REINTERPRETATION OF THE LOWER ORDOVICIAN CONODONT APPARATUS *PAROISTODUS*

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ABSTRACT. The lower Ordovician conodont genus *Paroistodus* has previously been interpreted as a two-element apparatus, although with wide variation among its 'drepanodontiform' elements. Collections of conodonts from a series of Swedish sections include almost 75000 elements of four successive species of *Paroistodus*: *P. numarcuatus* from the upper Tremadoc, *P. proteus* from the uppermost Tremadoc and lowermost Arenig, *P. parallelus* from the lower Arenig, and *P. originalis* from the lower middle Arenig to the lower Llanvirn. These species are probably those best known of the genus, and it is shown here that they all have a seven-element apparatus, closely comparable to that of *Drepanodus*.

NICOLL (1990) established a seven-element apparatus model for *Cordylodus angulatus* Pander and some other species of the same genus, the earliest conodonts with ramiform (denticulate) elements. That investigation showed the importance of large collections of elements when making such reconstructions. His careful and detailed descriptions of all element types recognized in *C. angulatus* enabled me not only to identify these in my own collections, but also to find what I consider to be the homologous elements in the coniform (non-denticulate) apparatus of *Drepanodus arcuatus* Pander. Although my interpretation of apparatus reconstructions of these two species differs slightly from those of Nicoll (1990, 1994, 1995, p. 253), his investigations put me 'on the right track'.

The apparatus for *Drepanodus arcuatus* arrived at is also close to that suggested by Dzik (1994). It is intriguing that *Cordylodus*, with a stratigraphical record from the Upper Cambrian to the upper Tremadoc, and *Drepanodus arcuatus*, which first appeared in the Tremadoc, should have such similar element arrangements. The element model in these early taxa should be close to the original seven-element conodont apparatus. The next step was to test this model for other Tremadoc taxa. As *Paroistodus* is the genus that most closely resembles *Drepanodus*, observations were concentrated on *Paroistodus numarcuatus* and its successors.

In faunas with *D. arcuatus* and *P. numarcuatus*, the Pb elements in particular, and also some of the S elements of the two species are very similar. Like *Drepanodus*, *Paroistodus* has a recurved Sa (symmetrical) element, unlike the suberect Sa elements of *Paltodus* and *Drepanoistodus*. This investigation was started by looking for those elements in the earliest species of *Paroistodus*, the Tremadoc *P. numarcuatus*, that were homologous with those distinguished in *D. arcuatus*. On discovering these, similar homologies were sought in the later species *P. proteus* (Lindström), *P. parallelus* (Pander) and *P. originalis* (Sergeeva). A general septimembrate model for *Paroistodus* was thus produced, which is presented below.

MATERIAL

The conodont elements used for the apparatus reconstructions presented here are from Ordovician (Tremadoc to Llanvirn; Text-fig. 1) rocks from various parts of Sweden. Localities from which material has been used are: Kalkberget, Kloxåsen and sections in the Brunflo area (Löfgren 1978)

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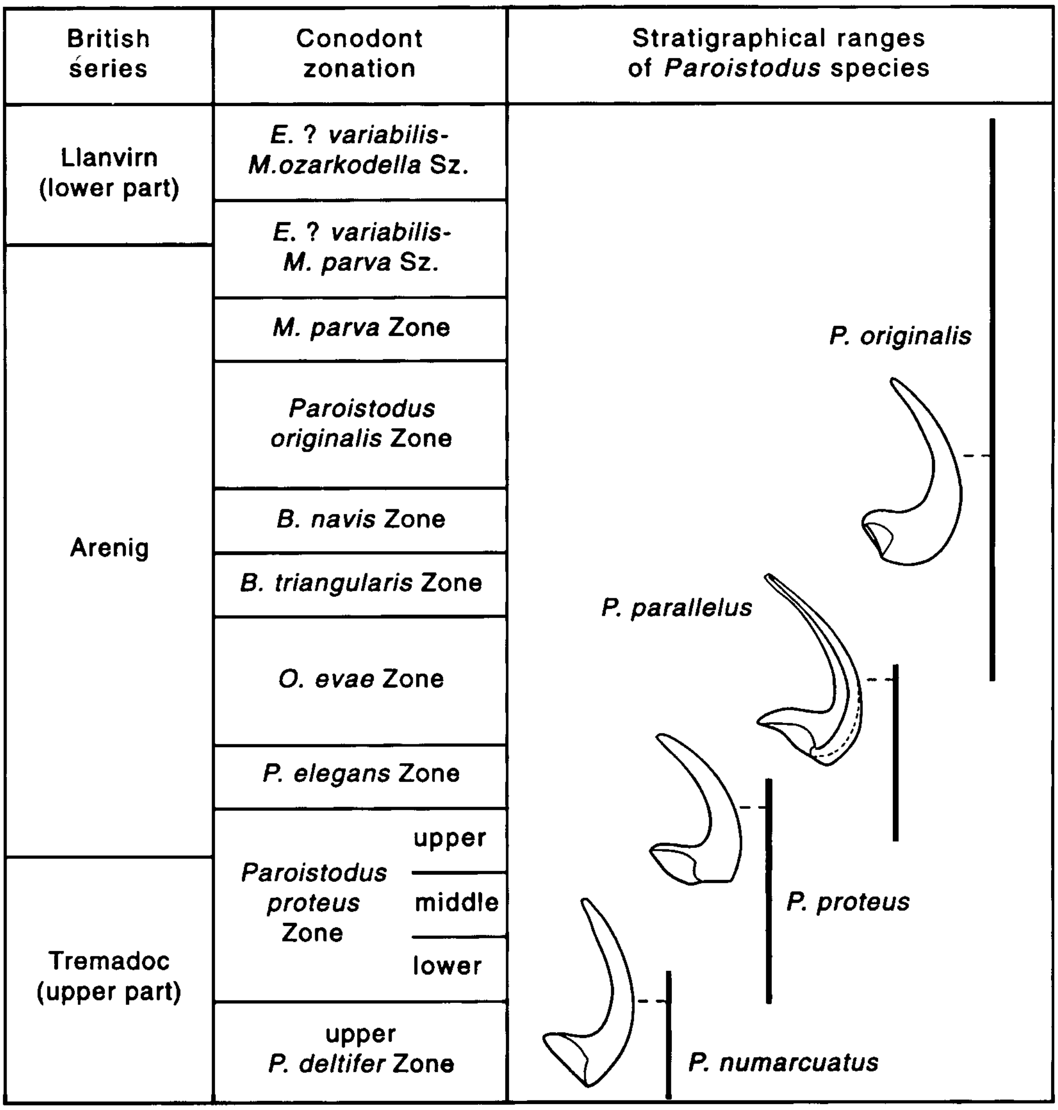


TEXT-FIG. 1. The four successive species of *Paroistodus* in Baltoscandia and their stratigraphical ranges.

and Sommartjärnen (Löfgren 1993*b*) in Jämtland; Finngrundet in the Bothnian Bay (drill core, Löfgren 1985); Sjurberg, Fjäcka and Djupgrav (Löfgren 1994), Talubäcken (Bergström 1988; Löfgren 1995*b*), Rävanäs, Kårgärde and Leskusänget (locations in Löfgren 1995*a*) in Dalarna; Gymninge (Löfgren 1993*b*) and Lanna (Löfgren 1995*b*) in Närke; sections at Hunneberg (Löfgren 1993*a*), Gullhögen, Hällekis and Orreholmen (locations in Löfgren 1995*b*), Brattefors (Teves and Lindström 1988) in Västergötland; Gillberga and Sandvik on North Öland (location in Löfgren 1995*b*) and Ottenby on South Öland (locality description in Tjernvik 1956).

