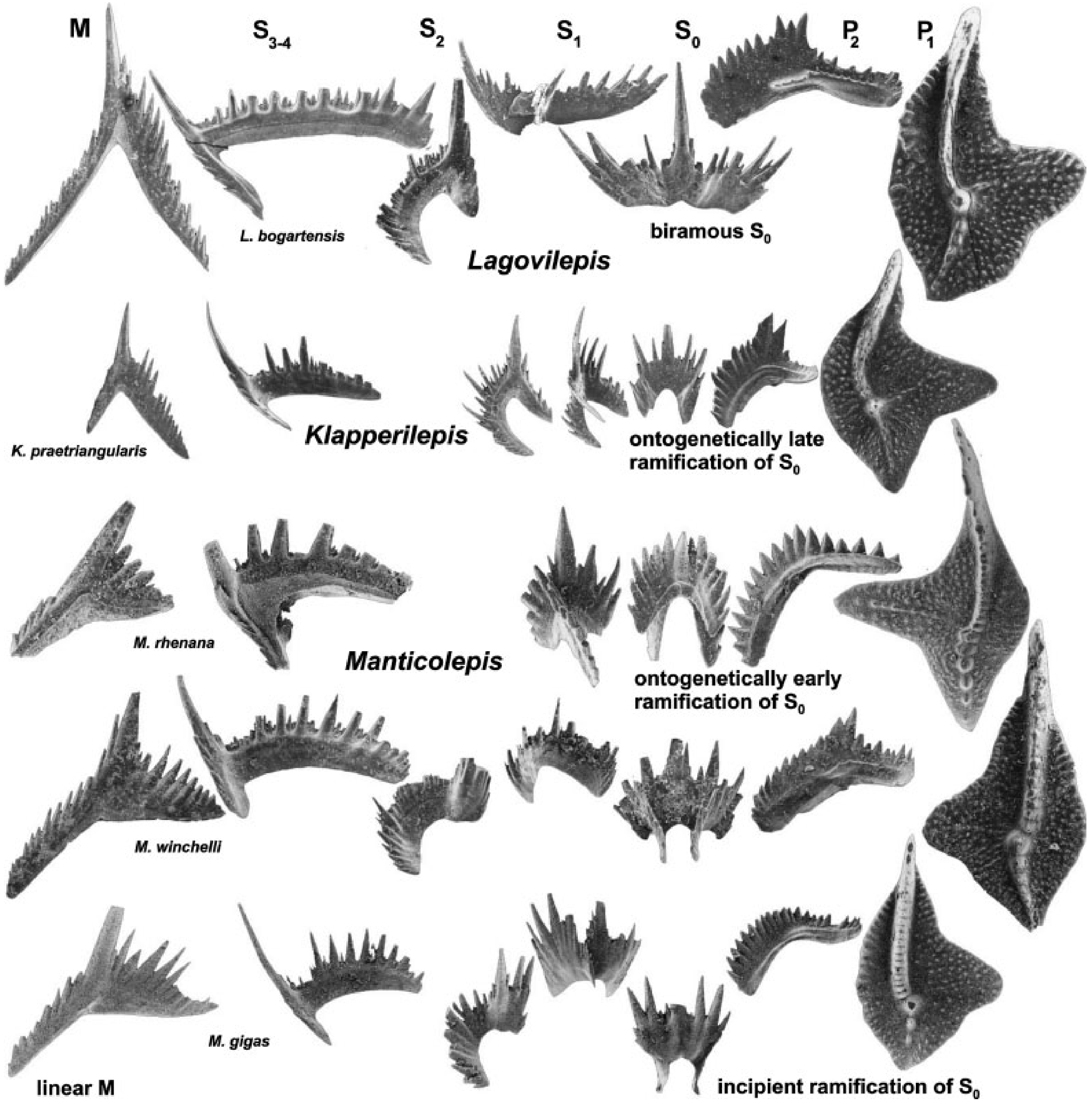
The geographical distribution of Frasnian palmatolepidids of the Holy Cross Mountains shows some regularity (Text-Fig. 13). As expressed by per cent contributions to samples, their frequencies are different in deeper- and shallower-water environments; some seem to be restricted to specific facies. For instance, the phylogenetically important *K. praetriangularis* lineage occurred in the extreme black shale environment in the marginal parts of the area (Text-fig. 13). It is not surprising that its origins remain cryptic.

