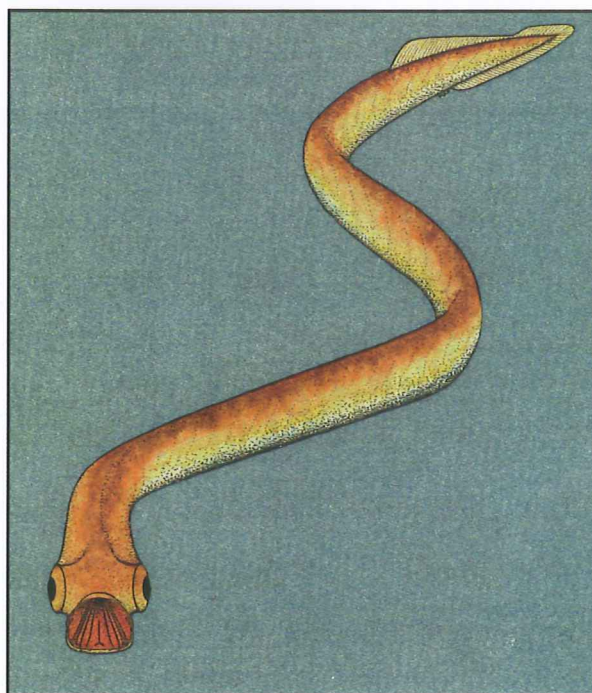


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# A model of reconstruction for the oral apparatus of the Ordovician conodont genus *Protopanderodus* Lindström, 1971

*Johanna S. Mellgren*

Examensarbeten i Geologi vid  
Lunds universitet - Berggrundsgeologi, nr. 180



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## A model of reconstruction for the oral apparatus of the Ordovician conodont genus *Protopanderodus* Lindström, 1971

Johanna S. Mellgren

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**Abstract:** Elements from the Ordovician conodont genus *Protopanderodus* Lindström, 1971 have been investigated to provide a model of reconstruction of the oral apparatus of this genus. In total, 4202 elements from the only five species representing *Protopanderodus* in the Swedish Middle Ordovician conodont fauna were included in the study. Four of the species, *P. rectus*, *P. robustus*, *P. graeai* and *P. parvibasis* have similar morphological characters and are thought to belong to the same evolutionary lineage. However, the fifth species, *P. calceatus*, is morphologically different and thus not so closely related, possibly representing a separate evolutionary lineage.

Well-preserved elements from adult specimens have been studied in detail for the identification of distinct element types, while all other identifiable elements (for example juveniles or somewhat broken elements) were also included in the calculation of element ratios, to statistically determine the lowest number of elements in a single apparatus. Three element groups were recognized for all five species; M-, S-, and P-elements according to the element notation system used. The number of element types in each group were quite different in *P. calceatus* (M1, M2, Sa, Sb, Sc, "Sd", Pa, Pb1, Pb2) compared to M, Sa, Sb1, Sb2, Sc, Pa, Pb in the other four species. The element ratios for the M, S and P element groups for *P. rectus*, *P. robustus*, *P. graeai* and *P. parvibasis* are indicative of an apparatus containing a minimum of 21 elements distributed as 4M (2 pairs), 1 Sa (symmetrical), 4 Sb1 (2 pairs), 4 Sb2 (2 pairs), 2 Sc (1 pair), 2 Pa (1 pair) and 4 Pb (2 pairs). The same minimum number of elements is recognized for *P. calceatus* but these are instead distributed as 2 M1 (1 pair), 2 M2 (1 pair), 1 Sa (symmetrical), 2 Sb (1 pair), 4 Sc (2 pairs), 4 "Sd" (2 pairs), 2 Pa (1 pair), 2 Pb1 (1 pair), 2 Pb2 (1 pair). At this moment it is uncertain if the dissimilarities between the apparatus of *P. calceatus* and the other four species suffice to refer the latter species to a new genus. Further investigations of other species, sharing the same morphological characters as *P. calceatus* would be desirable; the comparisons of element types in their apparatuses could show if these species belong to one single and separate evolutionary lineage.

**Keywords:** conodonts, *Protopanderodus*, apparatus reconstruction, Ordovician.

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## En rekonstruktionsmodell för tandapparaturen hos det ordoviciska conodontsläktet *Protopanderodus* Lindström, 1971

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**Sammanfattning:** Element från det ordoviciska conodontsläktet *Protopanderodus* Lindström, 1971 har studerats i syfte att sätta upp en modell för rekonstruktion av släktets tandapparat. Totalt har 4202 element från de fem *Protopanderodus*-arterna i den svenska mellanordoviciska conodontfaunan ingått i studien. Fyra av arterna, *P. rectus*, *P. robustus*, *P. graei* och *P. parvibasis* uppvisar många gemensamma morfologiska karaktärer och utgör troligast en utvecklingslinje, medan den femte arten *P. calceatus*, skiljer sig åt morfologiskt. Den sistnämnda arten är således inte lika nära besläktad, och representerar eventuellt en separat utvecklingslinje.

Välbevarade element från adulta individer har detaljstuderats för att identifiera och beskriva morfologiskt distinkta typer av element. Alla övriga identifierbara element (till exempel juveniler och trasiga element) har ingått i uträkningen av förhållandet mellan olika elementgrupper, i syfte att statistiskt uppskatta det lägsta antalet element i en apparat. Tre elementgrupper kunde urskiljas hos alla fem arterna; M-, S- och P-element enligt det i studien använda notationssystemet. Antalet elementtyper inom varje grupp visade sig vara annorlunda hos *Protopanderodus calceatus* (M1, M2, Sa, Sb, Sc, "Sd", Pa, Pb1, Pb2) jämfört med M, Sa, Sb1, Sb2, Sc, Pa, Pb hos de övriga fyra arterna. Förhållandet mellan elementgrupperna M, S och P för *P. rectus*, *P. robustus*, *P. graei* och *P. parvibasis* tyder på en apparat med minst 21 stycken element fördelat på 4M (2 par), 1 Sa (symmetriskt), 4 Sb1 (2 par), 4 Sb2 (2 par), 2 Sc (1 par), 2 Pa (1 par), 4 Pb (2 par). Samma minsta antal element gäller för *P. calceatus* men istället fördelat på 2 M1 (1 par), 2 M2 (1 par), 1 Sa (symmetriskt), 2 Sb (1 par), 4 Sc (2 par), 4 "Sd" (2 par), 2 Pa (1 par), 2 Pb1 (1 par), 2 Pb2 (1 par). Huruvida *P. calceatus* skiljer sig tillräckligt mycket från övriga fyra arter för att föras till ett separat släkte är för närvarande osäkert. En utökad undersökning som inkluderar andra arter med morfologiska karaktärer liknande de hos *P. calceatus* vore önskvärd, för att i första hand jämföra apparaternas elementtyper och på så vis se om dessa arter tillhör en separat, gemensam utvecklingslinje.

**Nyckelord:** conodoner, *Protopanderodus*, apparatrekonstruktion, ordovicium.

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Conodonts are small, extinct, marine animals, usually a few cm in length, with a laterally flattened, slender and elongate, eel-like body (Fig. 1). Body imprints are rarely preserved, and most of our knowledge about conodonts comes from their only mineralized parts, that were situated in their oral cavity (Briggs et al. 1983). These mineralized parts are called elements and together they built up what is called the conodont apparatus. An apparatus consisted of up to c. 20 different elements (cf. Aldridge et al. 1995). Conodont elements are commonly in the size range 0.1mm to 2.00 mm and a 1 kg sample of carbonate rock can yield thousands of them (cf. Löfgren 2000).

Conodonts were a successful group of animals; different faunas were adapted for a wide range of marine habitats; warm equatorial to colder waters, deep and shallow. Some faunas were very geographically wide-spread, some even cosmopolitan. These qualities, in combination with rapid evolution, make conodont elements invaluable as biostratigraphical markers.

The fossil record of conodonts extends from the middle Cambrian Period (~ 500 Ma) to the end of the Triassic Period (200 Ma). They seem to have been most flourishing during the mid-Ordovician, at least in terms of diversity and widespread distribution (Black 1989).

As full-body imprints only could be preserved under extremely favourable conditions, most of our current knowledge about conodont internal relations, evolution and extinction events, as well as different aspects of conodont palaeoecology relies on the elements and the apparatuses these once built up. Today there are only a few certain apparatus reconstructions based on findings of complete apparatuses of mid-Palaeozoic, rather complex forms. For the older and less derived forms, only a couple of reconstruction models have been suggested. A better understanding of the apparatus structure of older taxa is basal to our understanding of their phylogenetic relationships.

The purpose of this essay is to provide a model for the reconstruction of the coniform apparatus of the Ordovician genus *Protopanderodus* Lindström, 1971, of

which well-preserved material from the Middle Ordovician of Sweden was available, representing a rich fauna. By determining the number and arrangement of morphologically distinct element types and counting these, the element ratios can indicate the total number of elements included in one apparatus. In total, 4202 elements from five species of *Protopanderodus* Lindström, 1971 are included in this study. These five species are some of the oldest members of the genus, and together include the major morphological types present in the genus, thus making up a representative sample.

From each of the Middle Ordovician levels represented in the study, from the *B. navis* Zone to the *E. pseudoplanus* Zone, all available species of *Protopanderodus* have been investigated. Samples including only one of the species have been compared with samples containing two species or more, to minimize the risk of misidentification of elements between the species. The relative stratigraphic extensions of respective species also give some indication of their phylogenetic relationships.

## 1. The conodont enigma

Conodont research started in 1856 when the Russian palaeontologist Christian Heinrich Pander described the first conodont elements (Pander 1856). He called them *Conodonten* and regarded them as fossilized teeth/jaws of some unknown extinct group of fishes. Even though Pander's concept of *Conodonten* originally refers to the hard parts of an unknown animal, today the term "conodont" is used when referring to the whole animal, and the term element (or conodont element) for the mineralized mouth-parts (Sweet & Donoghue 2001).

Ever since conodonts started to gain interest amongst a few palaeontologists in the early 20<sup>th</sup> century, the discussion regarding what type of animal conodonts represent and where to place them in the animal kingdom has been a topic of debate. In 1983 the first more or less complete conodont specimen was described (Briggs et al. 1983). The specimen came from the Lower Carboniferous Granton Shrimp Bed of Edinburgh, Scotland, and



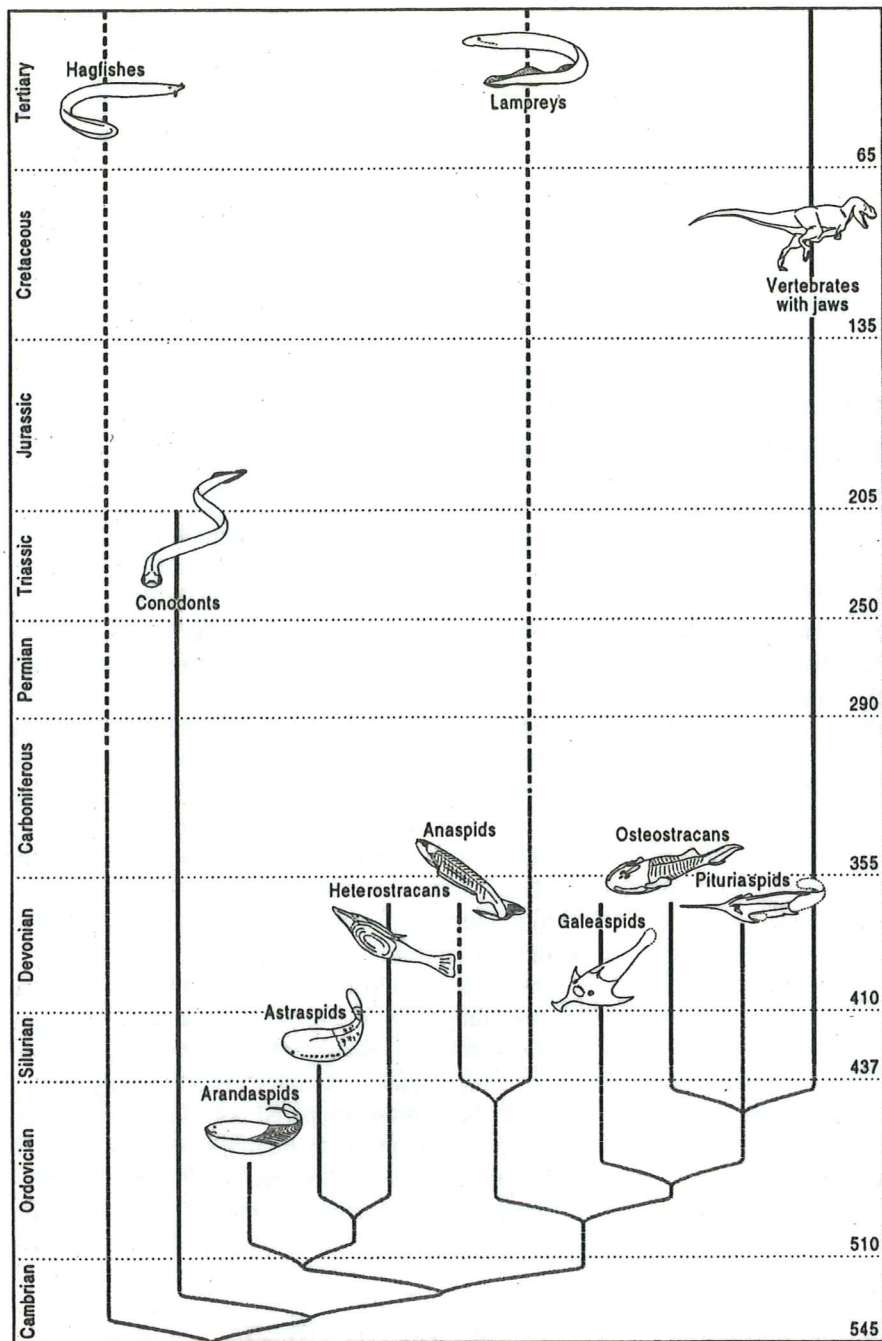


Fig. A. The fossil record of vertebrates and their evolutionary relationship, from the viewpoint that conodonts belong to the Subphylum Vertebrata. Solid black lines show the known fossil record of each group, grayish lines indicate relationship. From Purnell et al. (1995).

was soon followed by additional specimens from the same locality. A specimen from the lower Silurian of Wisconsin, USA was described by Smith et al. (1987) and finally in the 1990ies, gigantic specimens from the Upper Ordovician Soom Shale of South Africa were described by Aldridge et al. (1995). As of today 12 conodont body fossils are known (Aldridge & Purnell 1996). Even if these finds provided answers to some of the earlier questions they have also raised others. The highly debatable question regarding the insertion of conodonts into a phylum was not simply answered just because body fossils had been found. Sweet (1988) summarized some of the previous ideas that include connections to different invertebrate phyla like arthropods, mollusks, annelids and chordates.

Today most students agree that conodonts belong to the Phylum Chordata (Fig. A), and possibly even repre-

sent the first members of the Subphylum Vertebrata (Purnell et al. 1995). In the strongest competing theory the conodonts are instead regarded as representing some kind of "protochordates" (Nicol 1995). A small group of workers have not accepted the chordate affinities of conodonts and want to place them closer to the chaetognaths (Kasatkina & Buryi 1996). This is mainly a question how to interpret what can be seen in the imprints.

Although this matter is not completely solved, it seems fairly safe to shortly summarize the anatomical evidence for the chordate nature of the conodonts. As the first found conodont specimen is still the most well-preserved one, most conclusions have been drawn from studies of this particular impression.

The animal had no hard skeleton (except for the mouth parts) but the linear axial traces in the anterior and posterior part of the animal have been suggested as a rod of



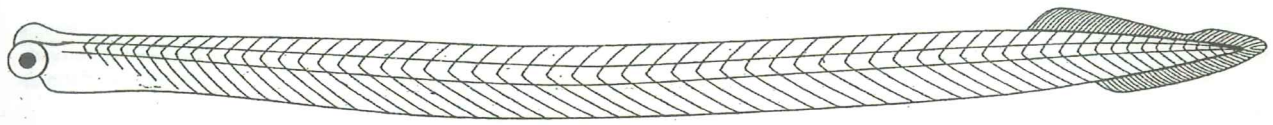


Fig. 1. Reconstruction of the anatomy of the conodont animal. From Sweet & Donoghue (2001).

cartilage along the back (notochord). The impressions of chevron-shaped structures likely represent segmentation and v-shaped blocks of muscle, similar to the myotomes in amphioxus and fish. The extensions in the posterior region of the animal likely were dorso-ventral, ray-supported fins. The bulbous anterior region is considered to be a separate head, with lobe-like structures that probably were a pair of eyes (Briggs et al. 1983; Sweet & Donoghue 2001).

## 2. The conodont elements

### 2.1 Element orientation

When describing a conodont element, the tip of the cusp is oriented upwards, the upper edge of the base or posterior process is horizontal and in most cases the concave side of the cusp is the posterior side which makes the convex side the outer side (Purnell et al. 2000). One has to be aware that this is purely for descriptive reasons and has little to do with the life orientation of elements. Even so, this standard-orientation is the starting point for additional terms used for description of elements. The basic terminology in this conventional system for describing orientation is; anterior, posterior, oral, aboral, upper, lower, inner, outer, left/sinistral and right/dextral.

When students started describing conodont elements, the only comparisons that could be made were between elements, as one basically did not have any knowledge at all about the organisms once possessing them. So, the terminologies that were developed are of universal biological meaning and made perfect sense as long as only discrete elements were described and all elements are oriented in the same way.

With increasing knowledge about the conodonts as animals, it has become clear to many scientists that this system has its weaknesses, for example when comparing

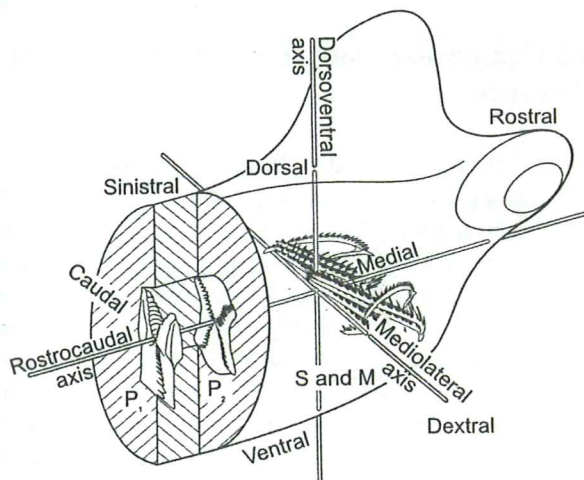


Fig. 2. Biological terminology applied on a reconstructed ozarkodid conodont and its elements. From Purnell et al. (2000).

conodonts to other organisms. The other alternative, even if it has not yet been used in any original description, is to apply the same basic biological terminology that is used when describing the anatomy of any (now living) animal, on conodont elements (Fig. 2) (Purnell et al. 2000).

### 2.2. Shapes of element crowns

As this essay treats the genus *Protopanderodus*, a so called coniform genus (with solely coniform element crowns; see below), this element type will be presented in more detail in this section. However, as additional element types also will be discussed in different contexts, it is necessary to sum these up (from Sweet 1988):

#### 2.2.1 General terminology

A conodont element, regardless of its outward appearance, consists of two parts; the crown and the basal filling. Basal fillings are only present in very well-preserved elements as the surface between the crown and the base is a surface of weakness. Instead, when describing an element, one usually describes the crown. Further, the crown is divided in two parts; the cusp and the base. The cusp is the rigid upper part of the crown and generally makes up the major part of the crown. The base is the lower part of the crown that contains a basal cavity, i.e., the surface of attachment between the crown and the basal filling that is enclosed in the crown. Basal cavities are most clearly seen in thermally unaltered crowns. Other element features include apex; the tip of the cusp, keels; very sharp edges, costae; sharp edges, carinae; smooth/rounded edges, anterior/posterior margins (Fig. 3).

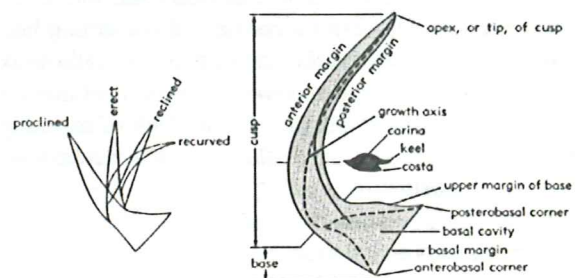


Fig. 3. Terminology used for describing different cusp curvatures in coniform elements, orientation and terminology of coniform elements. From Sweet (1981), after Lindström (1955).

