

# BEDDING PLANE ASSEMBLAGES OF *PROMISSUM PULCHRUM*, A NEW GIANT ASHGILL CONODONT FROM THE TABLE MOUNTAIN GROUP, SOUTH AFRICA

by J. N. THERON, R. B. RICKARDS and R. J. ALDRIDGE

**ABSTRACT.** *Promissum pulchrum* Kovács-Endrödy, 1986, originally described as the earliest vascular land plant or an ancestor of the same, is shown to be a conodont. The species is represented by several spectacular bedding plane assemblages which occur in the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, near Clanwilliam, South Africa. Invertebrate fossils from the Soom Shale indicate a late Ashgill (late Rawtheyan to Hirnantian) age. The conodont assemblages are the largest known, reaching 17 mm in length, with individual ramiform elements as long as 14 mm. The apparatuses are octomembrate with 2Pa, 2Pb, 2Pc, 2M, 1Sa, 4Sb, 2Sc and 2Sd elements. The possession of three pairs of P elements and a fully developed Sa-Sd symmetry transition series distinguishes *Promissum* from any other known conodont genus. The arrangement of the elements is unlike that shown by Carboniferous polygnathacean assemblages and implies a significantly different apparatus architecture. *Promissum* probably represents a cold-water Gondwanan lineage that survived the late Ordovician extinction event, and may well have given rise to the radiation of the Pterospirontidae in the warmer Llandovery seas.

THE name *Promissum pulchrum* is unlike those commonly used for conodonts, and reflects the fact that Kovács-Endrödy (in Theron and Kovács-Endrödy 1986) originally described these fossils as the earliest known vascular land plants or their ancestors. The binomen means 'beautiful promise', an allusion to the perceived potential of the species in interpreting early land plant evolution. The interpretation of *Promissum* as a plant was not readily accepted by Rayner (1986), a referee of the paper, whose objections were published immediately following the Theron and Kovács-Endrödy (1986) preliminary report. These largely revolved around the lack of information normally required to substantiate a claim for vascular land plant status, principally the presence of tracheids, a cuticle with stomata, and sporangia containing trilete spores with sporopollenin-impregnated walls. Kovács-Endrödy (1986, p. 103) pointed out that her conclusions were based on comparative morphology and that no attempt had been made to obtain tracheids because the specimens were so few in number (twelve, including parts, counterparts and fragments). Scanning electron microscopy had revealed no preserved cell structure, but she took as important criteria the facts that the fossils were distinct, clearly outlined and typical of plants with hard cortical tissues, and that they had well developed spines.

It should be said that identification of these fossils is far from easy, and the attribution of them to the plant kingdom on grounds of general comparative morphology is not so surprising. Only after painstaking study did the present authors manage to establish them unequivocally as conodont apparatuses. The possibility was raised at one stage that they might be graptolites, again not an unreasonable suggestion as some do superficially resemble monograptids (see, for example, Theron and Kovács-Endrödy 1986, fig. 5). Rayner (1986) in his review of Kovács-Endrödy's conclusion referred to one of us (R.B.R.) as having decided that the fossils were *not* graptolites. The same comment is made by Kovács-Endrödy (1987) in her fuller description of *Promissum pulchrum*. These statements are not absolutely correct. R.B.R. examined only one specimen, figured by Kovács-Endrödy (1987) as pl. 3.5 (Pl. 3, fig. 2 herein): his service identification file records it as 'not a

graptolite... looks like a primitive jaw apparatus'. On publication of the Theron and Kovács-Endrödy (1986) paper, R.B.R. borrowed, through the kindness of the Geological Survey of South Africa and J.N.T., the remainder of the collection, quickly confirmed that none were graptolites, and rather more slowly concluded that they were conodonts. At this stage the help of R.J.A. was enlisted.

#### STRATIGRAPHY AND BIOSTRATIGRAPHY

In the rugged mountain ranges of the Southwestern Cape Province of South Africa a laterally persistent argillaceous unit, the Cedarberg Formation, forms a conspicuous and critical marker horizon (c. 120 m) among predominantly arenaceous rocks (3000 m) of the Table Mountain Group (text-fig. 1). The Table Mountain Group is the basal unit of the Cape Supergroup and rests unconformably on Precambrian metasediments and the Cape Granite Suite, which has been dated radiometrically at 500 to about 610 Ma (Burger and Coertze 1973; Schoch, Leygoine and Burger 1975). It is overlain conformably by the fossiliferous Emsian Bokkeveld Group.

The Cedarberg Formation thins northwards with concurrent thickening of the underlying glacial Pakhuis Formation, and is broadly divisible into two members: a lower Soom Shale Member and an upper Disa Siltstone Member (text-fig. 2). The dark grey, predominantly thinly laminated, micaceous Soom Shale Member seldom exceeds 15 m in thickness. It grades into or is intercalated with the underlying tillite of the Pakhuis Formation. Towards the north these basal units of the Cedarberg Formation in places display varvites/rhythmites and dropstones.

