RELATIONSHIP BETWEEN RATES OF SPECIATION AND PHYLETIC EVOLUTION: STRATOPHENETIC DATA ON PELAGIC CONODONT CHORDATES AND BENTHIC OSTRACODS

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ABSTRACT - In the fossil record, distinction between the two basic aspects of evolution, i.e. branching of evolutionary trees (cladogenesis) and evolutionary transformations along lineages (phyletic evolution, "anagenesis"), is especially well visible. The process of allopatric speciation, presumably the most common, if not the only, way to split a lineage, cannot be recognised directly in any single geological section, as it proceeds in a geographic dimension. It has to be inferred from data preserved in many places, which makes the inference vulnerable to all the limitations of rock correlation. On the contrary, the course of phyletic evolution is potentially observable in a single geological section, with application of the Steno's rule of superposition as the only guide to the time distribution of evolutionary events. However, only rarely and in extremely stable environments can a complete time range of a morphologically recognisable segment of the evolution (chronospecies) be established. The stratophenetically documented phyletic evolution of both pelagic (Ordovician and Carboniferous conodonts) and benthic (Ordovician ostracods) organisms from such unusual sites provides evidence that ranges of chronospecies observed in particular sections represent generally only a minor part of their actual durations. As a result, rates of evolution estimated by counting reported ranges of taxa must appear much higher than they really were. Moreover, biometrically proven rates of evolution invariably appear to be much slower than expected. Ranges of fossils have thus little to do with the evolution of species they represent. In the studied cases, with a good geological time control, there is no evidence of any direct relationship between the speciation rate (or migration events) and the rate of morphological change. Generally, numerous slowly evolving lineages may develop in a varied environment, and a uniform environment may remain inhabited by a few, although fast evolving, lineages. Rates of speciation and extinction mostly reflect features of the physical environment and its transformations, being thus rather unreliable measures of the rate of biological evolution. Perhaps they may offer a measure of the evolution of complexity of ecosystems and/or effectiveness of their biocoenoses in exploiting resources. Nevertheless, they can hardly be used in empirical studies as neither speciations nor extinctions are directly observable in the fossil record and their identification requires a complex inference based on not obvious assumptions.

KEYWORDS: RED QUEEN HYPOTHESIS, PHYLOGENY, CONODONTS, OSTRACODS, ORDOVICIAN, CARBONIFEROUS.

RÉSUMÉ - Dans le registre fossile, la distinction entre deux aspects fondamentaux de l'évolution, ramifications des arbres évolutifs (cladogenèse) et transformations évolutives le long des lignées (évolution phylétique, "anagenèse "), est particulièrement bien visible. Le processus de spéciation allopatrique, sans doute le plus commun, sinon le seul pour partager une lignée, ne peut être reconnu directement dans une coupe géologique unique puisqu'il procède d'une dimension géographique. Il doit être déduit de données observées en divers points ce qui rend la déduction dépendante des limites de corrélation des couches géologiques. Au contraire, le cours de l'évolution phylétique est potentiellement observable dans une seule coupe géologique en appliquant la règle de superposition de Sténon comme unique guide de la distribution temporelle des événements évolutifs. Pourtant, c'est seulement dans de rares environnements parfaitement stables que peut être établie l'extension temporelle complète d'un segment morphologiquement reconnaissable d'une évolution (chronoespèce). L'évolution phylétique stratophénétiquement documentée d'organismes tant pélagiques (conodontes ordoviciens et carbonifères) que benthiques (ostracodes ordoviciens) de tels sites exceptionnels met en évidence que les extensions de chronoespèces observées dans des coupes particulières représentent, en général, seulement une faible partie de leurs durées réelles. Il en résulte que les taux d'évolution, estimés par le décompte des extensions rapportées des taxons, doivent apparaître beaucoup plus élevés qu'ils ne le sont réellement. De plus, des taux d'évolution biométriquement établis semblent être invariablement très inférieurs à ceux attendus. Les extensions des fossiles ont ainsi peu à voir avec l'évolution des espèces qu'ils représentent. Dans les cas étudiés, avec un bon contrôle géologique, il n'y a pas de preuve de relation directe entre le taux de spéciation (ou d'événements de migration) et le taux de changement morphologique. En général, de nombreuses lignées évoluant lentement peuvent se développer dans un environnement varié et un environnement uniforme peut rester habité par un faible nombre de lignées, mais évoluant rapidement. Les taux de spéciation et d'extinction reflètent surtout des conditions de l'environnement physique et leurs transformations; ils sont ainsi des mesures plutôt incertaines du taux d'évolution biologique. Peut-être peuvent-ils offrir une mesure de l'évolution de la complexité des écosystèmes et/ou de l'efficacité de leurs biocénoses pour l'exploitation des ressources. Cependant, ils peuvent difficilement être utilisés dans des études empiriques car ni les spéciations ni les extinctions ne sont observables dans le registre fossile et leur identification requiert une inférence complexe fondée sur des suppositions non évidentes.

MOTS-CLÉS: HYPOTHÈSE DE LA REINE ROUGE, PHYLOGÉNIE, CONODONTES, OSTRACODES, ORDOVICIEN, CARBONIFÈRE.

INTRODUCTION

Evolutionary theory is traditionally presented as the problem of the origin of species. This preoccupation with species and taxonomy strongly determines also modern thoughts about evolution. Influenced by this approach to evolution, palaeontologists tend to focus their attention on speciation and taxonomic diversity in ancient environments (e.g., Sepkoski 1998). For some reason, probably an effect of psychological or philosophical inclinations, the belief that horizontal splitting of a genetic pool must result in an increase of the rate of evolution, is astonishingly vivid. Equally influential is belief that the phyletic evolution of organisms cannot be directly inferred from the fossil record because of its intrinsic limitations, whereas durations of species is considered to be the best tool in recognising the pattern of evolution. Although those limitations are obvious and fundamental, the actual potentials and deficiencies of palaeontological data are just opposite: the process of speciation is very difficult to be documented with fossils whereas phyletic evolution can be studied directly in geological sections. The palaeontological record is not as deficient as is usually believed (see Dzik 1991a for discussion and a review of earlier published evidence) although species durations are virtually impossible to be determined with acceptable precision (Dzik 1995), assuming that one knows what it actually means. In fact, taxonomic diversity is not only hard to estimate with palaeontological evidence but, even if known, says little about the rate of evolution.

The method of stratophenetics (Gingerich 1979) is the tool which may provide direct evidence on the pattern of evolution at the population level based on palaeontological evidence. This in turn may enable one to check its correspondence to environmental changes as well as the allegedly strict correspondence between the rate of evolution and speciation. In the present paper I will try to show that both those assumptions about the nature of evolution are rather questionable and cannot be taken as given. Because of limitation of the method of palaeontology I will rather focus on the direct record of phyletic evolutionary changes than on more speculative effects of lineage splitting.

EMPIRICAL APPROACH

Palaeontological evidence has its obvious limitations. Most of it depends directly on, and is a result of, the very nature of the geological record. However, the course of evolution can be potentially deciphered from fossil remains of populations if they form a time and morphologic series complete enough to prove their genetic continuity. This requires an overlap of morphologic variability in every pair of successive samples (Dzik 1991a). Unavoidably incomplete geological sections are the only source of data, with the ratio of gaps to recorded sedimentary events very variable, ironically being the highest (worst for palaeontologists) in environments of greatest biological interest, such as those of continental ecosystems (McKinney 1985).

Stratophenetics requires geological sections which contain (1) possibly complete record of geological (evolutionary) time. This means that sedimentary gaps were short enough not to miss significant segments of the evidence, although their number does not matter. A truly complete geological record is a rare case, but occurs. It is obviously much more common in open than in near-shore marine environments but palaeontologically good geological record can be found even in the extreme continental settings, as is the case with the Bighorn and Clarks Fork Basins (e.g., Gingerich & Gunnell 1995).

Another requirement is that the environment represented in a geologically complete section was stable enough not to be influenced too much by lateral shifts in geographic distribution of its ecosystems and migration of species. This means that (2) ecological record has to be continuous and complete. Again, marine pelagic environments, being vast and relatively uniform, tend to offer a good ecological record more frequently than others. Some ancient lake succesions may also yield good fossil material with such features (e.g., Gorthner & Meier-Brooks 1985).

Finally, we need that the fossil material is (3) complete enough to record an evolutionary change. This limits interest of palaeontologists doing this kind of research to organisms with skeletal parts of the body which easily fossilise, are easy to extract from the rock, and contain important information about functionally significant features of the anatomy.