#### 2.2.2 Coniform crowns

Coniform elements ("coniforms" or simple cones) are as the name implies basically conical in shape. The coniform element is divided in two parts, the shorter base that encloses a basal cavity and the solid, longer cusp whose curvature can be either proclined, erect, recurved or reclined in relation to the base (Fig. 3). There are only



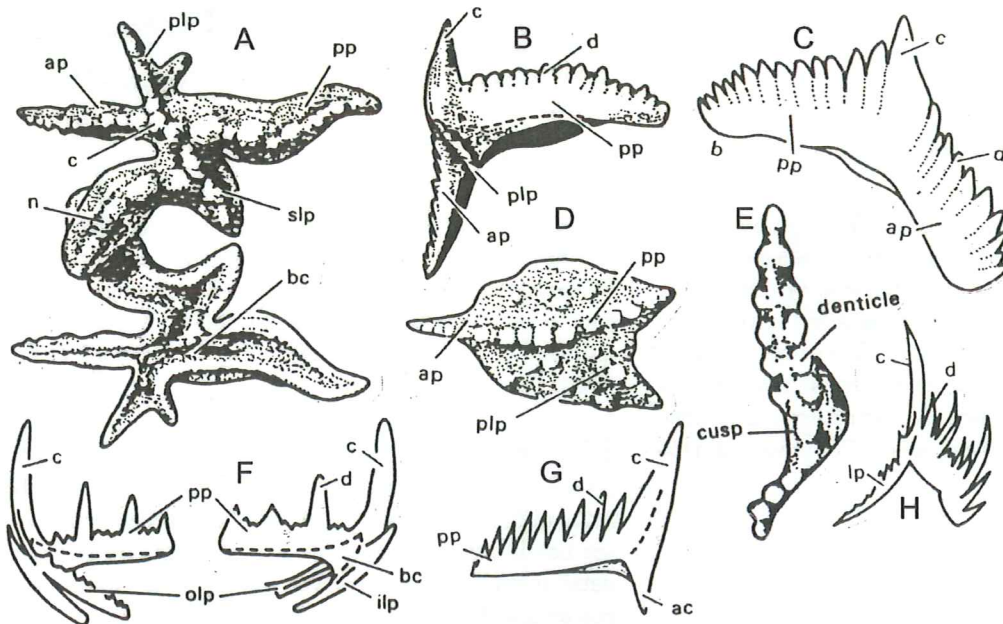


Fig. 4. Some examples of pectiniform elements (A-E) and ramiform elements (F-H). Terms to describe them include: ac=anticusp; ap=anterior process; bc=basal cavity; c=cusp; d=denticle; ilp=inner lateral process; lp=lateral process; n=node; olp=outer lateral process; plp=posterior lateral process; pp=posterior process; slp=secondary lateral process. From Sweet (1988).

two established basic divisions of coniforms; geniculate elements where the upper edge of the base joins the posterior margin of the cusp in an acute angle, and the non-geniculate elements where there is a smooth transition from the upper margin of the base to the posterior edge of the cusp.

### 2.2.3 Other kinds of crowns

Ramiform elements ("ramiforms"; also called bars, Fig. 4; F-H) have a base that is extended in different directions to form so called processes. These processes are named due to their orientation relative to the cusp (e.g. lateral process, posterior process or anterior process). The processes are usually denticulated, which means that the processes have individual serrations (denticles) on the upper edge, but adenticulated processes (no denticles) also occur. Eight morphologically different types are recognized, according to the orientation of the processes in combination with the number of denticles.

Rastrate elements can be considered something between coniforms and ramiforms, as they basically look like coniform elements that have developed denticles on the posterior margin of the cusp. The lack of anything comparable to processes makes them easy to separate from ramiform elements.

Pectiniform elements ("pectiniforms"; include so called blades, plates and platforms, Fig. 4; A-E) is a collective name for comb-shaped elements that occupied similar positions in different kinds of apparatuses and thus had basically the same function. Platformless pectiniforms have one to four processes; the difference between these and the processes found in ramiforms is that the pectiniform processes are laterally flattened and thus higher, and extend away from the cusp and not from the base. In addition, so called secondary processes can develop and branch out from the primary ones. Five main categories are recognized according to the number and arrangement of processes. The platformed analogues of these categories are named according to the shape of the attachment

surface (the basal cavity). In total, twelve different types of pectiniforms are known.

### 2.2.4 Crowns building up apparatuses

The variety of elements presented in previous sections also indicates a wide variety of apparatuses. As mentioned in the introduction, conodonts range from the Cambrian to the Triassic and in addition conodont elements had, at least periodically, a rapid evolution. Generally, one might say that the simplest types of apparatuses were built up solely by coniform elements while the more derived and complex apparatuses instead had ramiform- or a combination of ramiform-pectiniform elements. Of course, there were more or less derived types of all kinds of apparatuses.

Despite of the element types included, all conodont apparatuses had the same basic arrangement; the apparatuses were bilaterally symmetrical and thus separated in two halves with the elements working against each other in a side-to-side manner, instead of up-and-down as our own teeth. (Fig. 5)

## 2.3 Composition and structure of conodont elements

### 2.3.1 Internal structure, histology and growth

A conodont element, regardless of outward shape, is built up of several layers of growth lamellae that were formed by outer apposition around a nucleus, which means that the new lamellae were added to the outer surface of the growing element. The lamellae, usually 0.2 to 1.2  $\mu\text{m}$  thick, contain organic matter in which crystallites of calcium phosphate are embedded. The crystallites are oriented differently depending on the growth of the element; if the crystallites remain perpendicular to the lamellae it is called isometric growth, whereas in positions of accelerated growth the crystallite axis points in the direction of pronounced growth.



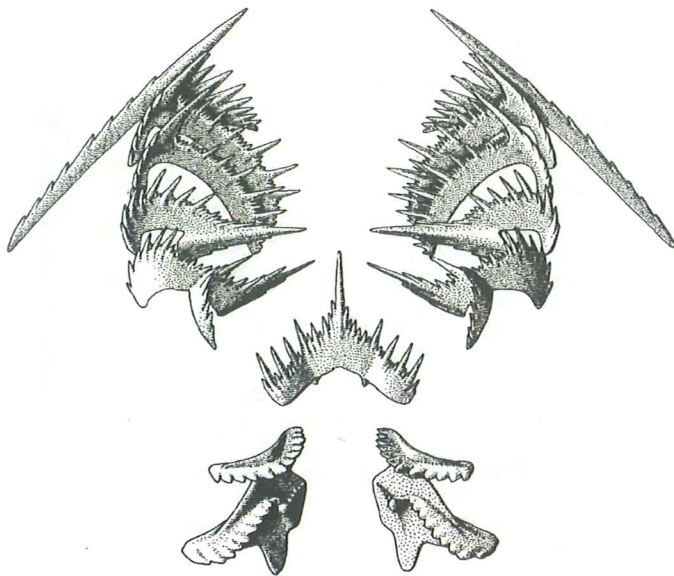


Fig. 5. A proposed arrangement of the elements in a ramiform-pectiniform apparatus (conodont species *Manticolepis subrecta*). Modified from Dzik (1991).

So called localized anisometric growth is responsible for the outer features of the element, or simply the element shape. This is seen as individual lamellae are thicker in the direction of pronounced growth and thinner in the areas between (Fig. 6).

Even if the growth lamellae are continuous between element crowns and basal fillings and the chemical composition is the same in both, there are still some differences between these two parts; in the crowns the lamellae are built up of relatively coarser crystallites compared to the basal filling. The basal fillings also contain more organic material. This is likely the explanation for the surface of weakness between element crown and basal filling. There are also differences in preservation; during diagenesis of the rock containing the elements, the organic matter in the basal fillings shrinks and this is seen as undulations in the lamellae, while the crown becomes less affected as the crystallites are packed closer. The preserved basal filling is generally considerably darker than the crown. This difference in colour is also due to the organic content and how it is affected by diagenesis.

All elements have one more important thing in common, the presence of "white matter". This feature is seen

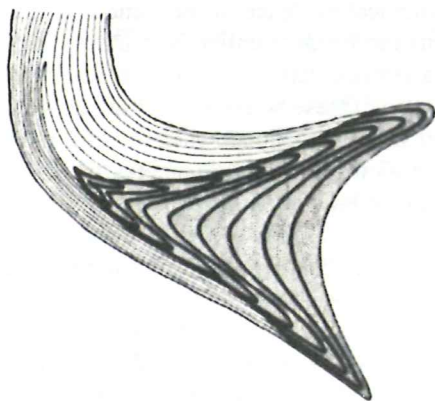


Fig. 6. Growth lamellae in the base and lower part of the cusp of a coniform element. From Müller (1981).

as white areas in thermally unaltered elements (hyaline amber colour), and appears at the tip of the basal cavity and continues into the cusp. Chemically, white matter is identical to the rest of the element, even if the white matter is regarded as re-crystallized. The white matter is believed to have formed during element growth, as it is covered with lamellae and seen in areas of prevalent growth (Ziegler & Lindström 1981; Müller 1981).

### 2.3.2 Chemical composition

As mentioned in the previous sector, a conodont element consists of both organic matter and crystallites. In short, an element is described as mainly consisting of calcium phosphate. In detail, the mineral part has been interpreted as a carbon apatite called francolite according to the formula (Ziegler & Lindström 1981)



with room for slight variations in the amount of each component.

The chemical qualities of elements make them soluble in hydrochloric, sulphuric and nitric acids and less soluble in acetic, formic and citric acids. Thus, the latter are to prefer when extracting conodonts from surrounding rock matrix. Acetic acid is currently used, and with the relatively new technique described by Jeppsson et al. (1999), where the solution is buffered with calcium acetate before use to a pH greater than 3.6, even most elements in size fraction 63  $\mu\text{m}$  can be retained.

The organic content of an element can actually be seen with the naked eye. If the element is dissolved slowly in a weak hydrochloric solution, a "ghost-element" remains after the demineralization. This could indicate that the mineralization once took place within the organic framework (Sweet 1988).

### 2.3.3 Elements as indicators of metamorphism

Conodont elements are, thanks to their organic content, good indicators of grade of metamorphism in rocks, that is the process of chemically altering in rocks due to increased burial depth and thus increased temperature.

As the element is heated together with the enclosing rock due to the gradually raising temperature in the metamorphic process, the organic carbon becomes more and more fixed and as a result the element gradually takes on a darker colour. The elements are affected by the temperature, time and burial depth; the pressure factor in itself does not change the element.

It has been discovered that the colour of conodont elements can be used as a thermal index that indicates the maximum temperature and burial depth that the enclosing rock has been exposed to, as well as the organic maturity of enclosed organic matter. The index developed is called CAI (Conodont Alternation Index) and is of value in the oil and gas exploration business as well as in structural and metamorphic analyses. The scale runs from 1 to 8; at CAI 1 (<50°-80°C) an element is assumed thermally unaltered and the colour is generally pale yellow. At CAI 5 (+300°C) the element is black and at CAI





Fig. 7. Natural assemblage of the ozarkodinid genus *Idiognathodus*, from the Carboniferous of Illinois, USA. From Purnell et al. (1995).

8, the element is instead nearly crystal clear. This is because when the temperature reaches a critical point, the organic carbon in the black element is driven out as a result from the release of water of crystallization. There are of course certain factors to consider; the type of rock (carbonate rock, sandstone etc.) and the shape and size of the elements have some influence on the colour (Epstein et al. 1977).

### 3. Apparatus reconstruction

#### 3. 1. Preservation of apparatuses as clusters and natural assemblages

It would be virtually impossible to try to reconstruct an apparatus without any information about the three-dimensional organization. This knowledge is received from so called natural assemblages (Fig. 7) and fused clusters (Fig. 8). A natural assemblage is an aggregate of elements found on a rock bedding surface, either articulated or slightly disarticulated, that represents a conodont apparatus. A fused cluster usually consists of elements that are held together by cement (a mineral or an organic substance) that is insoluble in acid. A cluster usually represents a fragment of the apparatus, while an assemblage can represent a complete apparatus (Dzik 1991). Findings of elements preserved in this way give invaluable information about the apparatus in question. Unfortunately, both these kinds of preservations are comparably

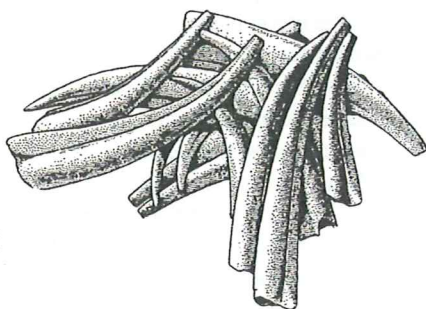


Fig. 8. Drawing of a fused cluster with elements from the coniform genus *Panderodus*. From Sweet (1988).

rare. The best preserved natural assemblages, from which the most confident reconstructions have been made, represent the complex ramiform-pectiniform apparatuses of two conodont groups called ozarkodinids and prioniodontids. For older conodont groups with less derived apparatuses, most of the obtainable material for reconstruction consists of discrete elements and sometimes fused clusters.

#### 3. 2 Element notation systems; location from homology or analogy?

In the early days of conodont studies, a discrete element could be classified as a separate taxon according to the so-called form taxonomy. When it eventually became clear that one animal could have several different types of elements in their oral apparatuses, the study of conodonts took a new turn and what is now referred to as multielement taxonomy started to develop. In the work of bringing together the right elements to the right taxa, several schemes of anatomical notation developed.

An element notation system is a terminological system, or one might say a tool for identifying different elements representing the same type. An element type is further a unit that groups corresponding elements from different apparatuses. The purpose is usually to express homology; that is, identifying elements that are equivalent (representing the same type and function) and show morphological evidence of the same origin, even if the elements can be quite unlike each other (Dzik 1991).

In a system, particular notion symbols are used for designation of these homologues. Further, a notation system can also be locational when used for indicating element position in the oral apparatus which is desirable when attempting to do a reconstruction (Dzik 1991). At last, when only aiming to describe the form of an element, a descriptive system can be used (e.g. Lindström 1971).

There are several reasons for not yet having a pervading notation system that is valid for all apparatus reconstructions. The problem partly lies in the huge variations in element types and proposed apparatus architectures between different conodont groups, due to their ra-



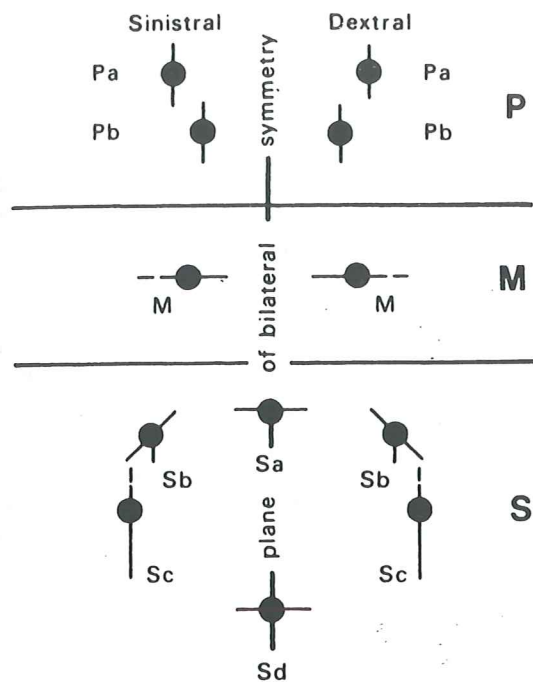


Fig. 9. Scheme of locational notation for the M, S, P system. Observe that the map is not intended to show actual positions of various element types, but to provide a system for designating major positions. From Sweet (1988).

pid evolution. Systems that seem to make perfect sense for some apparatuses can be totally unsuitable for others.

As Sansom et al. (1994) pointed out, if conodonts form a monophyletic clade (with one common ancestor), it should be possible to develop a unified locational apparatus notation that would allow us to draw direct homology between ramiform-pectiniform and coniform apparatuses. Thus, Sansom et al. (1994) indicate that it might be necessary to better understand the relationships between the different conodont groups before we are able to develop a functional notation system that gives us information about both location and homology.

However, the consequence of not having a fully accepted reference standard for reconstruction is mainly that confusion now and then arises, especially in cases when the same notation is used in different ways by different authors, sometimes to indicate homology and sometimes not (Purnell et al. 2000).

### 3.2.1. The element notation of Sweet (1981)

Today the most commonly used notation system is the one developed by Sweet (1981), as it can be applied to most conodont apparatuses. This system refers to three morphologically distinct groups of elements in the apparatus; the P (principal)-element group, the M (medial)-element group and the S (symmetrical) element group. The elements in each group have certain positions relative one another; the position is indicated by a small letter after the capital letter (Fig. 9).

The P position can be occupied by pectiniform elements, specialized ramiform elements or small coniform elements. There are two positions recognized; Pa and Pb.

In the M position Sweet (1981) placed pick-shaped elements, either ramiforms or alternatively geniculate coniforms. It has been shown that also nongeniculate coniforms could be placed in M position.

Four main positions in the S-series (termed Sa, Sb, Sc and Sd) are recognized. A symmetrical element is placed in midline (Sa) position, and the elements in Sb- and Sc positions showing increased asymmetry. These three positions thus form a symmetry transition series (*sensu* Lindström 1964). The Sd position was originally meant for a bilateral symmetrical element found in some complex apparatuses. However, as the M, S, P notation scheme now is used for elements of a wider morphological range, the Sd position is seen being used in other ways, for example as an extension of the symmetry series. In reconstructing the apparatus model of the coniform conodont genus *Cornuodus* Fähræus 1966, Löfgren (1999b) placed two pairs of strongly asymmetrical concavo-convex elements in Sd1 and Sd2 positions. Ramiform elements or nongeniculate coniform elements occupied the different S-positions.

Notice that the positions mentioned for these three element groups (capital letter followed by small letter) are so called end-member positions. All positions (except for the Sa with the single symmetrical element) can be inhabited by more than one type of element. If, for example there were two elements in the Sb-positions on each side, the positions of these two elements can be distinguished as Sb1 and Sb2. Further, there could also have been for example two pairs of Sb1 and Sb2, respectively.

Depending on the number of morphologically distinguishable elements, an apparatus can be described as either uni- or multimembrate (Sweet 1981). According to Sweet (1981), a unimembrate apparatus only has one kind of element, while a multimembrate one has several different kinds. Today the concept "unimembrate" is no longer used, as all apparatuses reconstructed in this way have been reinterpreted as having a higher number of element types. Multimembrate apparatuses are further subdivided into bi-, tri-, quadri-, quinqui/penta-, sexi- or septimembrate (or even octomembrate and so on). This means that two apparatuses can be very unlike each other, but still belong to the same category.

Clearly Sweet's (1981) intention was not to develop a system that could be applied to any kind of element in any apparatus reconstruction. He developed the system from studies of complex ramiform-pectiniform apparatuses of Ordovician age, and did not mention that this notation could be applied to apparatuses with for example solely coniform elements. This was because he believed that the coniform apparatuses only contained one or two element types. Sweet wrote (1981, p. 19) "...description of an element as the occupant of, for example, a Pa or Pb position does not (or should not) imply that it is necessarily homologous with elements described as occupants of Pa or Pb position in other apparatuses." This scheme was thus not originally designed to indicate homology, but instead, as he continues on page 20 "...the scheme of locational notation proposed...is designed to be a vehicle for expressing analogy."



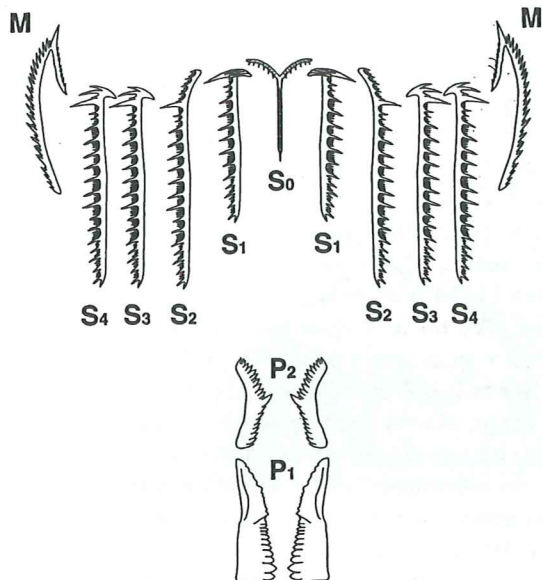


Fig. 10. The alternative, numerical M, S, P element notation applied on the elements of the ozarkodinid apparatus. From Purnell et al. (2000).

The intended (original) function of this system is thereby made clear; to propose relative positions and compare elements in these positions belonging to different taxa, without indicating homology. Even so, the M, S, P notation system is frequently used for demonstrating homologies based on similar morphological characters in elements of different genera. For example, Nicoll (1994, 1995) used this notation for apparatus reconstruction of coniform genera, as he observed a consistent morphological pattern in these genera that was agreeable with the use of the M, S, P notation system.