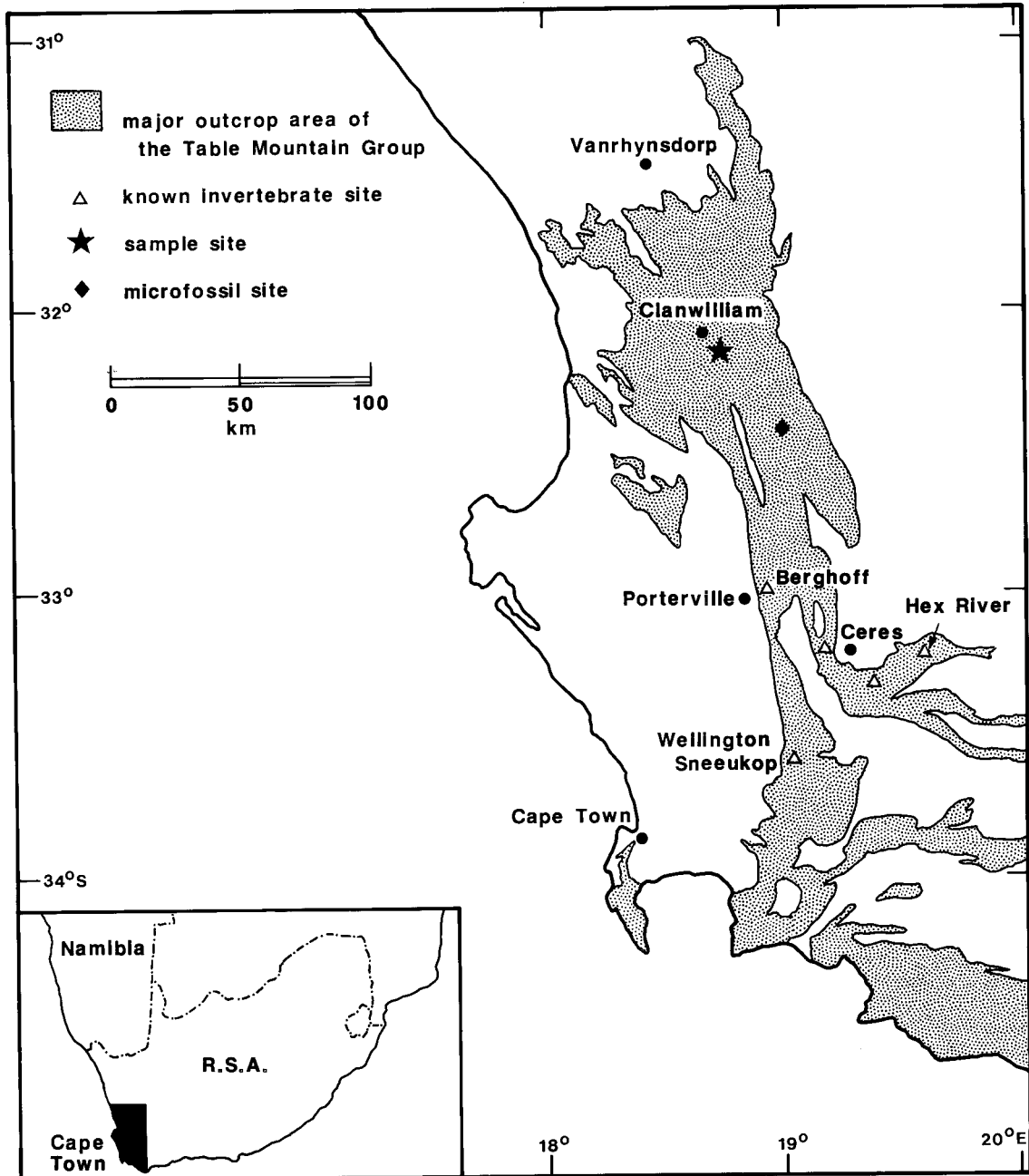
The Disa Siltstone Member is a thin-bedded argillaceous, fine-grained, sandy siltstone. Rare thin sandstone lenses become more prominent upwards, resulting in a gradational contact with the overlying Goudini Formation of the Nardouw Subgroup. Approximately in the middle of the Disa Siltstone Member in the Porterville-Wellington area occurs the 'brachiopod zone' in which Rust discovered a shelly fauna (Cocks *et al.* 1970; Cocks and Fortey 1986).

Body fossils from the Cedarberg Formation are as yet restricted to the western outcrops, and those on the farm Keurbos, about 11.5 km south-east of Clanwilliam, represent the northernmost fossiliferous occurrence known (text-fig. 3). The specimens of *Promissum* described in this paper all come from the base of the Soom Shale Member on Keurbos and were collected by J. N. Theron, J. H. Bredell and D. J. Barnardo of the Geological Survey in 1981. The associated fossils include rare scolecodonts, unidentified trace fossils, and a dark-coloured tube-like fossil which Kovács-Endrödy (1987) referred to the plant *Eohostimella* Schopf.

Quarrying for road metal has revealed that the Soom Shale locally attains a thickness of 6.5 m and contains a variety of invertebrate fossils. A 50 cm thick layer of partly bedded reworked glacial sediment interposes here between the underlying Pakhuis tillite and the shale unit. Systematic investigation of the quarry face has revealed two distinct levels at which *Promissum* and '*Eohostimella*' preferentially occur, 1.2 and 2.5 m above the Pakhuis/Soom contact. *Promissum* fragments are also present in the uppermost 5 cm of the reworked glacial bed, only 45 cm above the Pakhuis tillite. The Soom Shale Member at Keurbos is often conspicuously finely laminated with the individual laminae extensively characterized by linear and/or sinuous surface trails. *Promissum* and '*Eohostimella*' are infrequently present on the same laminar surface as brachiopods.

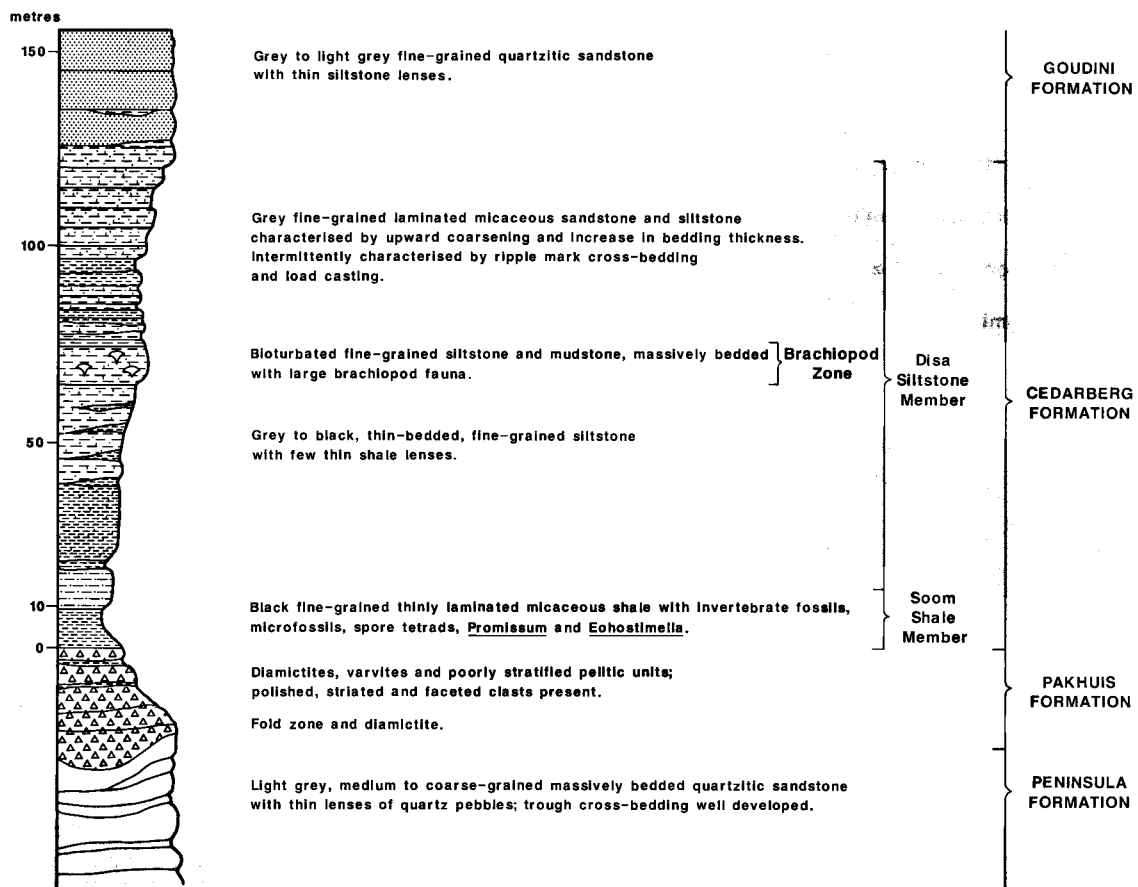
At least two major advances of the Gondwana ice sheet are registered in the glaciogenic deposits of the Pakhuis Formation (Rust 1967, 1981). The concurrent glacioeustatic fall in sea level resulted in partial reworking of glaciogenic deposits by coastal processes in a shallow marine embayment. The Cedarberg Formation was deposited during the succeeding glacioeustatic rise in sea level and represents the outwash silt and mud from the retreating ice sheets. Downwasting of the ice would have uncovered local embayments (ice-dammed?) along the northern shoreline which were probably flooded with fresh glacial melt-waters. The fine mud was clearly deposited towards the north in glaciolacustrine to shallow marine environments as shown by the presence of chitinozoans, marine phytoplankton, brachiopods, algae and spore tetrads in the same samples or in close proximity (Cramer *et al.* 1974; Gray *et al.* 1986). Varvites do not form in seawater (Flint 1971; Wright and Moseley 1975), but are commonly deposited seasonally in glacial lakes as graded layers. The finely laminated sediments at Keurbos with their biota of *Promissum*, '*Eohostimella*' and brachiopods manifestly accumulated in a protected still-water marine environment rather than in a proglacial lacustrine setting as previously envisaged (Theron and Kovács-Endrödy 1986).

