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# Conodont affinity of the enigmatic Carboniferous chordate *Conopiscius*

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*Conopiscius* shares V-shaped myomeres with the co-occurring conodont *Clydagnathus* but instead of a complex oral apparatus it has only a single pair of conical elements, and structures resembling scales are associated with its myomeres. Moreover, the coarsely crystalline crown tissue typical for conodonts has not been identified in the *Conopiscius* elements, which show only a finely lamellar skeletal tissue. The gap between conodonts and *Conopiscius* may be filled by isolated elements of similar morphology and structure occurring in the Late Devonian. They reveal a very thin external layer developed mostly at the tooth tip and resembling conodont crown tissue. The pulp cavity is partially filled with layered or spherulitic phosphatic tissue of the kind known also in conodonts (basal filling tissue) and early vertebrates (lamellin). Conodont elements of similar morphology and representing uni-membrate oral apparatuses have not been previously reported from the Devonian or Carboniferous but occur near the Cambrian–Ordovician transition (*Proconodontus*) and in the Late Permian (*Caenodontus*). It is proposed that *Conopiscius* represents a mostly cryptic conodont lineage extending from the Early Ordovician to the Permian, instead of being directly related to the agnathans. ☐ *Agnatha*, *Anaspida*, *conodonts*, *Early Carboniferous*, *evolution*, *histology*, *Late Devonian*, *microstructure*.

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The early Carboniferous Granton Shrimp Bed exposed near Edinburgh, Scotland, is famous for the first discovery of conodont animals with soft tissues preserved (Briggs *et al.* 1983; Aldridge *et al.* 1993). The anatomy of conodonts resembles that of Recent lamprey, with elongate body and narrow asymmetric tail fin but with *Branchiostoma*-like V-shaped myomeres. Such myomeres and general body appearance characterize also the second Granton chordate – *Conopiscius*. What makes *Conopiscius* rather basically different from conodonts is the presence of probable weakly mineralized scales associated with myomeres and its oral apparatus composed of only two elements of simple morphology (Briggs & Clarkson 1987).

No Late Palaeozoic conodont element of similar morphology has been known until recently, except for the enigmatic Permian serrated conical elements of *Caenodontus* (Behnken 1975). Typically, conodonts bore a complex oral apparatus composed of fifteen (sometimes even more) phosphatic elements. The apparatus was complex even in conodont groups characterized by a very simple, conical shape of their elements (e.g. Sweet 1988; Dzik 1991; Donoghue & Purnell 1999). Such morphologically simple conodonts did not survive the Frasnian–Famennian boundary (Dzik 2002), although some elements of the Famennian icriodontid conodonts developed secondarily simplified morphologies resembling those known from the Ordovician (e.g. Dzik 2006).

Two new observations make affinities of *Conopiscius* to the conodonts more likely than originally expected: (i) isolated specimens similar to the elements preserved *in situ* in the Granton material appear to be common in the Late Devonian, and (ii) the internal structure of these specimens is conodont-like, although more similar to Cambrian than to other late Palaeozoic conodonts. In the present paper, these new data are presented and discussed.

## Materials and methods

The Devonian specimens come from limestone samples dissolved in acetic (pure limestone) or formic (marls, dolomitized limestone) acids. Less acid was always used than necessary to dissolve completely the sample and this provided some buffering. Dried residues were enriched in an electromagnetic mineralogical separator. Specimens studied for microstructure were embedded in epoxy resin, ground and polished. They were etched with 0.5% orthophosphoric acid until a relief visible in reflected light under an optical microscope developed. The time of etching varied significantly (from 1 to 5 min) depending on the

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specimen. The blocks with embedded specimens were then attached to a stub and coated with platinum to photograph in a scanning electron microscope.

Specimens of *Conopiscius* are housed at the Royal Scottish Museum in Edinburgh, Scotland (abbreviated RSM), Devonian isolated elements at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland (ZPAL).

## Morphology of oral denticles in *Conopiscius*

The cone-shaped structures in the head region of *Conopiscius clarki* are preserved as flattened in both specimens found, but with some relief. This suggests that they were originally composed of a rigid organic matter, if not mineralized. Their surface is slightly wrinkled (Briggs & Clarkson 1987, p. 111), which suggests growth by marginal increments. The cones are filled with sediment for most of their length, so they had a deep pulp cavity and rather thin walls. As noticed by Briggs & Clarkson (1987, p. 111) at least RSM GY 1986.25.5 'preserves tenuous evidence of a tiny denticle near the proximal extremity of the outer margin'. Denticles are recognizable also in RSM GY 1986.25.6 (Fig. 1). They are rather prominent, and their arrangement suggests that the whole concave margin of the cone was originally armed with numerous serially distributed denticles, of which all except for the proximal two became exfoliated when the slab was split. This denticulated margin is thicker than the cone wall nearby, which means that it was reinforced with a skeletal tissue, and sharp-edged. The cross-section of the cone was thus lenticular. Its complete length from the base to tip exceeded 2 mm.