In total, almost 75000 elements of *Paroistodus* were studied. The samples yielding these elements were treated slightly differently over a 25-year period, but those heavily relied upon for the reconstructions and calculations of element ratios were treated with buffered acetic acid (method described by Jeppsson *et al.* 1985) and the residues washed through a 63-micrometer screen.

The preservation is variable; specimens from Leskusänget and Brattefors are in almost pristine condition, while those from Ottenby very often are broken, with some element types more seriously damaged than others. Elements from Hunneberg have been thermally altered, with CAI values (see Epstein *et al.* 1977) varying from 5 to 8; those from Jämtland have a CAI between 3 and 4. All other elements have CAI values of 1–1·5 (almost unaltered).

THE *PAROISTODUS* APPARATUS

Nicoll (1990, 1995) extended the designation system (P, S, and M elements) originally established for younger, ozarkodinid genera (see Sweet 1988 for review) to *Cordylodus* and *Drepanodus*, and it is used herein also for *Paroistodus*. Only well preserved natural assemblages could definitely prove that the element arrangement in these taxa was sufficiently similar to that of, for instance, the upper Ordovician prioniodontid *Promissum* (cf. Aldridge *et al.* 1995) to allow the same designations to be used. The very detailed analyses and comparisons of morphological characters in several taxa made by Nicoll (1990, 1995), however, seem to me to justify such usage. Homologies can be clearly demonstrated to exist between *Cordylodus* and coniform genera such as *Drepanodus* (Nicoll 1990, 1995). Current investigations confirm that the P, S, and M element notation system is applicable also to some other early coniform genera, such as *Rossodus* Repetski and Ethington (Huselbee 1996), *Paroistodus* (herein) and *Paltodus* Pander (Löfgren, unpublished data). For the more advanced coniform genera, such as *Panderodus* Ethington, comparisons using the P, M, and S designations are far more difficult, and alternative notations such as those proposed by Sansom *et al.* (1995) are more useful, at least for the time being.

General characteristics of the element types

Having homologized element types for *Cordylodus angulatus*, *Drepanodus arcuatus* and *Paroistodus numarcuatus* in a few samples with abundant and well preserved specimens (Text-fig. 2), I considered the three succeeding species of *Paroistodus*: *P. proteus*, *P. parallelus* and *P. originalis*. On checking through all the collections for the four *Paroistodus* species and comparing their elements, it soon became clear that seven element types could be distinguished, not only in *P. numarcuatus*, but also in each of the other species. A general description of these element types is given below; for details of each species, see the systematic section.

M element. Geniculate, i.e. there is a sharp angle between the oral edge and the posterior edge of the cusp. The cusp and the posterior part of the aboral margin are subparallel. The cusp is bent inwards in many specimens. The element is makellate *sensu* Nicoll (1990, p. 533).

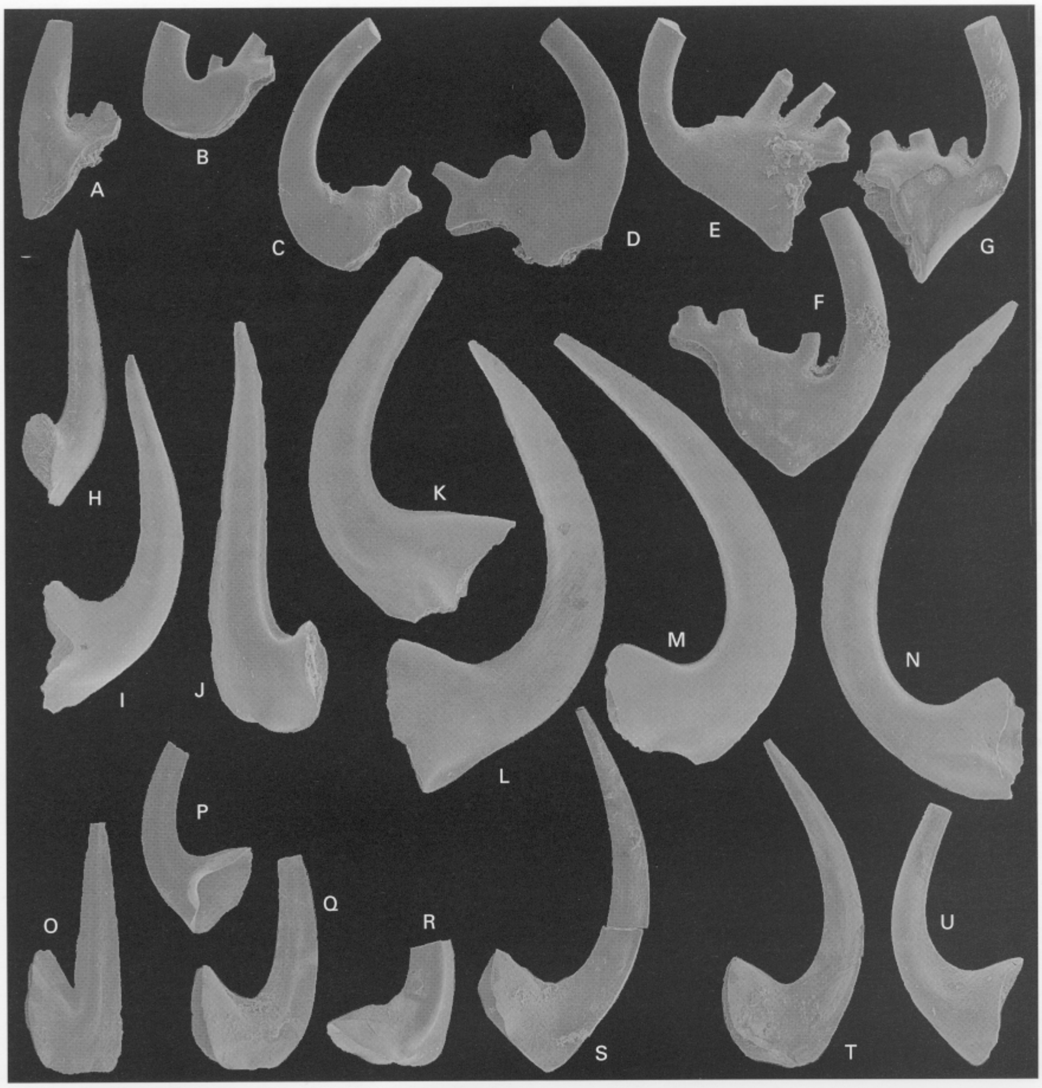
Pa element. Element with one flatter and one more convex side. Details of convexity of the sides, costae and carinae agree with those of the elements in the S series. Most distinctive of this element type is the notch and flare in the aboral margin on the outer side.