The literature data on stratophenetically documented evolutionary change is growing (reviewed in Dzik 1991a; also Gingerich 1991, 1993, Gingerich & Gunnell 1995). Planktonic foraminifers and radiolarians have provided most of the published evidence on continuous record of evolutionary transformations. For instance, Kucera & Malmgren (1998) documented gradual increase in mean shell conicity and decrease in mean number of chambers in the last whorl in a Late Cretaceous lineage of planktonic foraminifers. It is possible that those changes resulted from an alteration of the abiotic environmental conditions. Interpretation of morphologic changes in geometry of shells is difficult and unavoidably speculative. No doubt the amount of biologically understandable information which can be extracted from their morphology is not especially impressive (Norris et al. 1996; Huber et al. 1997). Moreover, it remains mostly unknown to what degree sexual processes are important in their biology, which makes application of the biological species concept a little unsafe. The latter refers also to another popular subject of evolutionary studies in palaeontology, the graptoloids.

The main deficiency of most biometrically documented transitions is that they refer to very simple morphological features of little anatomical importance and with poor control of ontogenetic change (this refers especially to data on ammonoids; reviewed in Dzik 1985, 1990a, 1995; Dommergues 1990). In the case of mammalian teeth, the ontogenetic change does not interfere with within-population variability (after eruption, the teeth do not change). Usually the only measured feature is the tooth size (e.g. Anderson et al. 1995) which does not assure that the observed change is not just phenotypic, but in some cases much more profound changes are documented stratophenetically (Rose & Bown 1984; Bown & Rose 1987). Although very attractive in this respect the mammalian dentition also has obvious deficiencies. Mammalian fossil occurrences are mostly limited to ecologically and geologically incomplete sections (with a few notable exceptions, e.g., Gingerich & Gunnell 1995). Comparable to the mammal teeth in complexity and functional significance (Dzik, in press c) but unbeatable by any other group of fossils in respect to the completeness of the fossil record of evolution are the conodont chordates.

Conodonts were well represented in various marine environments world-wide from the latest Cambrian to the end of the Triassic. The great content of information in morphologically complex apparatuses make conodonts excellent model subjects of evolutionary studies. Phosphatic denticles of their mouth apparatuses are very easy to extract from the rock. Their contribution to the pelagic sediment was commonly high and one kilogram of the rock may yield several thousands of elements. Methods of complete apparatus reconstruction are rather simple (Dzik 1991b). There may be up to eight separately evolving types of elements within the apparatus. Vast areas inhabited by species of the conodont chordates ensure that local occurrences were relatively insensitive of climatic changes. Still, a succession of conodont assemblages in a rock section may offer a clear and precise evidence of environmental changes, which can be calibrated on the basis of quantitative contribution of species typical for particular kinds of environment (Dzik in press b). Since many decades conodonts are the standard subject of stratophenetic evolutionary studies even if they continue to be considered a problematic and suspect group of fossils.

Obviously, even in the case of conodonts it is not easy to find geological sections fulfilling all those conditions listed above. I have chosen two such sections with a relatively good record of both the evolution and climate. One of them is representative for the first impulse of the late Palaeozoic glacial epoch, which apparently controlled the profound environmental changes at the Devonian-Carboniferous boundary. The sediments represented there were deposited in the tropics, which makes the influence of the glaciated regions on the local climate rather complex and indirectly expressed. More straightforward climatic effects will be shown by data derived from another section, with a good record of the Late Ordovician glaciation in temperate climate. Before the onset of the glacial epoch, the environment there was stable enough to provide a continuous fossil record of the evolution of benthic organisms. It took place in not so profoundly modified environment but still with some apparent alterations of the climate and abiotic environment. Those benthic organisms were mostly endemic to the ancient continent at which the section is located. All the associated conodont species had a much wider distribution. Of special interest are those which were able to invade epicontinental seas belonging to other biogeographic realms and to establish there allopatrically evolving lineages.

THE EVIDENCE

Periodic immigrations of species known to be abundant either in the tropics or subpolar regions can be used to determine precisely and to quantify changes in the climate. In the case of conodonts there are also some morphological features which allow, with much confidence, to distinguish cold- from warm-water species. Typical cold-water conodonts had wide basal cavities and thin walls of the crown of those elements of their apparatus which were apparently adapted to grinding (molarised); tropical species tended to develop a very thick crown and inverted basal cavity in these locations within the apparatus. The pattern of molarisation was different in each of the cases. In the former, denticle tips contributed mainly to the working surface (icrion) whereas basal thickenings of the crown (platform) dominated in the latter. This regularity, well documented in the Late Ordovician conodonts, can probably be extrapolated and used to determine polarity of climatic changes also at the beginning of the second great glacial epoch of the Palaeozoic, close to the end of the Devonian and in the earliest Carboniferous. Conodont assemblages of the Carboniferous black shales and radiolarites, deposited in deep water, are of low diversity and dominated by conodonts with thin crowns and icrions, whereas in brief periods of dominating carbonate sedimentation platform conodonts contribute significantly to high diversity assemblages. This seems meaningful. One of the best and most complete record of those changes is offered by the section Kowala in the Holy Cross Mountains, Poland.

LATE PALAEOZOIC GLACIATION AND THE EVOLUTION OF CONODONTS

Close to the Devonian-Carboniferous boundary a series of environmental (presumably climatic) events erased the extremely rich tropical faunas of the Late Devonian. Faunas of similar composition were re-established after a period of faunal impoverishment. Particularly in Europe, the end of the carbonate sedimentation of the *Wocklumeria* limestone coincides with the disappearance of a high-diversity warm-water assemblage of ammonoids and conodonts with elaborated platform elements. As a replacement, a low diversity fauna with the thin-crown conodont *Protognathodus* migrated to the area. The carbonate sedimentation was re-established at the beginning of the Carboniferous (*Gattendorfia* limestone). The new high-diversity ammonoid and conodont faunas represented again almost all the range of morphologies known from the Famennian. Migrations from unknown sources into the area dominated, with little contribution from the local phyletic evolution. This characteristic ammonoid-conodont community disappeared from this area with the sea-level rise in the Siphonodella crenulata Zone, to emerge at the same time in the North American Midcontinent. The reverse direction of migrations marks the latest Tournaisian *Scaliognathus anchoralis* event. No doubt glaciation of Gondwana was the main factor controlling the distribution of the latest Devonian and Carboniferous conodonts (for review see Dzik 1997).

The Kowala section in the Holy Cross Mountains in Poland, with its about 32.0 meters of rock thickness, represents probably the most complete continuous section of the Tournaisian in Europe. The strata range from the black shale at the base of the Famennian *Wocklumeria* limestone, through pale shales of the early Tournaisian Radlin beds with horizons of calcareous nodules, to the black shales and radiolarites of the middle Tournaisian Zareby Formation.

The carbonates and shales of the *Wocklumeria* age contain at Kowala conodonts and ammonoids typical for these strata. The clay immediately following the last limestone bed with *Wocklumeria* contains the same conodont assemblage as that below. Beginning at a tuffaceous shale, the ecologically opportunistic conodont *Neopolygnathus communis*, with insignificant occurrence in strata below, starts to substantially contribute to the assemblage. A tuffite bed located somewhat above contains numerous specimens of the morphologically simple ammonoid *Acutimitoceras prorsum*. Never before in the Holy Cross Mountains any single ammonoid species dominated the whole fossil assemblage. The thin-crowned, apparently cold-water conodont *Protognathodus,* associated elsewhere in Europe with *Acutimitoceras* ammonoids, joins *N. communis* and dominates the assemblage in the limestone beds higher up (Fig. 1). It is gradually replaced in the conodont assemblage by *Pinacognathus*? *praesulcatus,* which possibly evolves into *P. sulcatus*, steadily increasing its contribution to the assemblage. A complete evolutionary succession of the wide-platform conodonts *Siphonodella* and *Weyerognathus* enriches the species assemblage in the higher part of the section. *Siphonodella duplicata* is replaced there (by evolution?) by *S. carinthiaca*, then very advanced *S. belkai* appears by migration. Another immigration of populations probably representing *S. cooperi* follows, then *S. sandbergi,* and again the *S. cooperi* lineage represented by a more advanced chronospecies. The age correlation with other Tournaisian sections can be based on the succession of *Weyerognathus triangulus* and *W. inaequalis,* which at Kowala is an immigration event, but in the Chinese Muhua section the relationship is proven to be evolutionary (Dzik 1997).