The present picture of the phylogeny of palmatolepidids has been developed by arranging stratigraphically the data on populations and connecting them by a network of ancestor–descendant hypotheses. Particular hypotheses can be tested by increasing density of sampling and sample sizes within the area to meet the requirements of stratophenetics. Whenever the fossil record of a lineage is not good enough or terminates in local sections, sampling has to be extended to other areas. The lineages of allopatric origin have been attached basally to the morphologically closest of known lineages. The resulting hypotheses of ancestry have to be tested with evidence from elsewhere. If the basal extension of the lineage of the descendant meets another lineage, unrelated to that of the suggested ancestor, the hypothesis would eventually be refuted. Obviously, the whole phylogenetic tree has to be logically consistent. In cases of conflict between different interpretations, parsimony or common sense are the best guides. This means that any character distribution analysis is of much help, unless one enters circular reasoning.

The traditional palaeontological approach to evolution is fundamentally different from those preferred by neontologists. Although the fossil evidence is definitely less informative than data on recent organisms, only palaeontology may offer direct access to ancient evolutionary events. This makes the question of how to construct and test hypotheses on the course of evolution based on the fossil evidence (whatever methodology has been used to produce them) a matter of life-or-death for evolutionary palaeontology.

CLADISTICS VERSUS CHRONOPHYLETICS

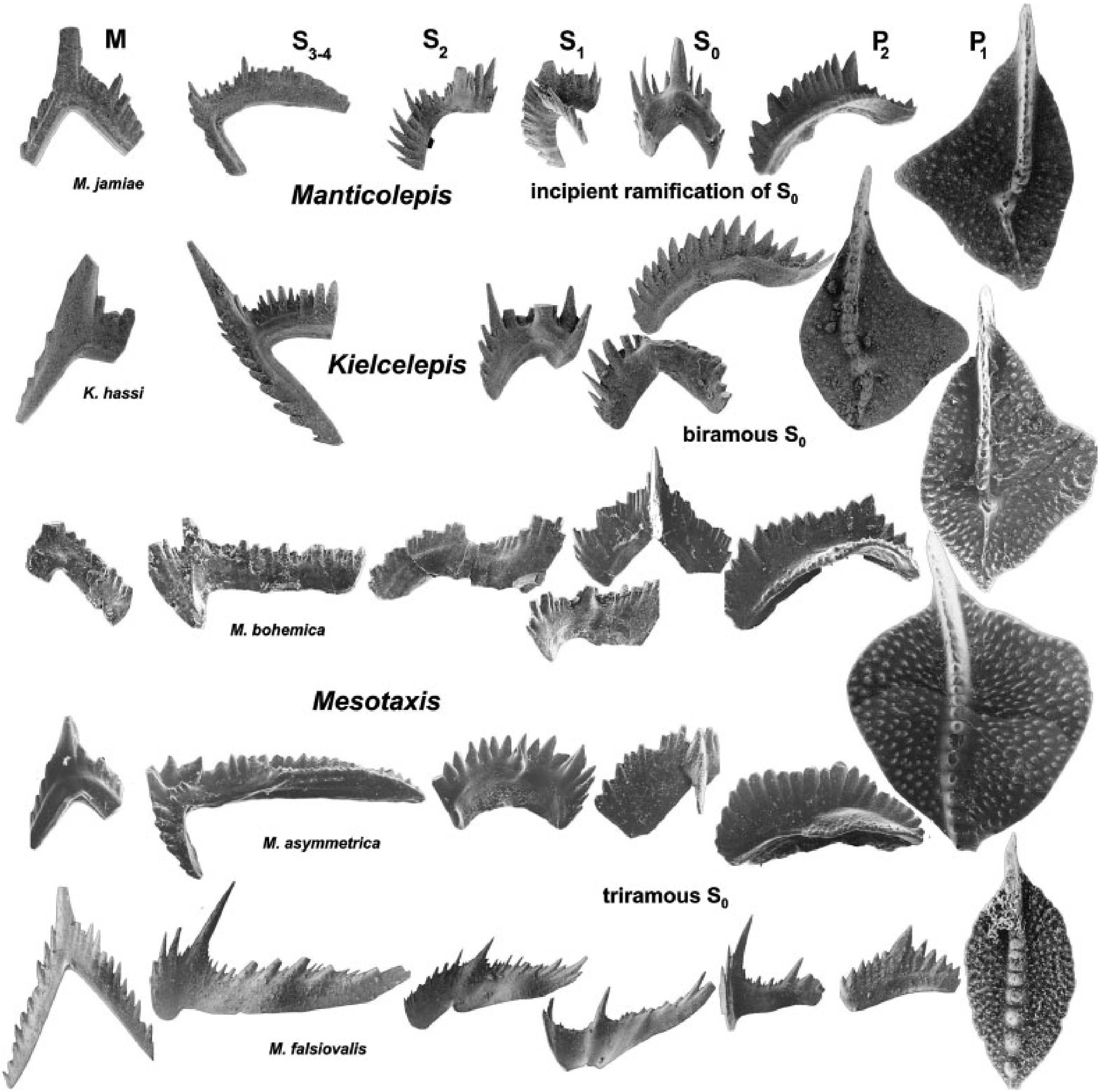
There can be no doubt that some aspects of evolutionary history of organisms can be extracted from the pattern of their present diversity. In fact, much of our knowledge of evolution is based exclusively on Recent organisms. Zoological or botanical data on the distribution of characters among organisms is widely used to infer their phylogeny. Several methods have been developed to perform this task. Any such method has to assume some correspondence between the morphological similarity and time