### 3.2.2 The element notation system of Purnell et al. (2000)

Purnell et al. (2000) stated that Sweet's (1981) notation scheme cannot be used for identifying homologous elements. The reason for this is that morphologically similar elements cannot be presumed as possible homologies without further evidence. Further, the morphology of an element is not a reliable guide to its position in the apparatus.

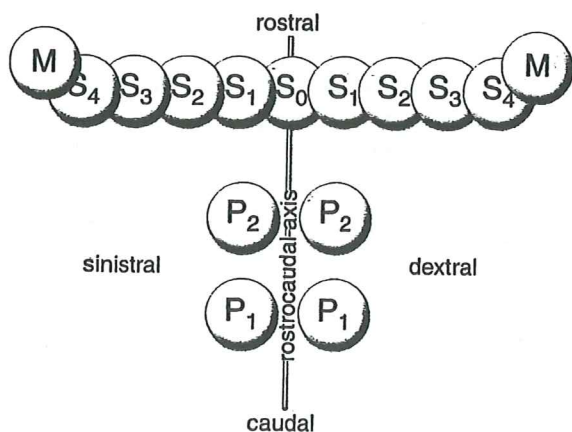


Fig. 11. Scheme of locational notation for the numerical M, S, P element notation system. From Purnell et al. (2000).

Purnell et al. (2000) also proposed a notation system for identification of homologies where the basis lies in the M, S, P scheme. The difference is that the three-dimensional arrangement of the apparatus is used as the starting point for notation, instead of the morphology of elements. The notations should thereby already be fixed.

After the development of the original M, S, P scheme, the knowledge of the actual life-positions for the elements in some complex ramiform-pectiniform apparatuses increased, and thus it became possible to directly compare these apparatuses in search of homologies. Purnell et al. (2000) suggested that as the ramiform-pectiniform apparatus of ozarkodinid conodonts is the best known one, this would make up the reference standard for any other apparatus to be compared with (Fig. 10). Instead of using a previous notation like for example Sc, the S positions should be numbered starting from the median axis (that is; the position for the symmetrical element named  $S_0$ ), with the first S position lateral to  $S_0$  becoming  $S_1$  and so on, regardless of the appearance of the element situated in this particular position (Fig. 11). For further precision one can differentiate the two lateral sides by adding a "d" in superscript referring to the dextral (right) side;  $S_1^d$ .

Purnell et al. (2000) were aware that their proposed system could not be applied to all conodont taxa. As already mentioned, there are not many conodont taxa for which there is direct evidence (e.g. clusters/natural assemblages) suitable for comparisons. This means that comparisons in that case would have to be made between the elements in the reference standard apparatus (or another fairly well-known apparatus) and discrete elements. This works as long as the elements compared are not too taxonomically distant from the reference apparatus of ozarkodinid conodonts. When it comes to apparatuses composed solely of coniform elements and the current knowledge about them, this is almost impossible. In such cases the M, S, P system of Sweet (1981) is preferable; as long as it is used in the way originally intended.

### 3.2.3 The notation used for panderodontid conodonts

Findings of fused clusters representing the genus *Panderodus* Ethington are not unusual, and in addition, this is the only coniform conodont genus that has been described from a natural assemblage with impressions of surrounding soft parts (Sansom et al. 1994).

The genus *Panderodus* Ethington possessed one of the most advanced coniform apparatuses with elements of very distinct form, to which application of the M, S, P notation system is difficult (cf. Löfgren 1997a). The apparatus architecture has, by some students, been interpreted to differ from other conodont forms known from natural assemblages and clusters (see also section 4.2).

For the description of the *Panderodus* apparatus, Sansom et al. (1994) developed a very detailed notation where descriptive terminology is combined with a locational notation (Fig. 12). This notation system is meant to express homology, at least for coniform genera, and is thus



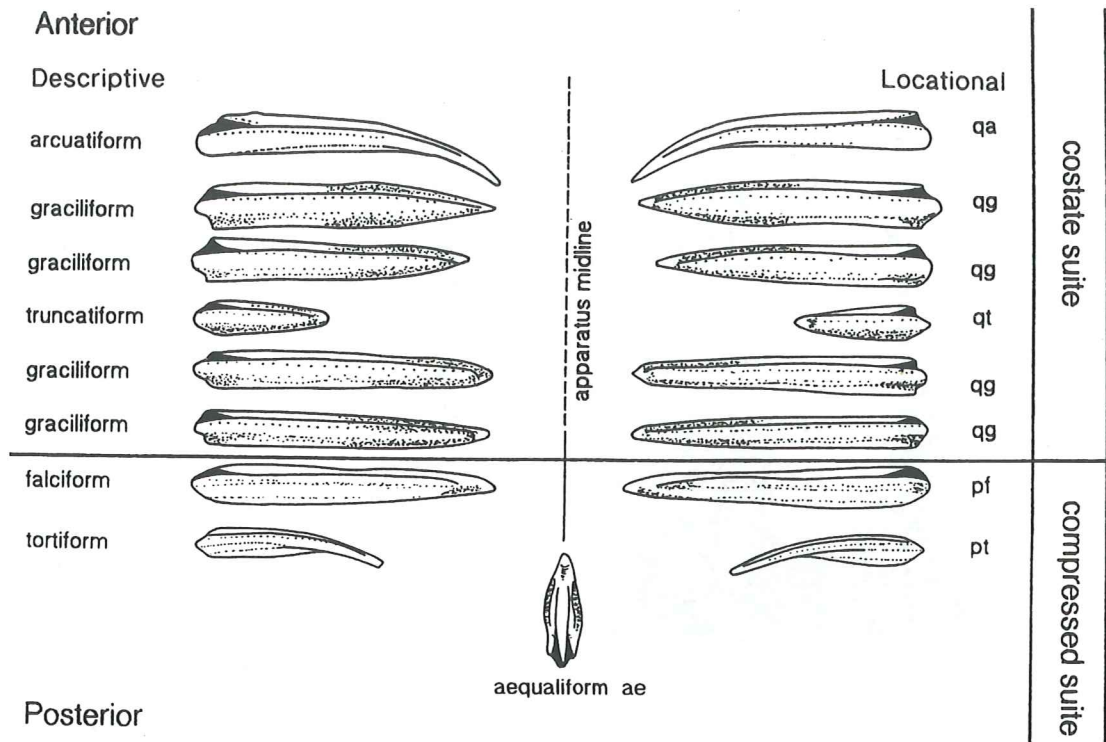


Fig. 12. Architectural reconstruction of the *Panderodus* apparatus, showing the descriptive terminology and the locational notation used. From Sansom et al. (1994).

also meant to be applicable to other coniform apparatuses. The system is strictly locational and based on three main positions; the ae position for the single symmetrical element, the p-position for posteriorly placed asymmetrical element pairs (compressed suite), and the q-position for anteriorly placed asymmetrical element pairs (costate suite). A second following letter indicates exact position in the apparatus.

#### 4. Function and evolution of the conodont apparatus

When discussing the function and evolution of the conodont apparatus, the main positions M, S and P according to Sweet's (1981) and Purnell et al's (2000) notation systems will be referred to.

##### 4.1. Function and feeding strategies

To be able to understand the evolution of the conodont apparatus it is important to first investigate the possible function, both for the entire apparatus and for the different M, S and P parts. During the process of reconstructing different kinds of apparatuses, a number of ideas for their function have been suggested. Today there are only two functions that are discussed; either the conodonts practiced suspension feeding or grasped their food. In other words; did these tooth-like elements really have a function analogous to teeth?

Despite the disagreements regarding the basic function, all students of conodonts that reconstruct conodont apparatuses seem to agree on the interpreted life-positions of the major element groups. Natural assemblages and clusters have shown that the M-elements were positioned anteriormost in the apparatus. The S-elements,

positioned posterior of the M-elements, have been interpreted to have been arranged to form an element-basket with the single symmetrical element in mid-position. The P-elements were positioned posteriormost in the apparatus, thus behind the S-array and closer to the throat (Fig. 13).

There is no question about the fact that conodont elements, especially the coniforms, resemble teeth (Jeppsson 1979). Jeppsson (1979) discussed conodont element function and compared elements with teeth from animals belonging to different taxa, and argued that the external shape of the element is enough to demonstrate a tooth-like function. A tooth-like function is often associated

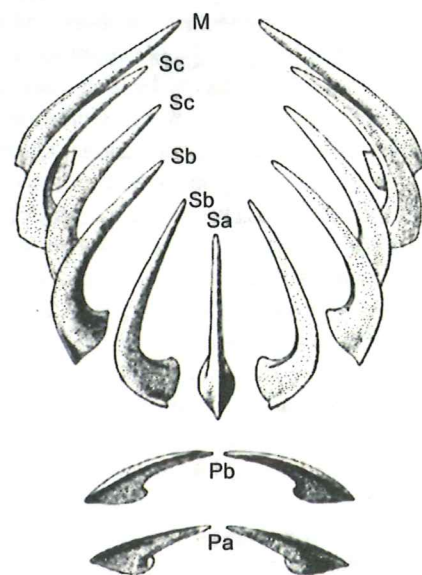


Fig. 13. Reconstruction of the coniform apparatus of the genus *Drepanodus* Hadding, 1913. Modified from Dzik (1991).



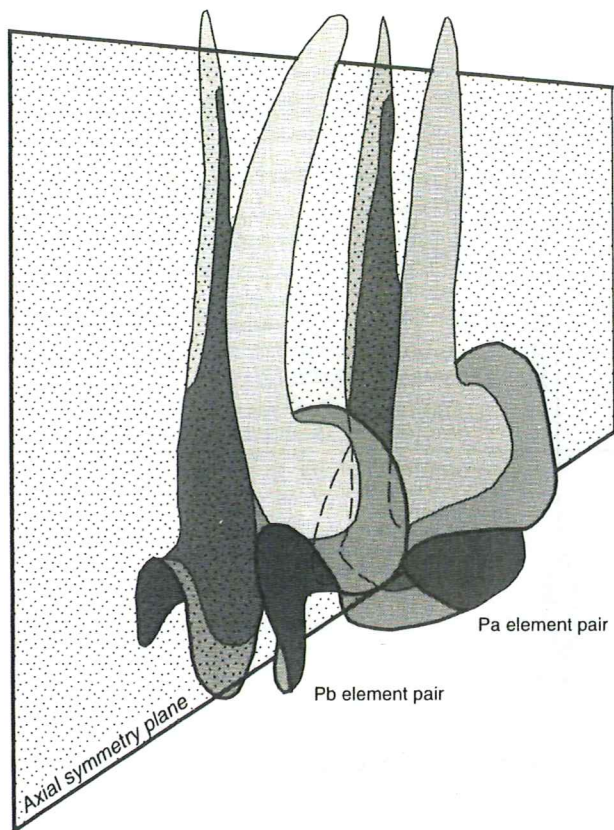


Fig. 14. Reconstructed positioning of coniform Pa and Pb element pairs. Drawing shows elements in conventional orientation. Observe the different functional interpretations for this element arrangement; the elements could have worked as scissors/knives-, alternatively mashing-tools when the pairs moved relative to each other. From Nicoll (1995).

with active hunting and thus a grasping function for the apparatus. The ramiform or coniform M-elements would have worked in an incisor-like manner, penetrating the food (Dzik 1991) while the P-elements took care of the necessary slicing and/or crushing (Purnell et al. 1995). It is quite easy to imagine how blade- and platform-shaped pectiniform elements in P position (see chapter 2) were suitable for occluding and thus crushing and shearing. But we know that many early conodont genera had an apparatus with only coniform elements; how did coniform P-elements perform this work? Coniform elements with the tips of their cusps pointing towards each other as shown in Fig. 13 could not have processed the food effectively. Nicoll (1995) presented models for the interrelationship of Pa and Pb elements for different conodont apparatuses, and suggested that the coniform P-elements should be placed with their basal cones next to each other (Fig. 14). In this way, these elements could have worked like a pair of scissors or knives, not able to crush effectively, but suited for slicing the food. Notice that this was not the function that Nicoll (1995) had in mind (see below).

There is mainly one thing that may be considered as speaking against a grasping tooth-like function, that it is the way that the elements grew. As mentioned in section 3:1, the lamellae that build up an element are added to the outer side of the growing element. Some sort of tis-

sue, secreting building material, must therefore have covered the element during growth (e.g., Purnell 1999). The question is then; were the elements constantly covered with this tissue or only periodically?

Followers of the competing, suspension-feeding theory (e.g., Nicoll 1995) argue that all the elements were tissue-covered throughout the lifetime of the animal, and this would certainly explain the growth-pattern. In this scenario, the S and M element array, anteriorly positioned in the apparatus, should have functioned as a tissue-covered ciliated suspension-feeding system. The difference between ramiform- and coniform elements building up this filter basket were, according to Nicoll (1995), only a function of efficiency. Microscopic food-particles first passed through the cilia and then continued to the posteriorly positioned P-elements, whose function would have been to mash up the food and then sweeping it into the throat and to the digestive tract. The P-elements moving in relation to each other should be enough to process the food, without any cutting action at all, as the potential prey (plankton) did not have to be cut (Nicoll 1987; 1995).

Followers of the grasping apparatus theory have been trying to explain the contradictory growth pattern, for example by suggesting that the elements could have retracted in epithelial pockets when they were not used (Fig. 15). In this way, periods of function were interrupted by periods of growth (Bengtson 1976; Jeppsson 1979). Another suggestion is that elements bore horny caps and that the tissue secreting material for additional lamellae was maintained in between the element and its cap (Purnell 1999).

Even if there are many uncertainties regarding the function of the conodont apparatus, the most popular, and probably also the most likely, theory is doubtless the one that conodonts grasped their prey. In an attempt to prove this, Purnell (1993) investigated the ontogeny of the ozarkodinid apparatus, with the assumption that the apparatus always functioned in roughly the same way through all the stages of animal growth.

Regardless of function, the apparatus had to increase

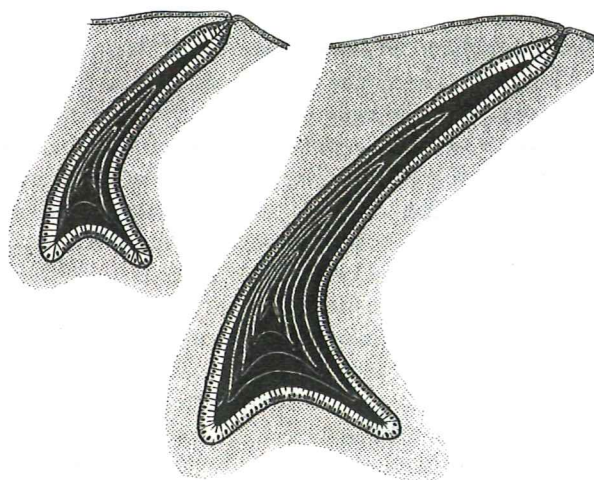


Fig. 15. Diagrammatic reconstruction of the relationship between a coniform element and its secreting epithelium during growth and/or periods when the element was not in use. From Bengtson (1976).



its size at such a rate that it could function as effectively as possible. Comparisons with extant organisms suggested that in the case of a grasping function, the size of the M and S elements only needed to increase in the same rate as the rest of the animal. If the function was filtering, the length of the M and S elements had to increase in a greater rate compared to the rest of the animal to match the growing conodonts' energy requirements. This is because the intake of food stood in direct proportion to the surface area of the filter. Measurements of the elements in question from natural assemblages show that the ozarkodinids could not have been suspension feeders as the M and S elements not are proportionately larger in larger apparatuses. Also, scanning electron microscopy has revealed wear-patterns on the functional surfaces of the elements, features that have not been noticed earlier but that could comprise verification for a grasping function. (Purnell 1993, 1999; Purnell et al. 1995)

As conodonts were such a successful and long-ranging group of animals with a variety of different element types, it is highly possible that different conodonts adopted different kinds of feeding strategies. Purnell (1999, p. 138) stated: "...the hypothesis that ozarkodinid elements functioned as teeth should not be extended to other taxa indiscriminately." Thus it is not safe to apply one single function to all conodont apparatuses. Generally, a grasping function is often associated with active hunting/predation or possibly scavenging, while suspension feeding would rather indicate a more inactive lifestyle (Purnell et al. 1995).

Löfgren (2003) discussed conodont palaeoecology and compared the feeding habits for at least the coniform conodont genera with some carnivorous bathypelagic fish that live in today's deep and low-productive seas. These fishes are generalists in terms of feeding and choice of prey as the distribution of food is very limited. The function of the jaws is thus to grasp and hold on to any prey as effectively as possible. This scenario seems applicable to conodonts with solely coniform elements; even if these conodonts lived in quite shallow waters, the availability of food was probably comparable to that of the deep seas of today. In this case the conodonts with more advanced apparatuses probably were comparably specialized in their choice of prey. Thus, these specialized conodonts must have occupied more productive parts of the seas where the food supply was comparably higher.

#### 4.2. The evolution of the conodont apparatus

Dzik (1991) discussed the evolution of the conodont oral apparatus and based the discussion on a grasping function for the most primitive types, comparable to the apparatuses of the chaetognaths. He suggested that the earliest Cambrian conodonts all had apparatuses entirely built up by coniform elements in which the entire apparatus was exposed. This means that these primitive conodonts did not have any elements in the posterior part of the oral cavity. The anatomical organization would therefore have to be different compared to later conodont as there were no obvious subdivisions into morphologically and

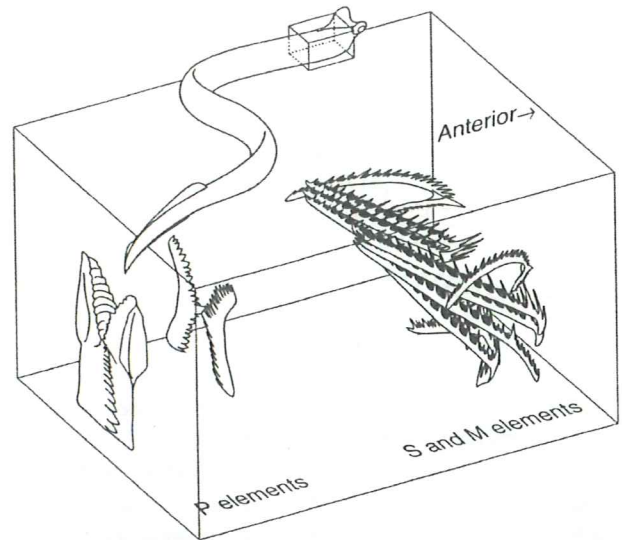


Fig. 16. Reconstructed architecture of the complex ramiform, pectiniform apparatus of *Idiognathodus*, showing the element orientation in relation to the animal and its plane of bilateral symmetry. From Aldridge & Purnell (1996).

functional groups of elements. All elements thus worked as grasping tools and there were no elements that further processed the food.

The next step in the evolution of the conodont apparatus probably was the reorganization of the coniform elements into functional groups to better the efficiency of the apparatus; that is the development of morphologically distinct M, Sa, Sb, Sc, Sd and Pa, Pb elements. In about the same time the development of ramiform element characters (e.g. denticles and processes) must have started in some genera, as conodonts with coniform as well as ramiform apparatuses co-existed already in the late Cambrian. The apparatus of the genus *Cordylodus* is one of the earliest ramiform apparatuses, and also a representative of the most archaic stage in the evolution of the typical conodont apparatus, with a complete set of S, M and P elements. According to Nicoll (1990), who described and discussed the apparatus of *Cordylodus*, this genus evolved from a coniform conodont lineage with all the distinct element types present. Other genera remained coniform but most likely still continued to evolve; the Ordovician genera *Cornuodus* and *Protopanderodus* are representatives of conodonts with more advanced and diversified coniform apparatuses.

The relationships between coniform apparatuses and the increasingly more complex ramiform apparatuses are still poorly understood. What was the cause of this phylogenetic split-up? It might have been a result of experimentalism in element morphology, due to the rapid evolution and diversification during the late Cambrian-early Ordovician (Smith 1990), or possibly connected to a change in lifestyle in some conodont groups. A change in habitat and feeding habits would require that the apparatus adapted to these changes. A wider variety of lifestyles for different conodont groups probably meant that they became more specialized and a gradually changing function for the different element groups caused a change in form for better efficiency.



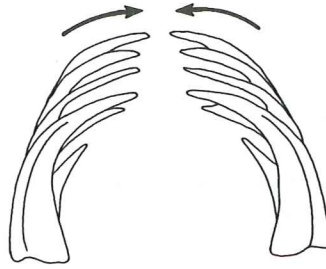
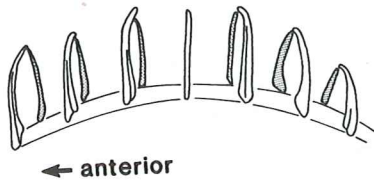


Fig. 17. Hypothetical linear architecture for the *Panderodus* apparatus. Left; lateral view. Right; anterior view, arrows show direction of occlusion. From Smith et al. (1987).