Within this generally smooth succession, partially evolutionary, partially migrational, there are three horizons of a rather profound and sudden change which are likely to represent climatic disturbances. The first one was already mentioned as the boundary zone dominated by cold-water *Protognathodus.* The second rebuilding of the fauna was not so profound but clearly recognisable and separates ranges of *Siphonodella duplicata* and *S. carinthiaca.* The ecological opportunist *Neopolygnathus* disappeared at that time from the record. Its sudden reappearance in high number together with *Protognathodus* marks the third, very thin horizon, probably climatically controlled. At the end of the uniform marly sedimentation and at the income of black radiolarites the fossils are rather rare at Kowala but close analogy with other sections (among others Muhua in south China) suggests that this corresponds to the world-wide transgression and incursion of the *Siphonodella crenulata* fauna. The Muhua section well compliments the fossil record of evolution of

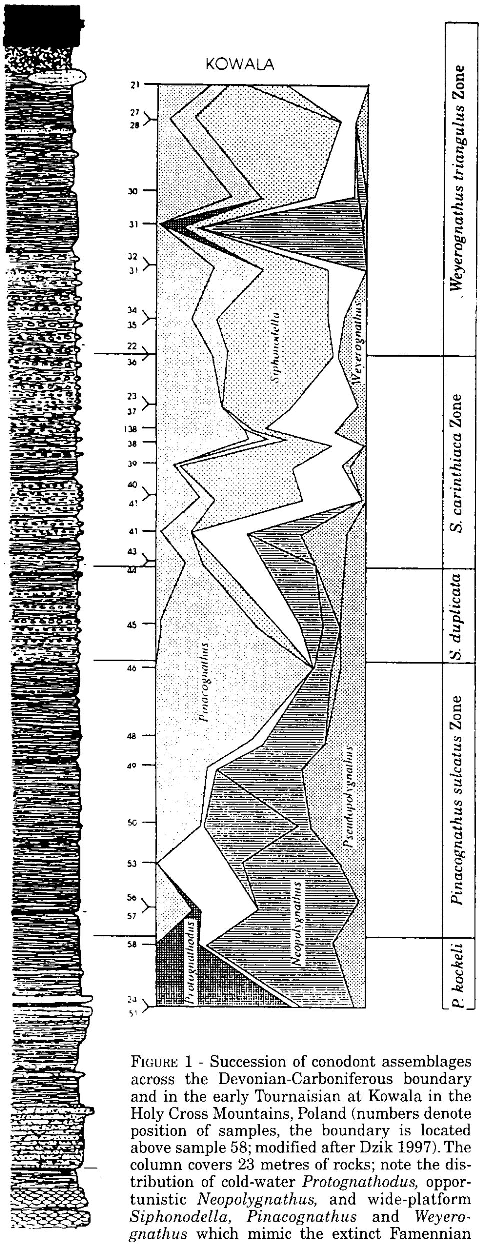


FIGURE 1 - Succession of conodont assemblages across the Devonian-Carboniferous boundary and in the early Tournaisian at Kowala in the Holy Cross Mountains, Poland (numbers denote position of samples, the boundary is located above sample 58; modified after Dzik 1997). The column covers 23 metres of rocks; note the distribution of cold-water *Protognathodus*, opportunistic *Neopolygnathus*, and wide-platform *Siphonodella*, *Pinacognathus* and *Weyerognathus* which mimic the extinct Famennian warm-water palmatolepidids and polygnathids.

Succession d'assemblages de conodontes à la limite Dévonien-Carbonifère et dans le Tournaisien inférieur à Kowala dans les Monts de Sainte-Croix, Pologne (les nombres indiquent la position des échantillons, la limite se situe au-dessus de l'échantillon 58; modifié d'après Dzik 1997). La colonne correspond à 23 mètres de sédiments ; noter la distribution de Protognathodus *forme d'eaux froides de* Neopolygnathodus *forme opportuniste, de* Siphonodella, Pinacognathus *et* Weyerognathus *qui miment les palmatolepidides et polygnathides, formes famenniennes éteintes d'eaux chaudes.*

conodonts represented at Kowala, as does also the Dzikowiec section in the Sudetes, Poland. Two conodont lineages represented at those localities have been documented biometrically, *Neopolygnathus purus* and *Weyerognathus triangulus*. Both at Muhua and Kowala the measured morphological features of those conodonts show a gradual shift in the mean values and the course of evolution seems to be virtually linear in respect to the rock thickness (Fig. 2). Remarkably, the migrational appearance of those lineages preceded the second climatic event indicated above and the *Weyerognathus triangulus* lineage at least at Dzikowiec terminated close to the end of carbonate sedimentation, being replaced by a more primitive species of the same genus, which apparently immigrated from other regions. If there was any response to the environmental change, it was migrational. The morphologic evolution of *Weyerognathus* and *Neopolygnathus* ignored the less fundamental changes of the abiotic environment.

The time extent of the observed evolutionary change covers most of the *Gattendorfia* stage and is difficult to estimate but may correspond to a couple of million years. One may possibly question the value of the presented evidence because ecological changes there were not fundamental and have been inferred on a rather speculative basis from the composition of fossil assemblages. This cannot be said about the other section, discussed below, where stratophenetics was also used to study the phyletic evolution.

LATE ORDOVICIAN GLACIATION AND THE EVOLUTION OF CONODONTS

The Mójcza section in the Holy Cross Mountains, Poland, is probably the most complete and uniform section of the Middle and Late Ordovician in Europe. A stable carbonate sedimentation continued there from the latest Arenig to the late Ashgill, that is about 25 million years (Fig. 3). This was mostly a result of unusually stable and slow pelagic carbonate sedimentation. In the Ordovician, this site was located at the northern margin of the separate Malopolska microcontinent. Originally probably associated with the margin of Gondwana, the continent migrated slowly northward from high latitudes to the equator, which was probably reached in the Devonian.

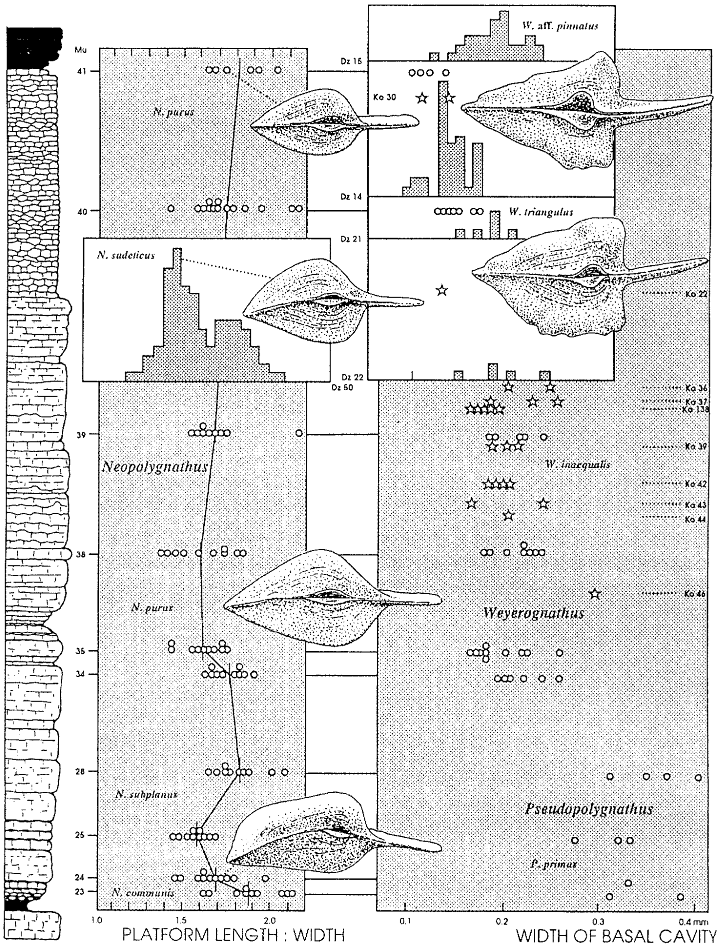


FIGURE 2 - Stratophenetically documented evolution of the conodonts *Neopolygnathus* and *Weyerognathus* based on the succession at Muhua in the Guizhou province of China (circles on plots; rock column on left which covers 4.5 metres of rocks), Kowala (asterisks), and Dzikowiec in the Sudetes, Poland (histograms) (modified after Dzik 1997). Note that in all the three sections changes are virtually linear in respect to the rock thickness although, except for at Muhua, where only short segments of their evolution are represented. No influence of climatic or migrational events represented by changes in fossil assemblage structure on log on Fig. 1 is recognisable. Two migrational events correspond to the incursion of *Neopolygnathus purus* in the lower part of the sections (between samples Mu 26 and 28) and the reintroduction of an archaic species of *Weyerognathus* with the beginning of the *Siphonodella crenulata* transgression (sample Dz 16). *Evolution stratophénétiquement documentée de l'évolution des conodontes* Neopolygnathodus *et* Weyerognathus *d'après la succession à Muhua, province de Guizhou en Chine (cercles; la colonne sédimentaire à gauche représente 4,50 mètres), à Kowala (astérisques) et à Dzikowiec dans les Sudètes, Pologne (histogrammes) (modifié d'après Dzik 1997). Noter que dans les trois coupes les changements sont virtuellement linéaires par rapport à l'épaisseur des sédiments, excepté à Muhua où ne sont représentés que de courts segments de leur évolution. Aucune influence d'événements climatiques ou migratoires, représentés par des changements dans la structure de l'assemblage fossile sur le log de la figure 1, n'est décelable. Deux événements de migration correspondent à l'incursion de* Neopolygnathus purus *dans la partie inférieure des coupes (entre les échantillons Mu 26 et 28) et à la réintroduction d'une espèce archaïque de* Weyerognathus *avec le début de la transgression à* Siphonodella crenulata *(échantillon Dz 16).*

A general trend toward climatic cooling is indicated in geological sections of the Holy Cross Mountains Ordovician by a steady increase in contribution of subpolar Gondwanan species, which was connected with a decrease in the assemblage taxonomic diversity. This transformation of the pelagic communities started in the middle Caradoc. Within the Late Ordovician epoch of domination of cold-water faunal assemblages, there was a series of at least eight brief increases in abundance of exotic temperate-climate species indicative of brief warmings. The topping shales with the brachiopod *Hirnantia* and trilobite *Mucronaspis* seem to mark the beginning of the terminal Ordovician transgression which culminated with the deposition of black graptolite shales.

