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# Evolution of morphogenesis in 360-million-year-old conodont chordates calibrated in days

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**SUMMARY** Highly rhythmic increments of crown tissue are identifiable in conodont oral apparatus elements from the Late Devonian of the Holy Cross Mountains, Poland; individual laminae being of thickness comparable with daily increments of vertebrate tooth enamel and fish otoliths. Abundant occurrence of such specimens enables bed-by-bed (stratophenetic) studies of the process of evolution at the population level and quantitative presentation of the evolution of ontogeny in the sampled geological section covering several million years. The morphologic transformation is expressed as expansion of a juvenile asymmetry to later stages of the ontogeny and in decrease of the mature element width, which was due to a change of the mineral tissue secretion rate. It was not just a simple extension of a juvenile character into the later stage of the ontogeny (heterochrony) but rather a true developmental novelty. The evolution was gradual and very slow. The proposed quantitative approach to growth increments in the mineral skeleton of ancient chordates introduces real-time units to evolutionary developmental studies connected with direct paleontological evidence on the course of evolution.

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## INTRODUCTION

Conodonts are extinct chordates known mostly after phosphatic denticles of their mouth apparatus, referred to as "elements." Loose elements may occur in large number in limestones deposited in pelagic marine environment, from which they can be easily extracted with dilute organic acids. Association of their various morphotypes within the apparatus can then be restored statistically. Rarely complete oral apparatuses of conodonts are preserved on the rock bedding surface ("natural assemblages") or can be extracted from the rock as clusters glued together with organic or mineral matrix. Based on the apparatus structure, the evolution of conodonts has been traced in detail from their origin in the Cambrian to extinction near the end of Triassic, that is, for about 300 million years. Imprints of whole bodies with mineralized soft tissue are also known. They show V-shaped myomeres similar to those of amphioxus, but also have large eyes with well-developed extrinsic musculature (Fig. 1A; Aldridge et al. 1993; Gabbott et al. 1995).

Conodonts are the oldest and least derived chordates (perhaps even vertebrates) that bore a well-developed mineralized dermal skeleton. The mode of formation of the phosphatic skeleton, which characterizes both conodont elements and vertebrate dermal scales, is unique for these two kinds of sclerites and unknown in any other organism. In conodont element crown tissue, successive lamellae of calcium phosphate were added from the outside, as in vertebrate enamel (Fig. 1C). Clear imprints of secretory cells on the oral surface of conodont elements provide insight, at the cellular level, into developmental processes in these extinct chordates, many of which are as much as 500 million years old.

Unlike vertebrate teeth, elements of the conodont apparatus are arranged in sets on lateral sides of the mouth. In the geologically oldest and least derived forms seven pairs of elements occur, which are of morphology similar to each other, but probably early in their phylogeny an additional medial element developed (Dzik 1991b). Oral apparatuses of most conodonts were thus composed of 15 elements (Sweet 1988). Usually elements of the anteriormost pair (referred to as M in standard notation denoting element homology) had a strong sharp cusp and functionally they presumably corresponded to incisors. The following set of eight paired ($S_4$–$S_1$) and single medial ($S_0$) elements are of delicate appearance, usually with numerous denticles. Elements of the two posterior pairs ($P_2$ and $P_1$) are of robust appearance and functionally they probably corresponded to molars (Fig. 1B). As many as eight distinct morphologic classes of conodont element may be represented in a single conodont apparatus. In rare instances, their number was reduced to just one pair (Dzik 2008) or enlarged to 19 (Purnell et al. 2000).

Irrespective of conodont element morphological complexity within the apparatus, increments of hard tissue were added in a similar manner and the rate of secretion was generally

