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# THE CURVATURE-TRANSITION SERIES: INTEGRAL PART OF SOME SIMPLE-CONE CONODONT APPARATUSES (PANDERODONTACEA, DISTACODONTACEA, CONODONTATA)

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Elements of species of *Drepanoistodus* Lindström, *Panderodus* Ethington, and *Protopanderodus* Lindström systematically vary from symmetrical to pronouncedly asymmetrical (symmetry-transition series) within each species, and a group of elements with systematic increase in curvature of the cusp can be recognized for each element type; each such group is named a curvature-transition series. *Panderodus* and *Protopanderodus*, both of the Panderodontacea, have essentially identical apparatuses with regard to symmetry and curvature-transition series whereas *Drepanoistodus*, of the Distacodontacea, differs in type of symmetry-transition series and number of curvature-transition series. The curvature-transition series is considered to represent a taxonomically distinct character at the suprageneric level.

Key words: conodont apparatuses, Ordovician, classification.

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## INTRODUCTION

More than twenty years ago Lindström (1964) introduced the concept of the symmetry-transition series to the study of conodont apparatuses. Lindström based this concept on the fact that one frequently can observe intergrading series of element morphologies varying from symmetrical to pronouncedly asymmetrical in a sample of disjunct conodont elements. Such symmetry-transition series occur both among ramiforms and coniforms. Costae, processes, and inclination of denticles display the symmetry relationships among ramiforms, whereas cross-section of the base and distribution of costae, carinae, and sulci largely characterize the symmetry of the simple cones.

The symmetry-transition series has proven to be one of the basic tools for reconstructions of conodont apparatuses which include ramiforms. Recognition of symmetry-transition series has, however, had less success with simple cone apparatuses. These latter apparatuses appear in many cases — to judge from the published literature — to either lack a symmetry-transition series or to have one that is poorly or incompletely developed (see e.g. Fåhræus and Hunter 1985).

In the mid-1960's several authors (e.g. Bergström and Sweet 1966; Schopf 1966; Webers 1966) began to reconstruct Ordovician conodont apparatuses along the lines suggested by Lindström (1964) and Walliser (1964). Most of these studies involved compound and platform conodont elements and only a few attempts were made at reconstructing simple-cone taxa.

Subsequently, Lindström (1971) reconstructed two types of Early Ordovician simple-cone apparatuses. One type of apparatus includes only two element types, as in *Paroistodus*, viz. one with obtuse cusp-to-base angle and one with acute cusp-to-base angle. The other type of apparatus (e.g. in *Oistodus*) displays a more or less well developed symmetry-transition series of the same type as found among in several genera with ramiforms.

In recent years numerous authors have reconstructed simple-cone apparatuses of Ordovician (e.g. Van Wamel 1974; Dzik 1976; Löfgren 1978; Sweet 1979) and Silurian (eg. Barrick 1977; Cooper 1976) conodonts.

Studies of Ordovician and Silurian conodonts have frequently demonstrated a high degree of morphologic variability among the coniforms. These various forms often intergrade almost completely. However, all of the above studies, and others not mentioned, have in common that they utilized a typological approach rather than trying to systematize and integrate the morphologic variability exhibited by individual conodont elements into a morphologically coherent apparatus with regard to symmetry relationships and general morphology. This approach we believe to have led to a spuriously high diversity of simple-cone taxa of some studies.

Morphologically similar simple-cone elements frequently show variation in curvature of the cusp. Although some students of simple cones have reported this variation in curvature of the cusp, no attempt has been made to consider the degree of curvature as an integral and regular part of conodont morphology and, thus, taxonomically important. Viira (1974) noted that several of her reconstructed simple-cone species included element types characterized by a variation in degree and type of curvature of the cusp. Viira (1974) also paid particular attention to the symmetry/asymmetry of the cross-section of the base of the elements she grouped together. However, she did not realize the presence of a continuous increase of the curvature of the cusp in some element types.

Dzik (1976) reconstructed several Early and Middle Ordovician simple-cone apparatuses. Dzik generally recognized more element types in his apparatuses than previous workers had done and gave greater emphasis to symmetry, but he did not regard the curvature of the cusp to be an important taxonomic feature. Dzik's (1976) approach had been largely anticipated by Viira (1974) and Van Wamel (1974), and later was followed by Löfgren (1978).