Sections from other regions of the world can be precisely correlated owing to the good record of evolution of the conodont *Amorphognathus*. Interestingly, the peak in domination of cold water species and fossil assemblages of the lowest diversity at Mójcza correlates with the epoch of maximum expansion of the Kullsberg Limestone mud mounds in the Baltic area, located that time

FIGURE 3 - Succession of conodont assemblages in the Middle and Late Ordovician in the Holy Cross Mountains, Poland. The sections represent different facies regions and are correlated with each other roughly on the basis of the evolution of conodonts (dotted correlation lines) and in more detail using numerous bentonite horizons (thick lines) and the distribution of phosphatic ooids and agglutinating foraminifers (controlled by availability of fine quartz silt). Note cold and warm events in the Late Ordovician (numbered) indicated by incursions of exotic faunal elements.

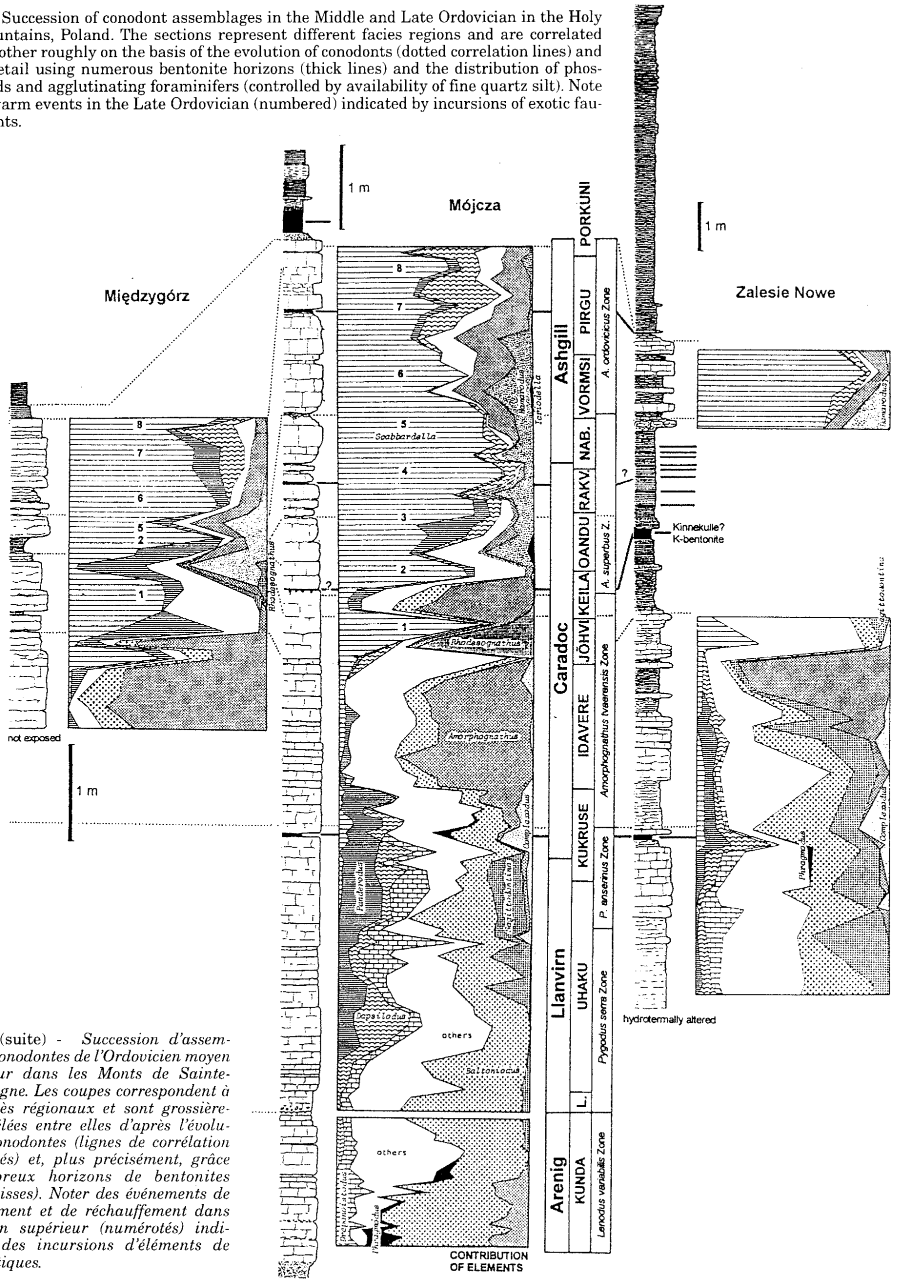


FIGURE 3 (suite) - *Succession d'assemblages de conodontes de l'Ordovicien moyen et supérieur dans les Monts de Sainte-Croix, Pologne. Les coupes correspondent à divers faciès régionaux et sont grossièrement corrélées entre elles d'après l'évolution des conodontes (lignes de corrélation en pointillés) et, plus précisément, grâce aux nombreux horizons de bentonites (lignes épaisses). Noter des événements de refroidissement et de réchauffement dans l'Ordovicien supérieur (numérotés) indiqués par des incursions d'éléments de faunes exotiques.*

close to the tropics (Smethurst et al. 1998). This suggests that a lowering of the sea level and increased climatic gradients were the main factors controlling the evolution of abiotic environment in the Late Ordovician.

The alternating periods of warm and cool climate effected very much distribution of the conodont lineages represented at Mójcza. Some of them invaded the area only during the most apparent warmings. These were especially the tropical (although with a long earlier evolutionary history in high latitudes; Dzik 1990b) species of *Rhodesognathus, Icriodella, Ozarkodina* and *Birksfeldia.* Several lineages of species with ecological preferences to relatively cold-water open-sea environments persisted continuously, although with varying relative frequencies. This was most likely controlled by the surface temperature in the case of generally subpolar conodont *Scabbardella* (which never entered the equatorial shallow seas of the North American Midcontinent) or by water depth (eventually also by temperature) in the case of *Amorphognathus.* Its increased contribution to fossil assemblages at Mójcza and global geographic extent fall clearly in epochs of the highest sea level stand in the Ordovician.

The rate of evolution within the lineages well represented at Mójcza is extremely variable. Some of them do not seem to change at all within the recorded time span of perhaps twenty million years. This refers especially to the aberrant *Strachanognathus* of cryptic origin but widely known in other regions, where its range represents only a fraction of that recorded at Mójcza. This clearly shows that the ranges of fossils in the rock, even pelagic, are of no value in estimating the rate of evolution (Dzik 1991a, 1996). *Scabbardella,* after a relatively short period of some, poorly documented, change in the late Llanvirn, remains virtually unchanged until its disappearance from the record in the late Ashgill. Similarly stable was *Hamarodus,* another widely occurring species of cryptic origin. Perhaps those slowly evolving but easily migrating lineages represented ecological opportunists of that time.

One of the earliest exotic immigrants at Mójcza was *Complexodus,* the lineage of which seems to have a complete record, not yet biometrically studied, in South China. There were at least three migrational events of this lineage recorded at Mójcza (Fig. 4). Its first incursion represents an early species which is very subordinate numerically and rather poorly represented in the material. It does not seem to change during its persistence at Mójcza but is suddenly replaced by another species of the same lineage, apparently during an environmental change which brought to the area also other exotic forms (*Phragmodus*). Before its disappearance after a relatively short time, this species underwent a biometrically recognisable morphological evolution (Dzik 1990b, 1994a). Then it gradually left the area with the beginning of the global Early Caradoc sea-level rise (*Nemagraptus gracilis* transgression). When *Complexodus* appeared again after the high water stand ended, it was represented again by the primitive species, which started to evolve at Mójcza in an opposite direction to that before. This is a good example that evolution proceeded effectively in periods of stable environment. Dramatic changes of the environment destroyed achievements of the evolution.