TEXT-FIG. 11. Apparatuses of the late Frasnian genera of the Palmatolepididae in the Holy Cross Mountains arranged partially according to their stratigraphic order of occurrence. Note that a gradual change in S_0 element marks their early evolution, followed by a split in morphology of the M element; the *Klapperilepis* lineage was confined to deeper-water facies.

that has passed since the separation of lineages of morphologically distinct members. The correspondence is hardly strict. Obviously, the rate of evolution may differ greatly between lineages. It may be quite irregular, resulting in misleading similarities from reversals, convergences and parallel evolution. As long as the purpose of the analysis is clearly stated (i.e. a restoration of the actual course of evolution) there is no disagreement between various methodological schools in dealing with these shortcomings of the evidence derived from Recent organisms. The tremendous recent progress in molecular phylogenetics, using both phenetic and cladistic ways of reasoning, exemplifies this very well.

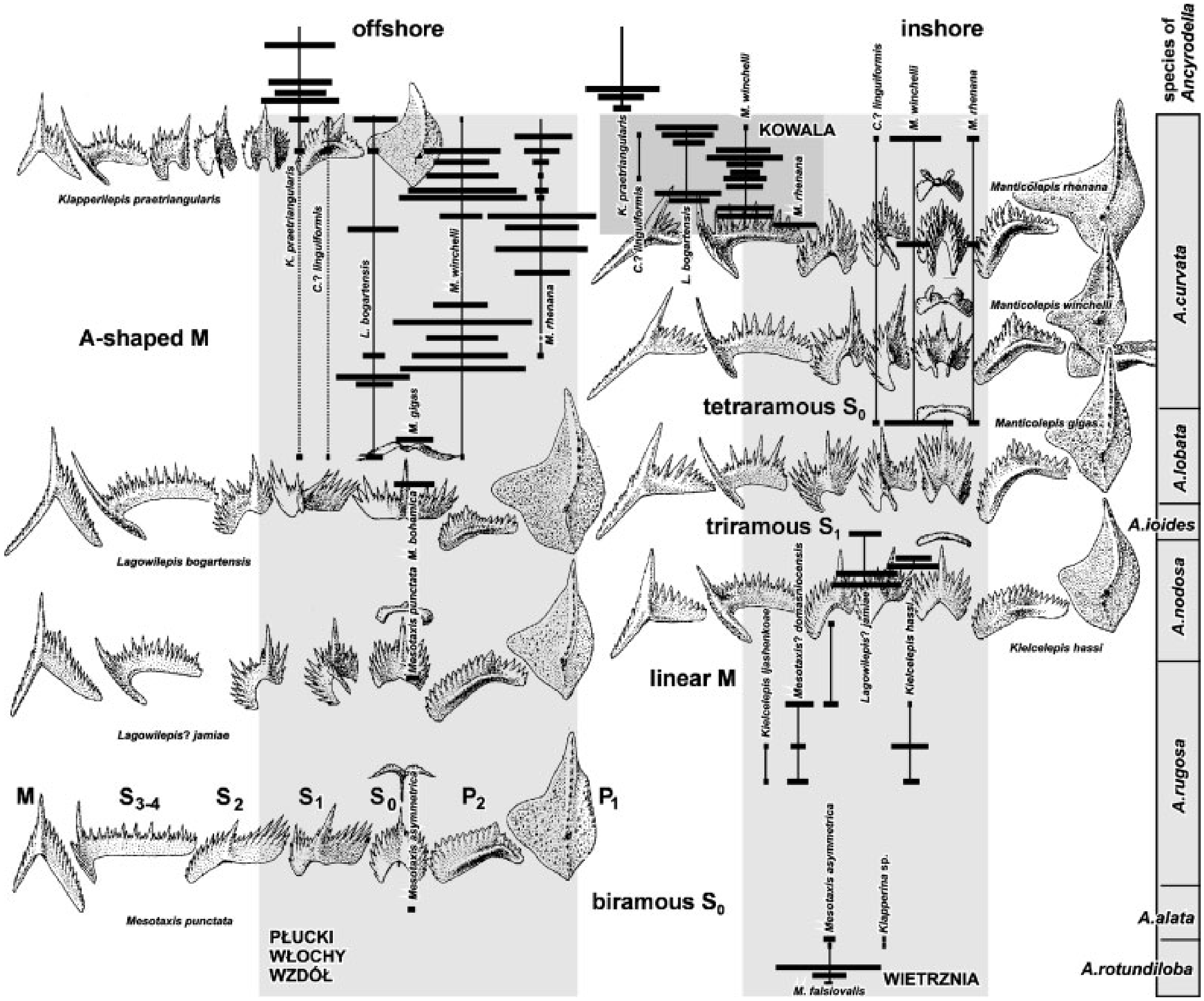
Nevertheless, the situation in morphology-based and molecular phylogenetics is fundamentally different in several aspects. The most troublesome distinctions of the analyses of phenotypic differences and molecular sequences are: (1) morphological characters are not