## The Late Devonian denticulated conical elements

Conical phosphatic (or perhaps secondarily phosphatized) elements with a deep basal cavity and denticulated concave margin occur widely, although sparsely, in pelagic sediments of the Late Devonian in the Holy Cross Mountains, Poland. They are usually referred to as *Caenodontus*, the type species of which, *C. serrulatus* Behnken, 1975 was originally described as a conodont from the Permian of Texas. Like associated unquestionable conodonts, the Polish conical elements are transparent, amber-coloured in samples with low diagenetic alteration (Kowala, Jabłonna) and dark, almost black in samples from strata which experienced significant burial heating (Płucki, Łagów). Some well-preserved specimens show folding and rupture of the wall proving their original flexibility,

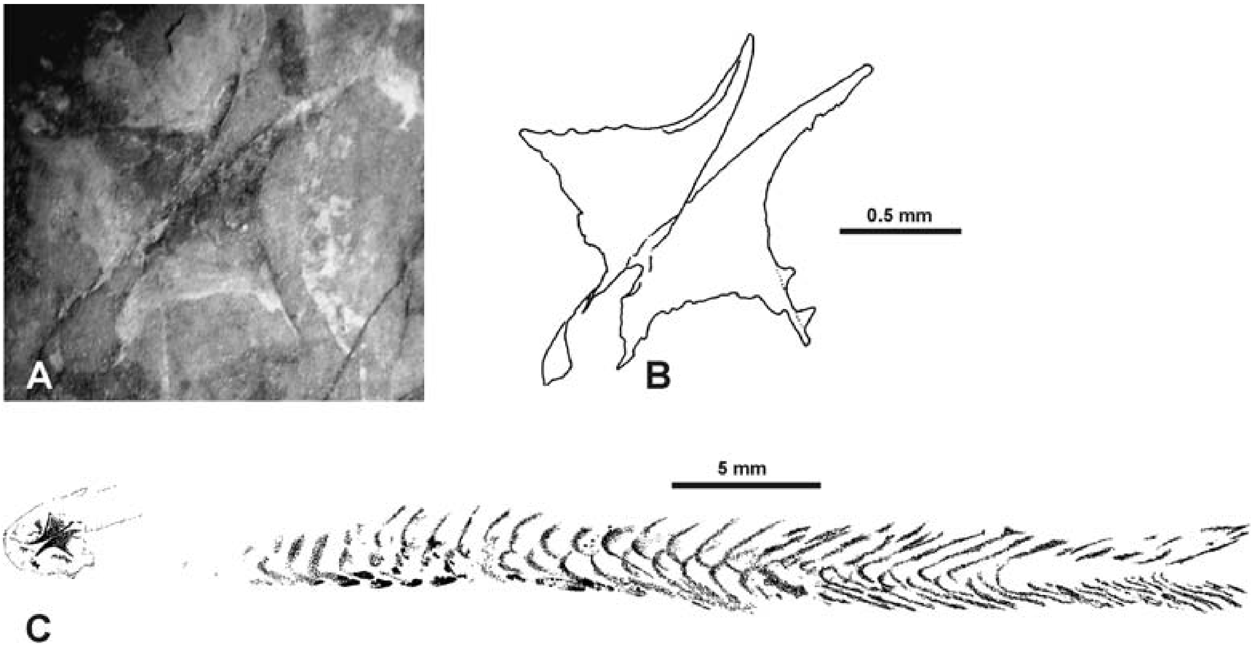

*Fig. 1.* □A, B. Elements from the head region of *Conopiscius clarki* Briggs & Clarkson, 1987 from the Viséan (Early Carboniferous) Granton Shrimp Bed exposed near Edinburgh, Scotland; specimen RSM GY 1986.25.6; photograph (A) and interpretive drawing (B). Note that phosphatic tissue of the elements is mostly exfoliated as a result of the slab splitting but a couple of preserved denticles are evident, presumably belonging to the series arming the cutting edge of the elements. □C. Composite drawings with the tail region of specimen RSM GY 1986.25.5 added to RSM GY 1986.25.6 (reversed) to show location of the mouth apparatus and inferred proportions of the body.

evidently owing to a high organic matter content. The element surface shows smooth transverse wrinkles, which seem to have resulted from incremental growth at the cone base. No true incremental discontinuities (growth lines) are discernible, however, suggesting that the secretory tissue formed a continuous cover from either the inside or the outside of the sclerite.