Barnes *et al.* (1979) formalized the concept of simple-cone apparatuses based on the cusp-to-base angle and curvature of the cusp, as proposed by Lindström (1971), but did not incorporate considerations of a systematicg increase in the survature of the cusp in any of their apparatus models.

However, as demonstrated below, it can be shown that many of the element types recognized in reconstructed simple-cone apparatuses show morphologic variation restricted to a gradual increase in the degree of curvature of the cusp. We refer to a series of such elements — representing one element type but showing a gradual increase in the curvature of the cusp — as a curvature-transition series. In the study presented herein we integrate the concept of the curvature-transition series with the symmetry-transition series, i.e. for each recognized element type a curvature-transition series can be recognized. We emphasize that we do not consider the varying degree of curvature to represent 'normal' variability but, rather, distinct, functionally determined, forms of the primary element types. By doing this systematically we have been able to homologize reconstructed simple-cone apparatuses representative of the superfamily Panderodontacea (viz. *Panderodus* and *Protopanderodus*) and to illustrate the fundamental differences between panderodontacean and distacodontacean (represented by *Drepanoistodus*) conodont apparatuses.

In this study we have paid particular attention to: (1) the recognition of a curvature-transition series; (2) the presence and type of symmetry relationships; (3) intergration of morphologic types; (4) recurrence over many samples of associations of morphologically distinct elements; and (5) the fact that the conodont elements, at least in some conodonts, appear to have been distributed in distinct units or segments along the mid-axis of the organism (Briggs *et al.* 1983). Finally (6) we have also kept in mind that it is highly likely that the apparatus itself had a bilateral or, in some forms, radial symmetry (Lindström 1964, 1974).

## PROPOSED COMPOSITION OF SOME SIMPLE-CONE APPARATUSES

Fåhræus and Hunter (1981) recently reported a large and varied conodont fauna from the Middle Ordovician (Chazyan, Llandeilian) Cobbs Arm Limestone of New World Island, north-central Newfoundland.

Among the more than 18000 identifiable conodont elements recovered from 72 samples — representing seven sampled sections — a large proportion consists of simple-cone elements (Fåhræus and Hunter 1981: Table 1). In a separate publication (Fåhræus and Hunter, 1985) we have discussed the symmetry and apparatus composition of several new and previously described simple-cone taxa that appear to lack curvature-transition series. Such series, however, appear to have been present in many other simple-cone taxa from the Cobbs Arm Limestone, as shown in the discussion that follows.

Our approach to some extent involves a considerable broadening of present species concepts of the taxa discussed, thus the results of our study should be looked upon as working proposals for further studies. Our reconstructed apparatuses, emphasizing the curvature-transition series, need to be confirmed by studies involving other localities and taxa of other ages.

## *Panderodus gracilis* (Branson and Mehl, 1933)
(fig. 1)

*Discussion.* — Bergström and Sweet (1966), in their study of Middle Ordovician conodonts from the Lexington Limestone (and lateral equivalents) in Kentucky, Indiana, and Ohio, proposed that the apparatus of *Panderodus gracilis* was composed of elements previously referred to the form-taxa *P. gracilis* s.f., *P. compressus* s.f. and forms similar to *P. unistriatus* s.f., a Silurian form. Carnes (1975, unpubl. Ph.D. dissertation) largely agreed with this synonomy with regard to included form-taxa but added the important distinction that five distinct morphologic types could be recognized, including one that is perfectly symmetrical. Sweet (1979), in a study which involved *Panderodus* species from the Ordovician western Midcontinent province, recognized essentially the same morphologic groups as Carnes but did not recognize the fully symmetrical element. Barrick (1977), in a study of simple cones from the Silurian Clarita Formation of Oklahoma, described a *Panderodus* species with four element types, one of which is nearly symmetrical. Cooper (1975), in a study of conodonts from the Silurian Brassfield Limestone of southern Ohio, recognized three morphologic groups in the *Panderodus* apparatus, none of them being fully symmetrical. Dzik (1976: fig. 15*a*, *b*, *e*, *f*) illustrated six different types of elements of *P. gracilis* from erratic boulders in Poland whose apparent ages range from the Middle to the Late Ordovician (?Silurian). Because Dzik did not provide a discussion to accompany his illustrations it is unclear what kind of relationship he envisioned for these forms. Finally, Löfgren (1978) recognized an early Llanvirnian *Panderodus* from Jämtland north-central Sweeden, and considered it to have the same general association of elements in its apparatus as the revised *P. gracilis* of Sweet and Bergström (1966).