TEXT-FIG. 12. Apparatuses of the genera of the early Frasnian Palmatolepididae. Note that ramification of elements in the middle of the apparatus starts from S_1 and expands to S_0; in transitional populations S_0 is polymorphic. Temporally ordered changes also took place in the S_2 and S_{3-4} elements.

objectively discrete, unlike nucleotides or amino acids; and (2) unlike the molecular data, morphological evidence can also be obtained for organisms from the geological past.

The consequence of a failure to define morphological characters objectively has been considered damaging to numerical methods of analysing raw data by opponents of 'computer cladistics' (e.g. Wägele 1994). Unavoidably, one has to assume the equal value of morphological characters or arbitrarily give them a weight. Some *a priori* weighting techniques have been developed in molecular phylogenetics. In simple cases such as the inequality between nucleotide and amino acid sequences, this can be easily overcome. Even differences in rates of mutations can be statistically estimated and the necessary correction introduced (Felsenstein 1978, 1981). However, there is no way to do this in practice with morphological characters and character states. Their delimitation is rarely objective.



TEXT-FIG. 13. Succession of the palmatolepidid conodonts in various facies zones of the Frasnian in the Holy Cross Mountains. Note the punctuated distribution of most lineages (especially *Klapperilepis*), appearing and disappearing together with their specific environments.