There are at least three distinct morphological types of conical element in the material studied, probably representing separate species. In all of them the denticles are pointed and sharp-edged. The prominence of denticles differs significantly, however. In the mid-Famennian specimens, the denticles are almost twice as high as wide (Fig. 2A–E). Such specimens have been previously illustrated from the late Famennian of Guizhou, south China (identified as *Belodella* sp. by Wang & Wang 1978, pl. 1:10–11), co-occurring with stratigraphically indicative *Pseudopolygnathus trigonicus*. Similar conical elements, representing the same species, also occur in the early Famennian of the Montagne Noire in France (Fig. 2F–I). The geologically older late Frasnian specimens are characterized by the denticles being not longer than wide and in some specimens being truly minute (Fig. 3). Rudimentary denticles characterize a coeval species with minute elements, almost round in cross-section (Fig. 4). It remains unclear whether this morphological series of species corresponds to any evolutionary succession but at least in the Frasnian two sympatric species are represented by *Caenodontus* (and *Conopiscius*)-like elements.

In the conical elements of the Viséan *Conopiscius clarki* only the proximal denticles are preserved and they are somewhat more robust than in the Famennian forms. Each element is also wider in general outline, although this may be partially due to its compression in the shale. The Permian *Caenodontus serrulatus* conical elements bear numerous minute denticles almost to the tip of the element (Behnken 1975). The