Pb element. With a flaring basal cavity, opening to the inner side.

Sa element. Symmetrical, with rather bulging sides. The cusp is at least slightly reclined or recurved, in contrast to Sa elements of *Paltodus* and *Drepanoistodus*.

Sb element. Slightly asymmetrical where the anterior margin is flexed inwards and there is only a small difference in convexity between the inner and the outer side. The distal part of the cusp can be twisted.

Sc element. Almost symmetrical. The base is flat and rhombic in side view and the asymmetry amounts only to a small difference in convexity between the sides.



TEXT-FIG. 2. Comparison of element types in *Cordylodus*, *Drepanodus* and *Paroistodus* from the upper *Paltodus deltifer* Zone. A–G, *Cordylodus angulatus* Pander, 1856; Orreholmen, sample Vg89-B1. A, M element; LO 7219t. B, Pa element; LO 7220t. C, Pb element; LO 7221t. D, Sa element; LO 7222t. E, Sb element; LO 7223t. F, Sc element; LO 7224t. G, Sd element; LO 7225t. A–C, ×50; D–G, ×60. H–N, *Drepanodus arcuatus* Pander, 1856; Brattefors, sample Vg84-26. H, M element; LO 7226t. I, Pa element; LO 7227t. J, Pb element; LO 7228t. K, Sa element; LO 7229t. L, Sb element; LO 7230t. M, Sc element; LO 7231t. N, Sd element; LO 7232t. H–K, M–N, ×60; L, ×65. O–U, *Paroistodus numarcuatus* (Lindström, 1955); Orreholmen, sample Vg89-B1. O, M element; LO 7253t. P, Pa element; LO 7254t. Q, Pb element; LO 7255t. R, Sa element; LO 7256t. S, Sb element; LO 7257t. T, Sc element; LO 7258t. U, Sd element; LO 7259t. O–Q, ×65; R–U, ×70.

Sd element. Strongly asymmetrical. The anterior margin and the anterio-basal corner are strongly flexed to the inner side, making the entire element concavo-convex.

White matter. In elements of *Paroistodus* white matter fills the entire cusp and base, except at the antero-basal corner and bordering the basal cavity. More extensive areas of hyaline material are thus only present in elements with drawn-out antero-basal corners, for instance Sd elements of *P. originalis*.

Previous interpretations of the apparatus

The apparatus reconstruction for *Paroistodus* given here is not the first attempted. Generally, most authors agree upon which specimens to include in respective species, but have suggested that the elements formed a simpler type of apparatus than the one described here.

Lindström (1971, p. 46; 1973, p. 327) described *Paroistodus* as having two element types, drepanodiform and oistodiform (= geniculate). In addition to these, van Wamel (1974, p. 78) distinguished a scandodiform type, clearly equivalent to the Pb element described here.

Barnes *et al.* (1979) concluded that *Paroistodus* belonged in their Type IIIC category, lacking an erect element type, and basically being a two-element apparatus. Subsequent authors including Bergström (1981) also considered the apparatus bimembrate, although Dzik (1983, fig. 4) indicated up to four element types in the apparatus, but without comment. Sweet (1988, p. 55, text-fig. 5.8) described *Paroistodus* as a bi- to quadrimembrate apparatus but the illustration does not indicate the kind of element categories that I have discerned.

The attribution to *Paroistodus* of elements otherwise referred to *Dapsilodus* Cooper, 1976 or to *Besselodus* Aldridge, 1982 is most probably erroneous (but see discussion in Nowlan *et al.* 1988). Details in element morphology as well as general apparatus type distinguish these taxa from *Paroistodus* as understood here. For an up-to-date interpretation of the apparatuses of *Besselodus* and *Dapsilodus*, see Sansom *et al.* (1995).

Element ratios

The number of each element type in an apparatus can be determined with certainty only in natural clusters or bedding-plane associations of conodont animals. No such assemblages have been found from the kind of coniform apparatus represented by *Paroistodus* except possibly the cluster described by McCracken (1989) as *Protopanderodus* n. sp. A. As noted by Nicoll (1995, p. 253), this is actually a *Drepanodus*. In that cluster there seem to be more than seven elements, among them a P pair. Better known clusters of ramiform and platform elements in Carboniferous ozarkodinid conodonts are usually interpreted as having 15 elements (Aldridge *et al.* 1987), and the giant *Promissum pulchrum* from the upper Ordovician of South Africa had 19 (Theron *et al.* 1990; Aldridge *et al.* 1995), including four pairs of P elements and two pairs of Sb elements.

Studies of isolated element collections and natural assemblages led Sansom *et al.* (1995) to reconstruct the coniform apparatus of *Panderodus* as having 17 elements. Earlier attempts at calculating relative ratios of element types in collections of separated coniform elements from dissolved limestone samples include those of Lindström (1971) and Löfgren (1978). Lindström's (1971, figs 9–12) diagrams show a ratio between drepanodontiform and oistodontiform elements of 2:1 or less, except for one large sample with *P. proteus* which has a ratio of 2·53. My own earlier calculations (Löfgren 1978, pp. 68–70) also led to ratios of 2:1 or even less. Apparently, oistodontiform (M) elements are often much over-represented, as these ratios would imply three or more pairs. The large sample with the 2·53 ratio gives an indication of two M pairs. It is also obvious, both from Lindström's (1971) and Löfgren's (1978) diagrams, that there is a wide variation in ratios from sample to sample, suggesting that preservational aspects may play a decisive rôle in the retrieval of different element types. Lindström (1984, p. 37) discussed hydrodynamic sorting of conodont elements that could lead to distorted ratios and Broadhead *et al.* (1990) and McGoff (1991) performed practical studies of this. Different abilities among element types to withstand crushing is probably also an important distorting influence on their ratios. I have observed that in all but the best preserved collections of *Paroistodus*, Sd elements in particular are much underrepresented and/or broken compared with the other, less concavo-convex S element types. To at least approach the 'true' element ratios one must choose particularly well preserved samples for calculations.

Among my collections, some are consistent with a *Paroistodus* apparatus of 4M, 2Pa, 2Pb, 1Sa, 4Sb, 2Sc and 2Sd elements (17 elements in all). Among these samples are D85-1 (Sjurberg; 509 elements of *P. proteus*), Nä87-1 (Gymninge; 1046 elements of *P. parallelus*) and Nä94-13 (Lanna; 583 elements of *P. originalis*), whilst other samples with rich and well preserved *Paroistodus* faunas indicate higher M ratios. To my knowledge, only one reconstruction so far has suggested more than one pair of M elements. *Gamachignathus* McCracken, Nowlan and Barnes, 1980 was interpreted as having two pairs of M (= e-1 and e-2) elements, although Aldridge *et al.* (1995) preferred a Pc or Pd position for the e-2 element type. However, there are apparatuses with three or four pairs of P elements; apart from *Promissum* from the Ordovician (Aldridge *et al.* 1995), there are some Silurian genera, e.g. *Pterospathodus* and *Pranognathus* (see Männik and Aldridge 1989), with this apparatus model. As M elements and Pb elements are very similar in some species of *Paroistodus*, it is conceivable that one pair of M elements could have functioned like Pb elements.