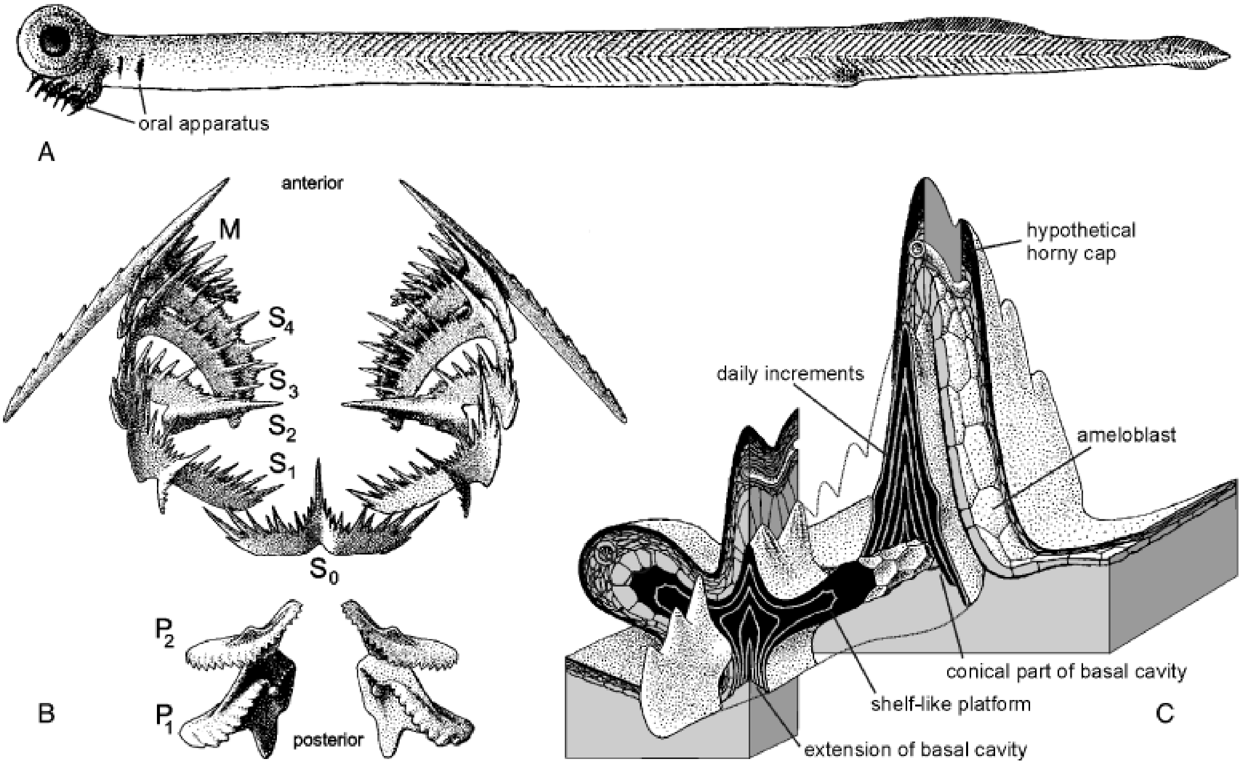

**Fig. 1.** Anatomy of advanced conodonts. (A) Restoration of Early Carboniferous (Viséan) *Clydagnathus* in lateral view (based on data from Aldridge et al. 1993). (B) Oral apparatus of the Late Devonian (Frasnian) palmatolepidid *Lagovignathus bogartensis* (Stauffer 1938) seen from its ventral side and notation of its elements expressing homology with elements in other apparatuses (after Dzik 1991b). (C) Diagrammatic cross sections of a juvenile $P_1$ element and one of possible models of its growth and morphogenesis assuming that the phosphatic tissue was an internal skeleton under a keratinous working surface (after Dzik 2006). Note that initially the basal cavity was of conical appearance even in elements of complex mature morphology.

similar. Local differences in growth rate at the element surface were presumably regulated by proliferation of ameloblasts (Dzik 2000). Such differences resulted in the formation of element- and taxon-specific morphologies such as denticles, ribs, or platform-like thickenings.

Conodont elements are attractive subjects for evolutionary studies because of their complex, highly informative morphology and easy extraction from limestone or chert. Among the relatively well-recognized conodont lineages is that of the palmatolepidids *Tripodellus schleizius*—*Tripodellus gracilis* (Schülke 1999; Dzik 2005, 2006), whose elements are widely distributed in the Famennian strata (361–376 Myr ago) of the Late Devonian over virtually the entire world.

These Late Devonian chordates, with their easily recognizable growth increments, their epithelial cell imprints and their unusually extensive fossil record, offer insight into the process of evolution and are unusually informative in this respect relative to other taxonomic groups within the phylum. In this report I attempt to calibrate in days the observed ontogenetic change using evidence from the Holy Cross Mountains area of central Poland.

## MATERIALS AND METHODS

The studied material comes from the quarry of the cement plant Nowiny II, which is located south of the village Kowala (50°47′37″N 20°33′ ± 41″E). Exposed in the quarry is the most extensive and thickest section of the Famennian in the Holy Cross Mountains, Poland. Conodonts occur throughout the entire section, but most samples are of low productivity. Apparatus reconstructions presented elsewhere (Dzik 2005, 2006) are based on much more productive samples from the same region.

Conodont samples were dissolved in formic acid. Throughout the procedure, less acid added than necessary was used to dissolve the carbonate, and this provided some buffering. Dry residues with a high content of non-phosphatic debris were separated in an electromagnetic mineralogical separator.

$P_1$ elements of genus *Tripodellus* were chosen for study. Measurements were made on SEM pictures of gold-coated specimens. All specimens were photographed in the same orientation, with the element cusp vertical (and thus the incremental units near the margin of the basal cone are visible in almost exact transverse section).