Thus, although the *P. gracilis* apparatus is recognized by most authors to include three or more element types, the presence of a fully symmetrical element in the typical *Panderodus* apparatus has not been included in most previous studies. However, Jeppsson (1983: 86), in an undocumented discussion report, stressed the importance of the fully symmetrical element in the Silurian *Panderodus* apparatus:

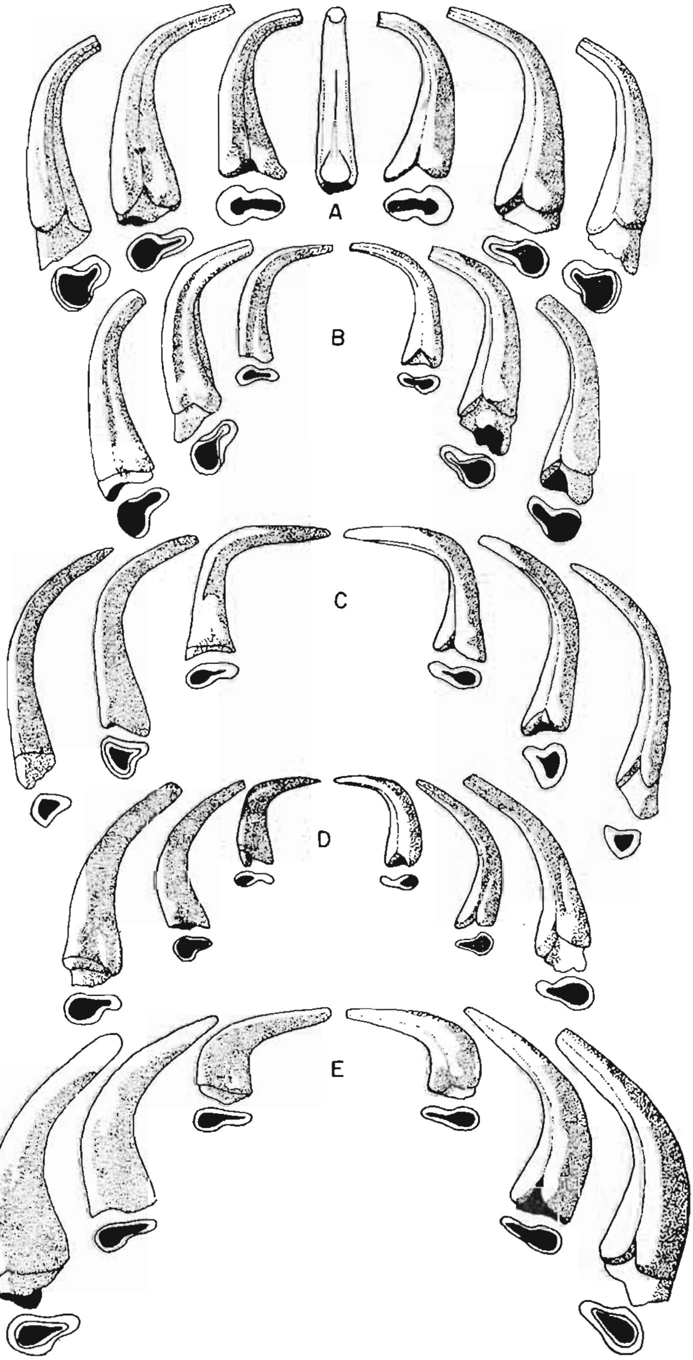


Fig. 1. *Panderodus gracilis* (Branson et Mehl): (*A*) symmetrical gracilid panderodontiforms; (*B*, *C*, *D*) asymmetrical gracilid panderodontiforms; (*E*) asymmetrical compressid panderodontiforms. Inner lateral views, left of centre; outer lateral views, right of centre. Illustrations are all × 40.