EVOLUTIONARY TRENDS IN *PAROISTODUS*

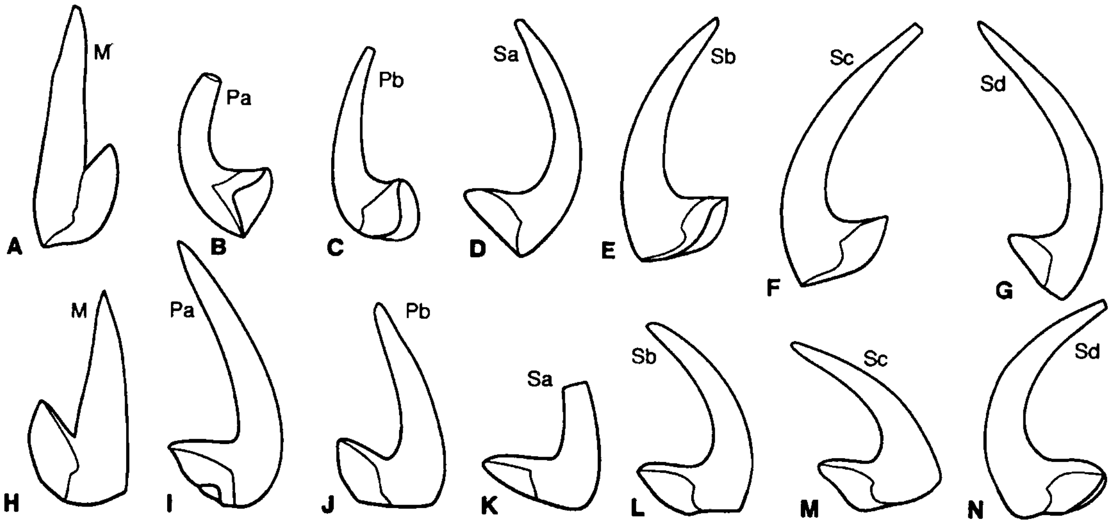
With four successive species of *Paroistodus* present in the same area, some general observations about direction of change in the genus can be made.

Inverted basal cavity. This feature occurs because younger lamellae do not cover older ones antero-basally. The character, which is also present in, for example, species of *Protopanderodus*, was noted and described in some detail by Lindström (1955, p. 537). It is present in specimens of all the *Paroistodus* species studied, but is extremely rare in *P. numarcuatus*, becoming successively more common in all element types in the younger species.

Similarities between element types. As discussed above, the elements of *P. numarcuatus* can be compared in detail with the homologous elements of *Drepanodus arcuatus*. In both these apparatuses the seven element types are quite distinct, possibly with the exception of some S elements. In particular, the Pa and Pb elements are very dissimilar with, in each species, the Pb elements being scandodontiform and morphologically closer to the M elements than to the Pa elements or the S series. Starting with *P. proteus* the Pa and Pb elements become progressively more similar, at the same time converging morphologically with the S series. In *P. originalis*, the youngest species investigated here, there is a striking resemblance between Pa and Pb elements in some long-based populations (cf. Text-fig. 5I–J). In populations with shorter-based elements, however, the two P elements remain more dissimilar, particularly where in some Pb elements the cusp is much more strongly reclined than in the corresponding Pa element (Pl. 1, fig. 19). Possibly, the convergent trend in P elements continues, as one of my youngest *Paroistodus* faunas includes a (probable) Pb element (juvenile) that resembles those of the S series (Pl. 1, fig. 16).

Lateral flattening of elements. In *P. numarcuatus* the sides of the elements, particularly those in the S series, tend to bulge laterally. The later species, *P. proteus* and *P. originalis*, lack lateral carinae and the sides are flatter, especially in the latter. Interestingly, this trend is present also in *Drepanodus arcuatus*, where Arenig specimens are noticeably flatter than Tremadoc ones.

The 'horridus' *trend.* Dzik (1983) postulated that the denticulated Llanvirn species '*Cordylodus*' *horridus* Barnes and Poplawski had connections with *Paroistodus*. An instance where denticles



TEXT-FIG. 3. *Camera lucida* drawings of elements of *Paroistodus*. A–G, *P. numarcuatus* (Lindström, 1955); Brattefors, sample Vg84-26. A, M element (same as Text-fig. 4A). B, Pa element (same as Text-fig. 4C). C, Pb element (same as Text-fig. 4F). D, Sa element (same as Text-fig. 4G). E, Sb element (same as Text-fig. 4H). F, Sc element (same as Text-fig. 4J). G, Sd element (same as Text-fig. 4I). H–N, *P. proteus* (Lindström, 1955); Sjurberg, sample D85-1. H, M element (same as Text-fig. 4L). I, Pa element (same as Text-fig. 4Q). J, Pb element (same as Text-fig. 4N). K, Sa element (same as Text-fig. 4O). L, Sb element (same as Text-fig. 4T). M, Sc element (same as Text-fig. 4U). N, Sd element (same as Text-fig. 4AB).

developed on the oral edge in *Paroistodus* was described by Löfgren (1995*a*) from the early Arenig *Oepikodus evae* Zone at Talubäcken, Dalarna. Another example is '*Drepanodus*' *cordylodiformis* Lehnert, 1995 from the older *Prioniodus elegans* Zone in the San Juan Formation of Argentina. Recently, Albanesi and Barnes (1996) described the transition from *Paroistodus originalis* to *P. horridus* in the lower Llanvirn in the San Juan Precordillera. It thus appears that the development of denticles on the oral margin of elements of *Paroistodus* occurred more than once. In '*Cordylodus*' *horridus* both P and S elements are denticulated (cf. Stouge 1984, pl. 1, figs 1–11) and mimic 'real' *Cordylodus* in their basal shape. Their corresponding M elements closely resemble those of *P. originalis* (cf. Stouge 1984, pl. 5, figs 1–4).

SYSTEMATIC PALAEONTOLOGY

The synonymies give only those references pertinent to the description of the respective apparatus. For fuller synonymy lists of *Paroistodus numarcuatus*, *P. proteus* and *P. originalis*, see Lehnert (1995), and for *P. parallelus*, see Stouge and Bagnoli (1988).

The figured specimens are deposited in the type collection of the Department of Geology, University of Lund, Sweden.

Genus PAROISTODUS Lindström, 1971

Type species. *Oistodus parallelus* Pander, 1856.

Age and distribution. Tremadoc to lower Llanvirn, pandemic.