The coniform apparatus of the genus *Panderodus* (also see section 2.2.3) has caused some debate; did coniform and ramiform-pectiniform apparatuses have a different architecture? Reconstructions of the latter show that the cusps of the M elements and S element array are parallel to the plane of bilateral symmetry, forming an anterior basket and with the P elements behind this basket (Fig. 16) (Purnell 1993). In the reconstructed *Panderodus*-apparatus, all element cusps are instead normal to the plane of symmetry. The elements thus become linearly arranged from anterior to posterior (Fig. 17). This could further indicate a fundamentally different body plan for *Panderodus*, being more dorso-ventrally flattened instead of laterally flattened, as have been suggested for other conodonts reconstructed with the help of both natural assemblages and imprints (Sansom et al. 1994; Smith et al. 1987; Smith 1990).

If these interpreted differences are correct, are they applicable to all coniform genera or were the panderodontid conodonts alone in having this apparatus architecture? Can it simply be a question of drawing conclusions from vague evidence? This is only one of many highly interesting questions that may not be answered soon, but it reflects how limited our understanding about the evolution and internal relationships among conodonts really is.

#### 4.3. The origin of the vertebrate teeth and the conodont problem

As conodonts became accepted (by most students) as representing the earliest vertebrates, the discussion about the evolution of the conodont apparatus suddenly became a discussion about the origin of vertebrate teeth. Purnell et al. (1995) presented the problems this brings up and stressed that it may be necessary to re-evaluate the scenario for the evolution of hard-parts in the earliest vertebrates.

According to the traditional view, the first vertebrates were relatively inactive suspension feeders. These animals would have needed to protect themselves from the invertebrate predators inhabiting the seas during the Cambrian and Ordovician. For this reason, these soft-bodied animals started to develop extensive armour of bony scales or plates. This kind of external armour is known to have existed in the jawless fishes from the Ordovician to the Devonian. Jaws should have developed during some 100 million years of evolution when the bony covering slowly migrated to the anterior parts and

eventually into the mouth. The jaws should ultimately have originated from a pair of skeletal bars that supported an anterior set of gills. When proper jaws in this way had developed, the animals could become predators. As a consequence of this new feeding strategy they became better physically adapted for a more active life, for example by the development of paired fins (Black 1989). According to this theory, the driving force behind the development of hard-parts was protection. This consequently makes teeth secondary features.

Conodonts as the first representatives of the vertebrate group makes them more primitive than the jawless fishes as conodonts came first and lacked any mineralized skeleton except for orally. Conodonts did not have any protective armour but still they managed to successfully inhabit the marine environments for over 300 million years. This indicates that the conodonts (or their ancestors) shifted from inactive suspension feeding to life as active predators considerably earlier than presumed in the traditional view of the evolution of vertebrate teeth. The reason for developing hard parts in the oral cavity should have been to improve their ability as predators. Further, this means that aggression rather than protection was the force driving the evolution of the vertebrate teeth and possibly also for the entire vertebrate skeleton (Purnell et al. 1995).

One crucial question arises; are conodont elements and vertebrate teeth really the same thing? They should be, at least if the interpretation of conodonts as vertebrates is correct. According to Purnell et al. (1995), investigations of the microstructure of the conodont elements and vertebrate teeth do in fact show similarities; the tissue building up the conodont elements is comparable with enamel, cellular bone, calcified cartilage and dentine; all of these components are unique to vertebrates. However, Müller (1981) described the histology of conodont elements as complex laminated structures that seem unique compared to other extinct or living animals, and after performing a histochemical analysis, Kemp & Nicoll (1997) declared that their results supported a link between conodonts and cephalochordates rather than to vertebrates.

My own conclusions are that the connection between conodonts on one hand and vertebrates as we know them (with a calcified skeleton) on the other is far from clear. Too many unanswered questions remain for us to say with certainty that earlier interpretations regarding the evolution of vertebrate hardparts would be wrong on several points. The discussion above merely presents one possi-



bility, based on the interpretation that conodont elements are basically the same as vertebrate teeth. This might seem a bit far fetched when one considers what we know about the arrangement in the oral cavity for conodont elements and vertebrate teeth, respectively. One should also keep in mind that just because a new theory is worked out, it does not have to prove the old theory wrong. In this case both scenarios can be accurate and make this a case of parallel evolution, just as in the lampreys and hagfishes.

## 5. *Protopanderodus*, material and methods

### 5.1 The genus *Protopanderodus*

The Ordovician genus *Protopanderodus* had an apparatus built up solely by coniform elements. All *Protopanderodus* elements are nongeniculate coniforms with slender cusps and sharp anterior and posterior margins. Ornamentations on the cusp are found as costae, carinae and striations; all running longitudinally along the cusp. The presence of costae is especially characteristic for this genus. Cusp curvature varies between proclined to strongly recurved. The basal cavities are triangular in shape and the bases are of variable height. White matter is distributed throughout the entire cusp.

The genus *Protopanderodus* evolved in the early Arenig or possibly in the late Tremadoc, most likely from an early species belonging to the genus *Drepanodus*. These two genera are no doubt closely related but are usually systematically placed in separate subfamilies in the Family Protopanderodontidae Lindström, 1971. The main character that separates them is the presence of costae in most *Protopanderodus*, and the lack of the same in most elements of *Drepanodus*. Also, in *Protopanderodus* the symmetry-transition in the S-series is based on the symmetry between costae, whilst in the *Drepanodus* S-series, a cusp-curvature and torsion transition is more apparent. It is therefore likely that *Protopanderodus* evolved as a consequence of further development of costae in a species somewhere early in the *Drepanodus*-lineage (McCracken 1989).

McCracken (1989) placed the species of *Protopanderodus* into two groups according to the degree of ornamentation (number of costae). The bicostate group includes species whose elements have two or less lateral costae, whereas the multicostate group have elements with more than two lateral costae; the latter evolved from a bicostate lineage in the Early Ordovician.

#### 5.1.1 Palaeoecology

For the Ordovician, two major conodont faunal provinces are recognized; the North Atlantic Province and the (North American) Mid-continent Province. The Mid-continent Province faunas generally developed in carbonate platform environments with shallow warm water and were probably restricted to equatorial regions, whereas in contrast the North Atlantic Province faunas developed in deeper and/or colder waters and are considered to

be more cosmopolitan (Barnes & Fåhraeus 1975). It must be mentioned that the provinces are not geographically restricted to North America and the North Atlantic; sub-provinces with depositional settings similar to these two are recognized in various parts of the world. Further, if for instance a succession of rocks represents a depositional succession of shelf – shelf edge – lower slope, the shelf deposits can contain a conodont fauna typical for the Mid-continent fauna while a North Atlantic type fauna can be found in the lower slope deposits; in this case one usually speaks of different biofacies representing different water-depth (Pohler 1994).

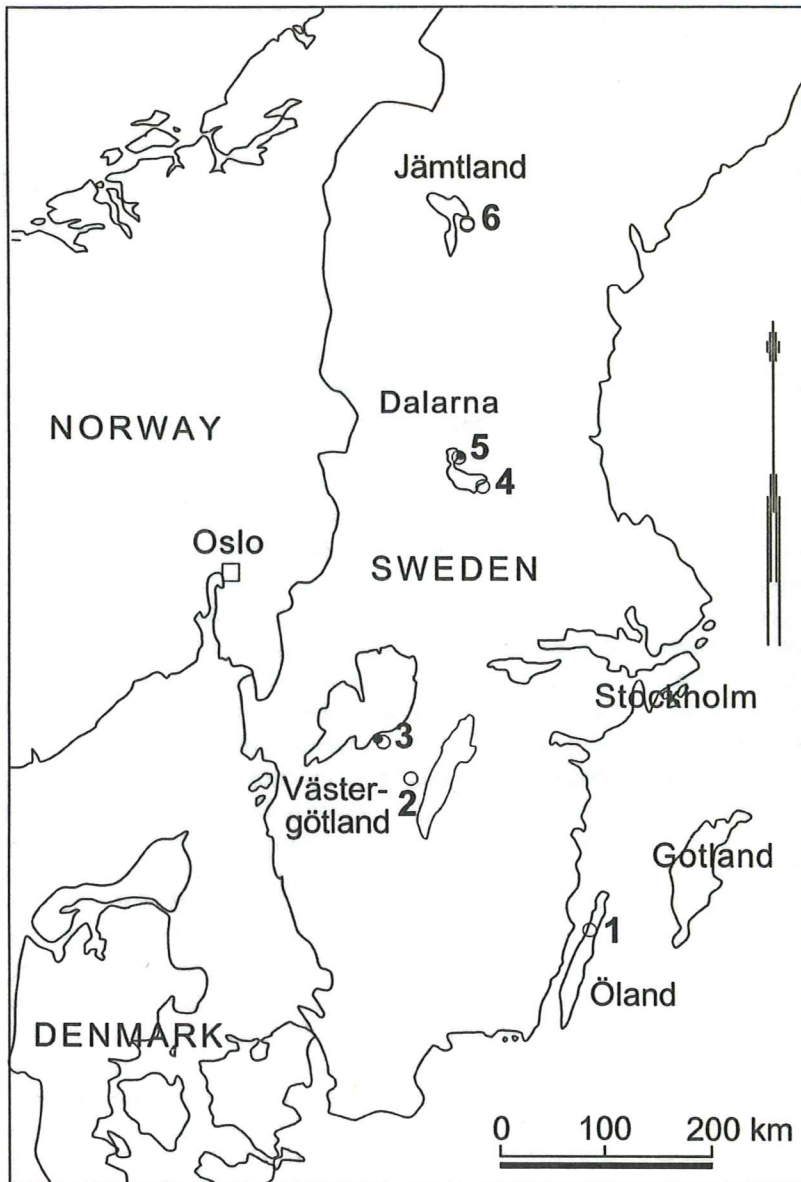
This kind of lateral segregation was recognized by Barnes & Fåhraeus (1975) and their interpretation was that the majority of the Ordovician conodonts were benthic or nektobenthic, with the exception for some coniform genera that instead would be pelagic. It seems reasonable that benthic or nektobenthic conodont groups lived in shallow waters and therefore were more restricted, whereas pelagic or planktic groups could inhabit deeper and therefore somewhat colder environments.

Considering the depositional environments and biofacies where *Protopanderodus* has been found, it seems as if the species of this genus inhabited fairly deep waters, corresponding to shelf edge – shelf slope environments. For example, Pohler (1994) described different Ordovician biofacies from a setting in western Newfoundland and found *Protopanderodus rectus* in a shelf-edge biofacies. Zhen & Percival (2004) described their entire conodont fauna (including three species of *Protopanderodus*) as consistent with a deep-water depositional environment, corresponding to a lower slope setting. According to Löfgren (2003, 2004), the *Protopanderodus* spe-

Table 1. The number of elements of the five investigated species in the samples used.

Taxa						
	P. rectus	P. robustus	P. parvibasis	P. graeai	P. calceatus	Total
Sample						
Total	1503	290	1140	559	710	4202
DLK86 H4	—	133	404	281	—	818
HK89-4	—	124	79	154	—	357
GB81-500	—	33	74	—	—	107
Rävanäs 5	—	—	345	—	337	682
Rävanäs 6	—	—	91	124	—	215
DLK86-H12	—	—	87	—	125	212
DLK86-H13	—	—	—	—	96	96
HK88-3	—	—	60	—	152	212
Öl94-2	592	—	—	—	—	592
Vg89-4B	141	—	—	—	—	141
DLK86 L4	492	—	—	—	—	492
DLK86 L5	278	—	—	—	—	278





### Localities:

- 1 Gillberga/Sandvik
- 2 Gullhögen
- 3 Hällekis/Sylten
- 4 Rävänäs
- 5 Kårgärde
- 6 Brunflo area

Fig. 18. Locations of the provinces and sections in Sweden where the actual samples derive.

cies in the Swedish fauna were all typical for fairly deep waters, and probably were amongst the most depth-dependent taxa; alternatively they were sensitive to oceanic influences. Löfgren (2004) also saw indications that multicostate forms seemed to prefer somewhat shallower waters compared to bicostate forms.

Thus, it seems as if *Protopanderodus* can be considered as a planktic/pelagic genus that inhabited the deeper parts of the shelf. From this perspective, *Protopanderodus* belongs to the North Atlantic Faunal Province.

### 5.2 Material and methods

In the Middle Ordovician Swedish conodont fauna, there are no less than five species representing the genus *Protopanderodus*: *P. rectus*, *P. robustus*, *P. parvibasis*, *P. graeai* and *P. calceatus*. Thus, elements from these five species have been investigated in the purpose of recognizing element types for the reconstruction of the *Protopanderodus*-apparatus. In total, 4202 elements of these species were sorted, categorized and counted (Table 1). All elements have been examined and included in the

counting of element ratios, but some of the samples were more suitable than others for reconstruction purposes, as they mainly contained elements from adult specimens. Elements representative of different element types were selected for free hand drawing, while others were coated with a thin layer of gold and photographed under a scanning electron microscope (SEM).

In addition, I have studied relevant literature and compared the results of my observations to previous reconstructions of similar conodont apparatuses.

The limestone rocks from which the conodont elements have been extracted are of Middle Ordovician age (see "Geological setting" below), and have been collected from six sections in southern and central Sweden (see Table 2 + Fig. 18). The elements are well to very well preserved, and the CAI value is 1 (unaltered) for all investigated elements. All samples were dissolved in dilute and buffered acetic acid according to the technique described by Jeppsson et al. (1999). The samples and microfossil slides are kept at the Department of Geology, Lund University, Sweden.

Table 2. Information about the samples used; the provinces and sections from where the samples have been collected, the conodont zones represented and where to find additional information.

Province	Section	Sample	Conodont zone	Sample description
Öland	Sandvik	Ö194-2	<i>P. originalis</i>	No descript.
Dalarna	Kårgärde	DLK86 H4	<i>E. pseudopl.</i>	Löfgren 2004
		DLK86 H12	<i>E. pseudopl.</i>	Löfgren 2004
		DLK86 H13	<i>E. pseudopl.</i>	Löfgren 2004
		DLK86 L4	<i>P. originalis</i>	Löfgren 1995
	Rävanäs	DLK 86 L5	<i>B. navis</i>	No descript.
		Rä 5	<i>E. pseudopl.</i>	Löfgren 2004
		Rä 6	<i>E. pseudopl.</i>	Löfgren 2004
Västergötland	Gullhögen	GB81-500	<i>E. pseudopl.</i>	Löfgren 2004
	Syften	Vg98-4B	<i>L. variabilis</i>	Löfgren 2003
	Hällekis	HK88-3	<i>Y. crassus</i>	Löfgren 2003
		HK89-4	<i>E. pseudopl.</i>	Löfgren 2004

### 5.2.1 Geological setting

During the Ordovician the world looked quite different from to the present (Fig. 19). The landmasses were basically assembled in three continents; the largest one named Gondwanaland, and two smaller known as Baltica (centered about midway between the equator and the South Pole) and Laurentia (positioned at the equator) (Torsvik & Smethurst 1999).

During the Middle Ordovician, much of Scandinavia was covered by an epicontinental sea at depths from c. 150 m to 250 m; shallower to the east (Estonia and the Gulf of Bothnia) and deeper to the west/southwest (Norway and southwestern Sweden). The sediment deposited during these conditions was mainly lime mud; this eventually resulted in the development of the characteristic Orthoceratite limestone. In areas representing deposition in deeper waters, mainly shale is found. Due to erosion, the only remains of these Ordovician formations are today found in Skåne, Öland, Västergötland, Närke, Östergötland, Dalarna, Jämtland and on the seafloor in the Gulf of Bothnia (Löfgren 2003).

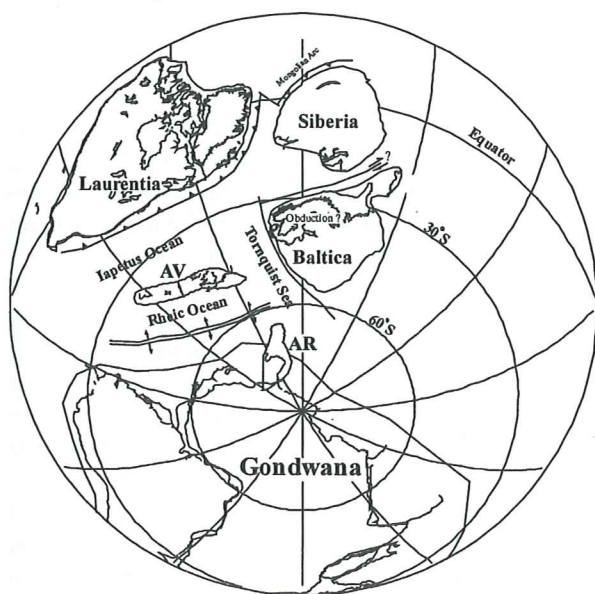


Fig. 19. The positions of the continents during the Middle Ordovician. From Torsvik & Smethurst (1999).

## 6. Element descriptions, discussions and results

### 6.1 Choice of notation system

For identification of the element types, I have used the element notation system of Sweet (1981). Other notation systems previously used for description of the elements of *Protopanderodus* are presented in Table 3.

A purely descriptive system like the one used by Löfgren (1978) describes the basic form of an element. Using this kind system as a base for reconstruction purposes requires a more detailed description that in an understandable way describes every single element type. Using a descriptive type of element notation instead of one with different letter-combinations is, in my opinion, a question of what the author prefers. Both ways work as long as only elements from the same genus are compared to each other; comparisons with other genera could be more difficult.

Sansom et al. (1994) suggested that their notation used for *Panderodus* should be applied to other coniform genera (see section 2.2.3). It would of course be possible to try to name the elements found in *Protopanderodus* ae, pt, pf, qg, qt and qa (cf. notation of *Panderodus*), but as this notation is meant to be strictly locational, it was highly speculative to even try to find elements corresponding to these positions, especially as no cluster or natural assemblage has been found representing *Protopanderodus*. Also, as the apparatus of *Panderodus* is a very derived one, it is difficult to compare with a less derived apparatus such as that of *Protopanderodus* and similar genera. This is evident when trying to compare the elements; the morphology differs considerably which complicates the comparisons of element types, regardless if one is aiming to identify homologies or analogies.

In this study I have instead chosen to work according to the notation system of Sweet (1981), and follow the concept of symmetry transition. In this way, a capital letter followed by a small letter could tell basically the same thing as a detailed description; compare for example "a Sc element" with "a very asymmetrical acontiodontiform element". In short, letter combinations are easier to work with.



Table 3: Notation systems previously used for description of *Protopanderodus*-elements.

Used by Löfgren (1978)	scandodontiform	acantiodontiform	acodiform
Used by McCracken (1989)	e	a/b - c	g, f
This paper (analogous)	M	S	P

The reason for not using the notation used by McCracken (1989, Table 3) is that a/b only refers to an asymmetrical element type and c to a symmetrical element type. It would of course be possible to distinguish two kinds of asymmetrical elements in that element group, a and b elements instead of a/b, but I felt that this probably was not sufficient, considering the number of element types found in previous reconstructions of coniform apparatuses. Also, the notation system of Sweet (1981) is the most commonly used today. Using this made it easier to understand previous reconstructions of coniform apparatuses and compare them with my own results, for example the apparatus of the closely related genus *Drepanodus* Pander, 1856, reconstructed by Löfgren & Tolmacheva (2003).

The only firm positions suggested are for the morphologically distinct element groups in the medial (M), symmetrical (S) and principal (P) positions that follow Sweet's (1981) scheme. The small letter in the S-series is here used to indicate increased asymmetry; a Sc element is therefore more asymmetrical than a Sb element and the Sa element is symmetrical. An "Sd" position is also used as an extension of this symmetry transition series. A similar principle is used for the P elements; the Pa element is less asymmetrical than the Pb element.

When describing the elements I have used the conventional terminology (see section 2:1). Even if I agree that applying correct biological terms on conodont elements is more appropriate, the conventional terminology is still the strongest alternative as the understanding of conodont anatomy needs to be improved, especially for coniform genera.