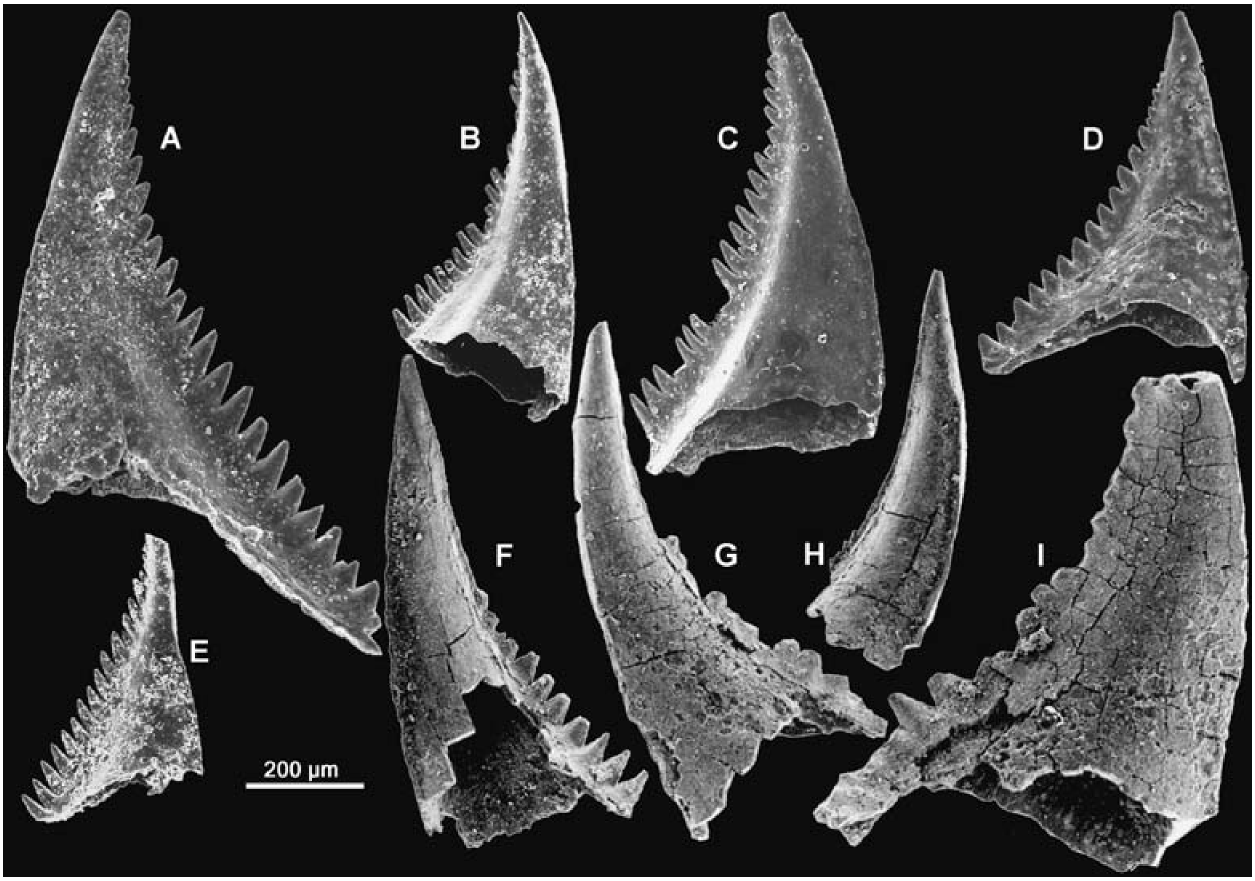

*Fig. 2.* Elements of the Famennian (Late Devonian) *Conopiscius*-like species A with prominent denticulation, as compared with other Devonian species. □A–E. Well-preserved translucent specimens from the mid-Famennian *Platyclymenia annulata* Event (black shale) at Kowala, Holy Cross Mountains, Poland; sample Ko-8a (A, B, D) and Ko-8 (C, E; for stratigraphy see Dzik 2006). Note variability in denticulation and curvature of the cusp. □F–I. Thermally altered black specimens from the early Famennian *Cheiloceras* Stufe limestone at Soreille d'Izarre near Cabriéres, France, with rather uniform and robust appearance. Specimens ZPAL CVI/3108, 3113, 3112, 3109, 3111, and 3125–3128, respectively.