TEXT-FIG. 4. Elements of *Paroistodus*. A–K, *P. numarcuatus* (Lindström, 1955); Brattefors, upper *Paltodus deltifer* Zone, sample Vg84-26. A–B, M elements; LO 7233t; LO 7234t. C, Pa element; LO 7235t. D, Pb element, outer side; LO 7236t. E, Pa element, inner side; LO 7237t. F, Pb element, inner side; LO 7238t. G, Sa element; LO 7239t. H, Sb element; LO 7240t. I, Sd element, inner side; LO 7241t. J, Sc element, inner side; LO 7242t. K, Sd element, outer side; LO 7243t. A–H, J, ×70; I, K, ×65. L–AB, *P. proteus* (Lindström, 1955); upper *P. proteus* Zone. L, N–R, T–W, AB, Sjurberg, sample D85-1. M, S, Z, Gullhögen, sample GB81-0FK. X, Y, AA, Diabasbrottet, Hunneberg, sample Vg86-12. L, W, M elements; LO 7271t; LO 7280t; ×70. M, Pa element, inner side with additional anterior edge; LO 7295t; ×60. N, R, Pb elements; LO 7272t; LO 7276t; ×70. O, Sa element; LO 7273t; ×75. P–Q, Pa elements, inner and outer side; LO 7274t; LO 7275t; ×75. S, Sa element; LO 7296t; ×60. T, Sb element; LO 7277t; ×75. U, Sc element, outer side; LO 7278t; ×80. V, AB, Sd elements, outer and inner side; LO 7279t; LO 7281t; ×75. X, Pb element; LO 7244t; ×65. Y, Pa element; LO 7245t; ×65. Z, Sb element; LO 7297t; ×60. AA, Sd element; LO 7246t; ×70.

Paroistodus numarcuatus (Lindström, 1955)

Text-figures 2O–U, 3A–G, 4A–K

1955 *Drepanodus numarcuatus* Lindström, p. 564, pl. 2, figs 48–49 [Sd and Sa elements], text-fig. 3I.
1955 *Acodus pulcher* Lindström, p. 546, pl. 2, fig. 38 [Sd element, holotype].
1955 *Drepanodus amoenus* Lindström, p. 558 (*pars*), pl. 2, fig. 26 [only; Sc element, holotype].
1955 *Oistodus parallelus* Pander; Lindström, pl. 4, figs 27–29, text-fig. 3N [only; M element].
1955 *Scandodus pipa* Lindström, pl. 4, fig. 38 [only; Pb element].
1971 *Paroistodus numarcuatus* (Lindström); Lindström, p. 46, fig. 8.
1981 *Paroistodus numarcuatus* (Lindström, 1955); Lindström, p. 227, *Paroistodus* pl. 2, figs 7–8.

Material. Approximately 15000 elements.

General description. In contrast to later *Paroistodus* species, elements of *P. numarcuatus* only very rarely have 'inverted basal cavity' lines antero-basally.

Sa element. Prominent carina present on each side of the recurved cusp. Both its anterior and posterior edges are sharp and the carinae are thickest anteriorly. They begin on the base, abutting against the basal cavity as seen in lateral view. The antero-basal corner is thin, with an angle of *c*. 100° between the anterior edge and the aboral margin. The aboral margin meets the slightly arched oral margin at an angle of *c*. 45°. The basal cavity is restricted to the posterior three-quarters to four-fifths of the base, and it bulges symmetrically on either side.

Sb element. More compressed laterally, and has a shorter and straighter oral edge than the Sa element. It is concavo-convex, the anterior margin facing the inner side and the antero-basal corner thin and slightly flexed inwards. The basal cavity has an inner bulge, the cusp is recurved, and its upper half is often somewhat rotated inwards.

Sc element. More compressed laterally than any of the other elements; the anterior edge of the cusp and the aboral edge of the base form a right angle. The element is almost symmetrical and the cusp strongly recurved.

Sd element. The anterior edge is strongly flexed inwards, making the entire element concavo-convex. In some elements an additional edge has developed anteriorly on the base. The base is short and the carinae are unevenly developed: strong on the outer, much weaker on the inner side. The cusp is recurved and bent inwards.

Pa element. The cusp is recurved and both sides are carinate. The anterior edge is flexed inwards on the base and in some elements an additional edge has developed anteriorly, as in the Sd element. The basal cavity flares towards the outer side, the aboral margin having the characteristic indentation of Pa elements.

Pb element. The cusp is very slightly recurved and each of its lateral sides has a prominent carina somewhat posterior to the mid-line. The anterior edge is slightly flexed towards the inner side. The cusp is only about twice as long as the base, and has a tendency to be bent inwards. The oral margin has a sharp edge, which does not reach the aboral margin. The basal cavity is wide and flaring, particularly towards the inner side. The element is similar to the Pb (pipaform) element of *Drepanodus arcuatus* but has a proportionally longer oral margin and shorter cusp.

M element. The sides of the cusp are carinate and often more bulging than in later representatives of the genus. The cusp is more strongly bent inwards than in the other *Paroistodus* species. In some populations a narrow extension of the basal cavity almost reaches the antero-basal corner, but is laterally pinched and the inner face of the base undulates. The element figured by Lindström (1955, pl. 4, figs 27–28) as *Oistodus parallelus* is a good example of this.

Remarks. In his description of multielement *P. numarcuatus*, Lindström (1971) included *D. amoenus*, with which I concur, except that I believe that one of his illustrated specimens (Lindström 1955, pl. 2, fig. 25) belongs to *Drepanoistodus* (as discussed by Löfgren 1994, p. 1365). Lindström (1971) also included in *P. numarcuatus* the specimens of *O. parallelus* listed in the synonymy above, but not *Acodus pulcher*. One of the illustrated elements of *Scandodus pipa* in Lindström (1955, pl. 4, fig. 38) is a Pb element of *P. numarcuatus*. In that publication, the holotype and other illustrated specimens of *Scandodus pipa* are homologous elements of *Drepanodus arcuatus*.

Stratigraphical occurrence. Tremadoc; upper *Paltodus deltifer* Zone to the lowermost subzone of the *Paroistodus proteus* Zone. The species co-occurs with its successor, *P. proteus*, in the lowermost part of the *P. proteus* Zone.

Paroistodus proteus (Lindström, 1955)

Text-figures 3H–N, 4L–AB

1955 *Drepanodus proteus* Lindström, p. 566, pl. 3, figs 18–21, text-fig. 2a–f, j.
1955 *Oistodus parallelus* Pander, 1856; Lindström, p. 579 (*pars*), pl. 4, fig. 26 (only).
1971 *Paroistodus proteus* (Lindström); Lindström, p. 46, fig. 8.
1981 *Paroistodus proteus* (Lindström, 1955); Lindström, p. 233, *Paroistodus* pl. 2, figs 5–6.

Material. Approximately 17000 elements.

General description. The basal cavity is restricted to the posterior half of the base in the S and Pa elements. Oral keels are better developed in S and P elements and 'inverted basal cavities' are more common in all element types of *P. proteus* than in *P. numarcuatus*.

Sa element. Biconvex, with the lateral sides only moderately bulging, with less prominent carinae than in *P. numarcuatus*. As seen in lateral view the basal cavity is drop-shaped with a poorly defined tip close to the oral margin. The base has a drawn-out antero-basal corner and the aboral margin makes a smooth curve up to the slightly arched and keeled oral edge. The angle between the oral edge and the posterior edge of the cusp is *c*. 90°. The distal part of the cusp is slightly reclined to recurved.

Sb element. There is an asymmetry in this element, as the anterior margin is slightly flexed inwards. In a few specimens the distal part of the cusp is slightly twisted. The outline of the base is similar to that in the Sa element, but the cusp is usually more recurved in the Sb element.