Theron and Kovács-Endrödy (1986) regarded the basal Soom Shale Member at Keurbos as probably early Silurian (Llandovery) on the basis of spore tetrads, phytoplankton and chitinozoans (Gray *et al.* 1986). However, Cocks and Fortey (1986) demonstrated that the Soom Shale Member at Buffels Dome in the Hex



TEXT-FIG. 1. Locality map showing the distribution of the Table Mountain Group, the microfossil site reported by Gray *et al.* (1986) and the sample site for the specimens of *Promissum pulchrum*.

River Mountains is late Ashgill (late Rawtheyan to Hirnantian) in age. The crucial element in the fauna is the trilobite *Mucronaspis olini*, which on all known records is late Ashgill; none of the other elements of the fauna contradict this. Buffels Dome is more than 100 km from Keurbos and diachronism cannot yet be ruled out, but the same authors reviewed the evidence for the age of the overlying Disa Siltstone Member and concluded from the presence of brachiopods, including *Trematis taljaardi* Rowell, *Marklandella africana* Cocks and



TEXT FIG. 2. Schematic stratigraphic profile.

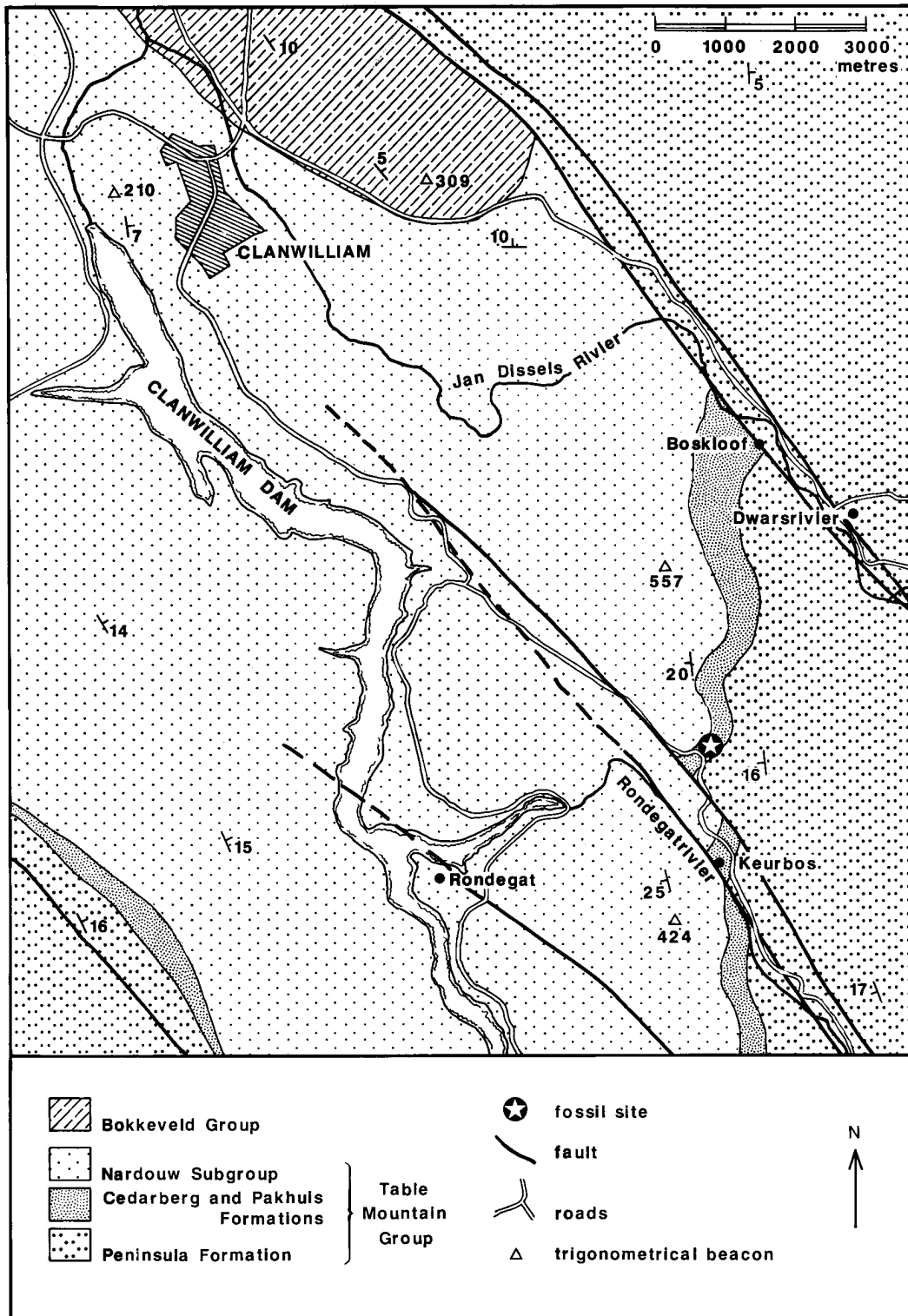
Brunton, *Eostropheodonta discumbata* Cocks and Brunton and *Plectothyrella haughtoni* Cocks and Brunton, that it is Hirnantian. Thus we regard *Promissum pulchrum* as more likely to be of late Rawtheyan to Hirnantian age, rather than Silurian.