Fossils cause difficulties of a different kind, and these are even more difficult to overcome. They involve the fundamental idea of correspondence between geological time and morphology. This assumption implies some regularity in distribution of morphologies in extinct organisms of different geological ages. In statistical terms fossil members of a lineage belonging to a monophyletic taxon (in cladistic terms, that is holophyletic: including all successors of the common ancestor) should be closer morphologically to each other than extant members of the same lineages. The similarity of their coeval sets should increase with the geological age of the horizon from which they come. This means that inclusion of fossil taxa in the same matrix of data as extant taxa must result in circular reasoning. This aspect of cladistics was addressed in a different way by Vermeij (1999), who pointed out that phylogenetic analyses derived from data matrices are not polarized, allowing data sets to be considered repeatedly even if they characterize long-separated branches of the evolutionary tree that could not possibly have interfered with each other's course of evolution. To be truly rigorous and logically consistent, one should restrict the analysis to organisms from the same time plane (it does not matter whether it is Recent or a segment of the past; Fortunato 1998).

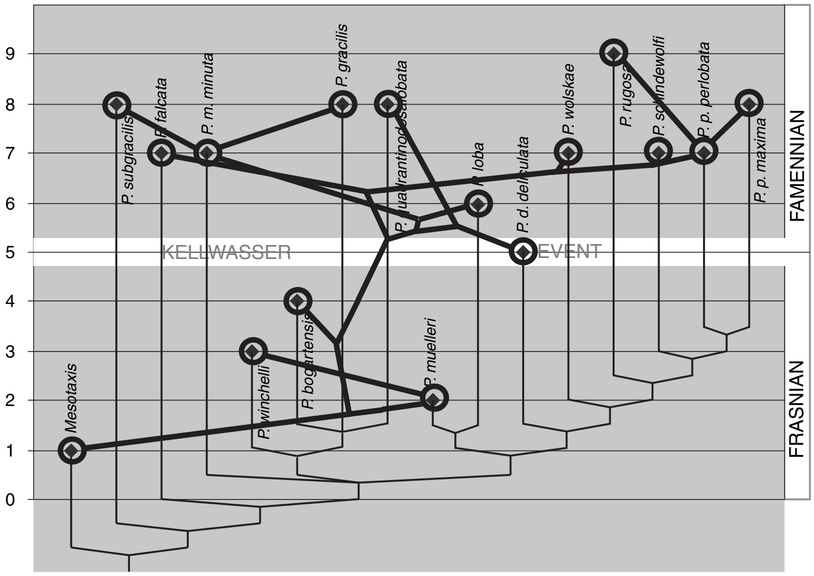
The above objections refer equally to all methods of inference on the course of evolution based on morphology. The method of cladistics (or at least approaches of those cladists who are interested in restoring phylogeny, not just the order behind the diversity of organisms) also assumes certain patterns in the process of evolution that raise controversy. Some followers of the method believe that evolution is always divergent and that all the change is concentrated in a sudden speciation event. Both of these assumptions are contradicted by palaeontological evidence and considered either false or unnecessary by followers of methods of inference exposing stratigraphical order in the fossil record (e.g. Dzik 1991*a*). Perhaps all this would be of secondary importance if the testing of phylogenetic trees based on morphological evidence was strict enough. This does not seem to be the case, as most cladists consider parsimony and congruency between different sets of data to be sufficient for testing the trees.

Parsimony (the Occam's Razor Rule) and testability (or falsifiability) are truly the fundamental qualities of scientific theories. The most parsimonious formulation of ideas based on available facts makes it easier to test them with new data and helps in clearing science of unnecessary assumptions and redundant explanations. However, parsimony by itself does not guarantee access to truth and a more parsimonious phylogenetic theory does not necessarily describe reality better than a more complex one (e.g. Sheldon 1996). This has already been treated in depth in discussion on the maximum likelihood method in molecular phylogenetics (e.g. Felsenstein 1978; Stewart 1993). Panchen (1982) showed that what cladists claim is a test of their hypotheses is actually a repeated application of the principle of parsimony. It is not enough to choose a more parsimonious solution to approach the truth. To use parsimony alone is definitely a good strategy in theology but science requires more. Those who follow the Popperian attitude to science (most cladists claim to be among them) and consequently Alfred Tarski's concept of truth insist rather on confronting theories directly with the empirical evidence of a physical process. The language of science has to be checked for correspondence with the real (although inadequately known) world in every possible point. Evolution is a process of the physical world as long as it is understood to be a result of Darwinian changes in populations. The most direct evidence on the history of evolution is offered by fossils. They are not just a source of information on phylogeny but physically parts of evolving lineages. All that is necessary is their arrangement into a phylogenetic tree by filling unknown parts with hypothetical junctions. Whether or not any character analysis is performed is irrelevant. Such hypotheses on ancestor–descendant relationship among ancient populations can be tested by checking for correspondence with any kind of evidence that refers to populations of the same lineage in any logically consistent way (including cladistic analysis).