Sc element. Almost symmetrical with flat sides. The outline of the base is rhombic, thereby resembling that in the corresponding element in *Drepanodus arcuatus* ('sculponeaform' element). The base is proportionally longer in an antero-posterior direction than in the other S elements, the oral edge is long and straight and the cusp is reclined to recurved.

Sd element. This is the most asymmetrical of the S elements in that the entire anterior margin is flexed to the inner side, making the element concavo-convex. The inner side is flat, whilst the outer one has a prominent carina. The basal cavity bulges almost equally on either side. The antero-basal corner can be seen only on the inner side. In a few elements there is a short additional anterior edge on the outer side of the base. The cusp is strongly recurved.

Pa element. The lateral outline of the base is similar to that in Sa, Sb and Sd elements. The aboral margin of the base has an indentation and flare on the outer side as in corresponding elements in other taxa. The basal cavity bulges, particularly to the outer side, and the antero-basal corner is flexed inwards. As in some Sd elements, an additional anterior edge may be present on the base. The cusp is slightly recurved, more prominently carinate on the outer than on the inner side, and the angle between the oral edge and the posterior edge of the cusp is *c*. 80°.

Pb element. This has similarities to the M element, but the transition from the oral edge of the base to the posterior edge of the cusp constitutes a smooth curve, and not a sharp angle as in the M elements. The angle between the oral edge and the cusp is usually more than 60°, and the basal cavity flares towards the inner side. The outer side of the reclined cusp is carinate, the inner side considerably flatter.

M element. The cusp is less inclined towards the inner side and more compressed laterally than in *P. numarcuatus*, but there is a rather weak central carina on the inner side and a stronger one posterior of the mid-line on the outer side. The antero-basal corner is thin, often broken or sightly flexed to the outer side. On the base, larger elements often display 'inverted basal cavity' lines. In some populations the base is typically squat and the cusp rapidly tapering. The element illustrated by Lindström (1955, pl. 4, fig. 26) as *Oistodus parallelus* is a good example.

Remarks. Lindström's (1955, p. 566) description included P and S elements, but he described the M elements together with those of *Paroistodus numarcuatus* and *P. parallelus* as *Oistodus parallelus*. The holotype is an Sa element with the characteristic basal shape described above. The Sa element in his text-figure 2j is similar, but more laterally compressed. The short-based element illustrated by Lindström (1955, pl. 3, fig. 19; text-fig. 2d–f) is an Sd element, as is that in his text-figure 2a–c, with its inwardly flexed anterior margin and short additional antero-lateral costa on the outer side. The specimen in Lindström's (1955) plate 3, figure 18 is a typical Pa element with its notched aboral margin, while his plate 3, figure 21 is a Pb element. He (p. 566) even commented on the similarity of this Pb element and '*Oistodus parallelus*' (= M elements of *Paroistodus*). Later, Lindström (1981, *Paroistodus* pl. 2, fig. 6) also included one of these illustrated elements (Lindström 1955, pl. 4, fig. 26) in *P. proteus*, as I have done above. Thus, all element types, except the flat-sided, square-based Sc element and the nearly symmetrical Sb element, were illustrated and described by Lindström (1955).

Stratigraphical occurrence. Upper Tremadoc to lower Arenig; from the base of the *P. proteus* Zone to the *Prioniodus elegans* Zone. The species co-occurs with *P. numarcuatus* in the lowermost subzone of the *P. proteus* Zone and with *P. parallelus* from the uppermost part of the *P. proteus* Zone to the (lower) *P. elegans* Zone.

Paroistodus parallelus (Pander, 1856)

Plate 1, figures 1–12, 17, 21; Text-figure 5A–G

1856 *Oistodus parallelus* Pander, p. 27, pl. 2, fig. 40 [M element].
?1941 *Acodus expansus* Graves and Ellison, p. 8, pl. 1, fig. 6 [Sa element].
?1941 *Oistodus pandus* Branson and Mehl; Graves and Ellison, pl. 1, fig. 34 [Sd element].
1955 *Distacodus expansus* (Graves and Ellison, 1941); Lindström, p. 555, pl. 3, figs 13–17, text-fig. 2g–i [Sa, Pb and Sb elements].
1955 *Oistodus parallelus* Pander, 1856; Lindström, p. 579 (*pars*), pl. 4, figs 30–31 [only; M element].
1971 *Paroistodus parallelus* (Pander); Lindström, p. 47, fig. 8.
1973 *Paroistodus parallelus* (Pander, 1856); Lindström, p. 329, *Paroistodus* pl. 1.

Material. About 9000 elements.

General description. The P and S elements have deeper basal cavities than in the other *Paroistodus* species and their lateral sides are costate. Characteristically, the basal cavity extends to more than half of the length of the base. There is an extensive area of inverted basal cavity anteriorly in most elements.

Sa element. This has equally strong costae, one on each side, and the basal cavity bulges symmetrically on either side. The costae extend from close to the aboral margin to the upper part of the recurved cusp. Basally, the costae are directed posteriorly, high up on the cusp more laterally. The antero-basal corner can be angular or rounded off. The oral edge is arched and strongly keeled.

Sb element. Similar to the Sd element in that the anterior edge is flexed inwards, but its antero-basal corner is less sharply inwardly flexed and its basal cavity less flaring. Its asymmetry consists mainly of a different degree of convexity of its inner and outer side.

Sc element. The base is square in lateral view, the aboral margin usually meeting the anterior edge of the cusp in an angle of *c.* 90°, but in some instances it is rounded off. The cusp is recurved. The costa on each side of the laterally flattened element is less strong than in the other S and P elements, and is sometimes less well developed on one side than on the other.

Sd element. Highly asymmetrical, having the anterior margin, including the antero-basal corner, flexed inwards, making the element concavo-convex. The distal part of the cusp is slightly rotated to the outer side. The costa on the outer side is stronger than that on the inner side. The oral margin is strongly arched and keeled, and the basal cavity flares almost equally to each side.

Pa element. Seen from the outer side the Pa element most closely resembles the Sa element. The Pa element can be distinguished by the indentation of the aboral margin on the outer side, and by the more lateral direction of the costae on its base.

Pb element. Has a costate inner side, the costa beginning on the base and continuing on the strongly reclined cusp. The outer side is broadly carinate or more weakly costate than the inner side. The angle between the oral edge, which is prominently keeled, and the posterior edge of the cusp is usually less than 60°.

M element. Very similar to the corresponding element in *Paroistodus proteus* and *P. originalis*. In some populations the outer side of the element has a bulge basally. According to Pander's (1856) original drawing and description the cusp is quite sharply carinate. In many instances in my collections, however, the cusp is only weakly carinate, particularly on the inner side.