## PALAEOLOGY

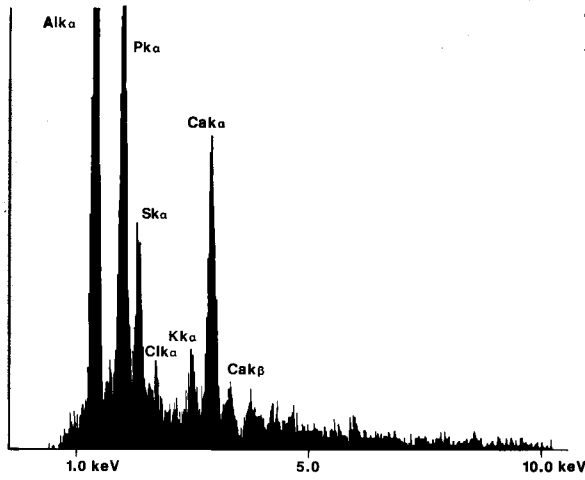
### Introduction

Our examination of the specimens of *Promissum pulchrum* has shown that they are bedding-plane assemblages and isolated elements of conodonts. They are remarkable in several ways, not least in their spectacular size. The ramiform elements in the largest assemblage are more than 14 mm long, with the whole assemblage having a length of 17 mm. The elements are robust with peg-like denticles, between some of which finer denticles are apparent. Preservation of the original apatite is poor, with several of the elements represented only by internal and external moulds. In others the phosphate has been leached or replaced by clay minerals to give a pale greenish appearance. On analysis, this material gave peaks in aluminium, silicon and potassium. Peaks in calcium and phosphorus were obtained from some relatively unaltered amber-coloured areas of one of the ramiform elements (text-fig. 4).

The anterior and posterior ends of the assemblages can be determined from the anterior cusps and posterior processes of the ramiform elements. Beyond this, orientation is problematical, as almost all the elements have their 'upper' surfaces directed inwards and it is impossible to tell whether the

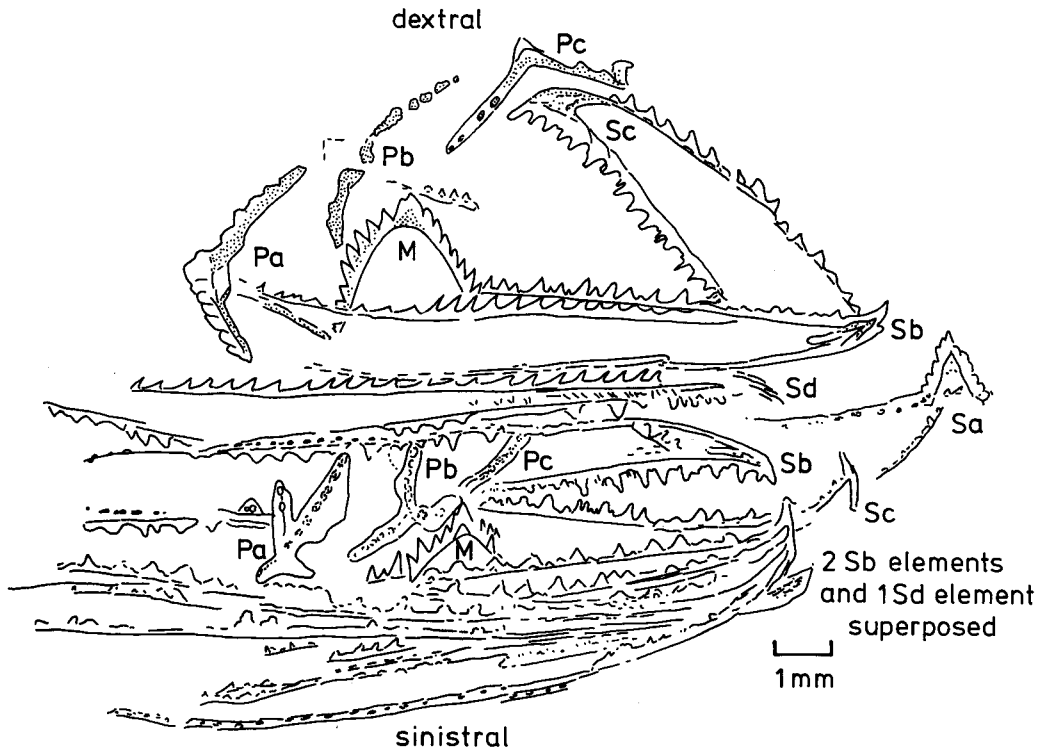


TEXT-FIG. 3. Geological map of the Clanwilliam area, showing the sample site.



TEXT-FIG. 4. Electron microprobe analysis of an amber-coloured area in a ramiform element of specimen C.1., showing principal excitation peaks.

assemblages are being viewed from above or below. The only guide is provided by the Pa and Pb elements in the central area of the holotype. On the counterpart (C.2b-I, text-fig. 5), these are preserved as deep external moulds, showing that their oral (conventionally 'upper') surfaces were directed into the bedding plane; they are thus being viewed from below, which indicates that they are situated on the sinistral side of the assemblage. This designation has been adopted in the description and discussion of specimens in this paper, but it should be emphasized that this is based



TEXT-FIG. 5. Camera lucida drawing of the counterpart of the holotype of *Promissum pulchrum*, specimen C.2b-I, for comparison with Pl. 1, fig. 2. The anterior of the apparatus is to the right.

on conventional orientation of the Pa and Pb elements alone and does not necessarily relate to actual left and right sides of the *Promissum* animal.

*Systematic palaeontology*

Genus PROMISSUM Kovács-Endrödy, 1986

*Type species.* *Promissum pulchrum* Kovács-Endrödy, 1986, from the basal Soom Shale Member, Cedarberg Formation, of Keurbos, near Clanwilliam, South Africa; by monotypy.

*Diagnosis (emend.).* Apparatus octomembrate, with 2Pa, 2Pb, 2Pc, 2M, 1Sa, 4Sb, 2Sc and 2Sd elements. Pa and Pb elements pastinate with deep basal cavities, M element arched, S elements with long processes.

*Remarks.* The apparatus is unlike that of any other known genus in possessing three pairs of P elements in conjunction with a fully developed Sa–Sd symmetry transition series.