The cladistic test by congruency superficially looks similar to that derived from Tarski's concept of truth. It is assumed that any pattern of relationship based on particular sets of homologous characters must be congruent with patterns based on other homologues. In fact, even the basic conviction that homology can be identified without any reference to evolution is an illusion. Regardless, leaving aside the question of what degree such congruency must be followed by any evolving lineage, tracing new congruencies hardly has anything to do with hypothesis testing (O'Keefe and Sander 1999, p. 589). By no means is this a case of a deduction confronted by a basic statement about empirical evidence. Different hypotheses are simply compared. To truly test a hypothesis of the course of evolution some predictions (or retrodictions) derived from it on populations precisely located in time and space have to be matched with the fossil evidence.

In the original Hennigian form of cladistics, retrodiction on the course of evolution was to some degree possible, by arranging derived characters (synapomorphies) into a time series. This is what cladists call 'evolutionary scenarios' and consider this type of presentation inferior with respect to presentation of 'horizontal' (blood) relationships. Advanced ('computer') cladistics offers no way to confront directly diagrams of relationships with empirical (fossil) evidence. This taxic approach to palaeontological data requires that to make its trees comparable with the fossil evidence the branches of the cladogram have to be complemented with the observed ranges of taxa.

This was done for the palmatolepidid conodonts by Donoghue (2001), who calibrated a computer-generated cladogram with stratigraphical data on the first appearances of species rank taxa (thus unavoidably understood as chronospecies, unless their sudden appearance, stasis and exact fossil record of extinction are assumed). Unavoidably, the cladistic dogma of the dichotomous nature of evolution introduced nonexisting ghost ranges in each of the proposed sister lineages. Such a tree cannot thus be easily transformed into a series of ancestor–descendant relationship hypotheses. Only the succession in branching of the tree and dating of bifurcations can be compared with those represented in the chronophyletic diagram of phylogeny. As it appears, there is virtually no correspondence between the trees (Text-fig. 14). The main reason for this is not only that there are so many reversals and parallelisms in the chronophyletically documented evolution of the palmatolepidids. The major problem is the unequal value of characters. As already commented above, the quite trivial upward bending of the tip of the platform that originated in the late Frasnian at the beginning of the *Klapperilepis* lineage is the only aspect that differentiates its Famennian successors from virtually all Frasnian palmatolepidids. Probably by adding more and more data the cladogram could be made more congruent with the real course of evolution. This would not, however, remove distortions resulting from the fundamental flaws in the basic assumptions of the method (especially the concentration of all evolutionary change in speciation events). The alternative is to consider ancient populations



TEXT-FIG. 14. Phylogenetic tree by Donoghue (2001) based on a computer cladogram with stratigraphical ranges of taxa added, and superimposed lines of ancestor–descendant relationships derived from the chronophyletic tree (Text-figs 5, 11–12). Note that there is virtually no correspondence between the cladogram and documented events except for a few species of *Palmatolepis* of questionable distinction (they do not differ in their apparatus structure at all). The problems with the results of the cladistic analysis result mostly from the unweighting of characters and several misleading reversals and convergent changes within the clade. Unnecessary 'ghost ranges', which are in contradiction to the generally accepted pattern of palmatolepidid evolution at the Frasnian/Famennian boundary, also represent a violation of the principle of parsimony.

restored on the basis of fossil samples the basic units of phylogeny reconstructions (Dzik 1985, 1991*a*). The chronophyletic approach is simpler and more efficient in achieving the goal.