"It is symmetrical, not nearly or almost. Earlier accounts of so called symmetrical elements in *Panderodus* referred to specimens with a furrow on one lateral side only; a genuine such element has one (furrow) on each lateral side." We fully concur with this statement and, on basis of our own and Carnes's observations, propose to extend it to typical Ordovician *Panderodus* species.

Our collections from the Cobbs Arm Limestone contain about 5700 specimens that collectively can be referred to the above three form-taxa of Sweet and Bergström (1966) included in the apparatus of *P. gracilis*. Among these specimens we can clearly distinguish the five morphologic groups recognized by Carnes (1975), including the fully symmetrical element. We are taking these conclusions one step further by showing that each of these element types is characterized by a curvature-transition series.

*Description.* — For the purpose of the following descriptions the five morphotypes and their respective curvature-transition series are referred to as Groups *A*, *B*, *C*, *D*, and *E* (fig. 1). We prefer this procedure as opposed to the descriptive terms proposed by Sweet (1979), viz. similiform, arcuatiform, asimiliform, tortiform, and falciform respectively, or the implied homology with ramiform and platform apparatuses proposed by Barrick (1977) in his usage of the *P*, *M*, and *S* positional terminology of Sweet and Schönlaub (1975). Barrick did not recognize any *P* elements in the *Panderodus* apparatus, but did not discuss their absence.

*Group A*: Cusp of symmetrical element with smooth broadly rounded posterior margin. Anterior margin sharp-edged from tip of cusp to near basal margin where it is rounded. Lateral costae symmetrically disposed and run from near basal margin to tip of cusp. Anterio-lateral surface smoothly convex. Postero-lateral faces slightly concave and ornamented with fine longitudinal striations. Along middle of each posterior lateral face runs a narrow furrow which begins as a notch at basal margin and continues to tip of cusp. The element has a very characteristic 'key-hole' cross-section.

*Group B*: Nearly symmetrical elements very similar to Group *A* but lack inner lateral furrow and basal notch. Sharp anterior edge of base occupies a slightly outer lateral position. Lateral costae not quite symmetrically disposed.

*Group C*: Slightly more asymmetrical elements with inward twisted cusp with inner lateral costa displaced anteriorly, becoming sharp anterior edge of cusp. Sharp posterior edge asymptotic to outer lateral furrow. Narrowly rounded outer lateral costa on base.

*Group D*: Has sharp anterior edge developed from inner lateral costa present in less asymmetric forms. Posterior edge very close and asymptotic to furrow on outer lateral face. Broadly rounded costa on outer lateral face.

*Group E*: Resembles Group *D* but with narrowly rounded anterior margin, wider base, and smooth outer lateral face.

*Remarks.* — We wish to emphasize (as is evident from fig. 1) that for each of the recognized element types a very well developed curvature-transition series can be recognized.

Only 969 elements, all from one sample, were studied in detail, the remaining specimens were surveyed as to element type. The proportions of the five forms (*A*:76; *B*:206; *C*:225; *D*:234; *E*:228) respectively suggest the ration 1:3:3:3:3. However, the form groups *C* and *D* intaergrade and are not easily subdivided, thus the numbers given are somewhat uncertain. Jeppsson (1983), on basis of Silurian material from Gotland, Sweden, was of the opinion that the symmetrical element usually accounts for less than 1% in *Panderodus* collections. In our collection it occurs with a frequency of about 8%.

*Material.* — 5756 specimens.

## *Protopanderodus varicostatus* Sweet and Bergström, 1962
(fig. 2)

*Discussion.* — The proposed reconstruction of this apparatus is in part a systematization and formalization of the high degree of variability of elements brought to this species that was already noted by Sweet and Bergström (1962) in their original description and subsequently by Löfgren (1978: 91—92) in her discussion of *Protopanderodus* sp. cf. *P. varicostatus.* Sweet and Bergström (1962) recognized three morphologic groups of costate elements whereas we recognize four. Sweet and Bergström did not include a non-costate element as we have done (fig. 2*E*) but the element was present in their collections and was described and illustrated as *Scandodus unistriatus* (Sweet and Bergström 1962: 1245, pl. 168: 12). Subsequent authors (Dzik 1976, Löfgren 1978, and Lindström in Ziegler 1981) recognized, and included, the fourth element. We agree with these latter authors and have included this element in our reconstruction because of overall morphologic similarity and persistent sample co-occurrence with costate elements. The ratio for the different element types is uncertain but would appear to be 1:2:2:2:2.