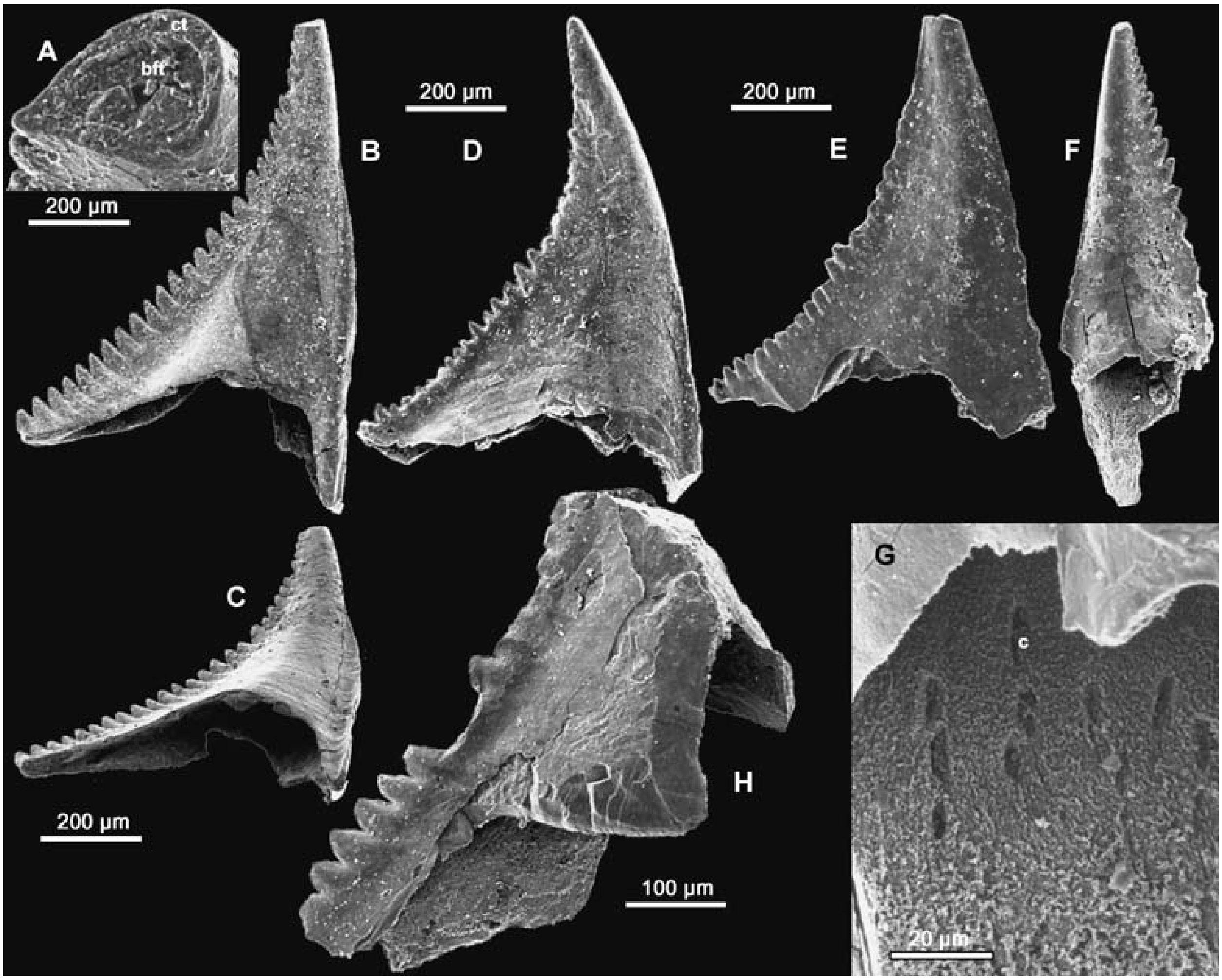

*Fig. 3.* Elements of the terminal Frasnian (Late Devonian) *Conopiscius*-like species B with sharp-edged denticulation from the Kellwasserkalk horizon at Płucki in the Holy Cross Mountains (for stratigraphy see Dzik 2002); specimens somewhat altered thermally (dark in coloration). ☐A–C. Broken apex exposing the crown (ct) and basal filling (bft) tissues, and the whole specimen in posterior and oblique views to show transverse wrinkles. ☐D. Specimen with partially exfoliated crown tissue. ☐E. Specimen with an abnormality in distribution of denticles indicating incremental growth at the base. ☐F–G. Unusually straight-cusped specimen and interior of its base with linear series of voids probably representing odontoblasts incorporated in the basal cavity tissue (c). ☐H. Incomplete specimen of large size comparable with that of the Viséan *Conopiscius clarki.* Specimens ZPAL CVI/3114, 3118, 3122, 3117, and 3120, respectively.

cusp is needle-like and the cone expands strongly near its base, more than in the Devonian specimens. Its general shape is thus somewhat closer to that of the Carboniferous *Conopiscius.*

## Microstructure of the Famennian cones

The Famennian conical elements are laterally bent and twisted. This makes sectioning of them difficult, as there is no symmetry plane to follow. Among several elements sectioned by myself, in only a few cases has the tip of the element been sectioned precisely enough to recognize its internal organization. Each element appears to be composed of two kinds of phosphatic tissue. The boundary between these is difficult to trace, but some specimens prove that it is rather abrupt (Fig. 5). Acid-resistant minerals may delimit the boundary in places, suggestive of a significant structural discontinuity.

The external layer is composed of a somewhat more regularly and coarsely crystalline tissue, with crystal axes probably arranged parallel to the surface, although the available evidence is not completely convincing (Fig. 6C). The layer forms a regularly conical unit, thickening distally, where it makes the sharp tip of the sclerite, but is extremely thin, less then 10 μm near the basal cavity tip. It thus roughly corresponds in thickness to a single increment (probably daily) in the platform margin of associated