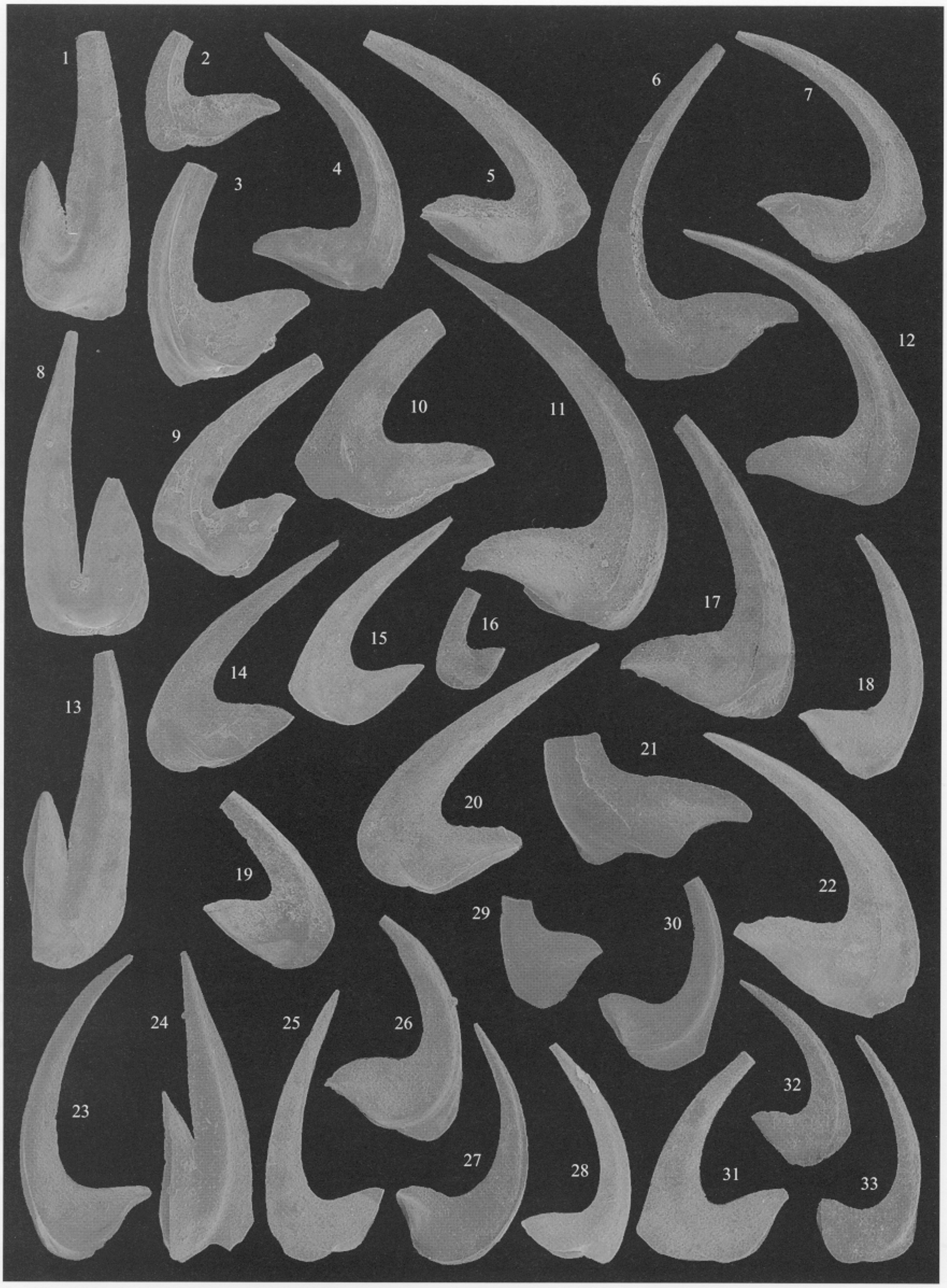
Remarks. Lindström (1971, p. 49) explained that he chose to combine Pander's (1856) type, an M element, with the other elements here described as *P. parallelus*, rather than with younger ones (those referred here to *P. originalis*) as there were no species of similar age to *P. originalis* among those described and illustrated by Pander (1856). I agree with Lindström, but note that even if most of my M elements are less sharply carinate than in Pander's (1856) drawing, it makes sense that in at least some populations of this species the costate S and P elements were accompanied by sharply carinate M elements. The elements described and illustrated by Graves and Ellison (1941) from the Marathon Formation of Texas and tentatively included in the synonymy list could belong to this species or to a closely related one. A closer study will be needed of most Laurentian reports of *Paroistodus* to demonstrate whether they represent Baltoscandian taxa, or parallel forms (the latter seems to be the case in *Drepanoistodus*, for example).

Stratigraphical occurrence. Arenig: from the uppermost *Paroistodus proteus* Zone to the upper middle *Oepikodus evae* Zone. The taxon co-occurs with its predecessor, *P. proteus*, in the uppermost subzone of the *P. proteus* Zone to the lower *P. elegans* Zone, and (rarely) with its successor, *P. originalis*, in the upper middle *O. evae* Zone.

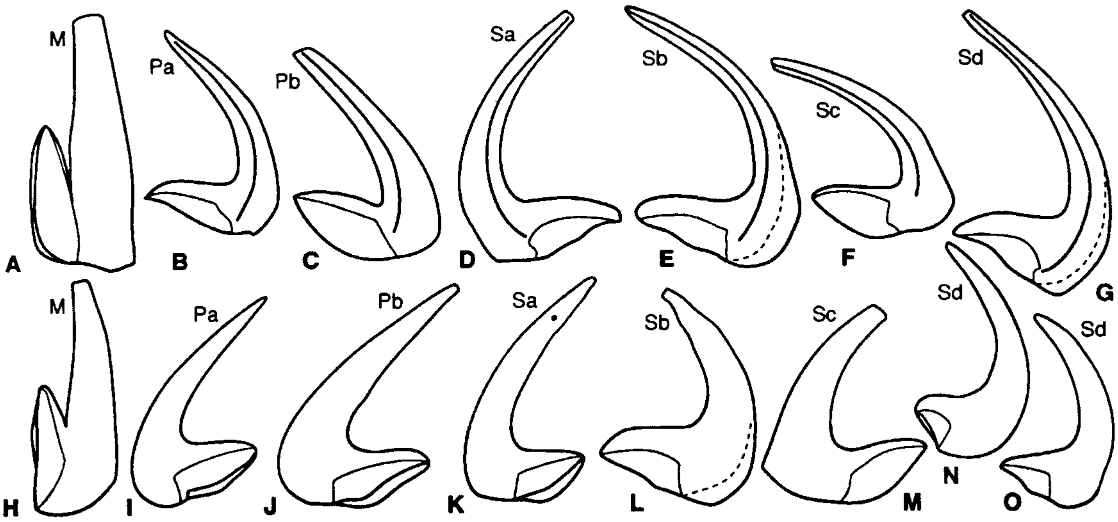
EXPLANATION OF PLATE 1

Figs 1–12, 17, 21. *Paroistodus parallelus* (Pander, 1856); *Oepikodus evae* Zone. 1–2, 4–7, 10–12, 17, 21, Gymninge, sample Nä87-3. 3, 8–9, Orreholmen, sample Vg89-B4. 1, 8, M elements; LO 7282t; LO 7247t. 2–4, Pa elements; LO 7283t; LO 7248t; LO 7284t. 5, Pb element; LO 7285t. 6, Sa element; LO 7286t. 7, Sc element; LO 7287t. 9–10, Pb elements; LO 7249t; LO 7288t. 11, Sd element, inner side; LO 7289t. 12, Sb element, inner side; LO 7290t. 17, Sb element, outer side; LO 7291t. 21, Sd element; LO 7292t. 1, ×50; 2–5, 7–8, 10, 17, 21, ×65; 6, 12, ×60; 9, 11, ×70.