*Description.* — The apparatus of *P. varicostatus* comprises one symmetrical and three asymmetrical multi-costate element types together with an asymmetrical non-costate element. We emphasize that each of these five element types exhibits a curvature-transition series. In the following descriptions the element types and their curvature-transition series are designated as Groups *A*, *B*, *C*, *D*, and *E* (fig. 2).

*Group A*: Symmetrical multi-costate elements with sharp anterior and posterior margins. Each lateral face carries 2 posterior costae separated by a deep furrow that begins near basal margin and extends to tip of cusp. Base one — third of length of cusp and with slightly sinuous basal margin.

*Group B*: Asymmmetrical tri-costate element with bases proportionally shorter than in Group *A*. Basal margins slightly sinuous in proclined forms and notched in reclined forms.

*Group C*: Asymmetrical multi-costate elements with sharp anterior and posterior margins. Cusp distally twisted with two low inner lateral costae. Outer lateral face with one well developed costa bounded by a furrow and one posterior costa which is well developed on the base but generally weakens towards tip of cusp.

*Group D*: Asymmetrical element nearly identical to Group *C* but with only one well developed outer lateral costa. Differs from Group *B* with proportionally shorter bases and slightly convex basal margin in proclined forms.

*Group E*: Non-costate elements with long robust and sharp-edged cusp that is laterally compressed and inward twisted. On anterior half of inner lateral face runs a shallow groove that begins near basal margin and continues to tip of cusp. Outer lateral face convex.

*Remarks.* — Form groups *C* and *D* intergrade to a larger extent than the same groups in *Panderodus gracilis* and are here accounted for in bulk. However, apart from the possibly differing ratios the two apparatuses would appear to have been largely identical in their basic composition with regard to symmetry- and curvature-transition series. For the descriptions and illustrations of Groups *C* and *D* we have used end members.

*Material.* — 1291 specimens (Group *A*: 157; Group *B*: 327; Groups *C*, *D*: 581, Group *E*: 226).