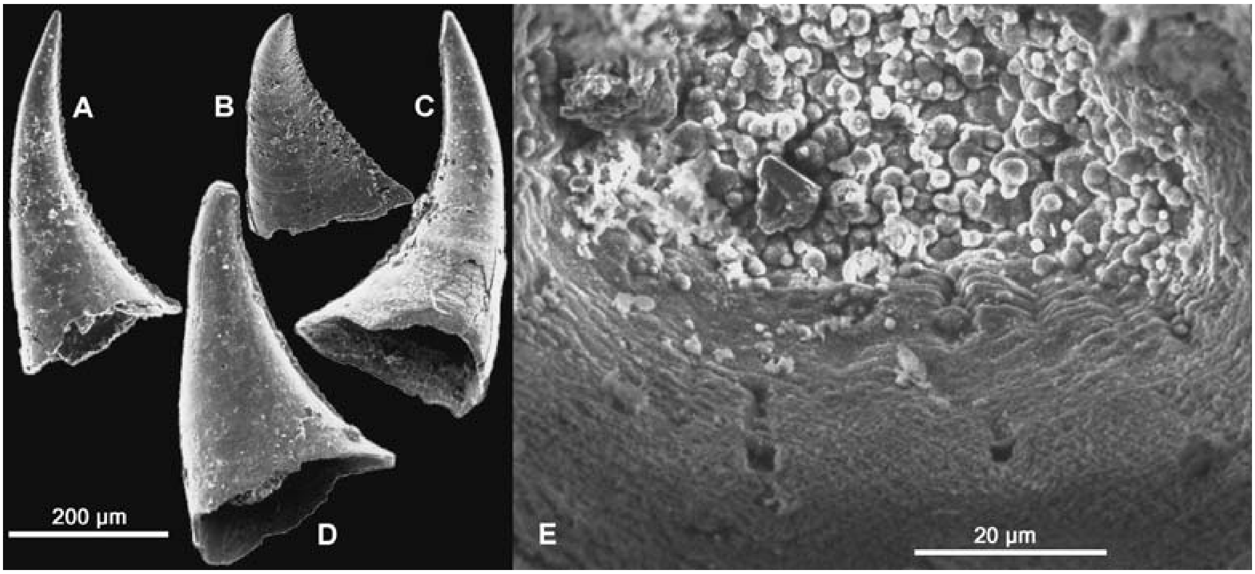

*Fig. 4.* Elements of the terminal Frasnian (Late Devonian) *Conopiscius*-like species C from Płucki. Note fine serration of the cutting edge and robust appearance of specimens. □A, B. Posterior and oblique views of specimen ZPAL CVI/3115 showing transverse wrinkles and disposition of minute denticles. □C. Specimen ZPAL CVI/3116 with partially exfoliated crown tissue. □D, E. Robust specimen ZPAL CVI/3119 and interior of its basal cavity with probable odontoblasts and spherulitic mineralization of the basal filling tissue at later stages of its secretion in the centre.

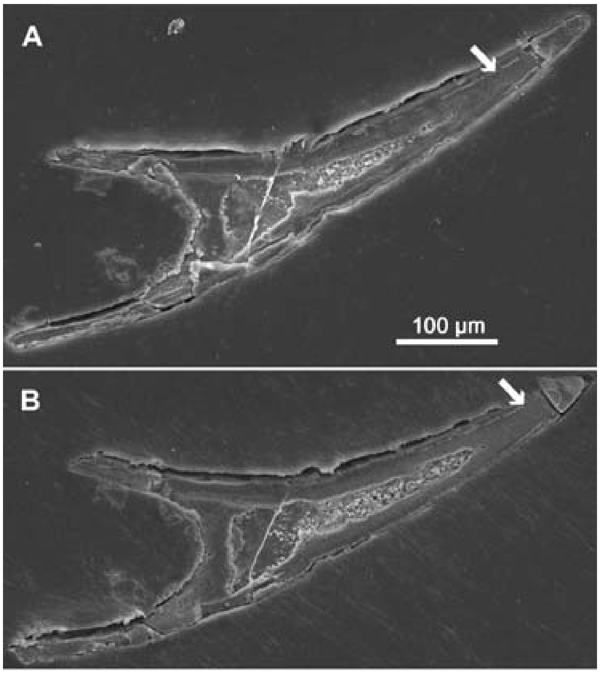

*Fig. 5.* Internal structure of the *Conopiscius*-like species A element. Two successive stages (A, B) in grinding of a well-preserved (translucent) specimen ZPAL CVI/3110 from the mid-Famennian at Ostrówka (sample Ost-12; for stratigraphy see Dzik 2006). Note the boundary between the crown and the basal filling tissues (arrowed) and disposition of the crown strongly suggesting conodont affinity.

conodont elements (Dzik 2006). Consequently, no internal layering is recognizable within this unit, which makes it difficult to determine whether it was deposited from outside (like conodont crown tissue, ganoin or enamel) or from inside the basal cavity. The completely smooth surface of the elements and the rather clear separation from the underlying tissue suggest that this is a homologue (or at least an analogue) of conodont crown tissue.

The tissue forming most of the element volume is distinctly lamellar, with crystal axes of each lamella oriented perpendicular to the surface. It resembles the atubular dentine (lamellin) that occurs in scales of Late Ordovician to Early Silurian agnathans (Karatajute-Talimaa & Smith 2004). The layers of the tissue close to the external layer run parallel to the boundary but material within this, secreted earlier or later, is wavy and has a spherulitic pattern (Fig. 6). The spherulites are visible within the basal cavity in its deeper part. In the proximal part of the cone, where the layer is thinner, series of empty cavities are recognizable in places (Fig. 3G, 4E). Their size, about 3 µm wide, 10 µm long, suggests that these are imprints of secretory cells (odontoblasts?), partially incorporated into the phosphatic tissue.