Data obtained using these methods were arranged on plots according to their stratigraphic position in the Kowala section. The method of studying evolution by dense sampling of geological sections and using solely stratigraphic superposition of biometrically characterized samples to detect polarity of change is called "stratophenetics," the term introduced by Gingerich (1979). Issues concerning strengths and criticism of stratophenetic methodology have been reviewed recently, elsewhere (Dzik 2005).

Within each sample of conodont element the pattern of variability appeared to be unimodal, which may be interpreted as a result of inbreeding within populations. In the present work, no other concept than the standard morphological species concept has been used; this is the same basic assumption that allows identification of any species based on morphology in zoology or paleontology. From this follows the conclusion that morphological continuity within samples corresponds to genetic continuity within a population, and that close morphological similarity or identity between two successive samples in the section is evidence of genetic continuity between the populations that they represent. Such hypothesized continuity between conodont populations can be tested by increasing density of sampling. Finally, in the studied geological interval, other species of *Tripodellus* known from other localities in the area, are practically missing (Dzik 2006), although occasional sympatric occurrences have been recorded.

## GROWTH OF ORAL APPARATUS ELEMENTS

The apparatus of *Tripodellus* is composed of 15 elements, which is the standard pattern inherited after the Early Ordovician common ancestor of the ozarkodinid and prioniodontid ancestor and probably dating even deeper in the geological past (Dzik 1991b). However, two pairs ($S_3$ and $S_4$) are of virtually the same shape (Fig. 1B), so seven kinds are distinguishable in acid-resistant residues of limestone samples. Element types representing the extreme locations in the apparatus evolved at the highest rate (Dzik 2005). The posteriormost $P_1$ elements of robust appearance are the easiest to recover as complete unbroken specimens and to study biometrically.

Particular conodont element types in most samples show great differences in size apparently representing different stages of their ontogeny. Frequent regeneration of broken or abraded conodont elements indicates that they functioned while growing, although there is controversy how such function throughout growth was actually achieved (Donoghue and Purnell 1999; Dzik 2000, here Fig. 1C). It is also likely that growth of most conodont elements terminated under genetic control. Growth termination is in some specimens marked by a change in direction of growth of element ramifications (processes). The tip of such a process is recurved and could grow further only in the height of its denticles, with the length of process remaining constant. This phenomenon is common in so many unrelated taxa that it suggests that the ontogeny of all conodonts was controlled in a similar way (Dzik 2006).

Like those of many other Devonian conodonts, *Tripodellus* elements initiated their growth as conical units with a deep basal cavity (Figs. 1, C and 2F). In subsequent growth, a thickening developed near the "$P_1$" element base on its sides, finally forming a wide, robust, and shelf-like platform (Figs. 1C, 2F, and 3). As shown by ameloblast imprints (Conway Morris and Harper 1988), this local increase in secretion rate was connected with the proliferation of ameloblasts (Dzik 2000) in a way resembling that associated with the formation of tooth cusps in recent mammals. In higher vertebrates the proliferation of ameloblasts is stimulated by a cluster of non-dividing epithelial cells (enamel knot) (Jernvall et al. 1994, 2000; Thesleff and Mikkola 2002). Possibly, much the same mechanism controlled morphogenesis of conodont elements, which are similar structurally and were presumably secreted under an epithelial cover in the same way as vertebrate teeth.

Although most of the conodont apparatus elements increase their size in a near-isometric manner, some complications in the pattern of growth may develop in the massive posteriorly located platform-bearing $P_1$ elements. In certain species, the early developmental stages of $P_1$ elements are morphologically distinct. Those of *Tripodellus* are of special interest, because of a profound change in proportions between this early stage and mature element morphology, in the course of the inferred sequence of evolutionary transformation.

## SINUOSA LARVA

In underived polygnathid conodonts, juvenile $P_1$ elements had a conical basal cone and developed a shelf-like thickening (platform) initially at some distance from the cone (Figs. 1C and 2F). This separation of structures was gradually obliterated as an effect of the expansion and thickening of the platform. At the end of growth the conical basal cavity is represented only by an indistinct pit, covered by new increments or resorbed. In some derived lineages, however, most of secretive abilities of the epithelium concentrated at the platform margin and the change from the cone to flat or inverted cavity of the massive platform was rather abrupt (Fig. 2, D–F). Even in mature elements a prominent basal cone is recognizable as a discrete unit. Such a drastic change in the ontogeny apparently represents a profound functional transformation. A similarly fundamental difference between modes of life and/or feeding strategies of juvenile and adult animals has already been suggested with respect to coniform protopanderodontid conodonts by Armstrong and Smith (2001). Whatever was its true biological nature (metamorphosis of a larva?), this is a convenient reference landmark in quantification of element morphogenesis (Fig. 3).