## 6.2 Identified element types

Lindström (1971) introduced the name *Protopanderodus* for genera with scandodontiform and acantiodontiform (M, S and P) elements combined. Löfgren (1978) and Dzik (1994) distinguished three to four separate element types in the apparatus (see also the systematic palaeontology in chapter 7). There is no natural assemblage or fused cluster described representing *Protopanderodus*. McCracken (1989) described a *Protopanderodus*-cluster that later was shown to consist of elements from *Drepanodus*, including smaller and larger nongeniculate coniform elements, likely to be S and P-elements. No M-elements can with certainty be identified, but this is probably due to incomplete preservation of the apparatus as Löfgren & Tolmacheva (2003) identified M-elements as well as S and P-elements in the *Drepanodus*-apparatus. Further, since these two genera are closely related, these results can be applied also to *Protopanderodus*, confirming that all three element groups were present.

In this study, four of the investigated species belong to the bicostate group; *P. rectus*, *P. robustus*, *P. graeai* and *P. parvibasis*. One multicostate species is included; *P. calceatus*. The four bicostate species are, according to Löfgren (1978) closely related, most likely as an evolutionary lineage starting with *P. rectus* as the ancestor to the other three species. The origin of *P. calceatus* is unknown at present.

The three morphologically distinct element groups (M, S and P) according to Sweet's (1981) notation system were first identified and sorted in all five species. The M-elements are recognized as being concavo-convex and generally the largest and most robust ones in the apparatus, and likely positioned anteriormost in the apparatus. The S-elements are cone-shaped with convex or more flat lateral sides and more slender than the M-elements. As these elements showed symmetry or asymmetry between costae to a variable degree, different S-element types could be distinguished, following the concept of a symmetry transition series. The P-elements have the same basic shape as the S-elements, but smaller and with shorter cusps and are believed to have been positioned posteriormost in the apparatus.

When identifying the different element types, I discovered that there is a difference in the element pattern between the four bicostate species and the single multicostate species.

In *P. robustus*, *P. rectus*, *P. parvibasis* and *P. graeai* the following element types were recognized:

M, Sa, Sb1, Sb2, Sc, Pa, Pb

Whilst instead in *P. calceatus*:

M1, M2, Sa, Sb, Sc, "Sd", Pa, Pb1, Pb2

Clearly, *P. calceatus* differs from the other four. The main differences, aside from purely external differences, such as number of costae, lies in the number of distinguishable element types and also in the element types included in the S array. In my opinion, there are two possible ways to interpret this:

1. If all five species belong to the same genus, they should probably also have the same numbers of element types in their apparatuses. The fact that *P. calceatus* has a different number of element types would in this case at least indicate that this species is not so closely related as the others are to one another. Further, the number of element types in *P. calceatus* should be applicable to the four bicostate species; that is they should also have at least two pairs of M and three pairs of P elements; with the difference that the M1 - M2 and Pb1 - Pb2 types are indistinguishable.



Table 4. The total number of M-, S-, and P-elements investigated, and the calculated average element ratio for the five *Protopanderodus* species.

Species/Element	M	P	S	Total nr	M	P	S
<i>P. rectus</i>	21.6%	19.6%	58.8%	1503	325	294	884
<i>P. robustus</i>	22.4%	15.2%	62.4%	290	65	44	181
<i>P. parvibasis</i>	25%	18.6%	56.4%	1140	285	212	643
<i>P. graeai</i>	15.7%	18.2%	66%	559	88	102	369
<i>P. calceatus</i>	22.2%	18.2%	59.6%	710	158	129	423

2. These differences in the number of morphologically recognizable element types suggest the possibility that *P. calceatus* should be placed in another genus.

With this in mind, the calculation and interpretation of the element ratios filled two purposes; first I got a good indicator to the lowest total number in every element-group and thus the smallest number of elements in one apparatus. Second, I could compare the results from the four bicostate species with the results from *P. calceatus*. The ratio percentage for M and P elements was of course especially interesting, as this practically is the only method to further investigate the relationship of *P. calceatus* to the other four species. To investigate the possibility of two pairs of Pb elements in the bicostate species, I compared the number of Pa relative to Pb (Table 5).

### 6.3 Element ratios

The calculation of number of elements and percentages for each sample is placed in the "Appendix". See also Table 4.

#### 6.3.1 Discussion

First the symmetrical elements (Sa) in *P. calceatus*, *P. graeai* and *P. robustus* were counted, but I soon realized that the Sa elements were strongly underrepresented, and could not give any precise information about the correct numerical relations between the elements. Instead I used the percentage ratios to calculate different scenarios that seemed realistic, with one symmetrical Sa element in each apparatus and with the observations from *P. calceatus* in mind.

A) The percentage of S elements relative to the other element groups should be the highest, and this is confirmed by the numbers in Table 4.

B) With only one pair of M elements and two pairs of P elements in the apparatus of the bicostate species, the percentage of P should be comparably higher. The same is valid for two pairs of M and three pairs of P.

The scenario that seems most probable at this point is an apparatus with four M (two pairs), 13 S (one symmetrical element + six pairs of asymmetrical elements) and finally four P (two pairs); that sums up to an apparatus comprising a minimum of 21 elements; 13 S (one Sa, four Sb1, four Sb2 and four Sc; c. 62%), 4 M (c. 19%) and 4 P (two Pa + two Pb; c. 19%) (compare with Table 4).

There are two problems with this scenario. First, from my own observations of the samples, I have noticed that in the bicostate species the amount of Sb elements is higher compared to the Sc elements. In the multicostate *P. calceatus*, it is instead the Sc and "Sd" elements that outnumber the Sb. So, from this perspective it is possible that the Sc position in the bicostate species was repre-

sented by one pair/two elements instead of two pairs/four elements like in the Sb positions. For *P. calceatus* there would instead be likely to be one pair in the Sb position and two pairs in Sc and "Sd" respectively. This adds up to a most probable number of 11 S elements.

The other problem is that in *P. calceatus* two types of Pb elements were recognized and therefore the same could be true for the other four species. In an attempt to test this, P elements from *P. parvibasis* (172), *P. graeai* (102), *P. robustus* (44) and *P. rectus* (145) from the samples with the best preservation and/or with as many P elements as possible were sorted and counted; 463 elements in all (Table 5).

The differences between the Pa and the Pb elements is mainly the width of the base in cross section, the oral margin/base-cusp bend and the shape of the cusp (see also Element descriptions below). In the work of dividing the P elements in two groups, those were the only criteria used. As seen in Table 5, the number of Pb elements is often much higher compared to the Pa elements. In my opinion, Pb numbers seem suspiciously high. Also, in the samples containing the highest number of elements, the Pb elements are always the most abundant and it is only in the samples with the lowest number of elements where the relations are the opposite.

The elements included in the Pb group of each species do not look exactly the same; there are some differences that can not be neglected as for example differences in size and the width of the base. These can be due to differences in age of the animals, sexual/gender- or population variations, to how much of the attachment cone is remaining or, most importantly in this context, could indicate differences between Pb1 and Pb2 elements. As there are several factors that could have caused these morphological differences, I have not been able to determine any criteria for distinguishing between Pb1 and Pb2 elements in the bicostate species. However, since the ratio of Pb to Pa elements is so high in *P. rectus*, I consider this to be an argument for the presence of two pairs of Pb

Table 5. Comparisons between the number of Pa and Pb elements in some representative samples.

Species	Sample	Nr Pa	Nr Pb	% Pb
<i>P. parvibasis</i>	DLK86H4	37	45	55
	Rä 5	20	51	71.8
	Rä 6	13	6	31.5
<i>P. graeai</i>	DLK86H4	23	39	62.9
	HK89-4	5	22	81.5
<i>P. robustus</i>	Rä 6	11	2	15.4
	DLK86H4	4	9	69.2
	HK89-4	7	12	63.2
<i>P. rectus</i>	GB81-500	0	12	100
	DLK86L4	12	89	88
	DLK86L5	13	31	70.5



elements in the *Protopanderodus* apparatus. The numbers are not so convincing for the other bicostate species, but since they are all descendants of *P. rectus* they should all have the same number of P elements in the apparatus. Further, since these species are so closely related morphologically, it seems unlikely that the numerical relations between the Pa and Pb elements could have changed in later species even if this possibility can not be completely ignored.

The calculation of element ratios between M, S and P elements (Table 4 and Appendix) shows that *P. calceatus* does not differ from the bicostate species in terms of the total number of elements in the oral apparatus. On the other hand, the conflicting number of distinguishable element types in combination with the external differences (see the element descriptions in section 6.5) and the fact that *P. calceatus* seems to have a different element organization clearly indicates a considerable difference. Possibly, this suggests that this species should be placed in a separate genus, but at the present, I prefer not to do so. This is mainly due to the relatively small number of elements investigated, and the lack of other multicostate species of *Protopanderodus* to compare with, except in the literature.

It would be very interesting to directly investigate elements of other multicostate *Protopanderodus* species to see if they follow the same pattern of element organization and element types as *P. calceatus*. Then another question would possibly be answered; do all multicostate species of *Protopanderodus* belong to one single evolutionary lineage, or has this character evolved more than once? If it would turn out that the element organization of *P. calceatus* is consistent with other multicostate species, I would suggest referring the multicostate lineage of *Protopanderodus* to a separate genus.

## 6.4 Proposed reconstruction model

My suggestion is that the conodont species included in the genus *Protopanderodus* had a minimum amount of 21 elements in their oral apparatuses, divided as follows:

For bicostate species (*P. rectus*, *P. robustus*, *P. parvibasis* and *P. graeai*):

- M (two pairs; four elements)
- Sa (one single element)
- Sb1 (two pairs; four elements)
- Sb2 (two pairs; four elements)
- Sc (one pair; two elements)
- Pa (one pair; two elements)
- Pb (two pairs; four elements)

For multicostate species (*P. calceatus*):

- M1 (one pair; two elements)
- M2 (one pair; two elements)
- Sa (one single element)
- Sb (one pair; two elements)
- Sc (two pairs; four elements)
- "Sd" (two pairs; four elements)
- Pa (one pair; two elements)
- Pb1 (one pair; two elements)
- Pb2 (one pair; two elements)

## 6.4.1 Discussion

The ideal percentage between the three element groups should be 52.4% S, 19% M and 28.5% P. Compared to the percentage received from my element count (see Table 4), it is basically only the P elements that fall outside the frame; there are simply too few of them. However, as P elements are the smallest, it is highly possible that many were "lost on the way"; many of the more juvenile P elements that should have been present in my samples were most likely not caught up by the 63  $\mu\text{m}$  sieve. For the high number of M elements the opposite scenario seems realistic; the M elements are the largest and also comparably robust, considering their morphology and position anteriormost in the apparatus.

Comparing this result with previous reconstructions of coniform apparatuses, a number of 21 elements seems a bit high but not at all unrealistic. Estimations for other coniform genera are: 17 elements in *Panderodus* (Sansom et al. 1994), 17 elements in *Paltodus* (Löfgren 1997b), 17 in *Paroistodus* (Löfgren 1997a), 17 or 15 in *Semiacoitodus* (Löfgren 1999a) and 21 or 27 in *Cornuodus* (Löfgren 1999b).

For *Drepanodus*, the genus that is considered to be closest to *Protopanderodus*, no element ratios have been calculated. However, the element types recognized by Löfgren & Tolmacheva (2003) are M, Sa, Sb, Sc, "Sd", Pa and Pb, which is quite similar to my own results in *Protopanderodus*.

## 6.5 Element descriptions

### 6.5.1 *Protopanderodus rectus*

Drawings of the element types of *P. rectus*, showing basal cavities, cusp curvature and costae in Fig. 25 (A-G).

**M** (Fig. 20 C, I): Recurved concavo-convex element with a long slender cusp. The inner side is carinate and has a shallow longitudinal groove on the anterior side of the carina. The base is moderately high with a smoothly rounded comma-shaped cross section.

**All S-elements:** The elements in the S-series of *P. rectus* are all bicostate; the postero-lateral costae extending from aboral margin to apex. The elements are slightly compressed laterally and the anterior and posterior margins are sharp. The asymmetrical S elements have a stronger costa on the outer lateral side compared to the one on the inner side. The bases are quite low and the triangular basal cavities are correspondingly shallow. The cross sections of the bases are quite narrow, pearshaped and less wide towards the anterior margin. All the S elements have a poorly developed anterio-basal "heel". The cusps are variously recurved.

**Sa** (Fig. 20 E): Symmetrical element with an almost erect to slightly recurved cusp; evenly curved along both margins. The oral margin is quite long.

**Sb1** (Fig. 20 B): Slightly asymmetrical element with the same cusp curvature as the Sa element. The oral margin is somewhat shorter than in the Sa element.



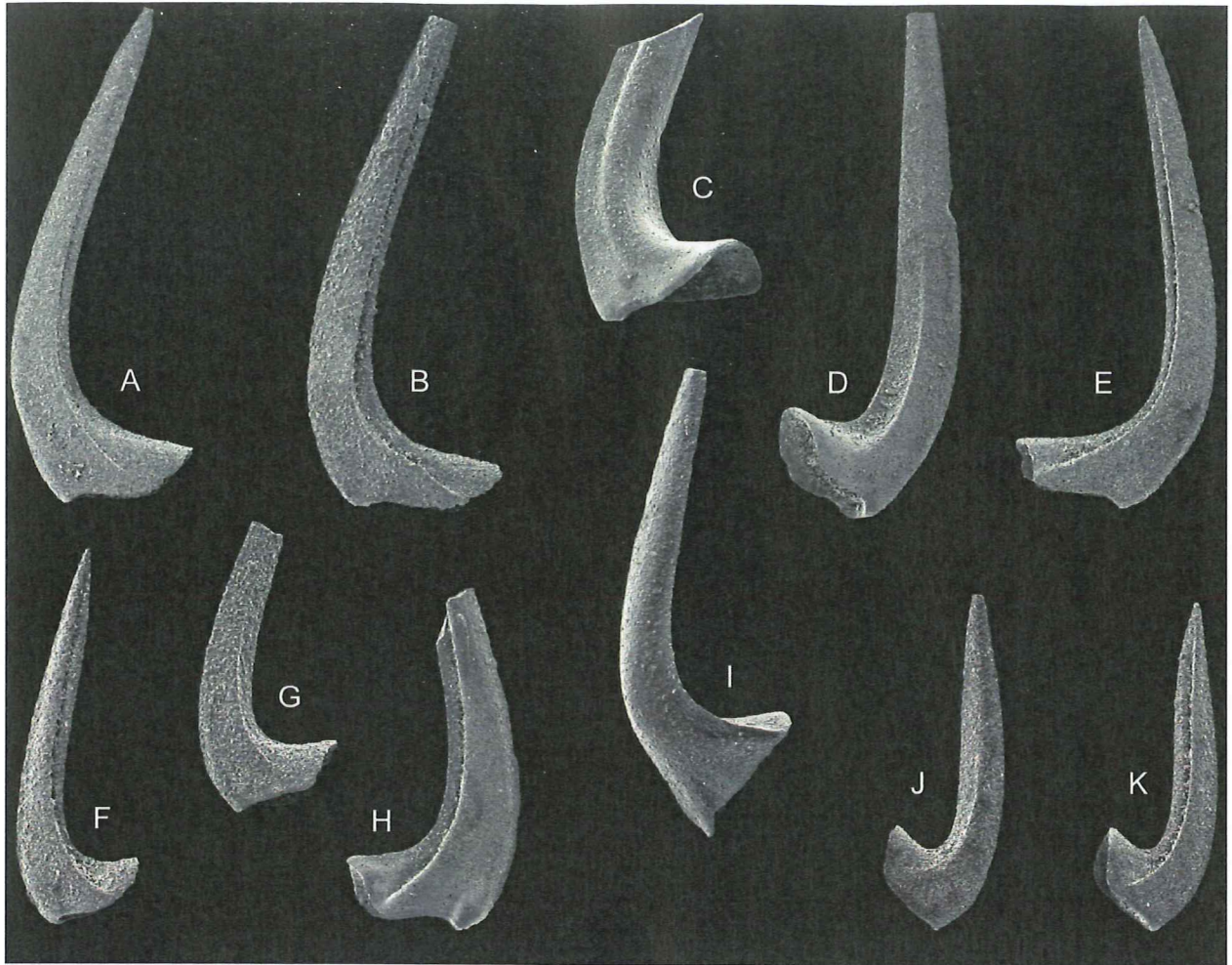


Fig. 20. A-K. Elements of *Protopanderodus rectus*. All elements from sample DLK86 L4, *P. originalis* Zone. A: Sb2 element, inner side, x63. B: Sb1 element, outer side, x73. C: M element, inner side, x49. D: Sc element, inner side, x57. E: Sa element, x52. F: Pa element, outer side, x72. G: Pa element, inner side, x71. H: Sc element, outer side, x49. I: M element, outer side, x55. J: Pb element, inner side, x61. K: Pb element, outer side, x55.

**Sb2** (Fig. 20 A): Like Sb1 but with even shorter oral margin and slight difference in cusp curvature along the anterior margin.

**Sc** (Fig. 20 D, H): Asymmetrical, slightly recurved element. The costa on the outer lateral side is sharp from base to apex. The oral margin is straight and shorter than in the other S elements.

**Pa** (Fig. 20 F, G): Asymmetrical, erect to slightly recurved element with sharp anterior and posterior margins. The costa on the outer lateral side is sharper than that on the inner, and runs from base to apex. The base cross section is pear shaped like in the S elements, but slightly wider than in these.

**Pb** (Fig. 20 J, K): Asymmetrical, strongly recurved element with a short oral margin and a low base. Both margins are sharp. Costae like in the Pa element. The base is wider in cross section than in the Pa element, and more flaring to the outer side, making it rather irregularly semi-pear shaped.

### 6.5.2 *Protopanderodus robustus*

Drawings of the element types of *P. robustus*, showing

basal cavities, cusp curvature and costae in Fig. 25 (H-N).

**M** (Fig. 21 F, I): Recurved concavo-convex element with a long slender cusp that is carinate on the inner lateral side. The base is slightly higher than in *P. rectus* and the basal cavity is correspondingly somewhat deeper. The base cross section is comma shaped but with a triangular outline.

**All S-elements:** The elements in the S-series of *P. robustus* are all bicostate and slightly laterally compressed, and with sharp anterior and posterior margins. The postero-lateral costae extend from the aboral margin to the apex. In the asymmetrical S elements, the costa is stronger on the outer lateral side than on the inner side. All S elements have a characteristic well-developed antero-basal "heel". The curvature of the cusps varies from slightly proclined to recurved. The bases are somewhat higher than in *P. rectus*. The cross sections of the bases are pear shaped, narrowing to the anterior margin like in *P. rectus*.

**Sa** (Fig. 21 A): Symmetrical element with an erect/slightly proclined cusp and fairly long oral margin. The ele-



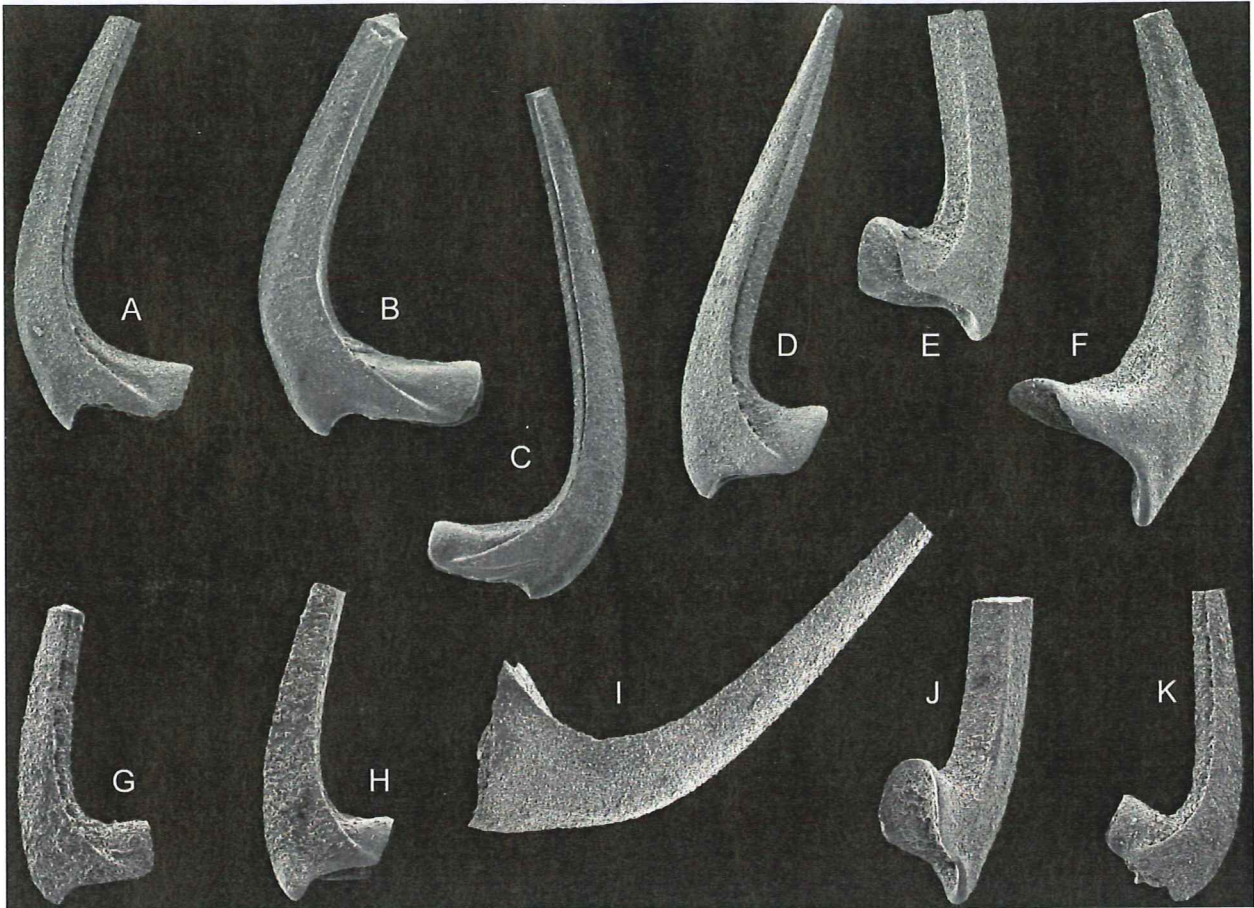


Fig. 21. A-K. Elements of *Protopanderodus robustus*. All elements from the *E. pseudoplanus* Zone. A: Sa element, x50. HK 89-4. B: Sb1 element, inner side, x71. DLK86 H4. C: Sb2 element, outer side, x65. DLK86 H4. D: Sc element, outer side, x46. HK89-4. E: Sc element, inner side, x59. HK89-4. F: M element, inner side, x41. HK 89-4. G: Pa element, outer side, x70. HK 89-4. H: Pa element, inner side, x54. HK 89-4. I: M element, outer side, x68. HK 89-4. J: Pb element, inner side, x57. DLK86 H4. K: Pb element, outer side, x60. DLK 86 H4.

ment is evenly curved along both the posterior and anterior margin.