The most time extended and morphologically complex changes were recorded at Mójcza in the evolution of the balognathid *Amorphognathus.* Almost certainly, this lineage is rooted in the Early Ordovician *Lenodus* but the transition has not been proven in any section in the world (Dzik 1994a). At Mójcza it appeared in the latest Llanvirn (Llandeilian, Pygodus anserinus Zone) and continues throughout the rest of the section (Fig. 5). The most apparent changes in the mouth apparatus of *Amorphognathus* concern the two elements located at its extremes, the anteriormost minute ne (or M in other notation system) and the posteriormost robust sp (Pa) elements.

The ne (M) element of *Amorphognathus* was progressively loosing its original similarity to its homologues in other Ordovician conodonts, gradually and convergently attaining shape similar rather to that in unrelated post-Ordovician ozarkodinids. Its character easiest to quantify is the number of main denticles (counted from the base of the external process to the bifurcation of the internal process, including the cusp which is frequently difficult to distinguish from them). In the oldest populations the denticle number was extremely variable, with the mean counting about five denticles. At the top of the section, all the specimens bear only the cusp, elongated and sharp (in early populations there are superficially similar rare specimens with cusp domination which resulted from concealing all the denticles in the histogeny). The change in the mean value for populations is almost linear in respect to the rock thickness (Fig. 5). Several other features which are not so easy to quantify change also in this element type. This especially refers to the length and orientation of the processes. The external process gradually reduces its length, in the latest populations being virtually missing and devoid of any denticulation. This seems to be the most persistent trend and the least variable character in the evolution of late *Amorphognathus* chronospecies. The internal process, being initially straight and weakly denticulated, became high arched and with strong denticles parallel to the cusp. The

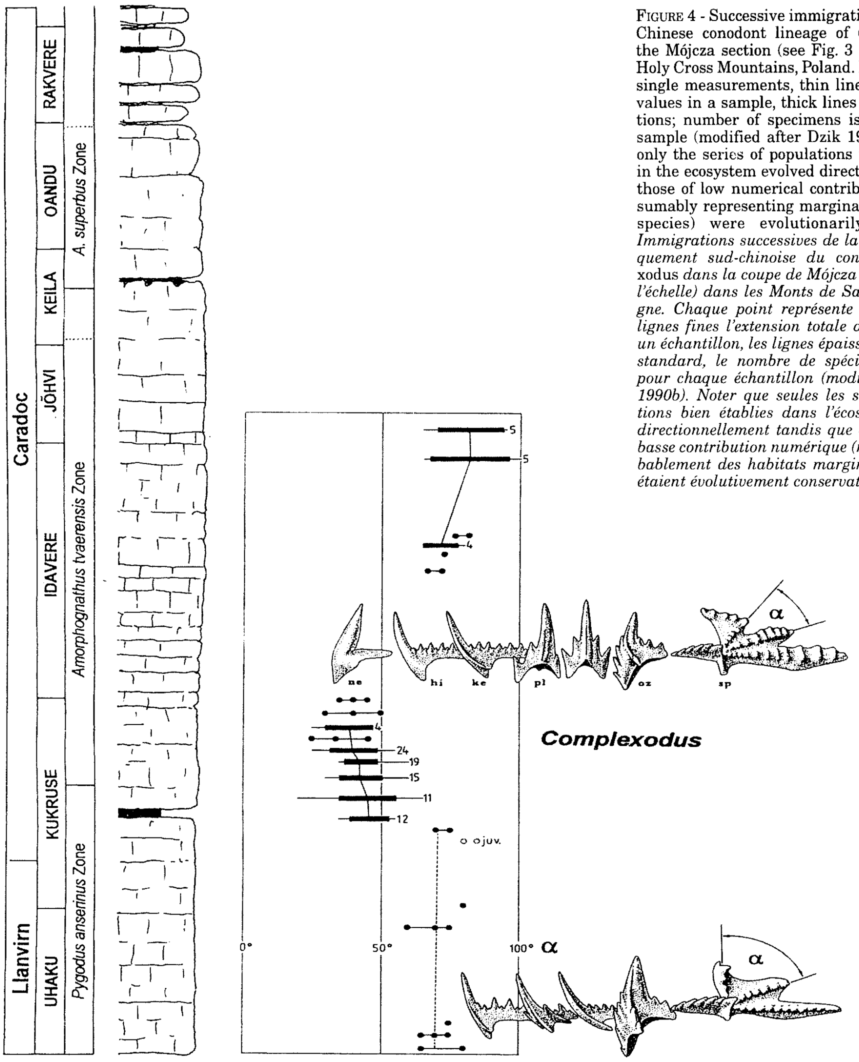


FIGURE 4 - Successive immigrations of the South Chinese conodont lineage of *Complexodus* in the Mójcza section (see Fig. 3 for scale) in the Holy Cross Mountains, Poland. Points represent single measurements, thin lines total range of values in a sample, thick lines standard deviations; number of specimens is given for each sample (modified after Dzik 1990b). Note that only the series of populations well established in the ecosystem evolved directionally, whereas those of low numerical contribution (thus presumably representing marginal habitats of the species) were evolutionarily conservative. *Immigrations successives de la lignée authentiquement sud-chinoise du conodonte* Complexodus *dans la coupe de Mójcza (voir Fig. 3 pour l'échelle) dans les Monts de Sainte-Croix, Pologne. Chaque point représente une mesure, les lignes fines l'extension totale des valeurs dans un échantillon, les lignes épaisses les déviations standard, le nombre de spécimens est donné pour chaque échantillon (modifié d'après Dzik 1990b). Noter que seules les séries de populations bien établies dans l'écosystème évoluent directionnellement tandis que celles qui sont à basse contribution numérique (représentant probablement des habitats marginaux de l'espèce) étaient évolutivement conservatrices.*

angle of ramification of the internal process was initially rather low (although variable), but became wider and wider, which finally resulted in location of a transverse denticle, emerging from the cusp, in the middle of the flat area spanning between the internal process and its posterior bifurcation. Only some initial stages of the development of this denticle, well represented in the Carnic Alps and Welsh materials, are seen close to the top of the Mójcza section. Although these transformations are difficult to be shown quantitatively with the material in hand (which is usually fragmented), there is no reason to expect that they were of different nature than others.

The elements sp (Pa) of *Amorphognathus* do not form a mirror image pair (Bergström 1971). The