It appears thus that only the use of fossil evidence with its time and space coordinates allows identification of the true course of evolution and testing of phylogenetic trees. This requires that the morphological evidence is processed in a proper way and that the phylogenetic tree should be designed to correspond directly to the fossil evidence. Neither the methods of analysing the morphological evidence nor the way of using fossils to test the results need to be especially rigorous. Only the presentation of the tree has to be truly strict.

PROPOSED SOLUTION

The basic question is, of course, what does one want to attain: a precise natural system of classification expressing the design of the living world or an approximation of the pattern of events that resulted in the observed complexity of life? Whatever we do, this has to be consistent with the basic aspect of science; the presentation of the story should be testable. It is claimed here that the method of chronophyletics results in the presentation of descendant-ancestor hypotheses that fulfil requirements of scientific methodology.

Some problems of evolutionary biology can be resolved only with fossil evidence. These include such questions as: (1) how old geologically are major groups of organisms, (2) what was the anatomical organization of their ancestors and (3) what moved phylogeny in specific directions? They refer to the course of evolution which makes ancestor–descendant relationships the only objectively accessible aspect of evolution, the pattern of 'blood relationship' remaining very difficult to specify in objective terms and virtually impossible to test without reference to the actual course of evolution (Panchen 1982; Dzik 1991*a*; O'Keefe and Sander 1999).

The question emerges of how to proceed with methods of inferring evolution from the distribution of characters in Recent organisms to reach results that can be tested with direct palaeontological evidence on the course of evolution. This requires thinking in terms of samples, populations and lineages with their time, geographical and morphological dimensions. The basic unit of empirical evidence in palaeontology is a sample that represents an extinct population living in a specified geological time and having a specified position in geographical space. These time and space coordinates are objective and unchangeable. The time dimension of fossil evidence is not just an addition to morphological characters. The populations located in time and space are elements of the network of lineages that remains more or less hypothetical but is objective and potentially can be documented with the fossil evidence wherever it exists. To propose a phylogenetic (chronophyletic) hypothesis the populations are thus connected by ancestor–descendant relationships. To do this it is not necessary to define or describe populations. It is enough to point to particular samples, their time and space coordinates being inherently connected with them. The question of evolutionary species, which emerges in this context, has been satisfactorily solved on the grounds of neontology (Mayr 1969) and can be easily applied to the fossil material (e.g. Gingerich 1985).

In cases where the real pattern of evolutionary relationship is difficult to decipher, analysis of characters based on the assumed correspondence between time and morphological difference may help in restoring the network of transitions. The analysis has to be restricted to a single time slice. The pattern of nesting in cladograms and the sequence of branching in phenograms can then be expected to approximate the actual time sequence of events (appearances of characters). The set of characters attached to each of the branching points in the diagram characterizes a real organism from a time horizon older than that on which the analysis has been based. Potentially, at least some of the nodes of the tree characterized in this way can be matched with actual fossil ancestors or their relatives, close in time, geographical space and morphology. In cases where identification of the real extinct population fails, the hypothetical description of it that has been obtained can be incorporated into the basic evidence coming from the time horizon from which another set of morphological evidence comes. The next steps of the analysis can then be performed.

Morphological characters as discrete units are mostly products of the human mind. Any phylogenetic approach referring to such understood characters ‘treats organisms as clusters of characters each one of which can be interpreted individually rather than as part of a functional complex’ (Campbell and Barwick 1988, p. 207). This is an inherent bias of cladistics and phenetics, if used to infer phylogeny from fossils, but references to discrete characters can be avoided within the chronophyletic approach. One possibility is to represent morphology and variability of organisms in a diagrammatic way (as ‘pictograms’; Dzik 1984, p. 11) to compare them as a whole. No formal algorithm to do this automatically is yet available, but there is probably no urgent need for it. It seems appropriate to quote in this place the maxim cited by Van Valen (1989 after Tukey 1962): ‘Far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made precise.’

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