In the main lineage of *Tripodellus* (Dzik 2006) a gradual evolution in the extent of the early developmental stage in $P_1$ elements can be traced. In early members of the lineage, there is virtually no recognizable morphologically separated conical-element stage in taxonomically identifiable juvenile specimens. This morphologically separated conical-element stage

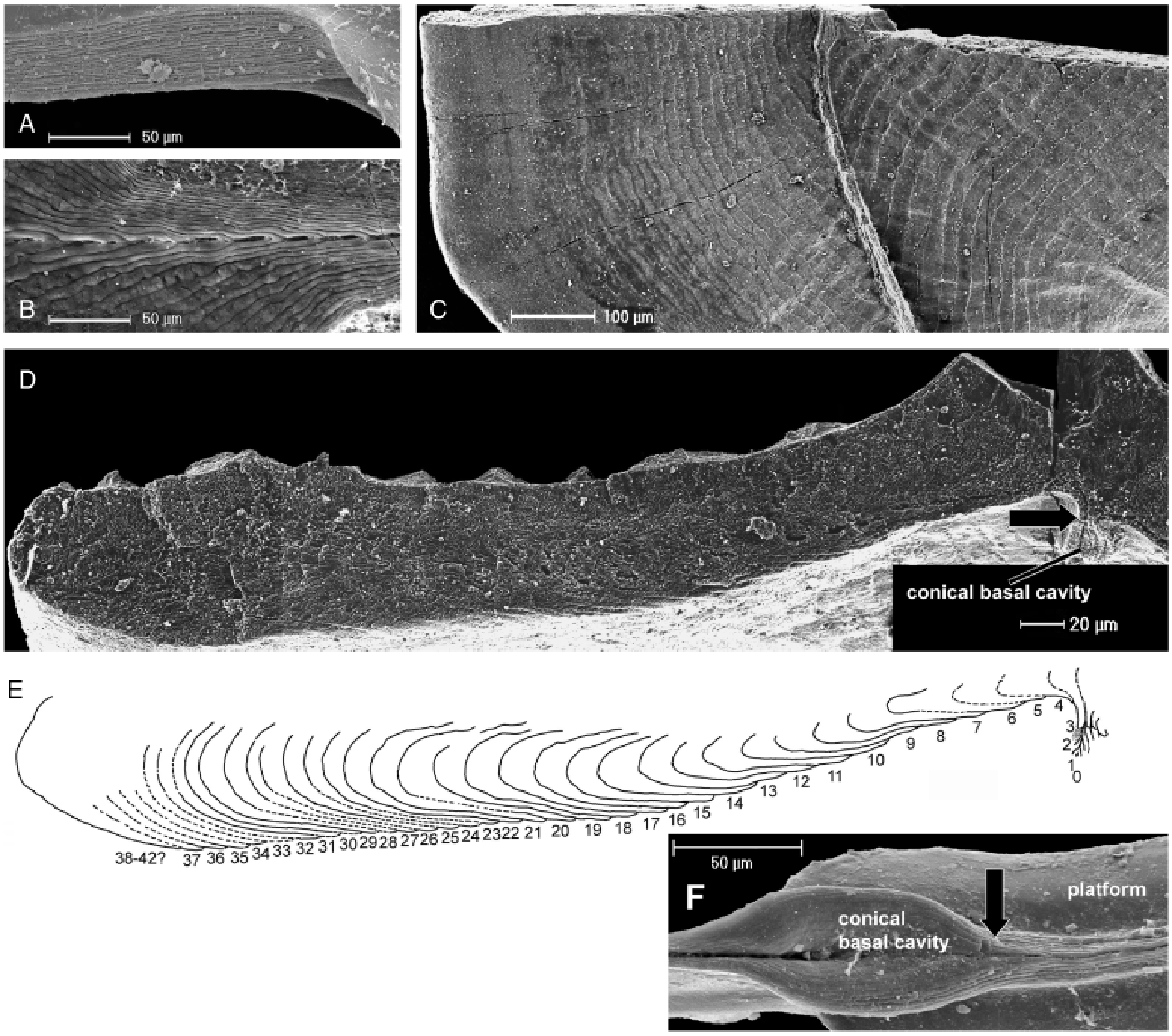

**Fig. 2.** Rhythmic growth increments in the basal cavities of conodonts other than *Tripodellus* but showing the same pattern (comparable aspects of *Tripodellus* elements are presented in this figure). Specimens collected from the Late Devonian strata of the Holy Cross Mountains, Poland. Note very regular distribution of increments and lack of any lower rank striation. (A) Lateral view of inverted basal cavity of the anteriormost M element of "*Polygnathus*" *streeli*, sample J-45, Famennian at Jabłonna. (B) Basal view of conical basal cavity of the posteriormost $P_1$ element of *Dasbergina ziegleri*, sample Ko-191, Famennian at Kowala. (C–E) Naturally broken $P_1$ element of *Mesotaxis*? sp., sample Wtr-13, Frasnian at Wietrznia; basal view (C), transverse section with the change from conical basal cavity of the "sinuosa larva" to its inversion (C; indicated with arrow) and interpretive drawing with proposed daily increments numbered (E). (F) Juvenile specimen of *Neopolygnathus communis* with well-developed conical basal cavity and its postlarval inversion (arrowed), sample Ost-12, Famennian at Ostrówka.