**Sb1** (Fig. 21 B): Asymmetrical element with a recurved cusp. The oral margin is longer than in the Sa and Sb2 elements.

**Sb2** (Fig. 21 C): Looks much like Sb1 but with the difference that the oral margin is shorter and the cusp curvature is closer to erect.

**Sc** (Fig. 21 D, E): Asymmetrical element with recurved cusp and a comparably short oral margin. The base is slightly wider than in the Sb elements with the base flaring more to the outer lateral side.

**Pa** (Fig. 21 G, H): Asymmetrical, almost erect element with a characteristic anteriobasal "heel", sharp anterior and posterior margins and a straight oral margin. The costa on the outer lateral side is sharper than on the inner side. The inner lateral side is more flattened than the outer, and the base is flaring slightly to the outer lateral side which gives the low base a semi-droplet shape in cross section.

**Pb** (Fig. 21 J, K): Asymmetrical, strongly recurved element that, compared to the Pa element has a slightly wider base that is flaring more to the outer side, and a shorter

oral margin. The height of the base, as well as the costae are comparable to those in the Pa element.

### 6.5.3 *Protopanderodus parvibasis*

Drawings of the element types of *P. parvibasis*, showing basal cavities, cusp curvature and costae in Fig. 25 (O-U).

**M** (Fig. 22 C, D): Recurved concavo-convex element that is thinner and more bladelikey than the M elements of the other species. The low base is flaring to the inner side which gives the comparably narrow base cross section a comma shape. The basal cavity is shallow. The inner side is carinate like in *P. rectus*, but the carina in *P. parvibasis* is less pronounced. A weak striation also can be detected on the larger elements. In large elements a very weak longitudinal groove runs close to the anterior margin. The outer side is smooth.

**All S-elements:** The elements in the S-series of *P. parvibasis* are bicostate and slightly flattened laterally. The cusp curvature varies from proclined to recurved and the anterior and posterior margins are sharp. The posterio-lateral costa on the outer side is sharper than the costa on the inner side; costae extend from base to apex. The elements have a poorly developed anteriobasal "heel", comparable with that in the S elements in *P. rectus*. Com-



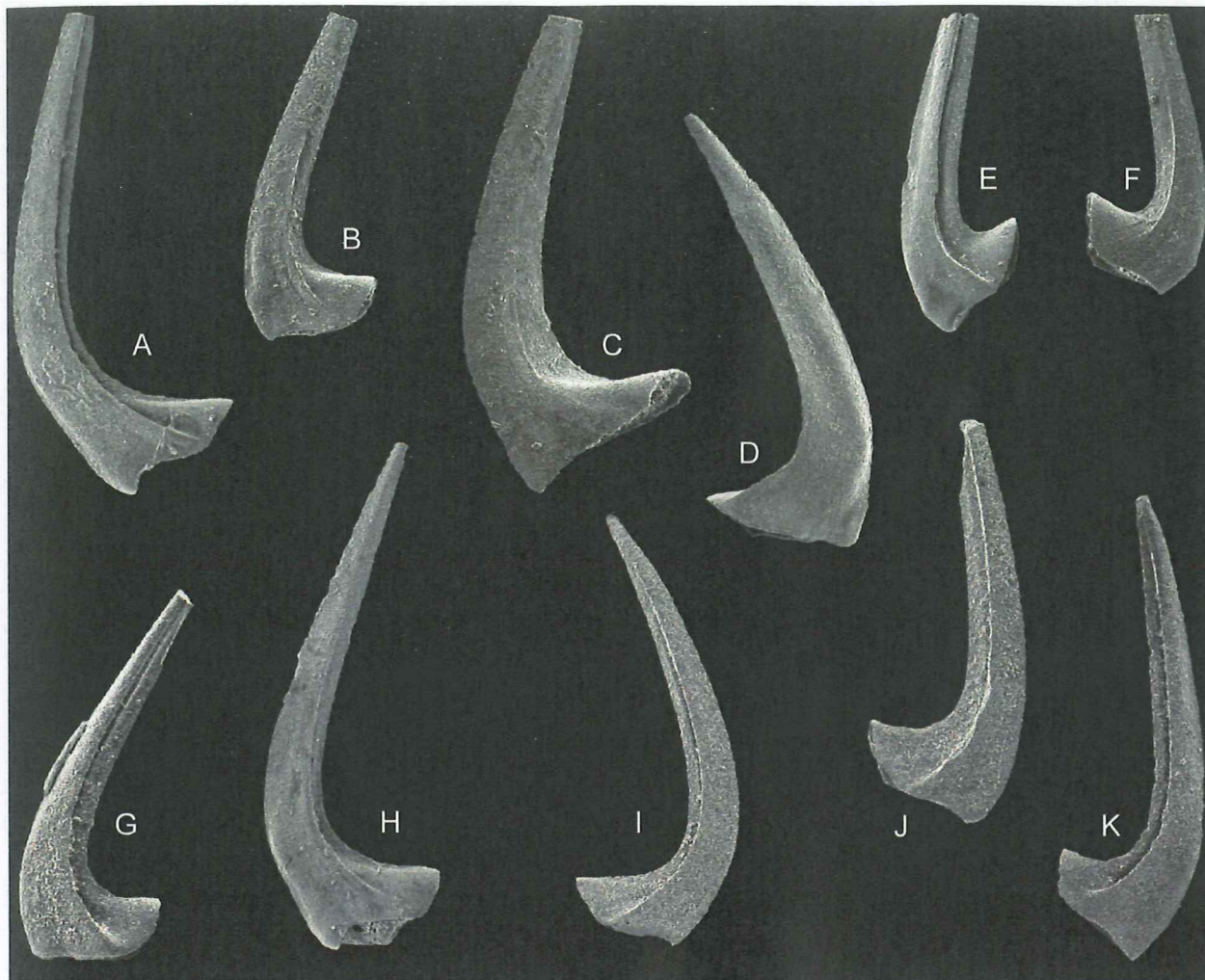


Fig. 22. A-K. Elements of *Protopanderodus parvibasis*. All elements from the *E. pseudoplanus* Zone. A: Sb1 element, outer side, x85. Rã5. B: Pa element, inner side, x73. Rã5. C: M element, inner side, x82. Rã6. D: M element, outer side, x61. Rã6. E: Pb element, outer side, x77. Rã5. F: Pb element, inner side, x86. G: Pa element, outer side, x86. Rã5. H: Sb2 element, inner side, x71. Rã5. I: Sa element, x72. DLK86 H4. J: Sc element, inner side, x74. DLK86 H4. K: Sc element, outer side, x86. DLK86 H4.

pared to *P. rectus* and *P. robustus*, the bases in *P. parvibasis* are quite high and the basal cavities have a slightly different triangular shape. The base cross sections are shaped like a narrow droplet, narrowing towards both margins but more towards the posterior margin.

**Sa** (Fig. 22 I): Symmetrical element with a recurved cusp; evenly curved along both anterior and posterior margins. The oral margin is fairly long and the costae are equally sharp on both sides and run from aboral margin to apex.

**Sb1** (Fig. 22 A): Slightly asymmetrical element with a proclined cusp.

**Sb2** (Fig. 22 H): Like Sb1, but the oral margin is shorter and the cusp curvature is closer to erect.

**Sc** (Fig. 22 J, K): Asymmetrical element with recurved cusp and a comparably short oral margin. The cross section of the base is semi-droplet formed.

**Pa** (Fig. 22 B, G): Asymmetrical, recurved element with straight oral margin and a low base. The costa is sharper on the outer lateral side than on the inner side. The base

is narrow and almost comma-shaped in cross section; narrowing towards both margins with a slight flare to the outer side.

**Pb** (Fig. 22 E, F): Asymmetrical element with a strongly recurved cusp and a short oral margin. Compared to the Pa element, the base cross section is wider and more flaring in the posterior part and is thus instead more semi-droplet shaped.

#### 6.5.4 *Protopanderodus graeai*

Drawings of the element types of *P. graeai*, showing basal cavities, cusp curvature and costae in Fig. 25 (V-BB).

**M** (Fig. 23 E, F): The recurved M element is not as obviously concavo-convex as the in other species; both the inner and outer lateral sides are laterally flattened and the inner side has a costa that runs close to the posterior margin. These characters make the element appear triangular and thus easy to recognize. The base is high with a correspondingly deep basal cavity. The basal cavity is flaring slightly to the inner side, and the base cross section has a distinct edge on the inner side.



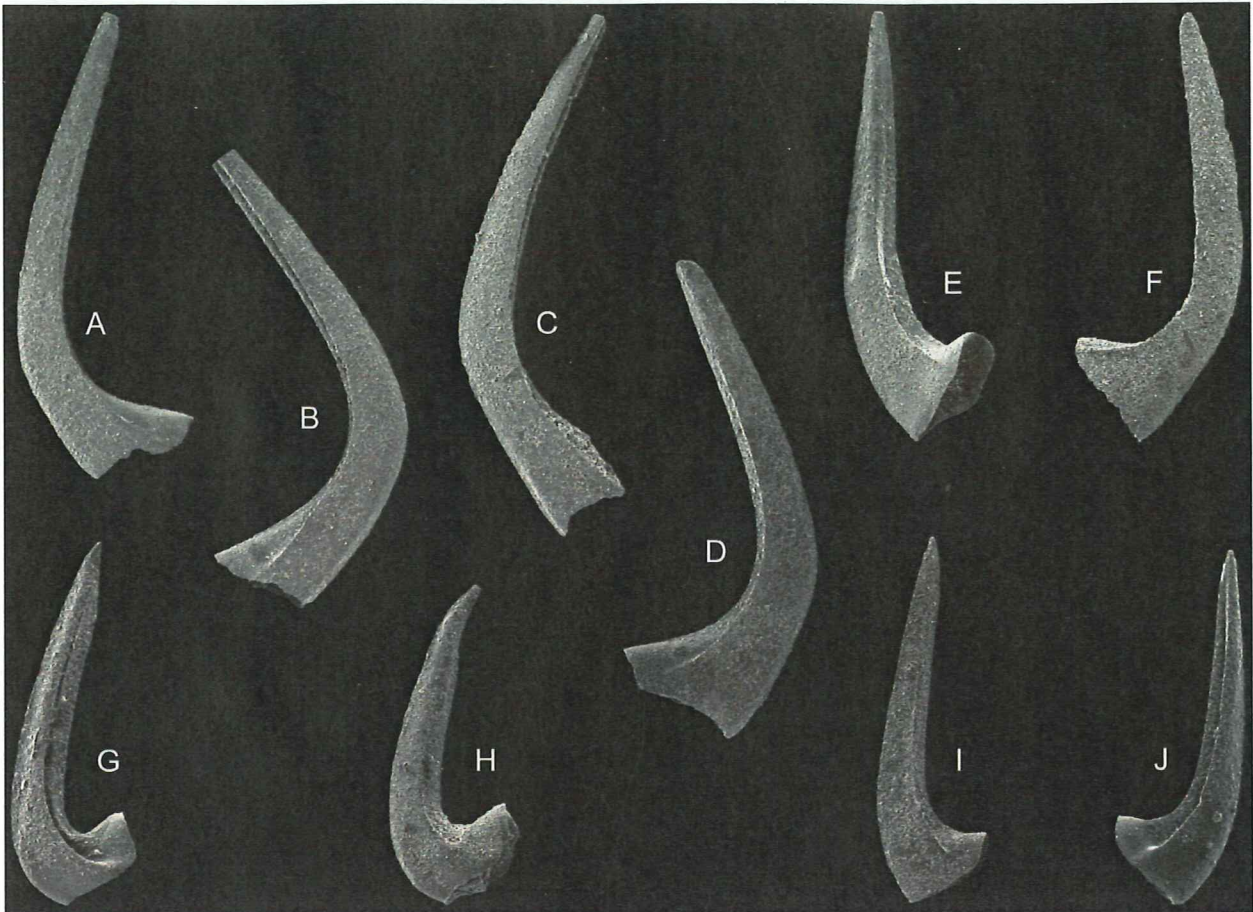


Fig. 23. A-J. Elements of *Protopanderodus graeai*. All elements from the *E. pseudoplanus* Zone. A: Sa element, x64. Ră6. B: Sb2 element, outer side, x74. Ră6. C: Sb1 element, outer side, x78. Ră6. D: Sc element, inner side, x70. Ră6. E: M element, inner side, x61. DLK86 H4. F: M element, outer side, x64. DLK86 H4. G: Pb element, outer side, x72. DLK86 H4. H: Pb element, inner side, x63. DLK86 H4. I: Pa element, inner side, x61. Ră6. J: Pa element, outer side, x63. Ră6.

**All S-elements:** The elements in the S-series of *P. graeai* show little asymmetry in placement of costae but instead there is a variation in cusp curvature, from proclined to recurved. All the S-elements are bicostate and slightly laterally flattened with the costae very close to the posterior margins. The postero-lateral costa on the outer lateral side is sharper than the costa on the inner side. The most notable character is the high bases and correspondingly deep basal cavities that are almost equilaterally triangular. The anterior margins are somewhat weaker compared to the sharp posterior margins; this gives the base a flattened ovoid shape, narrowing to the posterior margin.

**Sa** (Fig. 23 A): Symmetrical, bicostate element with an erect cusp. The postero-lateral costae are sharpest from mid-height of the base to the upper half of the cusp where they fade out somewhat.

**Sb1** (Fig. 23 C): Almost symmetrical proclined element with a base longer than in the Sa element. The base-cusp bend is wider than in Sb2.

**Sb2** (Fig. 23 B): Like the Sb1 element with the exception of an erect cusp that makes the base-cusp bend narrower than in Sb1.

**Sc** (Fig. 23 D): Slightly asymmetrical element with recurved cusp and a lower base that is broader in side view

compared with the Sb elements. The base is somewhat more laterally flattened than in the other S elements; the base cross section thus becomes narrower.

**Pa** (Fig. 23 I, J): Asymmetrical, almost erect element with a low base and short, straight oral margin. The base is quite narrow and almost comma-shaped in cross section, narrowing towards both margins but more anteriorly. The costa is more prominent on the outer lateral side compared to the faint costa on the inner side.

**Pb** (Fig. 23 G, H): Asymmetrical element with a strongly recurved cusp. The base is wider than in the Pa element and narrowing to the anterior margin only. Base height and costae are like in Pa, but the oral margin is shorter.

#### 6.5.5 *Protopanderodus calceatus*

Drawings of the element types of *P. calceatus*, showing basal cavities, cusp curvature and costae in Fig. 26 (A-N).

**M1** (Fig. 24 G, F): Recurved concavo-convex element with a low base. The outer lateral side is smooth while the inner side has a groove extending the length of the cusp, starting at the base. Weak striations also occur on the inner side. The base cross section has a smoothly rounded comma shape.



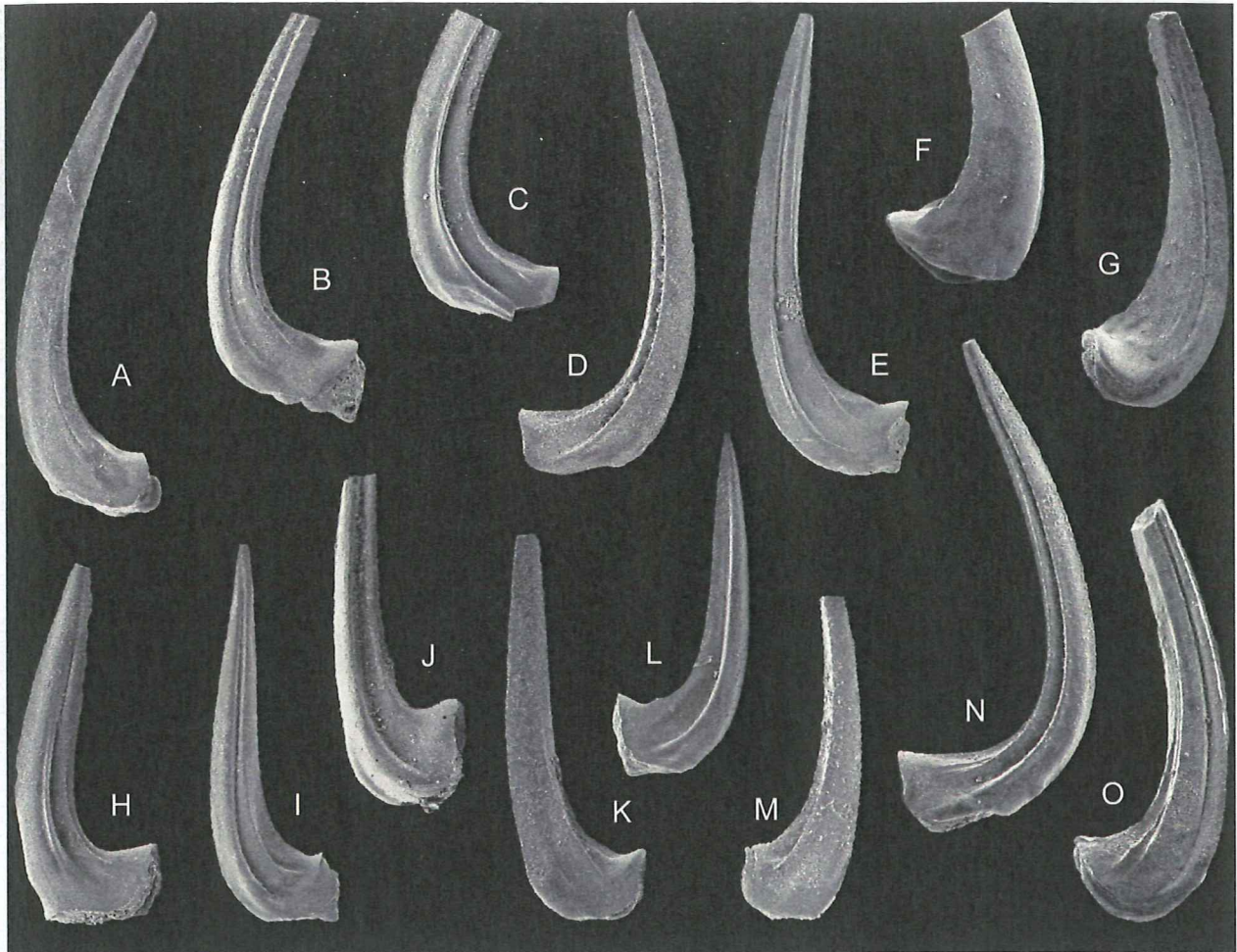


Fig. 24. A-O. Elements of *Protopanderodus calceatus*. All elements from sample Rå5, *E. pseudoplanus* Zone. A: Sc element, outer side, x50. B: Sc element, inner side, x71. C: Sb element, outer side, x62. D: Sd element, outer side, x54. E: Sd element, inner side, x50. F: M element, outer side, x62. G: M1 element, inner side, x47. H: Pa element, outer side, x70. I: Pa element, inner side, x51. J: Pb1 element, outer side, x63. K: Pb1 element, inner side, x68. L: Pb2 element, outer side, x62. M: Pb2 element, inner side, x62. N: Sa element, x66. O: M2 element, inner side, x50.