*Promissum pulchrum* Kovács-Endrödy, 1986

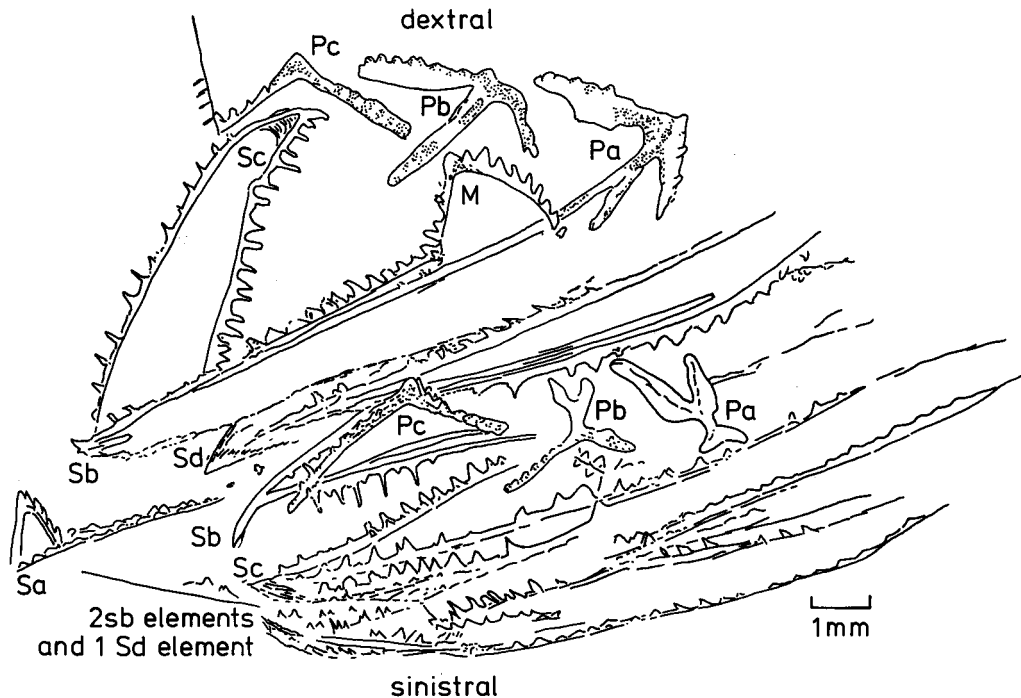
Plates 1–3; text-figs. 5–8

1986 *Promissum pulchrum* Kovács-Endrödy in Theron and Kovács-Endrödy, p. 102, figs. 4 and 5.

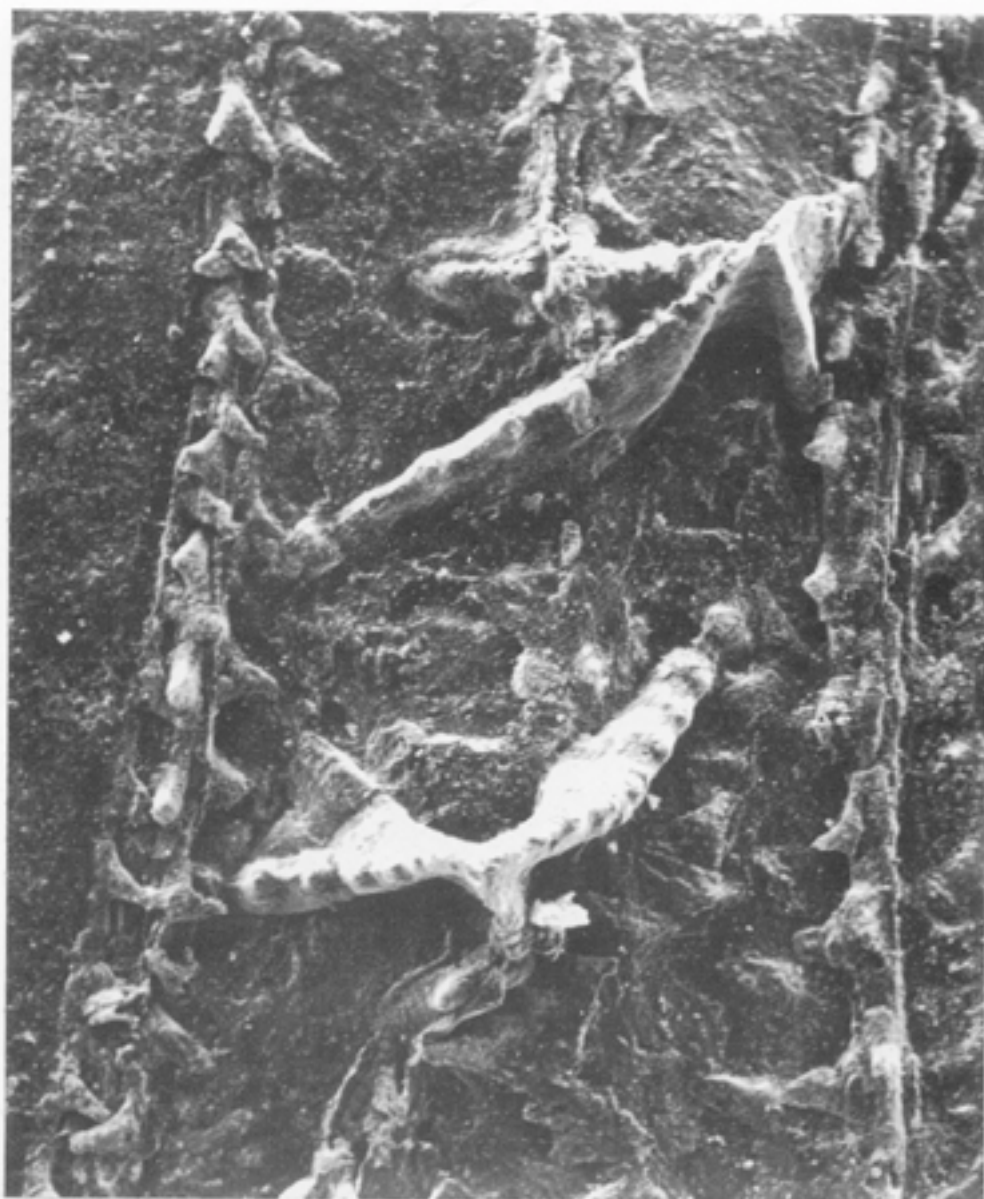
1987 *Promissum pulchrum* Kovács-Endrödy; Kovács-Endrödy, p. 99, pls. 3.1–3.22.

*Holotype.* Specimen C.2a, Geological Survey of South Africa, Pretoria.

*Material.* We have examined most of the specimens figured by Kovács-Endrödy (1987): the holotype C.2a (Pl. 2, text-fig. 6), its counterpart, C.2b-I (Pl. 1, fig. 2, text-figs. 5, 7, 8), assemblages C.1 (Pl. 3, figs. 1 and 4) and



TEXT-FIG. 6. Camera lucida drawing of the part of the holotype of *Promissum pulchrum*, specimen C.2a. The anterior is to the left.