developed first in geologically younger populations, and, furthermore, is recognizable on only one side of the element. Such specimens are referred to as "*Palmatolepis sinuosa*," so the name "sinuosa larva" was applied for this developmental stage (Dzik 2006). Admittedly, in the case of a long-extinct animal group an abrupt morphological change in early skeletal growth stages has to remain the only basis for this interpretation. In the most advanced *Tripodellus gonioclymeniae*, which possibly originated as a result of a relative shortening of the postlarval growth and earlier maturation (neoteny), the conical cavity existed until the end of element growth (Dzik 2006).

An impressive case of parallelism in this respect is the development at approximately the same time of a strongly asymmetric larval basal cone in the completely unrelated polygnathid *Lagovignathus*? *dissimilis*. The "sinuosa larva" also in this case expanded almost to the end of element growth (Dzik 2006).

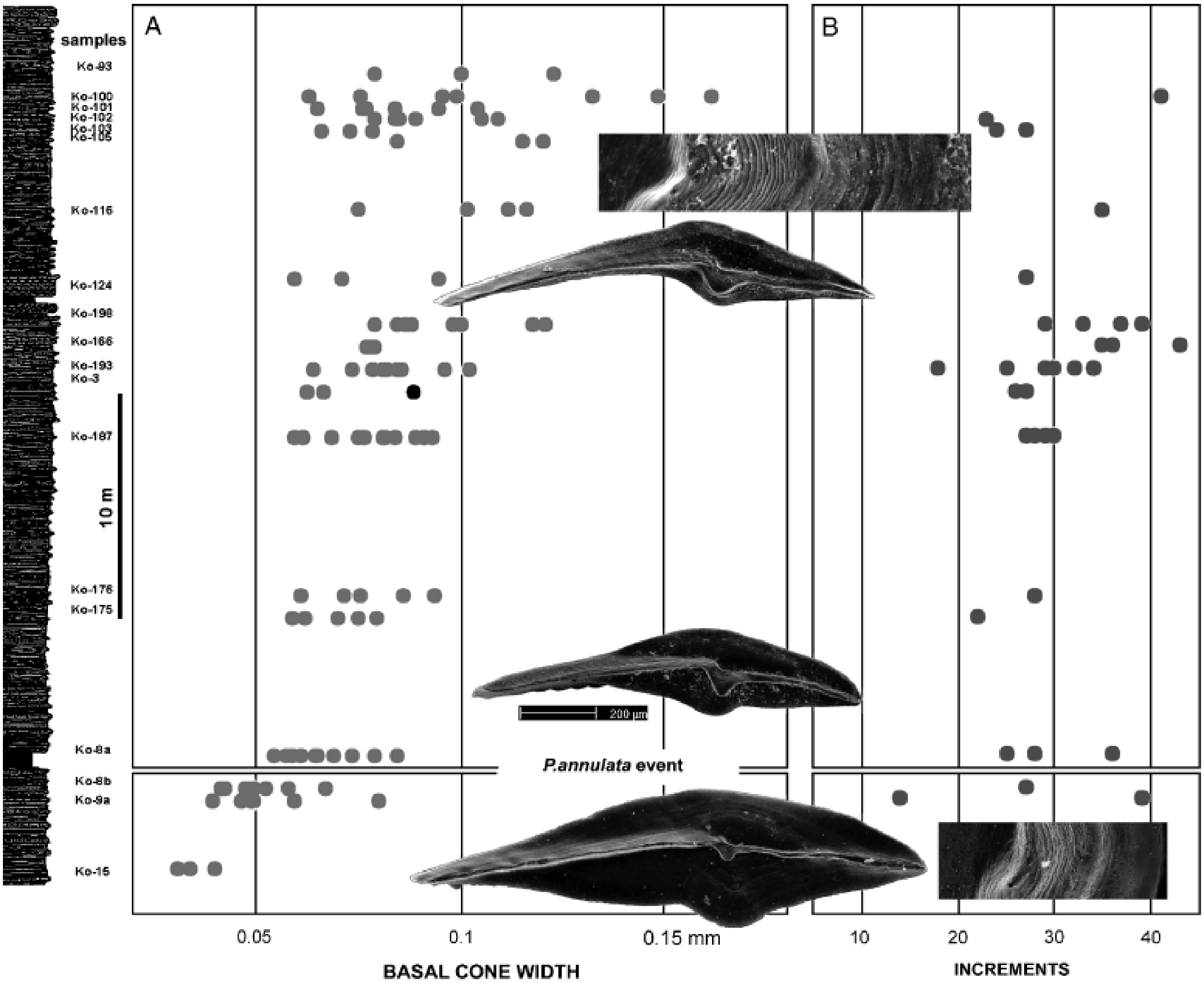

**Fig. 3.** The fossil record of the evolution of the *Tripodellus schleizius*—*Tripodellus gracilis* lineage (for taxonomy see Dzik 2006) in the Kowala quarry section, Holy Cross Mountains, Poland. Each gray dot represents a single $P_1$ element. (A) Distribution of width of the conical juvenile (larval?) basal cavity up the section (the cavity is developed only on the posterior side of the base); inserted SEM pictures show basal views of specimens typical of the lower, middle, and upper parts of the succession. Note that evolution of the juvenile and mature element outline proceeded in different directions and that the observed change was almost linear to the rock thickness except for a discontinuity at the black shale intercalation (between samples Ko-8b and 8a) corresponding to the *Platyclymenia annulata* event (sea level rise). (B) Change in number of daily increments in the juvenile conical base up the section (only a portion of elements in each sample is preserved well enough to enable counting all increments); inserted SEM pictures show patterns of increments distribution in the lowermost and topmost parts of the succession.

## DAILY INCREMENTS

Conodont crown tissue originated in a way closely similar to vertebrate enamel and may be homologous with it (Schmidt and Müller 1964; Dzik 1986; Smith et al. 1996; Donoghue et al. 2000; McCollum and Sharpe 2001), despite some microstructural differences (Kemp 2002) and controversies about its function in conodonts (e.g., Donoghue and Purnell 1999; Dzik 2000). Crown tissue secretion was rhythmic (Müller and Nogami 1971). Particular increments may be rather thick at the tips of denticles and very thin in the concave smooth areas of the element, but mostly they range from 2 to 5 µm (Figs. 1, C and 2; note that the distances between lines visible on the surface of inverted or deeply conical conodont element basal cavities are much larger than the actual thickness of increments).