**M2** (Fig. 24 O): Recurved cusp with smooth outer lateral side, and a comma shaped base like in M1, the difference is the inner side; the groove is notably deeper than that in M1, and instead of weak striations, the rest of the inner side has a number of costae, usually 2-4.

**All S-elements:** All the elements in the S-series of *P. calceatus* are slightly recurved. S-elements can be either bi- (Sa) or multicostate (Sb-“Sd”). Usually the elements have additional ornamentation in the form of lateral striations. The asymmetrical elements have a deep lateral groove on the inner side. The anterior margins are sharp while the posterior margins are blunter; especially in the asymmetrical elements, since the posterior side is slightly rounded and often possesses striations. The bases are low with correspondingly shallow, irregularly triangular basal cavities. Bases in cross section are quite narrow, droplet-formed with laterally flattened sides; narrowing towards the anterior margin.

**Sa** (Fig. 24 N): Symmetrical element with smooth, evenly convex lateral sides; only the base is somewhat laterally flattened. The cusp is recurved and there is one posterio-lateral costa on each side. The sharp posterior margin

bifurcates at the base-cusp bend so that the oral margin becomes more rounded with striations that extend over half the oral margin. These can also be interpreted short costae near the posterior edge.

**Sb** (Fig. 24 C): Slightly asymmetrical element with the same cusp curvature as the Sa element. The outer lateral side has one broad “twin” costa that begins on the central part of the base on each lateral side and runs up to about half the length of the cusp; then it converges into one single costa that continues up to the apex. The inner side also has one distinct costa, but without the twin character, and also a groove on the posterior side of the costa. There are additional weakly developed edges on both sides near the posterior margin.

**Sc** (Fig. 24 A, B): Asymmetrical, almost erect element. The inner lateral side is carinate and has a deep lateral groove running from the middle of the base to the cusp apex. An additional weakly developed edge is present close to the posterior margin. The outer lateral side is smoother with less prominent features on the lower part of the element; a weak carina on the anterior part and minor striations towards the posterior.



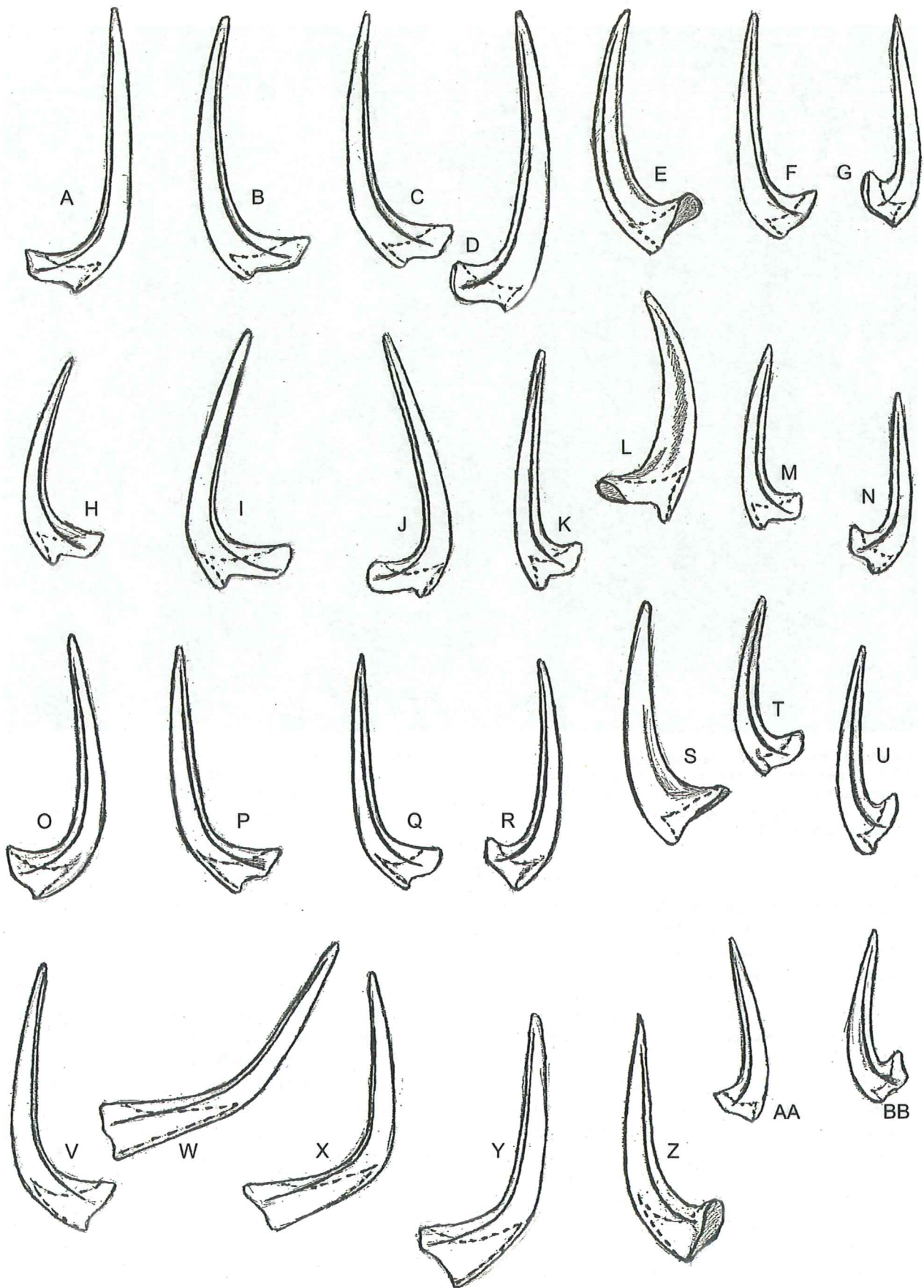


Fig. 25. Reconstructions of the seven identified element types of *P. rectus* (A-G), *P. robustus* (H-N), *P. parvibasis* (O-U) and *P. graei* (V-BB), showing basal cavity outlines (dotted lines), cusp curvature and costae. *P. rectus*: A: Sa element. B: Sb1 element. C: Sb2 element. D: Sc element. E: M element. F: Pa element. G: Pb element. *P. robustus*: H: Sa element. I: Sb1 element. J: Sb2 element. K: Sc element. L: M element. M: Pa element. N: Pb element. *P. parvibasis*: O: Sa element. P: Sb1 element. Q: Sb2 element. R: Sc element. S: M element. T: Pa element. U: Pb element. *P. graei*: V: Sa element. W: Sb1 element. X: Sb2 element. Y: Sc element. Z: M element. AA: Pa element. BB: Pb element.

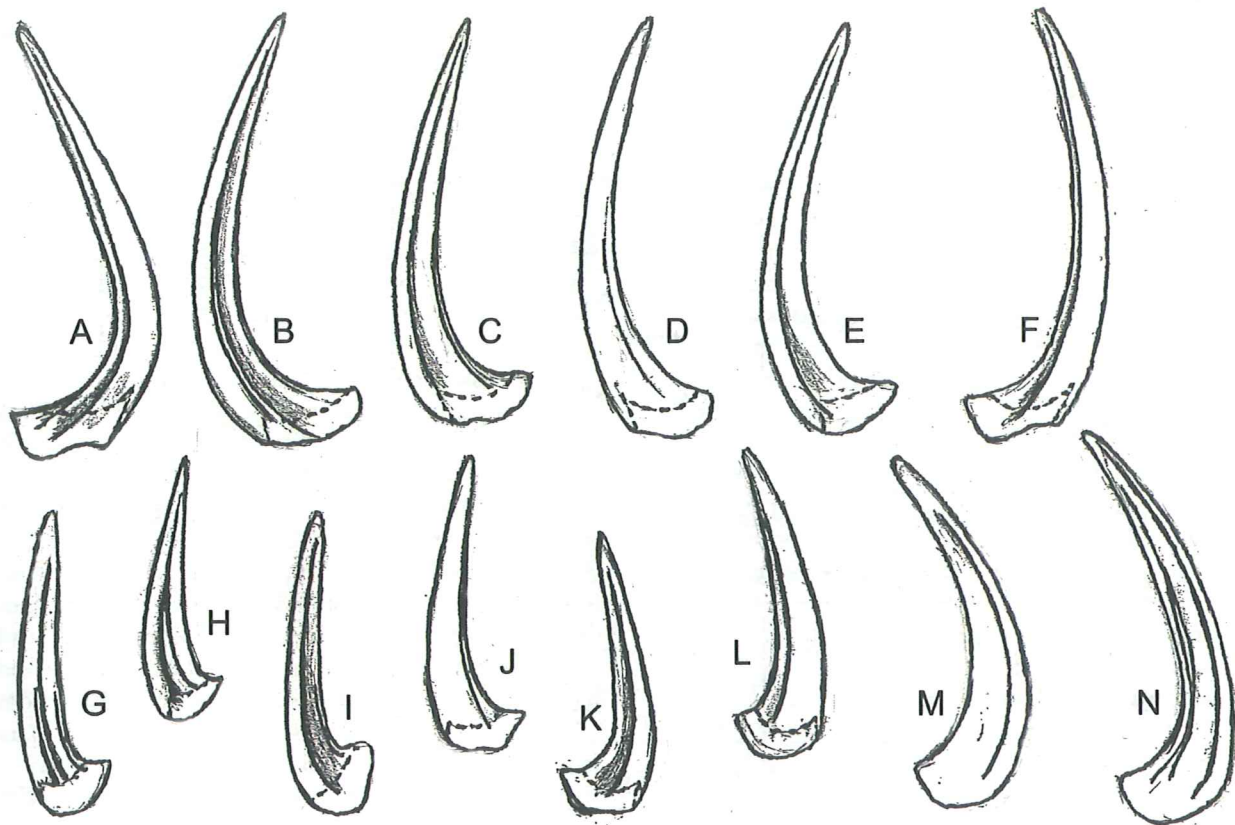


Fig. 26. Reconstructions of the nine identified element types of *P. calceatus* (A-N), showing basal cavity outlines (dotted lines), cusp curvature and costae. A: Sa element. B: Sb element, outer side. C: Sc element, inner side. D: Sc element, outer side. E: "Sd" element, inner side. F: "Sd" element, outer side. G: Pa element, outer side. H: Pa element, inner side. I: Pb1 element, outer side. J: Pb1 element, inner side. K: Pb2 element, outer side. L: Pb2 element, inner side. M: M1 element. N: M2 element.

**"Sd"** (Fig. 24 D, E): Asymmetrical, almost erect element with a concavo-convex outline. The convex outer lateral side has a postero-lateral costa; the rest of this side is smooth. The inner lateral side is straight or slightly concave and has a deep lateral groove and a twin costa on the lower part of the cusp on the anterior side of the groove. There is also an additional edge near the posterior margin, similar to that in the Sc element.

**Pa** (Fig. 24 H, I): Asymmetrical, almost erect element. The outer lateral side has a distinct longitudinal twin costa that extends from the base to about a third/half the length of the cusp; on the upper half of the cusp the costa is instead single. The inner side has longitudinal groove that can be followed from base to apex. The anterior part of the inner side is carinate. The base is low, with a cross section similar to that in the S elements but somewhat wider.

**Pb1** (Fig. 24 J, K): Asymmetrical element with an erect cusp and a low base. The outer lateral side has a distinct longitudinal groove centrally placed on the face, stretching from the top of the base to apex. This side also has a longitudinal, anterior carina. The inner side has striations and a weak edge on the lower part of the cusp, near the posterior margin.

**Pb2** (Fig. 24 L, M): Like the Pb1 element, but the grooved outer side is not carinate. The inner side is striated

like in the Pb1 element; the main difference is the sharp costa that extends from the top of the base to the apex.

### 6.6 Relations between species

As mentioned above, the four bicostate species are considered closely related. Löfgren (1978) noted that *P. robustus*, *P. parvibasis* and *P. graeai* all were morphologically closer to *P. rectus* than to any other *Protopanderosus* species, which suggested an evolutionary lineage beginning with *P. rectus*, as this species appeared considerably earlier than the other three (Fig. B). The internal relations in this evolutionary lineage were discussed by Löfgren (1978) as well as by McCracken (1989), both agreeing that *P. rectus* is in fact the direct ancestor to the other three bicostate species. Löfgren (1978) suggested divergent evolution, where different populations isolated from each other eventually gain species-status and then were able to co-occur, which also often is the case for these species.

The concept of heterochrony could explain the relatively quick evolution of these three new species from *P. rectus*. This evolutionary process takes two forms, either as pedomorphosis where ancestral juvenile characters are retained by the descendant adult, or as peramorphosis where ancestral adult characters appear in the descendant juveniles (McNamara 1990).

One thing that I noticed during the investigation and counting of elements was that the juveniles in all four



Series, stages, substages		Conodont zones and subzones		Ranges of <i>Protopanderodus</i> species	
Middle Ordovician	Darrivillian	Llanvirnian	<i>Pygodus anserinus</i> Zone		
			<i>P. serra</i> Zone		<i>Y. protoramosus</i> Subzone
					<i>Y. foliaceus</i> Sz
			<i>E. suecicus</i> Zone		<i>P. anitae</i> Sz
					<i>P. lunnensis</i> Sz
	<i>E. pseudoplanus</i> Zone	<i>M. ozarkodella</i> Subzone			
		<i>M. haegtiana</i> Sz			
	<i>Yangtseplacognathus crassus</i> Zone				
	<i>Lenodus variabilis</i> Zone				
	3rd Stage	Arenigian	<i>B. norrlandicus</i> Zone		<i>L. antivariabilis</i> Subzone
<i>T. quadrangulum</i> Subzone					
<i>Paroistodus originalis</i> Zone					
<i>Baltoniodus navis</i> Zone					
<i>Baltoniodus triangularis</i> Zone					
2nd Stage		<i>Oepikodus evae</i> Zone			
		<i>Prioniodus elegans</i> Zone			
		<i>Paroistodus proteus</i> Zone			
Tremadoc 1st Stage		<i>Paltodus deltifer</i> Zone	<i>P. rectus</i>		

Fig. B. The stratigraphical ranges for species of *Protopanderodus* in the Swedish Lower-Middle Ordovician succession. Conodont biostratigraphy after Zhang (1998) and Löfgren (2000).

bicostate species seldom had fully developed the characteristics that separate one species from the other. The smallest specimens were for this reason difficult to classify, but this further indicates a very close relationship and also suggests that the evolutionary processes mentioned above might have had something to do with this species-development. My suggestion for species-development is based on the characters typical for *P. robustus*, *P. parvibasis* and *P. graeai*, respectively. For details, see the element descriptions for each species in the previous section.

Comparing the four bicostate species, I consider the elements of *P. rectus* to be the most neutral, that is, they have not developed any distinctive characters like those found in the other three. On the other hand, morphological characters typical for the descendants can often easi-

ly be traced back to their ancestor, and so is also the case here.

*P. robustus* likely evolved gradually from *P. rectus*. In fact, these two species seem to have the most morphological characters in common, except for the form of the base. The well developed anteriobasal "heel" and long oral margin in the elements of *P. robustus* are probably due to a slight change in mineralization in the basal filling that covered this part of the element when the animal lived, as elements of *P. rectus* also have this heel-like form on the anterior part of the base, but poorly developed.

*P. parvibasis* could have evolved from *P. rectus* through pedomorphosis. I base this assumption on the appearance of the M-elements, where this is most obvious. The longitudinal groove and the carina on the inner side



of the M-elements of *P. rectus* can also be seen on the much thinner M-elements of *P. parvibasis*, but not nearly as prominent. In short, the characters typical for the M-elements of *P. parvibasis* are the same as found in juvenile specimens of *P. rectus*. Generally, these two species are very alike.

*P. graeai* likely evolved from *P. rectus* somewhat earlier compared to where this species turns up in the samples at hand (Fig. B). Löfgren (1978) suggested that this transformation took place in some other area from where there are no samples. The evolutionary process might have been peramorphosis, possibly from a population of *P. rectus* where the asymmetry between costae in the Sb and Sc elements had not yet fully developed/were not as pronounced, as the lack of obvious asymmetry between costae in the S-elements is characteristic for *P. graeai*. Further, the costa on the inner side of the M-elements of *P. graeai* could be a further development of the carina found on the M-elements in *P. rectus*. The particularly long bases in the M and S elements of *P. graeai* could have been due to a change in mineralization inside the basal filling, like for *P. robustus*. This kind of change in morphology can be due to slight differences in habitat and feeding compared to the other species.

The origin of *P. calceatus*, as well as the relation of this species to the four bicostate species is, as mentioned before, not clear. There is, however, a possibility that *P. calceatus* could have evolved from an early multicostate form of *P. rectus* in the earliest Arenig. Bagnoli & Stouge (1997) recognized what they called *Protopanderodus sulcatus* (first described by Lindström 1955a as *Acontiodus rectus* var. *sulcatus*) from the *O. evae* Zone, which actually looks like *P. rectus* with a few additional costae.

## 6.7 Conclusions

1. The investigation of elements lead me to conclude that the genus *Protopanderodus* possessed an apparatus containing three different groups of elements, referred to as the M, S and P element groups according to the notation system of Sweet (1981). Within these three element groups I distinguished a number of morphologically different element types (Figs. 20-26). It turned out that there is a difference in the number of identifiable element types between the four species belonging to the bicostate group of *Protopanderodus*-species, and the one species belonging to the multicostate group. The bicostate species *P. rectus*, *P. robustus*, *P. parvibasis* and *P. graeai* had the following seven element types: M, Sa, Sb1, Sb2, Sc, Pa and Pb. The multicostate species *P. calceatus* had instead the following nine element types: M1, M2, Sa, Sb, Sc, "Sd", Pa, Pb1, Pb2.

2. Having calculated the element ratios and combining numerical results with observations regarding the relative amount of element types, the result that I considered most probable was that all five species had an apparatus containing a minimum of 21 elements; two pairs of M-elements, five pairs of S-elements + one symmetrical S-element and three pairs of P-elements. One notable difference between the four bicostate species and *P. calcea-*

*tus* was the organization in the S-element array. In the latter, the pattern was one Sa, one pair of Sb, two pairs of Sc and two pairs of "Sd", compared with one Sa, two pairs of Sb1, two pairs of Sb2 and one pair of Sc for the other four species.

3. A comparison between the numbers of Pa and Pb elements for the bicostate species (Table 5) suggested that these species possessed two pairs of Pb elements in their apparatus, but that these elements cannot be distinguished from each other. The same seems valid for the M-elements, as the ratios clearly suggested two pairs of M-elements for all five species (Table 4).

4. The relationship between the four bicostate species included in this study is also discussed. Previous work has shown that *P. rectus* most likely is the direct ancestor to *P. robustus*, *P. parvibasis* and *P. graeai*. After comparing the morphology of their element types, my suggestion is that *P. robustus* developed gradually from *P. rectus*. This could have been due to a slight change in mineralization in the basal filling that led to the characteristic base found in *P. robustus*. The evolutionary process of paeomorphosis was likely responsible for the development of *P. parvibasis*, whilst instead in *P. graeai* peramorphosis, possibly also in combination with a change of habitat, could have been responsible for the evolution of this species.

5. Further studies could focus on the relationship between the bicostate group and the multicostate group of *Protopanderodus*-species, as well as the relationship between different multicostate species. My results for *P. calceatus* can be used for comparisons to investigate if other multicostate species show a similar pattern of element organization. This might give some clues whether multicostate species belong to one single, separate evolutionary lineage or if the multicostate character has developed independently more than once. Further, this can reveal whether or not it is sufficient to place bicostate and multicostate species of *Protopanderodus* in two separate genus.