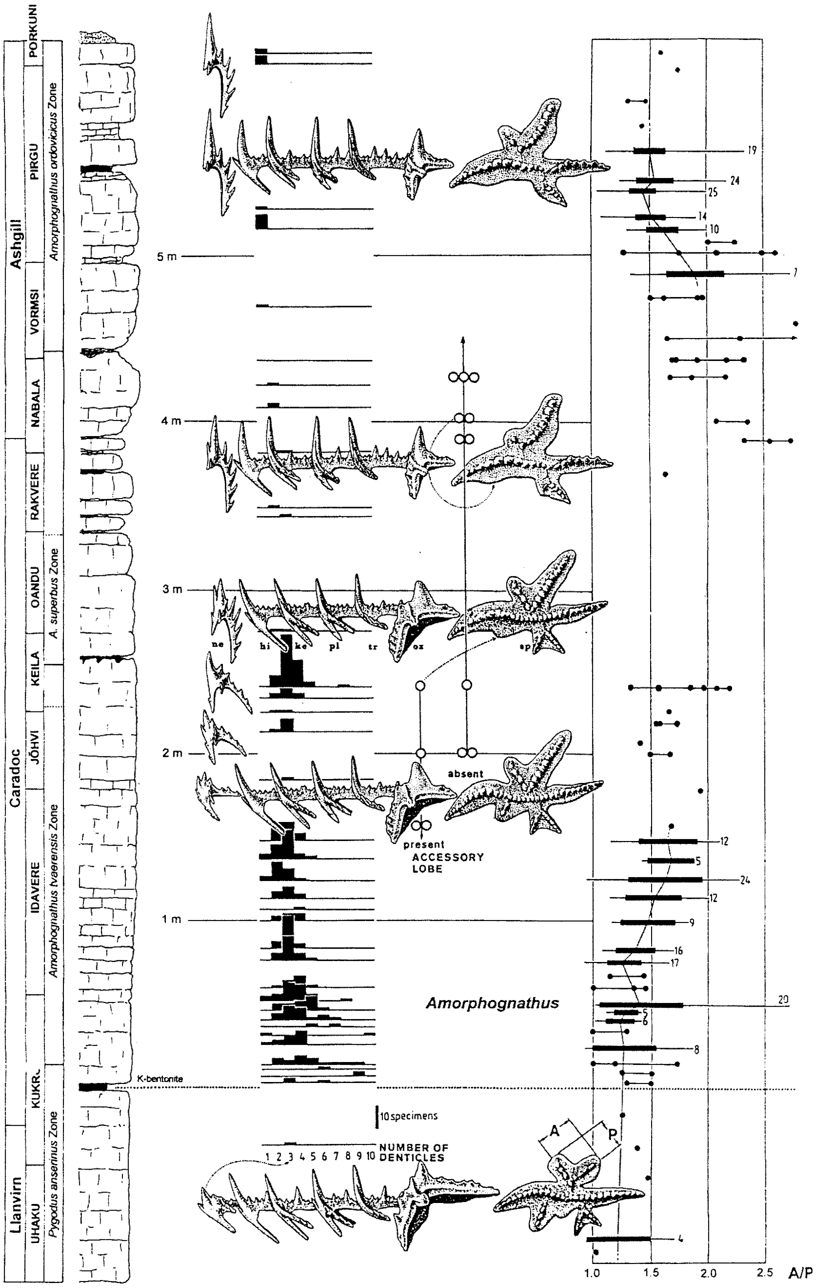
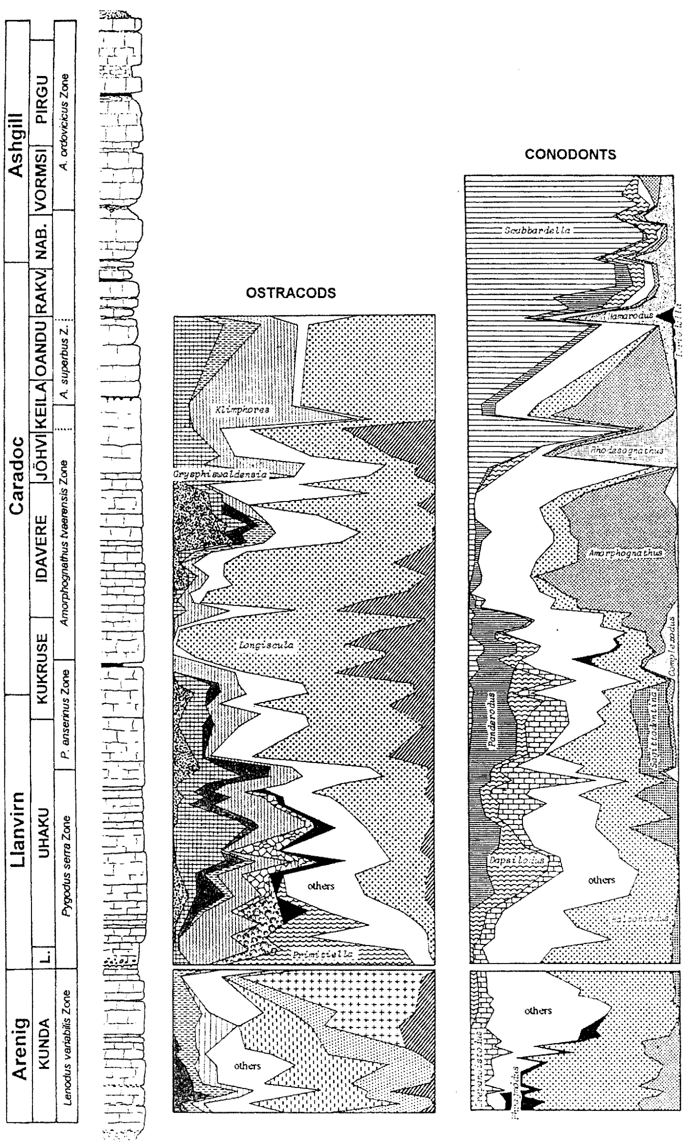


FIGURE 5 - Evolution of the conodont *Amorphognathus* at Mójcza in the Holy Cross Mountains, Poland (see Figs 3, 4 for explanations; modified after Dzik 1990b). Note that the lineage dramatically changed its geographic distribution, invading the epicontinental seas of the North American Midcontinent among others, in epochs of high water stand, which is well expressed at Mójcza by increases in numerical contribution to the fossil assemblage (see Fig. 3 where also scale is given). These fundamental changes in ecological conditions and the area inhabited by populations of the lineage had no expression in the rate of its phyletic evolution. It remains almost linear in respect to the rock thickness through the whole section. *Evolution du conodonte* Amorphognathus *à Mójcza dans les Monts de Sainte-Croix, Pologne (voir Fig. 3 et 4 pour explications, modifié d'après Dzik 1997). Noter que la lignée changea fortement sa distribution géographique, envahissant les mers épicontinentales du centre de l'Amérique du Nord entre autres, aux époques de haut niveau marin bien exprimé également à Mójcza par les accroissements de la contribution numérique à l'assemblage fossile (voir Fig. 3 où l'échelle est aussi donnée). Ces changements fondamentaux des conditions écologiques et l'aire occupée par des populations de la lignée n'ont pas d'expression dans le taux d'évolution phylétique. Il reste à peu près linéaire par rapport à l'épaisseur des sédiments tout au long de la coupe.*

FIGURE 6 - Succession of ostracod assemblages in the Middle and Late Ordovician in the Holy Cross Mountains, Poland, and its relationship to changes in conodont assemblages (modified after Olempska 1994; Dzik 1994a). Note that alterations in benthic arthropod communities parallel those in pelagic chordates, which proves that the controlling factor was not locally sedimentological but more general, probably climatic. *Succession des assemblages d'ostracodes de l'Ordovicien moyen et supérieur dans les Monts de Sainte-Croix, Pologne, et ses relations avec les changements dans les assemblages de conodontes (modifié d'après Olempska 1994; Dzik 1994a). Noter que les modifications des communautés d'arthropodes benthiques sont parallèles à celles des cordés pélagiques, ce qui prouve que le facteur contrôlant n'était pas sédimentologique et local mais plus général, probablement climatique.*



dextral element is always relatively flat and of a regular appearance, whereas the occlusal surface of the sinistral element is strongly convex and of more elaborate outline. Its internal process develops a posterior ramus, which in early forms is of almost the same length as the part of the internal process distal of the bifurcation point. This was because the bifurcation occurred initially late in the histogeny. In the course of evolution the point of bifurcation was closer and closer to the cusp until its complete disappearance. A lobe in the place of this process persisted for some time until the sinistral process reached a morphology not much different from that of its dextral counterpart. The process is developed in all sinistral specimens of early populations of *Amorphognathus* and is missing in all such elements of late populations. There is an interval in the middle of the section where both lobate and non-lobate elements co-occur. Generally, the shape of sp (Pa) elements is extremely variable and only when large samples are available it is possible to recognise with confidence which stage of their evolution is represented.

Also variable is the bifurcated anterior process in sp (Pa) elements of *Amorphognathus,* but its evolutionary transformation is roughly parallel in both dextral and sinistral elements. Its external lobe became more and more elongated in the evolution until the Early Ashgill, when in some elements the internal lobe may be missing. Then, in the topmost part of the Mójcza section the quantitative data seem to show a reversal of the trend. This may be an expression of the general reduction in size of the *Amorphognathus* elements in this part of the section. It is not clear whether this is a matter of true evolution or just an ecologically controlled change in population dynamics (an increase of juvenile mortality), which may have resulted in the sample being dominated by juvenile elements of a more primitive appearance than that of the adults. Unfortunately, there is no clear demarcation of juvenile or adult stages in conodont elements because their growth was not terminal. Apparently, the correspondence between size and age was there not especially strict. Small elements may quite well represent small adults or normal juveniles. There is no way to show precisely what was the pattern of evolutionary expansion of evolutionary novelties in their ontogeny. This lack of evidence on the timing of ontogeny modifications is the main deficiency of the conodont fossil record of evolution.

This can be overcome easily in case of arthropods, where moulting stages are very well represented in the fossil record and can be easily identified. The main problem with the arthropods is that their fossil record is rarely complete enough to enable stratophenetic study, as typical of benthic organisms. Also in this case Mójcza offers an unique opportunity of evolutionary studies owing to the secondary phosphatisation of calcareous skeletons in the rock.