The Famennian specimens from the Holy Cross Mountains are unusually well preserved and show that boundaries between increments are sharp-cut and that there is no other lower rank striation (Fig. 2, B–C). Some possibly lower rank bands recognizable in sections of other conodont elements (e.g., Armstrong and Smith 2001) are likely to correspond to irregularities in the process of mineralization or are diagenetic artifacts (Fig. 2D). Such artifacts are missing in the basal cavity of the best preserved specimens from the Holy Cross Mountains, which do not show signs of any postmortem surface corrosion.

The mean thickness and strict regularity of increments in conodont crown tissue, although varying in different parts of conodont elements and changing during their ontogeny and evolution, correspond to the daily growth rate of hydroxyapatite in mammalian enamel (e.g., Fitzgerald 1998; Hoppe et al. 2004). Similar rates of mineral deposition are known in the aragonite statoliths of fish and squid (Campana and Neilson 1985; Arkhipkin and Perez 1998; Yatsu 2000). Conodonts were marine, mostly pelagic animals and their remnants are usually associated with open-sea cephalopods (nautiloids and ammonites), bony fish, and sharks. They were under the influence of same environmental, and presumably also trophic, factors. The similarity in daily growth rate of recent statoliths and proposedly daily growth increments in the conodont crown tissue seems thus consistent with their autecology, although their precise position within trophic webs is likely to have differed.

Along with daily rhythms, other periodic changes may be expressed in incrementally growing skeletal tissues. In the mammalian teeth, the striae of Retzius are an expression of circaseptan intervals. They are spaced an order of magnitude wider than the increments observed in conodonts and may be compared with higher rank rhythms observed by Armstrong & Smith (2001). As stressed already above, the increments proposed to be daily in the Famennian Holy Cross Mountains material are of lowest rank and there is no rhythm to be expressed by each of them (Fig. 2B–C).

Platform-bearing elements of derived *Tripodellus* lack the basal filling tissue that commonly obliterates the growth record in conodonts. Growth increments, clearly visible within the basal cavity (or on the surface of the inverted basal cavity) of many specimens, show a surprisingly rhythmic and regular distribution (Fig. 3). In Late Devonian conodont elements of medium size there are 40–70 of them (Fig. 2E; Dzik 2006). If these are daily increments, conodonts reached their maturity after approximately 2 months. In some conodonts, the rhythm of daily increments was punctuated by several periods of rest, thus a higher rank rhythmicity developed (Zhang et al. 1997). This was perhaps related to formation of denticles at tips of the element processes that were added sequentially (e.g., Dzik and Trammer 1980) or, alternatively, to circaseptan intervals. Such periods of rest probably did not occur in the early ontogeny of the Famennian conodonts studied (Fig. 2).