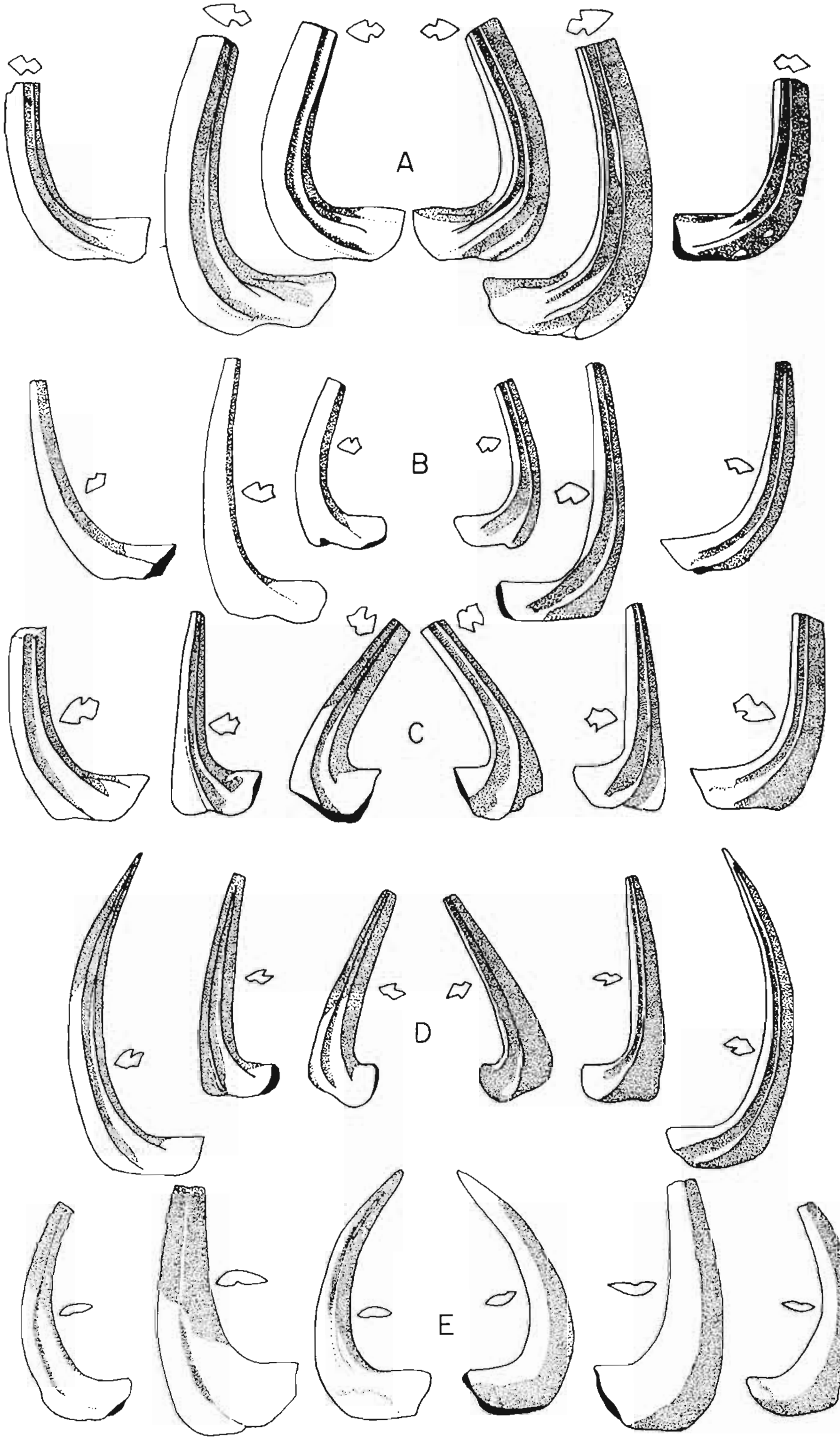


Fig. 2. *Protopanderodus varicostatus* (Sweet et Bergström): (*A*) symmetrical multicostate elements; (*B*) tricostate elements; (*C*, *D*) asymmetrical multicostate elements; (*E*) asymmetrical acostate elements. Inner lateral views, left of centre; outer lateral views, right of centre. Illustrations are all × 40.

## *Drepanoistodus* sp. aff. *D. suberectus* (Branson and Mehl, 1933)

(fig. 3)

*Discussion.* — The genus *Drepanoistodus* was introduced by Lindström (1971) who included two types of elements in the conodont apparatus of this genus, viz. drepanodontiforms and oistodontiforms. However, as already pointed out by Bergström and Sweet (1966) on basis of Middle Ordovician material from the Midcontinent of the United States and later reiterated by Löfgren (1978), who based her conclusions on Lower Ordovician material from north-central Sweden, two distinctly different types of drepanodontiforms can be recognized in the *Drepanoistodus* apparatus, namely homocurvatiforms and suberectiforms (typically fig. 3*E* and *C*, respectively). Our material strongly confirms the presence of these three basic types of elements in the *Drepanoistodus* apparatus. However, based on the overall morphology of the elements together with the outline of cross-sections of the base and the cusp, we recognize four groups of elements in this apparatus; each of these groups incorporates a curvature-transition series.