Figs 13–16, 18–20, 22–33. *Paroistodus originalis* (Sergeeva, 1963). 13–15, 18, 20, 22, 24–26, 28, 31, Orreholmen, sample Vg84-10, *P. originalis* Zone. 16, 33, Kårgärde, sample H6, upper *E.*? *variabilis* Zone. 19, Gillberga, sample Ö194-8, *P. originalis* Zone. 23, 29–30, Kårgärde, sample L4, *P. originalis* Zone. 27, 32, Gillberga, sample Ö194-9, *P. originalis* Zone. 13, 24, M elements; LO 7260t; LO 7266t. 14, Pa element; LO 7261t. 15–16, Pb elements; LO 7262t; LO 7298t. 18, Sd element; LO 7263t. 19–20, Pb elements, LO 7299t; LO 7264t. 22, Sb element, inner side with costa; LO 7265t. 23, Sd element; LO 7250t. 25, 28, 30, Sa elements; LO 7267t; LO 7269t; LO 7252t. 26, 29, Sb elements; LO 7268t; LO 7251t. 27, 33, Sd elements; LO 7293t; LO 7300t. 31–32, Sc elements; LO 7270t; LO 7294t. 13, 16, 23–24, 26–27, 29, 31–32, ×60; 14, 18, 20, 22, 33, ×70; 15, 19, 28, ×75; 25, ×65; 30, ×55.



LÖFGREN, *Paroistodus*



TEXT-FIG. 5. *Camera lucida* drawings of elements of *Paroistodus*, showing the outline of the basal cavity. A–G, *P. parallelus* (Pander, 1856); *Oepikodus evae* Zone, Gymninge, sample Nä87-3. A, M element (same as Pl. 1, fig. 1). B, Pa element (same as Pl. 1, fig. 4). C, Pb element (same as Pl. 1, fig. 5). D, Sa element (same as Pl. 1, fig. 6). E, Sb element (same as Pl. 1, fig. 12). F, Sc element (same as Pl. 1, fig. 7). G, Sd element (same as Pl. 1, fig. 11). H–O, *P. originalis* (Sergeeva, 1963); *P. originalis* Zone; H–M, O, Orreholmen, sample Vg84-10. N, Gillberga, sample Ö194-9. H, M element (same as Pl. 1, fig. 13). I, Pa element (same as Pl. 1, fig. 14). J, Pb element (same as Pl. 1, fig. 20). K, Sa element (same as Pl. 1, fig. 25). L, Sb element (same as Pl. 1, fig. 26). M, Sc element (same as Pl. 1, fig. 31). N, Sd element with small basal cavity (same as Pl. 1, fig. 27). O, Sd element with normal basal cavity (same as Pl. 1, fig. 18).

Paroistodus originalis (Sergeeva, 1963)

Plate 1, figures 13–16, 18–20, 22–33; Text-figure 5H–O

1963 *Oistodus originalis* Sergeeva, p. 98, pl. 7, figs 8–9, text-fig. 4 [the holotype (pl. 7, fig. 8) is most probably an Sd element, while the element in pl. 7, fig. 9 and text-fig. 4 seems to be an Sa element].

1971 *Paroistodus originalis* (Sergeeva); Lindström, p. 48, fig. 8.

1981 *Paroistodus originalis* (Sergeeva, 1963); Lindström, p. 231, *Paroistodus* pl. 2, figs 1–4.

Material. About 33000 elements.

General description. In this species there are specimens with basal cavities of approximately the same depth as in elements of *P. proteus*, but also, and often co-occurring with the deep-based elements, there are specimens with very shallow basal cavities. I have not been able to discover whether these two forms belonged to separate populations (there are intermediate forms), and for the present they will be treated together. Anteriorly, all element types have a wide zone of 'inverted basal cavity'. Some populations have costate rather than carinate sides.

Sa element. The cusp is more strongly laterally compressed than in corresponding elements of older taxa of the genus. In some populations the element is very similar to the homologous element of *P. proteus* with an angular antero-basal corner with the basal cavity occupying about half the length of the base. In most populations, however, the basal cavity is shallower, the antero-basal corner is rounded off and it has a wide section of thin translucent material. The cusp is recurved.

Sb element. The anterior edge is flexed to the inner side and the distal part of the cusp bent inwards. In long-based specimens the antero-basal corner is angular, in short-based ones it is well rounded.

Sc element. The base appears angular in side view, and the entire element is laterally flattened. The cusp is recurved and has a strong anterior keel. The antero-basal corner is rounded in a few specimens. There are no short-based Sc specimens, but some elements have a very restricted basal cavity which occupies much less than half the length of the base.

Sd element. Concavo-convex, as the cusp and the entire anterior edge are bent inwards, but in contrast with the homologous element in *P. parallelus* the cusp is rarely rotated. The antero-basal corner is rounded, and the basal cavity bulges, particularly to the inner side. The oral margin is keeled and arched.

Pa element. Similar to the Sa element, but its cusp is more strongly recurved. The anterior edge is slightly flexed inwards and the characteristic indentation of the aboral margin is present, although weaker than in the older *Paroistodus* species.

Pb element. Similar to the M element, but the oral and posterior edges of the cusp are more divergent (*c.* 60°) and separated by a smooth curve rather than a sharp angle. In contrast to earlier species of the genus, the oral edge may be slightly arched, particularly in short-based specimens. The base is expanded on the inner side.

M element. Some of these elements are practically indistinguishable from those of *P. proteus* or *P. parallelus*, but in *P. originalis* the base is generally lower and the cusp is proportionally shorter. Some populations have more distinct mature M elements with a prominent carina on each side and a well-rounded antero-basal corner with a wide, thin edge, slightly flexed outwards. The illustration in van Wamel (1974, pl. 7, fig. 17) of '*Oistodus parallelus*' is an excellent example of this.

Remarks. Specimens of *P. originalis* are uncommon above the *P. originalis* Zone. Those from the overlying *Microzarkodina parva* Zone agree in all details with those from older strata. The youngest representatives come from beds of Llanvirn age in Dalarna (the Kårgärde section) and from latest Arenig strata in Öland (the Gillberga section), and are rare. Most of them are juvenile and thus difficult to assess, but they appear to fall within the limits of variation of *P. originalis*. This taxon, or a similar one, is also present in the upper Arenig and lower Llanvirn of Laurentia and Argentina, often found associated with elements of '*Paroistodus horridus*' (cf. Löfgren 1995*a*, and discussion above).

Stratigraphical occurrence. Arenig to lower Llanvirn; from the upper part of the *Oepikodus evae* Zone to the *Eoplacognathus*? *variabilis-Microzarkodina ozarkodella* Subzone. The species co-occurs rarely with its predecessor, *P. parallelus*, in the upper middle *O. evae* Zone.

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