## RESULTS

All apparatus elements of the studied *Tripodellus* lineage underwent some morphologic change but the transformation of ontogeny recorded on the basal side of the posteriormost element pair is especially informative and easy to quantify (Fig. 3A).

The rapid growth of the conodont element platform resulted in a change from conical basal cavity to its inversion. The change is abrupt, which might suggest a separate larva-like developmental stage, but this is purely inferential and based on the striking change in element geometry (Dzik 2006). In *Tripodellus*, the width of the platform in the posteriormost $P_1$ elements of the apparatus decreased significantly but, at the same time, the conical juvenile base expanded (Fig. 3A). Eventually, in the advanced species *T. gonioclymeniae* (representing a separate lineage of *Tripodellus*) such cavity persisted until the end of element growth (Sandberg and Ziegler 1979). At first glance, this seems to be an expression of paedogenesis, with an increase of importance of the larval stage in the life cycle. Such cases of shortening of postlarval growth and earlier maturation (neoteny) are not rare in paleontological material. The *Tripodellus* specimens are unique in that they enable calibration of the observed morphologic transformation in real-time units. This tempting interpretation of *Tripodellus* evolution as heterochrony can easily be tested.

The testing is possible owing to the increments exposed over the basal surface of the *Tripodellus* $P_1$ elements. Rather surprisingly, the number of daily growth increments inside the conical base of the “larval” element unit does not show any apparent change in the succession, although there is a wide range of population variability in this character (Fig. 3B). Unfortunately, the exposed margin of the basal cone is abraded in most specimens and the densely distributed growth increments are difficult to discern there. Nevertheless, there seems to be little reason to suggest any significant evolutionary change in the duration of the “larval” stage; at least it was disproportionately small with respect to the change in growth rate. This was thus not so much a matter of the exact timing of basal cavity inversion, but rather of the element secretion rate. Indeed, the growth rate changed significantly in the evolution of *Tripodellus* (Fig. 4). In the lowest set of samples (Ko-8b-9b) the mean base width did not reach 50 μm even after 50 increments (probably days) but this size has been achieved before 20 increments in sample Ko-8a, before 15 increments in a series of samples above and before 10 increments in the topmost set of samples (Ko-93-105). In later growth of the larva not only are particular increments thicker, but also the population variability in growth rate had increased.

Perhaps the most striking aspect of the evolution of *Tripodellus* is its extremely gradual nature, almost linear relative to rock thickness. The sampled Kowala section seems to represent a case of relatively deep-water stable sedimentation, as suggested by the expression of probable Milanković cyclicity in bedding and faunal succession (Dzik 2006). In fact, the only part of the section, in which the linear evolution of *Tripodellus* seems somewhat distorted is the black *Platyclymenia annulata* Event shale, apparently related to a global sea-level rise and break in limestone sedimentation at Kowala (Fig. 3). This is a carbonate-poor, organic-rich sediment that probably accumulated at a much lower rate than the rest of the Kowala succession. To accommodate the plot to a real-time succession, its part corresponding to the black shale thickness should thus be significantly enlarged. Although differences in degree of diagenetic compaction between marly and carbonate-poor beds also remain to be considered, the resulting picture would probably show the course of *Tripodellus* morphological evolution virtually linear to time. Such pattern of the change is not predicted, or even expected, by the classical theory of evolution and requires some additional assumptions.

In fact, the above-presented empirical evidence supports numerous earlier observations that phyletic evolution, whenever well documented, is virtually linear in respect to time (e.g., Dzik 1995). Its rate is not influenced by speciation events (i.e., splitting of lineages). Migrations and changes in environmental conditions tend to hamper the evolution and destroy its earlier effects. There is hardly any paleontological support to the generally held belief that environmental change, either abiotic or biotic, drives evolution. The rate of evolution seems rather enhanced by the stability of the environment. This phenomenon was referred to as The Ancient Lake Concept (Gorthner & Meier-Brooks 1985) or *Plus ça change* Model (Sheldon 1996).

The crucial point of the concept is that in stable conditions, the lineages evolve directionally at a great rate even if they originated from species that are extremely conservative morphologically in not so stable environments (as is the case with viviparid or planorbid snails inhabiting ancient lakes).