EVOLUTION OF ONTOGENY IN ORDOVICIAN OSTRACODS

Among several lineages of benthic ostracods from the Mójcza Limestone (Fig. 6) studied by Olempska (1994) at least one of them shows excellently documented gradual transformations of the carapace morphology (Olempska 1989, 1994). Olempska's (1989) lineage of *Mojczella* extends from the end of Arenig to the middle of Caradoc, thus for about fifteen million years. This seems to be one of the longest in time biometrically documented continuous records of the evolution (note that it corresponds to the time span from the Middle Miocene to today!). Among evolving features of the *Mojczella* carapace the easiest to measure is the development of junction between two curved ribs at its surface. Initially, there were two separate ribs throughout the whole ontogeny, although the gap between their lower ends decreased somewhat in extent during growth. In late populations of the lineage there was a continuous, sinuous rib in late ontogenetic stages and only earliest moults preserved two separate ribs. There is a complete gradation between these extreme stages of the evolution, with the evolutionary novelty (junction between ribs) expanding towards earlier and earlier stages of the ontogeny. Although this pattern of the evolution of ontogeny is easy to infer from less direct evidence, the Mójcza lineage is probably the only one in palaeontological literature which documents it in full. What is the most surprising, the change is almost linear in respect to the rock thickness (Fig. 7).

The Mójcza lineage persisted in one place for unusually long time. Its particular members may have invaded for a brief period also other regions (Olempska 1994), notably with the *Nemagraptus gracilis* transgression, in the epoch of the extreme world climate uniformity. There is no indication of any significant alteration of the rate of evolution in the time spans, when the geographic extent of the lineage expanded or shrunk. There is also no reason to suggest that the evolution of *Mojczella* was governed by different mechanisms than that of other Ordovician ostracods.

The unavoidable conclusion is that both in the case of pelagic chordates and of benthic arthropods, the observed ranges of species in the rock sections have nothing to do with the real durations of morphologies in the phyletic evolution. Moreover, the evolution was very slow and successions of the basically different morphologies we usually see in the fossil record is almost exclusively a result of ecologically controlled migrations and shifts in distribution of species. This is frequently misunderstood as directly connected with the evolutionary change.

GENERAL CONSIDERATIONS

The horizontal flow of genetic information among particular genealogical lines of descent (crucial for the theory of speciation), is not necessary for selection forces to act and the evolution to proceed. One may easily imagine evolution without species, in which all genealogical lines of descent are separate from each other (prokaryotes evolve

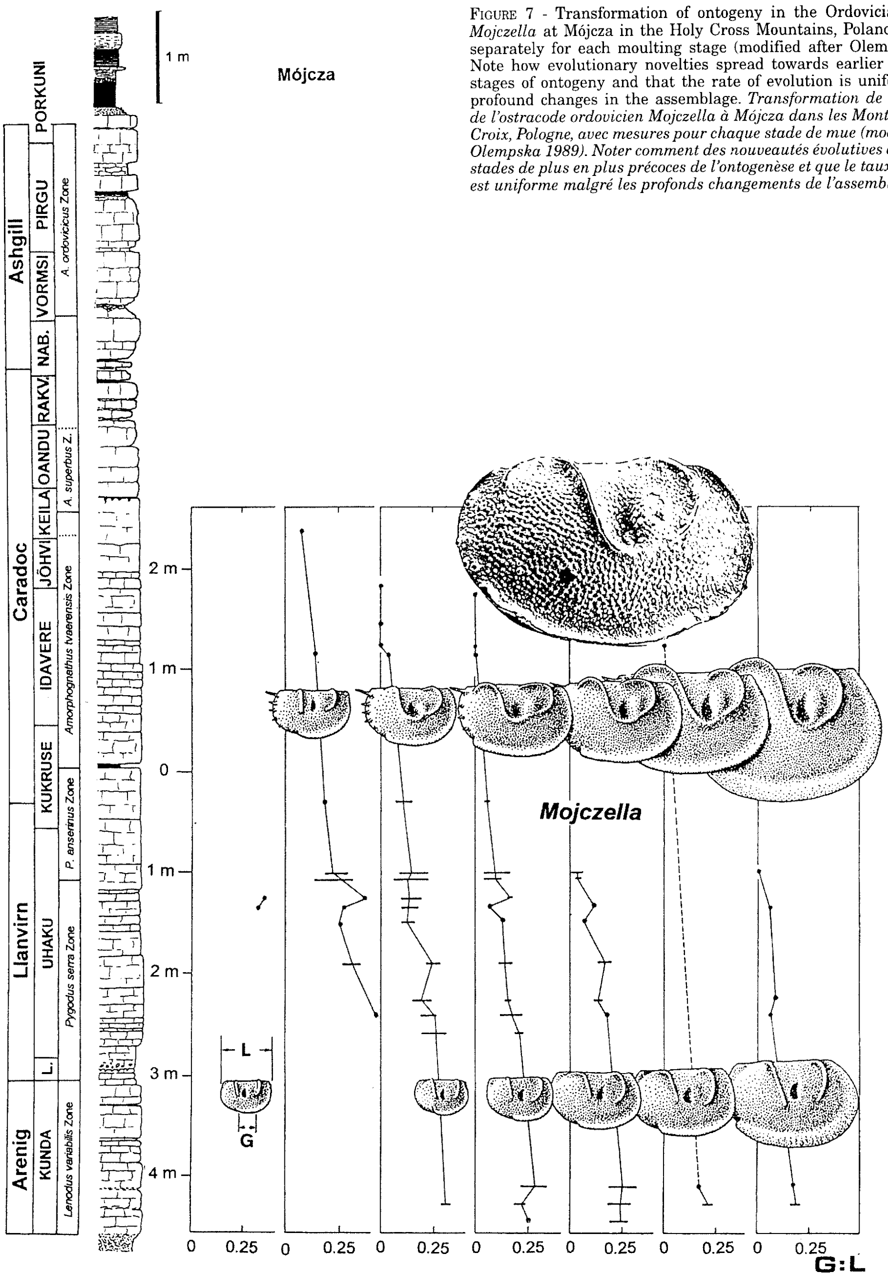


FIGURE 7 - Transformation of ontogeny in the Ordovician ostracod *Mojczella* at Mójcza in the Holy Cross Mountains, Poland, measured separately for each moulting stage (modified after Olempska 1989). Note how evolutionary novelties spread towards earlier and earlier stages of ontogeny and that the rate of evolution is uniform despite profound changes in the assemblage. *Transformation de l'ontogenèse de l'ostracode ordovicien Mojczella à Mójcza dans les Monts de Sainte-Croix, Pologne, avec mesures pour chaque stade de mue (modifié d'après Olempska 1989). Noter comment des nouveautés évolutives affectent des stades de plus en plus précoces de l'ontogenèse et que le taux d'évolution est uniforme malgré les profonds changements de l'assemblage.*

in fact in this way, even if there is some insignificant horizontal transfer of genes). Less obvious, but possible, is evolution within a panmictic population without speciation. It is enough to compare the number of species with anatomical distance between extreme members of particular taxonomic groups to see that there is evidently no clear correspondence between the rate of speciation and the rate of morphologic evolution. Insects, which tend to speciate especially easily, are generally very conservative in their anatomical evolution, most of Recent morphologies ranging back to the early Mesozoic or even Palaeozoic. On the contrary, whales and humans, with their few species, are among the fastest evolving organisms.

The theory of allopatric speciation claims that whenever environmental barriers separate parts of a population, splitting thus its genetic pool into segments, they may start divergent evolution eventually leading to development of genetic barriers. As a result, such transformed populations are no longer able to interbreed with each other and remain separate genetic units (species) even if they meet spatially again. Thus a geographic space and spatial discontinuity of the environment is needed to explain the observed disparity in number of species between various taxonomic groups. The concept of "allopatric" speciation is sometimes narrowed to a special case of evolutionary changes being supposedly fastened at the moment when a small marginal population invades a new environment (Gavrilets & Hastings 1996; see also Koeslag 1995). If true, such a mode of the evolution would make its tracing inaccessible to palaeontology being beyond resolution of its method. However, the factual evidence (Dzik 1991a) proves that this is at least not the dominant mode of evolution. All the palaeontologically documented cases of evolutionary change show a rather slow rate also in populations clearly changing their geographic range. The first observable departures from the original morphology of invaders to new marginal environments appear with much delay (in terms of geological time; e.g. Dzik 1983). Such pattern is close to what White (1968) named "stasipatric" speciation, but nomenclatorial problems are obviously secondary to the subject which is to be discussed here.

The question why the number of kinds of organisms is not virtually infinite is thus explained by the theory of sex belonging to the field of population genetics. Why there are so many kinds of organisms and not just a single panmictic population is a question which has to be addressed to population ecology. The correspondence between the number of species and area is generally apparent, even if many additional factors have to be consulted to explain fully particular patterns. This factor may be responsible for both objective changes of diversity in the geological past and bias in their estimation caused by unequal knowledge of particular time segments (Sepkoski 1993). Any method to estimate precisely rates of extinction and origination of lineages might thus be a powerful tool to describe evolutionary partitioning of the ecospace. Unfortunately, this is not an easy task and definitely there is no simple correspondence between originations and extinctions of lineages and their ranges observed in rocks (Dzik 1995). Moreover, the estimation of diversity based on fossils is strongly biased by common application of vertical (typologic) instead of population concepts of chronospecies (Dzik 1985, 1990a) or even completely obscured by taxonomic methodologies.