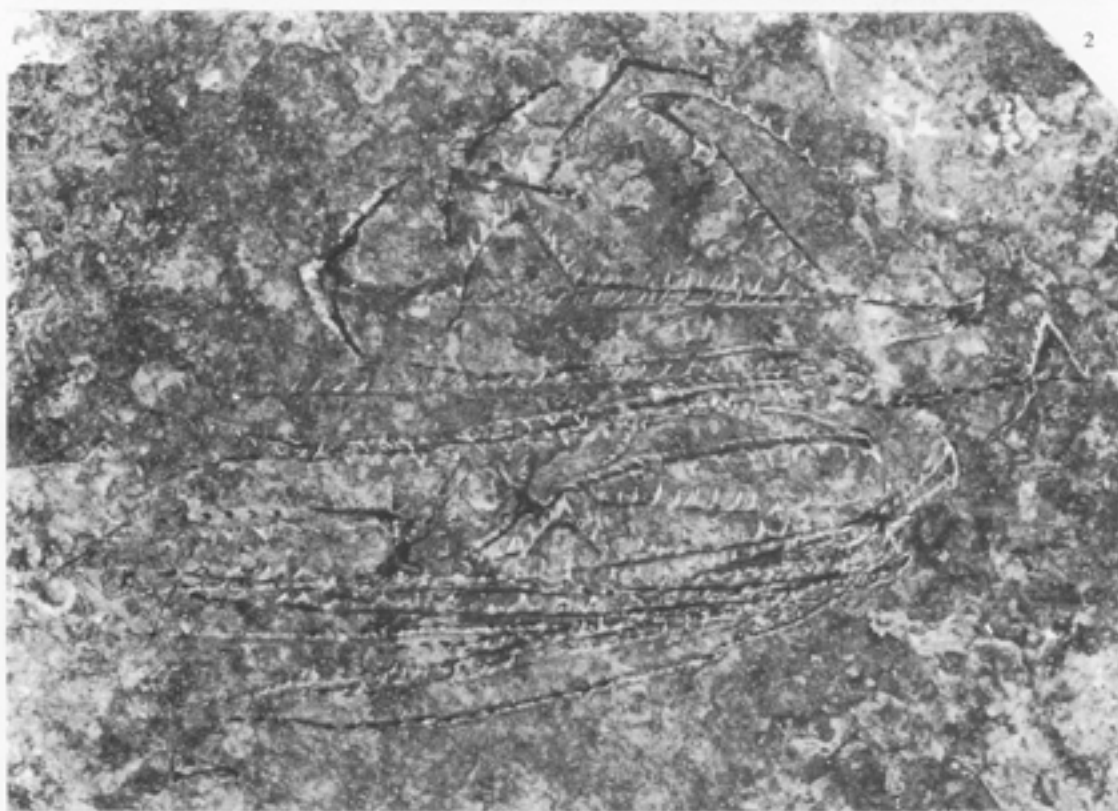


TEXT-FIG. 7. Scanning electron micrograph of latex cast of portion of counterpart of holotype, specimen C.2b-I, showing Pa element (above, centre), Pb element (below, centre) and portions of the processes of ramiform elements; posterior towards top,  $\times 35$ .

#### EXPLANATION OF PLATE I

Figs. 1 and 2. *Promissum pulchrum* Kovács-Endrődy. 1, latex cast of specimen C.2b-II. Anterior to the right,  $\times 13.5$ . 2, specimen C.2b-I, counterpart of holotype. Anterior to the right,  $\times 7.5$ . For annotation of the elements see text-fig. 5.





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C.2b-II (Pl. 1, fig. 1), and isolated element C.6 (Pl. 3, fig. 2). The poorly preserved specimen numbered C.81 (Kovács-Endrödy 1987, pl. 3.6) and the unfigured specimen C.3 have not been included in our study.

*Diagnosis.* As for genus.

*Description.* Pa element: pastinate, high, with deep basal cavity; probably thin-walled. Cusp apical, stout; anterior, posterior and primary lateral processes with discrete nodose median denticles. Primary lateral process long, secondary lateral process short and apparently adenticulate.

Pb element: pastinate, high, with deep basal cavity; probably thin-walled. Anterior, posterior and primary lateral processes with discrete nodose median denticles. Primary lateral process long; distribution of secondary lateral processes unclear, but process disposition appears to differ from that shown by Pa element.

Pc element: indistinct, but with at least two denticulate processes diverging widely from a prominent triangular cusp.

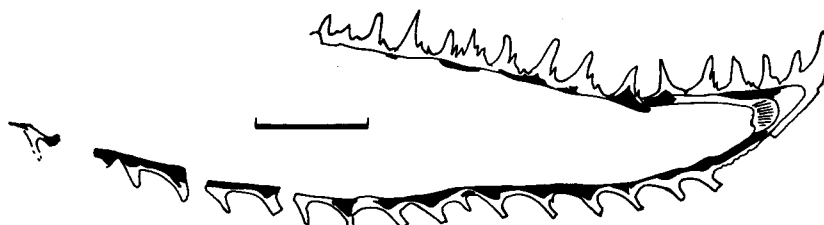
M element: symmetrically arched, with a prominent cusp and discrete, erect, robust denticles on each process. Basal cavity at apex of arch, with lip on outer side.

Sa element: alate, probably with long posterior process. Lateral processes diverge at 40–50° to form an anterior arch; very long, but broken about 1 mm from apex on all specimens, distal portions extend posteriorly for several millimetres. Proximal denticles stout, widely-spaced with u-shaped separations and no evidence of intercalatory smaller denticles; denticulation beyond 1 mm indistinct. Basal cavity apparently conical with small lips.

Sb element: teriopodate, with very long posterior process bearing regular, stout, erect, large denticles between which smaller, slender denticles are irregularly recognizable. Antero-lateral process also long, curved proximally to become sub-parallel to posterior process, with widely-spaced, stout, conical denticles of subequal size. Outer lateral process not clearly preserved on any specimens, may be short and adenticulate or perhaps broken. Basal cavity small and conical beneath small erect cusp.

Sc element: bipennate, with very long posterior process displaying similar denticulation to that of the Sb element (text-fig. 8). Antero-lateral process strongly curved proximally to become nearly parallel to posterior process; very long and bearing widely-spaced conical denticles that are directed inwards and somewhat downwards. Basal cavity conical beneath a relatively small, erect cusp.

Sd element: quadriramate, with all four processes probably very long. Posterior process with similar denticulation to that of the Sb and Sc elements; other processes may have widely-spaced conical denticles, but they are difficult to distinguish. Cusp small and erect.



TEXT-FIG. 8. Camera lucida drawing of dextral Sc element of specimen C.2b-I, showing details of denticulation; scale bar 1 mm.

*Remarks.* Since Kovács-Endrödy (1987) considered *Promissum* to be a plant, she provided interpretations of various features of the specimens on that basis. These features are highlighted on the twenty-two illustrations of *Promissum* in her paper. Our recognition of the specimens as conodonts necessitates a re-interpretation, and we would caption her figures as follows:

#### EXPLANATION OF PLATE 2

*Promissum pulchrum* Kovács-Endrödy, specimen C.2a, holotype, photographed under alcohol. Anterior at the top,  $\times 9$ .