## 7. Systematic palaeontology

Class CONODONTA Pander, 1856

Order CONODONTOPHORIDA Eichenberg, 1930

Superfamily DISTACODONTACEA Bassler, 1925

Family PROTOPANDERODONTIDAE Lindström, 1970

Subfamily PROTOPANDERODONTINAE Lindström, 1970

Genus *Protopanderodus* Lindström, 1971

Type species *Acontiodus rectus* Lindström, 1955



*Protopanderodus rectus* Lindström, 1955

Fig. 20 A-K and Fig. 25 A-G

*Synonymy.* –

- 1955a *Acontiodus rectus* n. sp. – Lindström, p. 594, pl. 2: 7-11, Fig. 3B.  
1955a *Acontiodus rectus* n. sp. var. *sulcatus* nov. – Lindström, p. 550, Pl. 2: 12, 13, Fig 3D  
1955a *Scandodus rectus* n. sp. – Lindström, p. 593, Pl. 4: 21-25, Fig. 3K.  
1960 *Acontiodus rectus* Lindström – Lindström, p. 90, Figs. 2: 8, 3: 7 (non Figs. 6: 10, 8: 8)  
1961 *Acontiodus rectus* Lindström – Wolska, p. 345, Pl. 1: 2.  
non 1963 *Acontiodus rectus* Lindström – Spassov & Teller, p. 78, Pl. 1: 4.  
non 1964 *Acontiodus rectus* Lindström – Hamar, p. 258, Pl. 1: 10, 12, 13, 17, Fig. 4: 4a-b  
1964 *Acontiodus rectus* Lindström – Lindström, p. 108, Figs. 10 (o), 47j.  
1965 *Acontiodus rectus rectus* Lindström – Ethington & Clark, p. 188, Pl. 2: 12.  
? 1965 *Acontiodus rectus sulcatus* Lindström – Ethington & Clark, p. 188, Pl. 1: 15.  
1967 *Acontiodus rectus* Lindström – Viira, Fig. 1: 12.  
1967 *Scandodus rectus* Lindström – Viira, Fig. 1: 13.  
1969 *Acontiodus rectus* Lindström – Bednarczyk, Pl. 1: 7.  
1969 *Acontiodus rectus sulcatus* Lindström – Bednarczyk, Pl. 1: 10.  
1969 *Scandodus rectus* Lindström – Bednarczyk, Pl. 1: 9.  
1971 *Protopanderodus rectus* (Lindström) – Lindström, p. 50.  
1974 *Acontiodus rectus* Lindström – Viira, p. 48, Pl. 4 21-23, Fig. 29.  
1974 *Protopanderodus rectus* (Lindström) – van Wamel, p. 93, Pl. 4: 7-10.  
1976 *Protopanderodus rectus* (Lindström) – Dzik, Fig. 16 (l) (only).  
1978 *Protopanderodus rectus* (Lindström) – Löfgren, p. 90-91, Pl. 3: 1-7, 36A-B, Fig. 31 A-C.  
1981 *Protopanderodus rectus* (Lindström) – Nowlan, p. 15, Pl. 1: 6-7.  
1987 *Protopanderodus rectus* (Lindström) – Olgun, p. 54, Pl. 7W-Z, AB, CD.  
1990 *Protopanderodus rectus* (Lindström) – Stouge & Bagnoli, p. 23, Pl. 8: 1-5.  
1991 *Protopanderodus rectus* (Lindström) – Rasmussen, p. 283, Fig. 8 F-H.  
1993b *Protopanderodus rectus* (Lindström) – Löfgren, Fig. 5A-D.  
cf. 1994 *Protopanderodus rectus* (Lindström) – Dzik, p. 72, Pl. 13: 27-30, Text-fig. 10a.  
1994 *Protopanderodus rectus* (Lindström) – Löfgren, Fig. 7: 7-10.  
2000 *Protopanderodus rectus* (Lindström) – Löfgren, p. 324, Fig. 4 N-O.  
2001 *Protopanderodus rectus* (Lindström) – Rasmussen, p. 124-125, Pl. 16: 1-4.

2003 *Protopanderodus rectus* (Lindström) – Löfgren, p.432, Fig. 8 R-U.

2004 *Protopanderodus rectus* (Lindström) – Löfgren, p. 581, Fig. 13 d-f.

*Holotype.* – Lindström, 1955a, p. 549, Pl. 2, Figs. 7, 8. – Department of Geology, Univ. of Lund, LO 3562 T.

*Original diagnosis.* – (Of *Acontiodus rectus* Lindström, 1955a) An erect *Acontiodus* with strong posterior lateral costae, rounded basal outline and rather shallow basal cavity.

*Remarks.* – The original diagnosis only refers to the S elements. Löfgren (1978) was the first to describe all three morphologically different element types in *P. rectus*, using a descriptive notation system; acontiodontiform for the S elements, scandodontiform for the M elements and acodontiform for the P elements.

*Type locality and type level.* – Lanna quarry 15 km WSW of Örebro, Sweden, NE end of the quarry, sample 12 c. 3.0 m above base of Ordovician, upper part of Billigen Substage.

*Stratigraphical range.* – (Lower Ordovician: Arenigian Billigen Substage (conodont Zone of *Oepikodus evae*) to lower Llanvirnian (lower part of conodont Zone of *Amorphognathus variabilis*).

Lower Ordovician: Conodont Zone of *Oepikodus evae*, possibly even from the *P. proteus* Zone, to the middle Darriwilian; *E. pseudoplanus* Zone.

*Regional occurrence.* – Europe: Sweden (Lindström 1955a, 1960, 1971; van Wamel 1974; Löfgren 1978), St. Petersburg area (Sergeeva 1962), Estonia (Viira 1967, 1974), Åland (Merrill 1980), Norway (Rasmussen 1991, 2001), Southern Uplands of Scotland (Lamont & Lindström 1957). North America: Texas: Marathon Basin (Bergström & Cooper 1973), Canada (Ethington & Clark 1965; Nowlan 1981). Australia: Canning Basin (McTavish & Legg 1976).

*Protopanderodus robustus* (Hadding, 1913)

Fig. 21 A-K and Fig. 25 H-N

*Synonymy.* –

- 1913 *Drepanodus robustus* n. sp. – Hadding, p. 31, Pl. 1: 5  
1955b *Acontiodus robustus* (Hadding) – Lindström, p. 108, Pl. 22: 1, 2, 4, 6.  
1960 *Acontiodus rectus* Lindström – Lindström, Figs. 6: 10, ?8: 8 (non Figs. 2: 8, 3: 7).  
1962 *Acontiodus robustus* (Hadding) – Sweet & Bergström, p. 1222, Pl. 169: 11, Fig 1 (I)  
? 1962 *Scandodus* sp. – Sweet & Bergström, p. 1246, Pl. 168: 13, 16.  
1963 *Acontiodus rectus* Lindström – Spassov & Teller, p. 78, Pl. 1: 4.



- 1964 *Distacodus* n. sp. – Hamar, p. 263, Pl. 1: 19-20, Fig. 6: 3a.
- ? 1964 *Scandodus rectus* Lindström – Hamar, p. 282, Pl. 2: 6-7, Fig. 6: 9, 11.
- 1966 *Acontiodus robustus* (Hadding) – Fåhraeus, p. 16, Pl. 2: 5a-b, Fig. 3E, F, G.
- 1966 *Scandodus formosus* n. sp. – Fåhraeus, p. 30, Pl. 3: 11, Fig. 2K.
- 1966 *Acontiodus unciformis* n. sp. – Fåhraeus, p. 17, Pl. 2: 7a-b, Fig. 3B.
- 1969 *Acontiodus robustus* (Hadding) – Bradshaw, p. 1148, Pl. 131: 8, 10, 13, 14.
- ? 1969 *Scandodus dubius* n. sp. – Bradshaw, p. 1161, Pl. 134: 19-20.
- 1970 *Acontiodus robustus* (Hadding) – Uyeno & Barnes, p. 104, Pl. 21: 18-19, Fig. 7G.
- 1973 *Acontiodus robustus* (Hadding) – Barnes & Poplawski, p. 768, Pl. 2: 15.
- 1974 *Acontiodus viruensis* (Fåhraeus) – Viira, Fig. 31 á (only).
- 1976 *Acontiodus robustus* (Hadding) – Landing, p. 629, Pl. 1: 8.
- 1978 *Protopanderodus robustus* (Hadding) – Löfgren, p. 94, 95, Pl. 33, Figs. 32-35, text-fig. 31G-J.
- 1989 *Protopanderodus robustus* (Hadding) – McCracken, p. 20-22, Pl. 1, Figs. 1-10, text-fig. 3E.
- 1989 *Protopanderodus robustus* (Hadding) – Rasmussen & Stouge, Fig. 3N.
- 1991 *Protopanderodus robustus* (Hadding) – Rasmussen, p. 283, Fig. 8J-M.
- ? 1995 *Protopanderodus robustus* (Hadding) – Lehnert, p. 118, Pl. 13: 16.
- 1998 *Protopanderodus cooperi* (Sweet & Bergström) – Zhang, pp. 81-82, Pl. 14: 13-17.
- 1998 *Protopanderodus robustus* (Hadding) – Albanesi, p. 129, 130, Pl. 11, Figs. 17-20, text-fig. 14A.
- 2001 *Protopanderodus robustus* (Hadding) – Rasmussen, p. 125, Pl. 16: 5-8.
- 2004 *Protopanderodus robustus* (Hadding) – Zhen et al., p. 155, 157, Fig. 8J-M.
- 2004 *Protopanderodus robustus* (Hadding) – Zhen & Percival, p. 172, Fig. 11G-O.
- 2004 *Protopanderodus* cf. *robustus* Hadding – Löfgren, p. 518, Fig. 13 j-n.

*Holotype*. – Hadding, 1913, Pl. 1, Fig. 5b. – Department of Geology, Univ. of Lund, LO 2344 T.

*Original diagnosis*. – (Translated by Lindström 1955b) A long, rather slender, slightly recurved *Acontiodus*, sharply keeled anteriorly and with a marked tendency to develop additional costae. Basal cavity roughly conical.

*Type locality and type level*. – Fågelsång area, Skåne, S. Sweden. E14, lower part.

*Stratigraphical range*. – From the Middle Ordovician into the Late Ordovician.

*Regional occurrence*. – Europe: Sweden (Hadding 1913;

Lindström 1955b; Fåhraeus 1966; Löfgren 1978). Norway (Rasmussen 1991, 2001). Estonia (Viira 1974).

Canada (Uyeno & Barnes 1970; Barnes & Poplawski 1973; McCracken 1989). Argentina (?Lehnert 1995; Albanesi 1998). China: Yangtse Valley (Zhang 1998). Australia (Zhen et al. 2004; Zhen & Percival 2004).

### *Protopanderodus parvibasis* Löfgren, 1978

Fig. 22 A-K and Fig. 25 O-U

*Synonymy*. –

1978 *Protopanderodus parvibasis* Löfgren – Löfgren, p. 93, Pl. 3, figs. 11-18, Fig. 31D-F.

1989 *Protopanderodus parvibasis* Löfgren – McCracken, p. 20, Pl. 1, figs. 25-29, Fig. 3D.

2004 *Protopanderodus parvibasis* Löfgren – Löfgren, p. 518, Fig. 13 a-c.

*Holotype*. – Löfgren, 1978, p. 93, Pl. 3, Fig. 18. – Department of Geology, Univ. of Lund, LO 5165 T.

*Original diagnosis*. – A *Protopanderodus* with scandodontiform (M) elements with a very low base, a shallow basal cavity slightly expanded on the inner side, a short, sharp oral edge, and an erect cusp with a poorly developed rounded carina on the inner side. The species also has symmetrical (S) and slightly asymmetrical acontiodontiform (P) elements (Löfgren 1978).

*Remarks*. – The holotype is an M element. All three element groups were included in the original description.

*Type locality and type level*. – Lunne quarry about 2.5 km E of Brunflo, Jämtland, sample J 70-10 of Löfgren (1978), orthoceratite rich limestone, 11m below the top of the quarry. Conodont Subzone of *E. pseudoplanus* – *M. ozarkodella*.

*Stratigraphical range*. – Middle Ordovician.

*Regional occurrence*. – Sweden (Löfgren 1978) and Canada (McCracken 1989).

### *Protopanderodus graeai* (Hamar, 1964)

Fig. 23 A-J and Fig. 25 V-BB

*Synonymy*. –

1964 *Acontiodus rectus* Lindström – Hamar, p. 258, Pl. 1: 10, 12, 13, 17, Fig. 4: 4a-b.

1966 *Acodus graeai* n. sp. – Hamar, p. 47, Pl. 3: 11-14, Fig. 3: 5.

1966 *Acodus triangulatus* n. sp. – Fåhraeus, p. 11, Pl. 2: 1, Fig. 2C.

1966 *Acontiodus coniformis* n. sp. – Fåhraeus, p. 15, Pl. 2: 3, Fig. 3C.

1967 *Scandodus* n. sp. B – Viira, Fig. 4: 17.

1974 *Acodus triangulatus* Fåhraeus – Viira, p. 46, Pl. 5: 25, 26, Figs. 25, 26.



- 1974 *Acontiodus* aff. *rectus* Lindström – Viira, p. 49, Figs. 30a, á, ? á, 34a, á.  
 1974 *Acontiodus viruensis* (Fåhraeus) – Viira, Fig. 31 ? (only)  
 1976 *Protopanderodus rectus* (Lindström) – Dzik, Fig. 16i.  
 1978 *Protopanderodus graeai* (Hamar) – Löfgren, p. 93, Pl. 3: 19-25, Fig. 31K-M.  
 ? 1994 *Protopanderodus graeai* (Hamar) – Dzik, p. 72, Pl. 13: 14-22, Fig. 10b-c.  
 1998 *Protopanderodus graeai* (Hamar) – Zhang, pp. 84-85, Pl. 15: 1-5.  
 2001 *Protopanderodus graeai* (Hamar) – Rasmussen, p. 124, Pl. 15: 17-19.  
 2004 *Protopanderodus graeai* (Hamar) – Löfgren, p. 518, Fig. 13 o-r.

*Holotype*. – Hamar, 1966, p. 47, Pl. 3, Figs. 11, 13. – Paleontological Museum of the Univ. of Oslo, PMO 69708.

*Original diagnosis*. – (Of *Acodus graeai* Hamar, 1966) An *Acodus* with proclined cusp and a posterior lateral costa. The cross section is triangular.

*Remarks*. – The original diagnosis refers to M elements only.

*Type locality and type stratum*. – North of Rodelökken café, NE side of Bygdøy Peninsula, Oslo, Norway. Sample 187 of Hamar (1966), from lower part of a 20 cm thick limestone bed in the uppermost 10 m of the Ampyx Ls.

*Stratigraphical range*. – Ordovician: Darriwilian; conodont Subzone of *E. pseudoplamus* – *M. ozarkodella* to lower part of Upper Ordovician.

*Regional occurrence*. – Europe: Sweden (Fåhraeus 1966; Löfgren 1978). Norway (Hamar 1966; Rasmussen 2001). Estonia (Viira 1974). China: Yangtse Valley (Zhang 1998b). Questionably in Poland (Dzik 1994).

### *Protopanderodus calceatus* Bagnoli & Stouge, 1997

Fig. 24 A-O and Fig. 26 A-N

*Synonymy*. –

- 1969 *Scolopodus varicostatus* Sweet & Bergström – Bradshaw, p. 1163, Pl. 134: 12-13.  
 1969 *Scandodus unistriatus* Sweet & Bergström – Bradshaw, p. 1161, Pl. 135: 5-6.  
 1976 *Protopanderodus rectus* (Lindström) – Dzik, Fig. 16b-d.  
 1978 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Löfgren, p. 91, Pl. 3: 26-31.

- 1983 *Protopanderodus* sp. – Dzik, Fig. 3: 30-31.  
 1987 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Olgun, Pl. 7: P-S.  
 1990 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Stouge & Bagnoli, p. 23, Pl. 8: 9-12.  
 1991 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Rasmussen, p. 283, Fig. 8D-E.  
 1994 *Protopanderodus gradatus* (Serpagli) – Dzik, p. 73, Pl. 13: 23-26, Fig. 11a.  
 1994 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Löfgren, Fig. 7: 3.  
 1995 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) – Lehnert, p. 118, Pl. 13: 17, Pl. 17: 5-6, 8-9.  
 1997 *Protopanderodus calceatus* n. sp. – Bagnoli & Stouge, p. 154, Pl. 8: 13-19.  
 1998 *Protopanderodus calceatus* Bagnoli & Stouge – Zhang, pp. 82-83, Pl. 15: 6-13.  
 2000 *Protopanderodus calceatus* Bagnoli & Stouge – Löfgren, p. 324, Fig. 4 V.  
 2001 *Protopanderodus calceatus* Bagnoli & Stouge – Rasmussen, pp. 122, 124, Pl. 15: 20-21.  
 2001 *Protopanderodus* cf. *P. varicostatus* (Sweet & Bergström) – Viira et al., Fig. 9 (r) (only).  
 2003 *Protopanderodus calceatus* Bagnoli & Stouge – Löfgren, p. 432, Fig. 8 O-Q.  
 2004 *Protopanderodus calceatus* Bagnoli & Stouge – Löfgren, p. 518, Fig. 13 g-i.

*Holotype*. – Bagnoli & Stouge, 1997, p. 156, Pl. 8, Fig. 18. – Mineralogic and Geologic Museum of Copenhagen, MGHU 24149.

*Original diagnosis*. – The elements of *Protopanderodus calceatus* n.sp. have a low, small and hyaline base. The asymmetrical elements have a prominent antero-lateral groove (Bagnoli & Stouge 1997).

*Remarks*. – The holotype is a scandodiform (M) element, but all three element groups were included in the original description. There are only slight morphological differences between the originally described fauna, and the stratigraphically younger faunas included in this study.

*Type locality and type stratum*. – Section North of Horns Udde, 7.10m above the base of the section, sample HU 649, *Baltoniodus norrlandicus* Zone.

*Stratigraphical range*. – Ordovician: Upper *Oepeikodus evae* Zone (Lower Ordovician) into lower part of the Upper Ordovician, at least through the Darriwilian.

*Regional occurrence*. – Europe: Sweden (Löfgren 1978; Bagnoli & Stouge 1997). Norway (Rasmussen 1991, 2001). Estonia (Viira et al. 2001). Poland (Dzik 1994). China: Yangtse Valley (Zhang 1998).



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## Appendix: Element ratios

### *Protopanderodus rectus*

DLK86 L4: M-22% P-20.5% S-57.5%  
 DLK86 L5: M-22.3% P-15.8% S-61.9%  
 Ö194-2: M-21.5% P-21.6% S-56.9%  
 Vg98-4B: M-19.9% P-14.9% S-65.2%

Average%: M-21.6% P-19.6% S-58.8%

Sample \ Element type	M	P	S
DLK86 L4 (2 slides)	108	101	283
DLK86 L5	62	44	172
Ö194-2 (3 slides)	127	128	337
Vg98-4B	28	21	92

### *Protopanderodus robustus*

DLK86 H4: M-15.8% P-9.8% S-74.4%  
 HK89-4: M-28.2% P-15.3% S-56.5%  
 GB81-500: M-27.3% P-36.3% S-36.4%

Average %: M-22.4% P-15.2% S-62.4%

Sample \ Element type	M	P	S
DLK86 H4 (2 slides)	21	13	99
HK89-4	35	19	70
GB81-500	9	12	12

### *Protopanderodus parvibasis*

DLK86 H4: M-23% P-20.3% S-56.7%  
 HK89-4: M-27.8% P-8.9% S-63.3%  
 DLK86-H12: M-29.9% P-12.6% S-57.5%  
 GB81-500: M-18.9% P-8.1% S-73%  
 Rävånäs 5: M-25.8% P-20.9% S-53.3%  
 Rävånäs 6: M-29.7% P-20.9% S-49.4%  
 HK88-3: M-23.3% P-25% S-51.7%

Average %: M-25% P-18.6% S-56.4%

Sample \ Element type	M	P	S
DLK86 H4 (2 slides)	93	82	229
HK89-4	22	7	50
DLK86-H12	26	11	50
GB81-500	14	6	54
Rävånäs 5 (2 slides)	89	72	184
Rävånäs 6	27	19	45
HK88-3	14	15	31

### *Protopanderodus graeai*

DLK86 H4: M-14.6% P-22.1% S-63.3%  
 HK89-4: M-14.3% P-17.5% S-68.2%  
 Rävånäs 6: M-20.2% P-10.5% S-69.3%

Average %: M-15.7% P-18.2% S-66%

Sample \ Element type	M	P	S
DLK86 H4 (2 slides)	41	62	178
HK89-4	22	27	105
Rävånäs 6	25	13	86

### *Protopanderodus calceatus*

Rävånäs 5: M-15.7% P-21.4% S-62.9%  
 DLK86 H12: M-25.6% P-17.6% S-56.8%  
 DLK86 H13: M-31.3% P-15.6% S-53.1%  
 HK88-3: M-28.3% P-13.1% S-58.6%

Average %: M-22.2% P-18.2% S-59.6%

Sample \ Element type	M	P	S
Rävånäs 5 (2 slides)	53	72	212
DLK86 H12	32	22	71
DLK86 H13	30	15	51
HK88-3	43	20	89



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