In most samples containing the elements, phosphatic detritus is abundant, including pieces of crustacean cuticle among taxonomically identifiable fossils (Rolfe & Dzik 2006). Originally, the cuticle was apparently organic, so the taphonomic conditions during formation of these fossiliferous strata were suitable

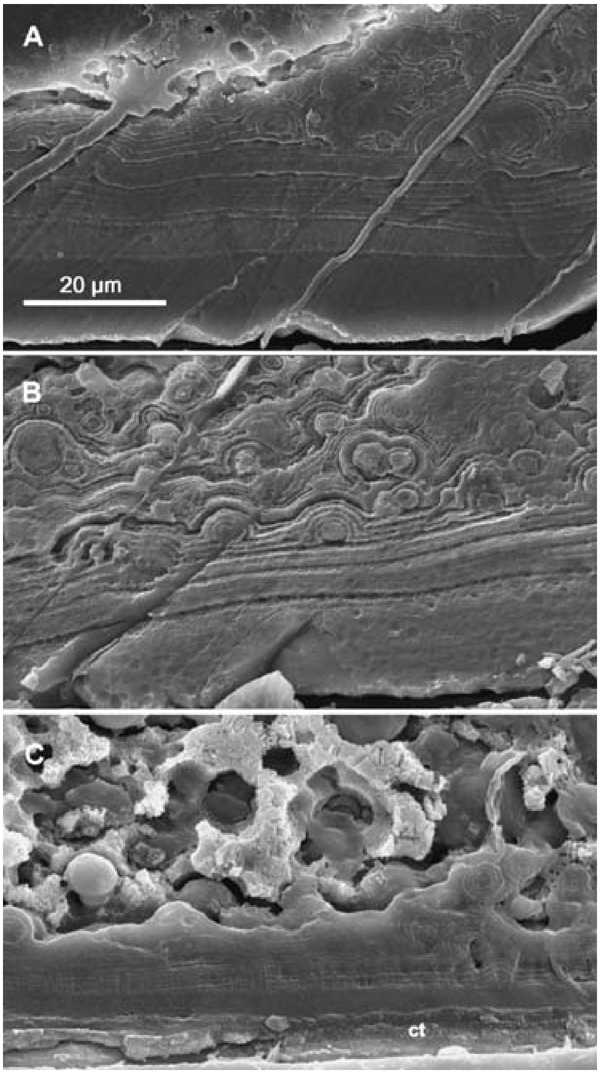

*Fig. 6.* Wall microstructure of the Devonian *Conopiscius*-like elements. ☐A, B. Weakly and more intensely etched translucent specimens ZPAL CVI/3123 from the mid-Famennian at Ostrówka (sample Ost-2; for stratigraphy see Dzik 2006) showing transition from laminar to spherulitic increments of the basal filling tissue. Etching sufficient to expose layered structure of the basal filling tissue did not differentiate the crown tissue. ☐C. Deeply etched dark specimen ZPAL CVI/3124 from the terminal Frasnian at Płucki showing somewhat more coarsely crystalline structure of the crown tissue (ct; compare Fig. 3A).

for secondary phosphatization. It is thus possible that the spherulitic apatite in the basal cavity of the Devonian *Conopiscius*-like elements developed partially post-mortem. This may explain uneven representation of these fossils in sampled sections, similar to that of the mineralized basal tissue of associated conodonts. More likely, however, is that it represents a gradual mineralization of a cartilagineous tissue, as suggested by the disposition of spherules in the pulp cavity showing marks of incremental growth on its walls (Fig. 4E).

## Possible Cambrian relative

Some Late Cambrian species of *Proconodontus* are almost undistinguishable externally from the Late Devonian conical elements of probable *Conopiscius* affinity. For instance, *P. serratus* Miller, 1969 (Müller & Hinz 1991; Szaniawski & Bengtson 1993, 1998) closely resembles the *Conopiscius*-like species B. The crown tissue in *Proconodontus* is somewhat thicker and clearly shows perpendicular orientation of apatite crystals, and this seems to be the main difference between these forms. According to Szaniawski & Bengtson (1993) the crown tissue of early conodonts developed after formation of the basal body and layers of both units were in continuity. They proposed an origin for the typical (eu)conodont *Cordylodus* lineage from *P. serratus*. Clusters composed of several elements of *Cordylodus* are known (e.g. Andres 1988), and it is generally accepted (Nicoll 1990, 1991) that its apparatus composition was similar to that of typical conodonts, that is with 14 elements in seven pairs (or 15 if a symmetrical medial element was present). It is thus unlikely that the *Proconodontus* oral apparatus differed in its composition from other conodonts. Despite the similarity of the general appearance of *Conopiscius* elements and internal structure of the Famennian conical elements to *Proconodontus serratus*, they apparently differed in organization of the oral apparatus. The inferred presence of either 14 or 15 elements in *Proconodontus* and only two in *Conopiscius* appears to preclude classification of the latter in the family Proconodontidae Lindström (1970). It remains a possibility, however, that in the course of evolution between the Late Cambrian and the Late Devonian, the apparatus was simplified and the thickness of the crown tissue in the elements was reduced.