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- pl. 3.1 holotype of *P. pulchrum*, C.2a; complete octomembrate bedding-plane assemblage (see Pl. 2 herein).
- pl. 3.2 dextral portion of counterpart of holotype, C.2b-I; elements mostly preserved as external moulds. To the left are the P elements, the arrow points to the M element and the long processes of the S elements are evident in the centre and right of the picture. The displaced dextral Sc element is at top left.
- pl. 3.3 faintly preserved complete assemblage, C.2b-II; (a) cusps of ramiform S elements, (b) P element, (c) distal portion of S elements (see Pl. 1, fig. 1 herein).
- pl. 3.4 complete assemblage, C.1 (see Pl. 3, fig. 1 herein).
- pl. 3.5 isolated quadriramate Sd element, only proximal portion preserved (see Pl. 3, fig. 2 herein).
- pl. 3.6 poorly preserved processes of an S element.
- pl. 3.7 anterior portion of assemblage C.1, arched Sa element at the top of the picture (see Pl. 4 herein).
- pl. 3.8 cusps and proximal parts of two dextral S elements, C.2a.
- pl. 3.9 holotype, C.2a; (1) sinistral Pb element, (2) sinistral Pa element, (3) dextral Pa element, (4) dextral Pb element, (a) dextral Sb element, (b) axial portion of ramiform element group, (c) displaced dextral Sc element.
- pl. 3.10 dextral Pa element, C.2a.
- pl. 3.11 dextral Pb element, C.2a.
- pl. 3.12 portion of specimen C.2a, to show process disposition on Pa elements.
- pl. 3.13 sinistral Pa element, C.2a.
- pl. 3.14 Pa element, C.1.
- pl. 3.15 Pc element, C.1.
- pl. 3.16 central portion of complete assemblage, C.1.
- pl. 3.17 proximal portion of dextral Sb element, C.2a; the process on the right side of the photograph is part of the lateral process of the displaced dextral Sc element and shows robust denticles in lateral view.
- pl. 3.18 axial portion of the ramiform element group, showing opposition of denticulate surfaces, C.2a.
- pl. 3.19 proximal portion of dextral Sc element and dextral Pc element, C.2a.
- pl. 3.20 part of a process on the quadriramate Sd element C.6, showing robust denticles in apical view.
- pl. 3.21 enlargement of processes on S elements of C.1, showing robust denticles in apical view.
- pl. 3.22 cusp of dextral Sb element and portion of lateral process of displaced dextral Sc element, C.2b-I.

*Arrangement of the assemblages and the architecture of the Promissum apparatus*

The arrangement of the elements is most clearly displayed by the counterpart and part of the holotype (text-figs. 5 and 6), in which two integrated sets are evident:

(i) The elements of the first symmetry transition series (*sensu* Barnes *et al.* 1979). The Sb, Sc and Sd elements are orientated with their posterior processes parallel; other processes of these elements diverge at the cusp, but become parallel to the posterior processes distally. On the sinistral side of the assemblage these elements are piled on each other, with the cusps and denticulate surfaces of the posterior processes directed inwards. On the dextral side the elements are more widely separated. One of the dextral Sb elements and the probable Sd element are orientated in opposition to the sinistral elements, whereas the second Sb element has become overturned to face outwards. The dextral Sc element is also overturned and the proximal portion is displaced so that the long processes are directed inwards and somewhat anteriorly. The Sa element is positioned to the anterior of the other elements, displaced dextrally from the axis with the cusp pointing dextrally; the lateral processes are broken, with the distal portions parallel or subparallel to the processes of the other S elements.

(ii) the elements of the second transition series (*sensu* Barnes *et al.* 1979). The P elements are arranged in two parallel rows, aligned along an axis at 30° to that of the S elements. Those of the sinistral side are superposed on the processes of the S elements, but those on the dextral side are

EXPLANATION OF PLATE 3

Figs. 1 and 2. *Promissum pulchrum* Kovács-Endrődy. 1, specimen C1. Anterior at the top of the picture, ×9. Specimens of '*Eohostimella*' are apparent around and across the apparatus. 2, specimen C.6. Single, isolated quadriramate Sd element. Anterior at the top, ×22.





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positioned largely outside the members of the first transition series. On the dextral side the Pa and Pb elements are in lateral aspect, whereas on the sinistral side of the part they are in upper view. The M element on each side is immediately to the left of its companion Pb element, with the cusp directed dextrally. As with the M elements, the Pc elements are in similar positions but apparently in opposing orientation on the two sides of the assemblage. The dextral Pc element on the counterpart has its denticulate posterior process directed away from the bedding surface while the equivalent process on the sinistral member is preserved as an external mould. The revealed face of the sinistral M element has a clear lip to the basal cavity that is not apparent on that of the dextral element.

The bilateral symmetry retained by the two sets of elements shows that the assemblage has been compacted in close to a dorso-ventral configuration. The displacement of the outer Sb and Sc elements on the dextral side, together with the apparent dextral shift of the axial Sa element, indicate that the apparatus was tilted a little to that side before it collapsed onto the bedding plane. This tilting has also displaced the P and M elements towards the right and may account for the different orientations of the Pa and Pb elements on the two sides.

The other two assemblages we have examined add little information about the relative dispositions of the elements in the apparatus. The second, less well preserved, assemblage (C.2b-II, Pl. 1, fig. 1) on the same slab as the counterpart of the holotype displays a similar arrangement of the two sets of elements, except that the upper surfaces of the Pa and Pb elements face inwards. The elements of the third assemblage (C.1, Pl. 3, fig. 1) are superposed on each other, giving a much more crowded arrangement in which the P and M elements cannot all be clearly distinguished; the anterior portion of the Sa element is separated from the others at the front of the apparatus in exactly the same manner as in the holotype (Pl. 4). The fact that all three specimens are preserved in close to dorso-ventral compaction may suggest that the *Promissum* animal was dorso-ventrally flattened in life, in contrast to the lateral flattening deduced for Carboniferous polygnathaceans (Aldridge *et al.* 1987).

In the absence of an assemblage compacted in lateral aspect, it is impossible to produce a reconstruction of the three-dimensional architecture of the *Promissum* apparatus. However, the evidence from these three specimens does place constraints on that architecture and reveals several important differences from the structure of polygnathacean apparatuses, as deduced from the study of several Carboniferous bedding-plane assemblages preserved in different orientations by Aldridge *et al.* (1987). In the polygnathaceans, the elongate, ramiform S elements were aligned at a steep angle to the long axis of the conodont animal, with their cusps to the anterior and an M element flanking them on each side; to the posterior of this group were one pair each of Pb and Pa elements, lying nearly vertically and nearly normal to the trunk. In *Promissum*, the M elements are clearly associated geometrically with the P elements, rather than with the S elements. In addition, unless the head of the *Promissum* animal has collapsed anteriorly on to the bedding-plane in all three known specimens, it appears that the P and M elements may not have been positioned posterior to the S elements in this apparatus. The superposition of the P and S elements suggests that the former were situated above or below the denticulate processes of the latter, although with the currently limited material it cannot be discounted that the two sets of elements may have been brought into juxtaposition by muscular contraction. Whether the cusps of the P elements were directed inwards or towards the S elements cannot be determined, but their position at least suggests that an analogy with the palatal tooth of the myxinoids is worthy of investigation.