The problem of relationships between the rate of evolution and stability of environment is usually addressed within the frames of the Red Queen hypothesis (Van Valen 1973) versus Stationary Model (Stenseth & Maynard Smith 1984) controversy. The Red Queen hypothesis is based on a zero-sum assumption that what one species gains, other species must loose or counter with evolutionary change. In such conditions evolutionary change must took place irrespective of the influence of abiotic environment. According to the Stationary Model evolution occurs only in response to changes in the environment. "The rate of evolution of any particular species will depend on how far the species is from a local adaptive peak" (Stenseth & Maynard Smith 1984: 871). The main shortcoming of this concept of the evolutionary lag is that there is practically no way to determine what does it actually mean "a local adaptive peak". What is even worse, as admitted by Stenseth & Maynard Smith (1984: 878) there may be no such peak in case of organisms exploring new regions of the ecospace.

Attempts of testing those opposing interpretations were based on an assumed correspondence between the origination of species and their ranges in rock sections (Hoffman & Kitchell 1984; Kitchell & Hoffman 1991) which, in fact, was the starting point of Van Valen's (1973) considerations. This assumption is highly questionable, however, as pointed out above and discussed more extensively elsewhere (Dzik 1995). A statistical approach to the problem does not seem to remove any of the problems. Mean species duration will remain biased, as shown by Solow & Smith (1997), because (1) the observed range of a fossil species is almost always less than its true duration and (2) species for which there is a high probability that no individual is preserved will not be observed. Longer-lived species will thus be over-represented and original durations of preserved species are biased upwards (Foot & Raup 1996). Although those two bias act in opposite direction, the resulting counts give hardly a reliable approximation to the truth. We have to admit that stratigraphic ranges of species are actually useless as a measure of the rate of evolution, giving either overestimate or underestimate of its rate in unknown extent. There is also no correspondence between the observed ranges of species and speciation events. Morphologic distinction in allopatric populations may develop much before genetic isolation develops (a good case is the profound difference between brown bear *Ursus arctos* and polar bear, classified once as *Thalarctos maritimus*) or much after it (which may be the reason of seemingly sympatric speciation in stratophenetic record). Because of the fundamental limitations of palaeontology, speciation events are practically out of reach of its method, unavoidably requiring complex inference to be identified, not a direct observation from the fossil record (Dzik 1985, 1991a, 1995).

Even if one claims to be able, in some mysterious way, to determine frequency of speciations in fossil record, this would be hardly of much use in quantifying the rate of evolution. The process of speciation refers to other dimension of the evolution than its rate. It mostly expresses a complexity of the environment in which organisms evolve or special features of their biology (for instance mating behaviour) with no direct correspondence to the intensity of the process of transformation.

Those comments refer as well to estimates of diversity based on higher rank Linnean taxa, although additional aspects of the problem then emerge. Is taxonomic diversity a measure of evolution or complexity of environment? The number of Linnean taxa of various rank into which temporally co-occurring species were classified on the basis of fossils described in the literature is the most commonly used measure of diversity, dating back to the classic book of Phillips (1860; reviewed recently e.g., by Conway Morris 1998). Also in this case particular steps in the procedure of obtaining data, collecting fossil (mostly limited to skeletal remains), their description, and finally classification, are biased in a non-random way. This is the obvious shortcoming of this kind of evidence (commented e.g., in Sepkoski 1993). Perhaps the most serious bias is that resulting from subjectivity of supraspecific Linnean taxa. Ironically, this last aspect of the Linnean taxonomy gives it a special value and strength. Although there is no generally accepted standard for the morphological extent of a taxon of given rank, taxonomers tend to give similar ranks to groups of organisms of similar internal diversity. This, in lack of strict objective methods of quantifying diversity makes Linnean taxonomy, despite all its shortcomings, the best tool to express differences and similarities among both fossil and Recent communities of organisms. Unfortunately, the recent expansion of cladistics, despite its claim of objectivity, makes taxa even less informative and eventually will remove any informative value from the palaeontological taxonomy.

The main problem is what the number of Linnean taxa actually describes. To know whether it is truly useful we need to know what kind of distortion of the evidence results from its natural biases. Obviously, it would be unrealistic to expect that the fossil evidence is complete enough to give a good representation of the total diversity of the biosphere. Sampling is evidently too uneven and enough non-random to make direct reasoning impossible. It is known well enough that even the localities with extremely good preservation of fossilised soft-bodied organisms do not provide undistorted evidence and are restricted to a very few special environments, different in particular segments of geological time in non-random mode. For instance, the Ediacaran type of preservation seems to be restricted to the epoch preceding evolutionary origin of scavengers (Dzik in press a), "small shelly fossils" kind of phosphatisation was erased with the expansion of bioturbators in the early Palaeozoic (see Dzik 1994b), and the "orsten" type of phosphatisation seems to be strongly controlled by climate and eustacy, being represented only in very special epochs of the Earth history. It is even not completely safe to compare fossil assemblages which originated in similar sedimentary conditions as it is easy to be involved in a circular reasoning. Organisms were much more sensitive environmentally than it can be shown by the sediment alone. Results of counting species and comparing their numbers may thus be very misleading and the real meaning of differences recognised in this way is difficult to identify.

The only reasonable method to determine rate of evolution is thus by restoring the course of the phyletic evolution. This can be done by proving evolutionary continuity at the population level (the method of stratophenetics), or by presenting ancestor descendant hypotheses (the method of chronophyletics), which are fully falsifiable in Popperian sense as proven elsewhere (Dzik 1991a). Some evidence of this kind has been presented above. To explain the observed patterns we need additional data about the environment, in which the evolution took place. This is necessary because the main point is whether there was mostly an abiotic control of change or only intrinsic biological factors were involved in the process. The main difficulty in applying palaeontological evidence of this kind in testing the Red Queen Hypothesis versus Stationary Model dilemma envisaged by Stenseth & Maynard Smith (1984) is that continuous small changes in physical conditions could result in continued evolutionary changes which would be indistinguishable from Red Queen dynamics in an unchanging physical environment. This does not seem to apply to the empirical evidence used in this paper, as the evolution of environment has been determined by independent evidence and was of various nature, not necessarily directional. Generally linear character of the evolution in respect to time (in the studied sections the rate of sedimentation was apparently rather stable) strongly supports intrinsic control of the evolution.

Paradoxically enough, it is not only that a change in environmental conditions does not increase the rate of evolution. It is in fact enhanced by the stability of the environment (Dzik 1991; Sheldon 1996). This is a phenomenon well documented in several ancient lakes. The Ancient Lake Concept (e.g., Gorthner & Meier-Brooks 1985) does not necessarily include any assumption about changing biotic environment as the main motor of the evolution but at least it requires that a fast and directional evolution needs a stability of the abiotic environment. The crucial point of the concept is that in specific conditions of the ancient lakes, the lineages evolve directionally at great rate even if they originated from species which are extremely conservative morphologically in not so stable environments (for instance, viviparid or planorbid snails). Although fast, the evolution in ancient lakes is slow enough to leave a good fossil record in geological sections. The evolutionary conservatism of invertebrates living in ephemeral continental fresh-water environments seems consistent with the destructive effects of migrations in the evolution of Ordovician conodonts, reviewed above.

CONCLUSIONS

It follows from the above presented empirical evidence that not only profound changes in local, climate controlled, environmental conditions, but even expansions of a marginal population to a new environment does not necessarily influence the rate of evolution. Migrations rather tend to hamper the evolution and destroy its earlier effects. Whenever well documented, the phyletic evolution seems virtually linear in respect to time. This must have a rather fundamental bearing on the theoretical explanation of the forces controlling the evolution of natural environments. Palaeontological empirical evidence hardly supports the idea of a strict correspondence between the rate of speciation and the rate of phyletic evolution. Both the Red Queen Hypothesis and the Stationary Model are based on the same paradigm: that it is always an environmental change which drives evolution, biotic in the first case, abiotic in the second. The extremely time-extended stable rate of evolution documented with palaeontological evidence does not seem to be consistent with this paradigm, although no direct evidence against it can be offered now. Whether the "arm race" mechanism of the Red Queen Hypothesis is truly involved in the apparent enhancement of the rate of evolution and its directional character in both ancient lakes and stable marine environments is disputable. Equally probable is that the supply of new genetic material for selecting evolutionary novelties is the most important. If true, the mutation rate would be the main limiting factor in the evolution.

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