## Conclusions

It is proposed that these Late Devonian conical serrate elements, with an internal structure resembling the most underived Cambrian conodonts, belong to the same clade as *Conopiscius*, which may continue to the Permian as *Caenodontus* (Fig. 7). If true, reduction of the oral apparatus to a single pair of morphologically simple elements marked the origin of this mostly cryptic evolutionary branch of Palaeozoic chordates. The possible presence of mineralized scales protecting the myomeres, as suggested by Briggs & Clarkson (1987), places *Conopiscius* between the conodonts and the agnathans (it has even been classified as the geologically youngest member of the Anaspida;

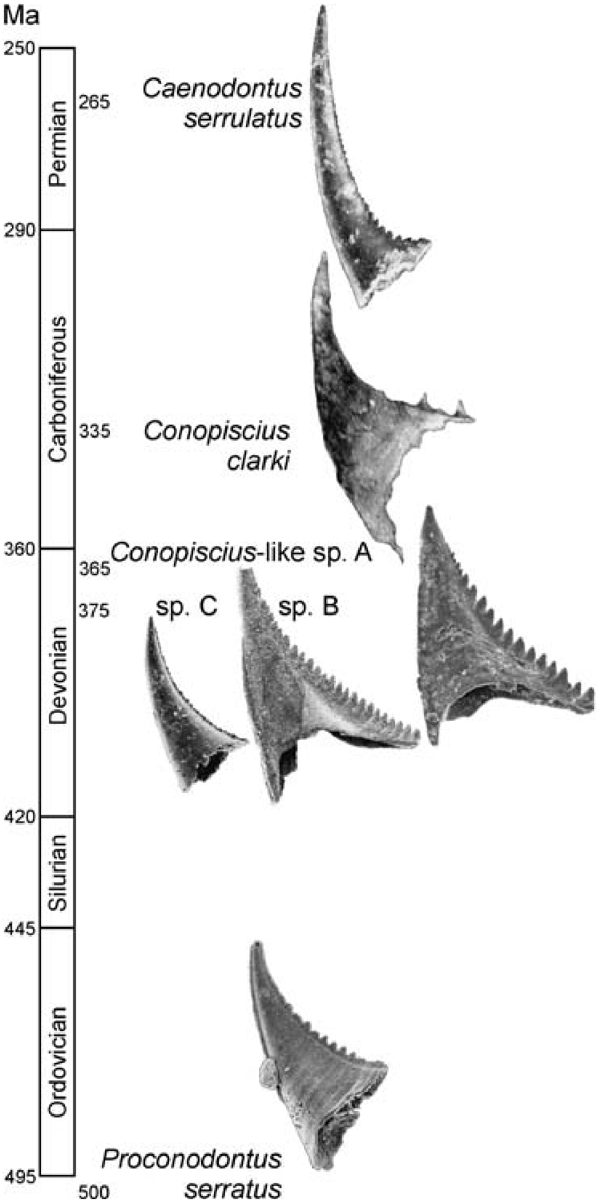

*Fig. 7.* Geological time distribution of serrate phosphatic elements possibly representing the *Conopiscius* lineage. *Caenodontus* adopted from Behnken (1975), *Proconodontus* from Szaniawski & Bengtson (1998).

Sepkoski 2002) but more evidence is necessary to exclude possible diagenetic phosphatization of originally organic tissue. A conodont affinity for the oral apparatus of *Conopiscius* would imply that it was covered with soft tissue during growth and growing while functional. It remains to be determined whether the surface of each mineralized element was repeatedly exposed while piercing the food and covered with the epithelial secretive organ while being secreted (Bengtson 1976; Donoghue & Purnell 1999), or alternatively, if the secretive tissue was covered with a permanent keratinous cup (Priddle 1974; Dzik 2000). The proposed conodont affinity of *Conopiscius* is consistent with its soft anatomy. Its V-shaped myomeres point forward in the same way as in the coeval conodont *Clydagnathus* but also as in the early Palaeozoic Anaspida and Recent *Branchiostoma*; (e.g. Gemballa *et al.* 2003). In apparently more derived (in this respect) hagfish and lamprey, as well as in the gnathostomes, additional dorsal and ventralmost anteriorly pointed arms of myomeres are developed (Vogel & Gemballa 2000).

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