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#### EXPLANATION OF PLATE 4

*Promissum pulchrum* Kovács-Endrődy, specimen C1. Anterior area of apparatus, showing proximal portions of ramiform S elements. Anterior at the top,  $\times 30$ .

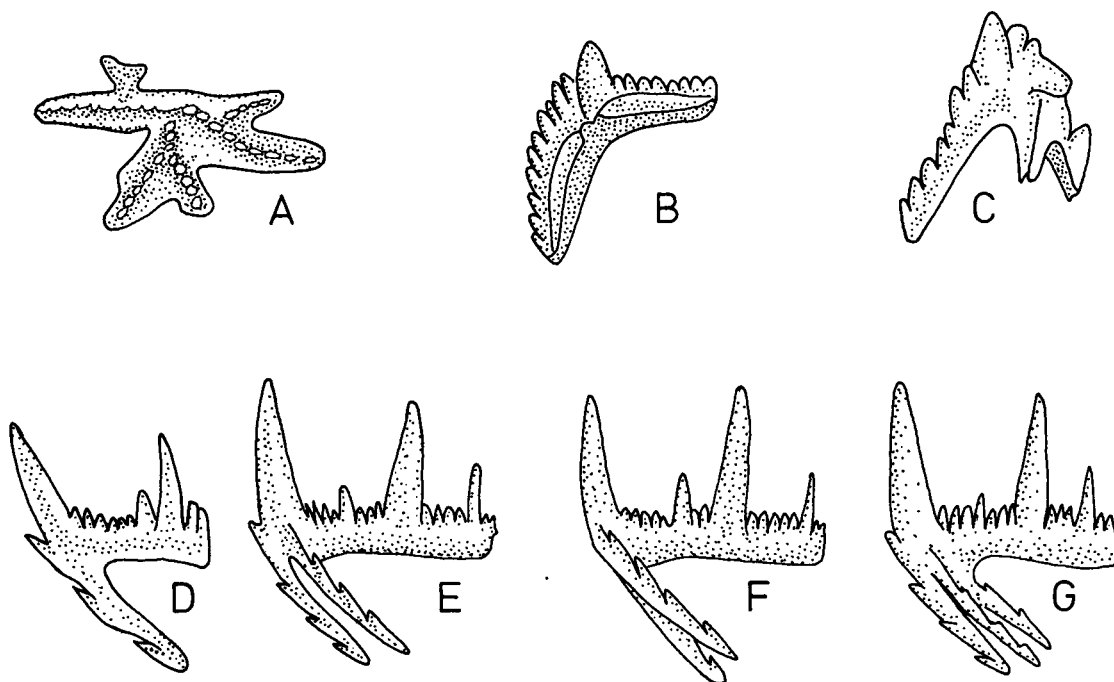


THERON, RICKARDS and ALDRIDGE, *Promissum*

RELATIONSHIPS OF *PROMISSUM* AND EVOLUTIONARY IMPLICATIONS

One of the striking features of *Promissum* is its extremely large size. Gigantism is not uncommon in cold-water taxa, although the controls in this case are uncertain. In other features, *Promissum* differs less spectacularly from other coeval conodont taxa. The apparatus structure broadly conforms to a prioniodontacean plan, although differing somewhat from all other genera whose apparatuses are known. The Sa–Sd elements compare in general pattern with those of the Ordovician genera *Prioniodus* Pander and *Amorphognathus* Branson and Mehl (Bergström 1971, 1983; see text-fig. 9), but the very long processes are distinctive. The M element is totally unlike that of *Prioniodus*, which is falodiform, or that of *Amorphognathus*, which is holodontiform. The Pa and Pb elements do resemble specimens that have been assigned to *Prioniodus*, but are most similar to the Pa element of *Sagittodontina* Knüpfel. The apparatus of *Sagittodontina* has been reconstructed by Bergström (1983), who included ramiform elements with very short processes, dissimilar from those displayed by the South African specimens. The material illustrated by Knüpfel (1967) from the same collections as the original specimens of *Sagittodontina* does include some broken specimens that may be comparable with some of the ramiform elements in *Promissum*, but nothing resembling the arched M element is reported. There have been no suggestions that *Sagittodontina*, *Prioniodus* or any other Ordovician genus possessed three pairs of P elements.

Some Silurian genera may well have had Pa, Pb and Pc elements homologous with those of *Promissum*. A quinquemembre apparatus with three pairs of P elements has been reconstructed for *Pterospathodus* Walliser by Männik and Aldridge (1989), who also recognized Pa, Pb and Pc elements in their new genus, *Pranognathus*. Three P elements, termed Pa<sub>1</sub>, Pa<sub>2</sub> and Pb were described in *Apsidognathus* Walliser by Uyeno and Barnes (1983), and comparable elements occur in



TEXT-FIG. 9. Element types in the apparatus of *Amorphognathus tvaerensis* Bergström for comparison with *Promissum pulchrum*; redrawn after Bergström (1983). A, Pa element, upper view; B, Pb element, lateral view; C, M element, lateral view; D, Sc element, lateral view; E, Sb element, lateral view; F, Sa element, lateral view; G, Sd element, lateral view.



*Astropentagnathus* Mostler. None of these genera have first transition series comparable with that of *Promissum* and quadriramate Sd elements, in particular, are unknown in Silurian taxa. Only in *Astropentagnathus* does the M element have a symmetrically arched morphology.

*Pterospathodus*, *Astropentagnathus* and *Apsidognathus* were all included by Klapper (1981) in the family Pterospathodontidae, which appears cryptically in the mid-Llandovery (Männik and Aldridge 1989). The earliest representatives are currently assigned to *Pranognathus*, which possesses thin-walled Pa, Pb and Pc elements, a dolabrate M element and a first transition series of Sa, Sb, Sc<sub>1</sub> and Sc<sub>2</sub> elements; related later Llandovery genera have more robust P elements, and in *Pterospathodus* the first transition series comprises only an Sa/Sb element. It is possible that *Promissum* represents a stock from which this group of genera descended by reduction of the first transition series. The radiation of the Pterospathodontidae may thereby reflect a spreading into warm Llandovery seas of a cold-water Gondwanan lineage that survived the late Ordovician extinction event.

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