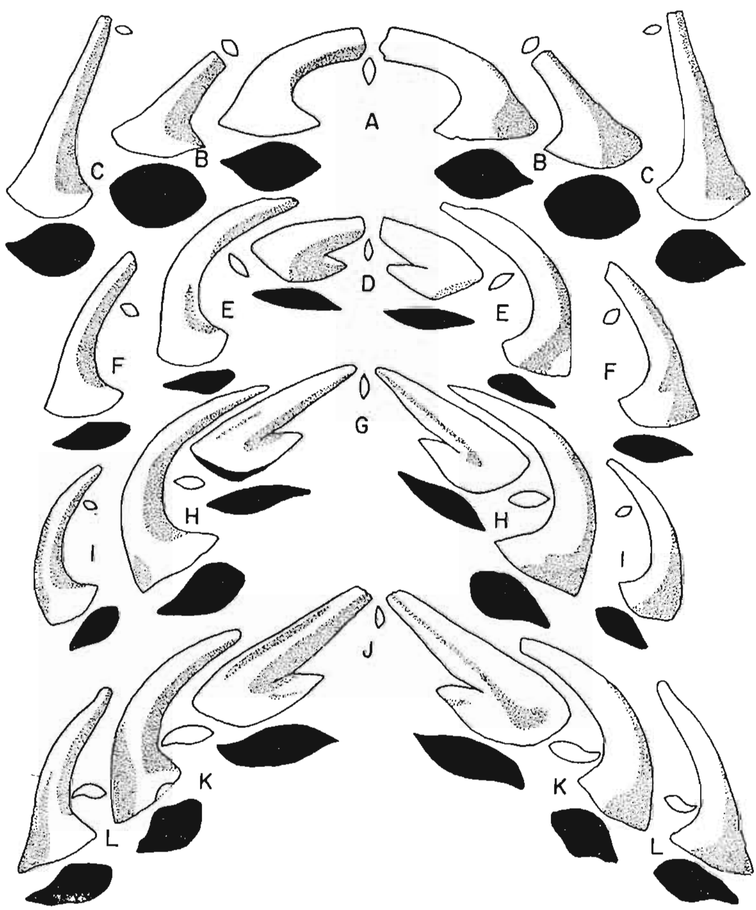


Fig. 3. *Drepanoistodus* sp. aff. *D. suberectus* (Branson et Mehl): (*A*) symmetrical drepanodontiforms; (*B*, *C*) symmetrical drepanodontiforms; (*D*, *G*, *J*) asymmetrical oistodontiforms; (*E*, *F*, *H*, *I*, *K*, *L*) asymmetrical drepanodontiforms. Inner lateral views, left of centre; outer lateral views; right of centre, Illustrations are all $\times 40$.

Rather than grouping the oistodontiforms separately they are considered parts of the individual curvature-transition series (fig. 3). This conclusion is based on the observation that the symmetry and outline of the cross-section of the bases of the oistodontiforms appear to conform with the basal cross-sections of the different element types of the drepanodontiform that we recognize. There is also an overall similarity in the morphology of the cusps (fig. 3).

*Description.* — Drepanodontiforms have long and slender proclined to reclined cusps that generally are slightly compressed laterally and sharp-edged. Symmetrical forms have straight or slightly curved biconvex cusps and broadly flaring short and shallowly excavated bases. Asymmetrical forms have curved cusps with outward convex faces. Inner faces vary from weakly convex to planar to concave with increasing asymmetry of form. Basal margins only slightly flaring.

Oistodontiforms have compressed, pointed and sharp-edged cusps that are about three times as long as upper basal margin. Basal margins laterally biconvex but asymmetric due to more pronounced inward flare. This inward flare is variable among the different types recognized but largely constant within each curvature-transition series (fig. 3). Posterio-basal angle appears to vary inversely with magnitude of basal flaring. Oistodontiforms with pronounced flare have postero-basal angle of about 80 degrees, whereas nearly symmetrical oistodontiforms have postero-basal angle of about 40 degrees.

*Remarks.* — Our total collection of drepanodontiforms and oistodontiforms (see below) supports the ratio 4:1 calculated by Lindström (1971) for the *Drepanoistodus* apparatus. Löfgren (1978) also arrived at the same ratio.

(This species is listed as *Drepanoistodus* n.sp. A in Fåhraeus and Hunter 1981: Table 1).

*Material.* — 530 specimens 344 homocurvatiforms, 63 suberectiforms, and 123 oistodontiforms).