Another non-trivial aspect of the studied lineage of *Tripodellus* is the rate of its evolution. The estimated duration of the Famennian is 14.5 million years (Tucker et al. 1998; Trapp et al. 2004) and the succession presented here covers about half of this time range. The rather minor modification in the morphology of the *Tripodellus* oral apparatus required a lot of time to be achieved. In fact, the rate of change in the molarized elements of conodont apparatus is similar to that in molars of Pleistocene mammoth (e.g., Lister 1993). Even the fastest evolution observed in other densely sampled geological

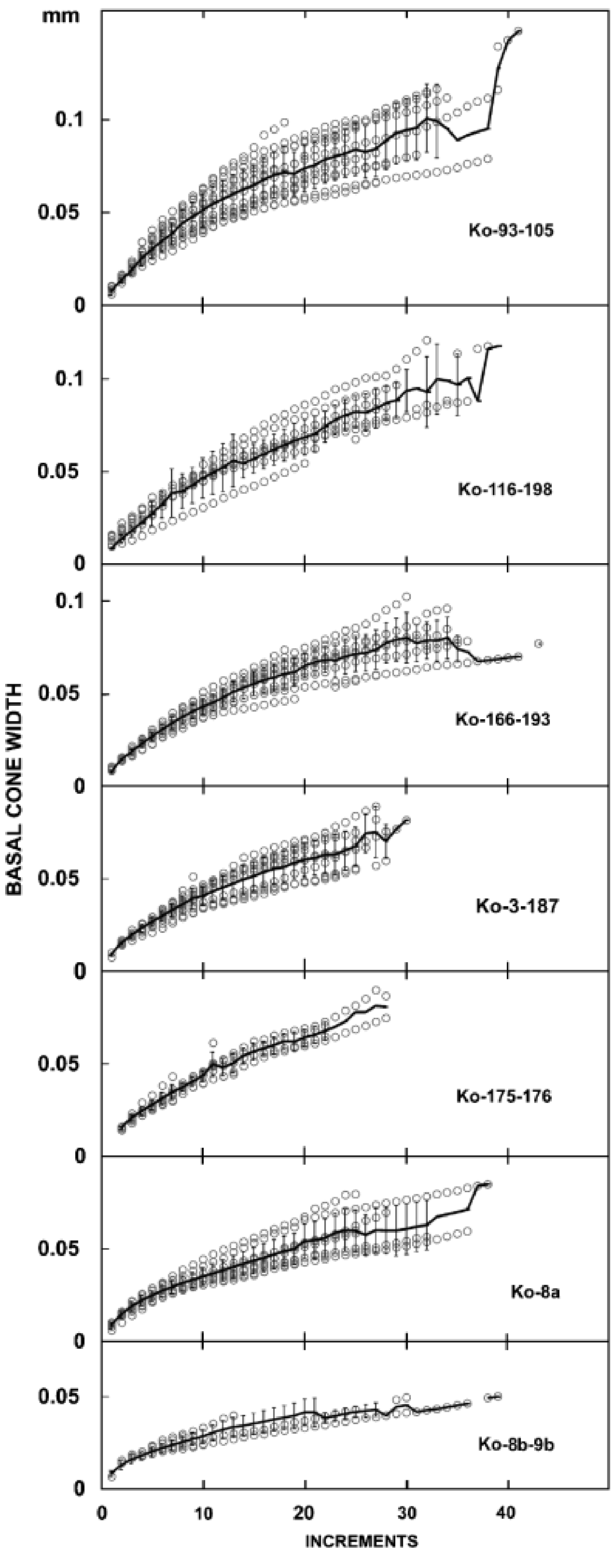

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**Fig. 4.** Evolution of the juvenile growth pattern of the $P_1$ element in *Tripodellus schleizius—Tripodellus gracilis* lineage as recorded in the Kowala quarry section. Circles represent individual measurements; their number in particular samples can be seen on Fig. 3. Specimens from neighboring samples are grouped together (their location in the section shown on Fig. 3; note that ranges of variability are not influenced by grouping); mean and standard deviation values for basal cavity width at each successive daily increment are shown. Note that ranges of standard deviation disproportionately increase in the course of evolution, influencing potential quantification of the evolutionary rate (Gingerich 1993).

sections is much slower than its rates inferred from population genetics of living populations. A possible cause of this discrepancy (referred to as the Haldane Paradox in Levinton 2001) is limited supply of new genetic material for selecting evolutionary novelties.

If true, the mutation rate would be the main limiting factor in the evolution.

## CONCLUSIONS

The skeletal remains of *Tripodellus* conodonts enabled tracing the development of a Paleozoic animal in successive days, as well as identification of its evolutionary change on the population level. The closest approximation of such evolutionary modifications of ontogeny to real time was achieved previously by the identification of particular molting stages in arthropods (Olempska 1989). Calibration in days of the evolving ontogeny of Devonian conodonts offers some refinement to the picture derived from stratigraphically dense data on evolution of other organisms (reviewed in, e.g., Dzik 1991a, 2005; Sheldon 1996; O'Keefe and Sander 1999; McCormick & Fortey 2002).

Evolution was rather slow, offering one more exemplification of the Haldane Paradox (Levinton 2001) and its directional pattern, virtually linear in respect to the rock thickness (thus, presumably, to geological time), makes contribution of randomness rather unlikely.

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