## DISCUSSION and CONCLUSIONS

In our reconstructions of the *Panderodus gracilis* and the *Protopanderodus varicostatus* conodont apparatuses we have shown that these apparatuses are essentially identical in their symmetry relationships and overall architecture. Thus, we are supporting the views of Lindström (1971) that these two genera should be referred to the same superfamily, despite their considerably different element morphologies. Our evidence does not support the reassignment of *Protopanderodus* to the Distacodontacea recently suggested in the Treatise on Invertebrate Paleontology (Bergström in Clark *et al.* 1981). The distacodontacean apparatus, if exemplified by that of *Drepanoistodus* as reconstructed herein, is different in its general structure: it has four rather than five curvature-transition series and the component elements show much less symmetric to asymmetric variation, and three of the curvature-transition series include a characteristic geniculate element.

The curvature-transition series, which we have recognized not only in the three genera discussed herein but also in *Distacodus* Pander, *Drepanodus* Pander, and *Strachanognathus* Rhodes (other possible simple-

-cone genera remain to be studied), we believe to reflect actual apparatus architecture such that each series represents an actual group of elements, i.e. in much the same way as the groups are represented in figs. 1-3. Such groupings would also agree with element groupings found in natural assemblages of apparatuses containing both platforms and ramiforms (cf. Briggs *et al.* 1983).

Although the curvature-transition series appear to be an integral part of some simple-cone apparatuses there are others in which it is not present, e.g. *Scalpellodus*, *Walliserodus*, and 3 new genera described in Fåhræus and Hunter (1985). That is, presence or absence of curvature-transition series would appear to be taxonomically indicative, however, at the present we are uncertain about which suprageneric rank it reflects.

It is also noteworthy, and probably not coincidental, that many ramiforms (e.g. of the genera *Chirognathus*, *Erraticodon*, *Hibbardella*, *Hindeodella*, and *Periodon*) show curvature-transition in the arrangement of cusp and denticles. It would seem reasonable to assume that such curvature-transitions in both simple-cone and more complex apparatuses represent functional constraints which could be assumed (as working hypotheses) to be phylogentically inherited rather than the result of isolated functional adaptations, i.e. an application of the curvature--transition series concept to the study of phylogenetic links between simple-cone conodonts and those with more complex apparatuses would seem to be a potentially fruitful avenue for future research.

The true potential of the concept of the curvature-transition series for phylogenetic and taxonomic studies of simple-cone conodont taxa remains to be tested on a larger material than presented herein, however, it does appear to offer certain possibilities.

In conclusion, the curvature-transition series would seem to be an integral part of the conodont-apparatus of several different simple-cone genera. In the study accounted for herein we have endeavored to show how the systematic variation in curvature of the cusp observable in some conodont elements, when considered in conjunction with the element types recognized in a symmetry-transition series, can result in the reconstruction of morphologically coherent simple-cone conodont apparatuses.

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# SZEREGI PRZEMIAN ZAGIĘCIA JAKO INTEGRALNE CZĘŚCI PEWNYCH PIERWOTNYCH APARATÓW KONODONTOWYCH (PANDERODONTACEA, DISTACODONTACEA, CONODONTATA)

## *Streszczenie*

W zespołach elementów każdego z gatunków konodontów z rodzajów *Drepanoistodus* Lindström, *Panderodus* Ethington i *Protopanderodus* Lindström objawia się zmienność stopnia asymetrii elementów i stopnia zagięcia ich zębów. W obrębie szeregów przemian symetrii (symmetry-transition series) identyfikuje się odrębne typy elementów, symetryczne i asymetryczne — o rosnącym stopniu asymetrii. Proponujemy wprowadzenie nowego pojęcia szeregów przemian zagięcia (curvature-transition series) obejmujących formy elementów o wzrastającym stopniu zagięcia zęba w obrębie każdego z członów szeregu przemian symetrii. Spośród rozpatrywanych rodzajów, rodzaje *Panderodus* i *Protopanderodus* (obydwa z nadrodziny Panderodontacea) obejmują aparaty o zasadniczo podobnych szeregach przemian symetrii i zagięcia, podczas kiedy *Drepanoistodus* (Distacodontacea) ma odmienny typ szeregu przemian symetrii i inną liczbę szeregów przemian zagięcia. Uważamy szeregi przemian zagięcia za odrębny rodzaj charakterystyki taksonomicznej jednostek rangi ponadrodzajowej.