

Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff & Ziegler, 1957) from the Upper Devonian of the Canning Basin, Western Australia

Robert S. Nicoll¹

More than 200 conodont clusters and 1300 discrete elements belonging to *Polygnathus xylus xylus* and *Ozarkodina brevis* were recovered from a sample of the Upper Devonian Napier Formation in the Oscar Range of the Canning Basin, Western Australia. A study of them indicates that both *P. xylus xylus* and *O. brevis* had a multielement structure of 15 elements, belonging to seven element types: M (2), Sa (1), Sc (4), Sb (2), Sd (2), Pb (2), and Pa (2). The better preserved and more complete

clusters of *P. xylus xylus* have been used as a basis, with reference to a recent find of an impression of a conodont animal, for a reconstruction of the head region, showing the position of the conodont elements. Two groups of elements with distinctly different functions are recognised. The anterior discernens elements (M, Sa, Sc, Sb, & Sd) serve to sort particulate food matter, and the posterior contundens elements (Pb, Pa), to crush the food particles prior to their entry into the gut.

Introduction

Fused conodont clusters were recovered from a sample of the Upper Devonian Napier Formation in the Oscar Range of the Canning Basin, Western Australia*. The geologic setting and general nature of the fauna have been discussed previously (Nicoll, 1981, 1982) and this paper deals with the apparatus structure and interpretation of *Polygnathus xylus xylus* and *Ozarkodina brevis*.

Uyeno (1978, 1982) recently described the apparatus structure of both *P. xylus xylus* and *O. brevis*, on the basis of collections of discrete elements. The present study, based on both discrete elements and fused clusters, basically confirms the composition of these species as recognised by Uyeno, but adds an additional element to *P. xylus xylus*.

The number of element types recognised as belonging to the apparatus structure of conodont species within the Polygnathidae has increased as more taxa have been revised in a multielement sense. Klapper & Philip (1971, 1972) recognised only six element types when they first proposed the apparatus structure of *Polygnathus*. More recently, several authors (Baesemann, 1973; Chatterton, 1974; Dzik, 1976; von Bitter, 1976; Nicoll, 1977, 1980, 1982; Sparling, 1981; Van den Boogaard & Kuhry, 1979) have suggested that seven element types may have been the normal complement in the multielement apparatus. This does not mean that some conodont taxa may not have had fewer element types, but it would appear that the majority had seven types of elements in the apparatus structure. This seven element type structure appears to hold for conodont taxa from the Ordovician to the Carboniferous, and over a wide range of conodont families, from the Icriodontidae to the Polygnathidae.

Grouping of elements

The recovery of well-preserved clusters, representing what must be partially preserved original element associations, provides a good insight into the grouping of elements in the conodont organism. The clusters found in this study can be divided into three basic types: those that contain only ramiform elements,

those that contain only pectiniform elements, and those that contain mixed ramiform-pectiniform element types. The clusters that contain ramiform elements only are the most abundant.

It is apparent from the preserved element distribution in the fused clusters of this study, the morphology of the elements, and the interpreted function of the elements, that there are two distinct groups of elements in the head region of the conodont animal. The anterior group of elements can be divided into two subgroups. This grouping is, in part, confirmed by the separation of ramiform (anterior) and pectiniform (posterior) elements in the conodont animal illustrated by Briggs & others (1983). Nicoll (1977, 1980) referred to these element associations informally as Groups One, Two, and Three. However, with the present level of understanding of the positional relationship and, possibly, the function of these groups, I think it appropriate here to give them formal names.

The first (anterior) group, consisting of ramiform-type elements, is here designated discernens elements. Two subgroups are recognised. The primary discernens elements are the M, Sa, Sc, and Sb elements, and are located just inside the anterior end of the food groove. Behind these are the secondary discernens elements, represented by a single pair of Sd elements. The name, discernens, refers to the function of these elements as sorters of food particles (discerno, L - to separate, as according to qualities).

The second (posterior) group of elements, consisting of the Pb and Pa elements, is designated the contundens elements. The name, contundens, refers to their function of crushing the food particles before they enter the gut. (contundo, L - to grind, crush, pound, break to pieces, to bruise).

Discernens elements (M, Sa, Sc, Sb & Sd)

The discernens elements are subdivided into two distinct functional groups in the conodont animal: the primary and secondary discernens element groups.

Primary discernens elements (M, Sa, Sc, Sb)

A study of the *Polygnathus* clusters has shown that the group structure that I suggested (Nicoll, 1977) for *Oulodus* is incorrect. In *Oulodus*, the elements of Group One were, in present element terminology, thought to be M, Sa, and Sc. In *Polygnathus*, the primary discernens elements are M, Sa, Sc, and Sb (Figs. 1, 3). Figure 3A illustrates the best preserved of the primary discernens element clusters, but Figure 5A and B are also nearly complete primary discernens element clusters. In Figure 3A, the cluster contains 9 elements: one pair of M elements, a single Sa element, two pairs of Sc elements and one pair of Sb elements.

¹Division of Continental Geology, BMR.

*Collecting localities

WCB 811/1-5 Sadler Limestone: in gully on west side of McWhae Ridge at southern end of the Lawford Range. Grid ref. 4160-919261, Bohemia 1:100 000 topographic map.

WCB 804/5 Napier Formation: at edge of small lamproite plug near eastern end of the Oscar Range. Grid ref. 3962-618132, Leopold Downs 1:100 000 topographic map.

The cluster of Figure 2A is complete except for the anterior part of the right side M element, which is missing, and the broken right lateral process of the Sa element. When the cluster was being turned for photography, the Sa and left M elements broke free (Fig. 3Ae, Af). The original position of the Sa element in the centre of the cluster is shown by the position of the broken posterior process (Fig. 3Ad) in the axis of the cluster. Lateral to the axial Sa element are the paired Sb elements, one on either side of the axis. Outside the Sb elements are two pairs of Sc elements. This nesting of one Sb element and two Sc elements is shown in many of the clusters (Figs. 3, 5).

The M elements are paired, but their position in the living organism cannot be exactly determined. My best guess is that the M elements were located slightly anterior to the Sa element. The right M element of the cluster in Figure 5B may represent the approximate position of the M element in the living organism. I believe, from the example of the *Oulodus* apparatus (Nicoll, 1977), where the basal plates were well preserved, and from the general morphology of the basal cavities and denticle curvature of most M elements, that the M element was located transversely to the axis of the other elements, with the main cusp near the cluster axis and the 'downwardly' curving 'posterior' process directed outward and maybe slightly posteriorly.

Secondary discernens elements (Sd)

The secondary discernens elements in *Polygnathus* consist only of the single pair of Sd elements. Only two clusters have an Sd element associated with another element and both of these appear to be fortuitous. From this evidence and on morphologic considerations, the Sd element must have been isolated in a separate position, between the primary discernens elements and the contundens elements. This would apply to the *Oulodus* and other apparatuses as well.

In the reconstruction of the *Oulodus* apparatus, I associated the Sb and Sd (Sb and M elements as used in that paper) in Group Two (Nicoll, 1977). This association was based on the well-preserved morphology of the basal plate of the *Oulodus* elements and the curvature of the denticles. In the Sb and Sd elements of *Polygnathus*, there is again a strong morphologic similarity between these two element types, especially in the shape of the basal cavity and the outline of the posterior process. The difference in basal cavity morphology between the Sc and Sb elements is clearly shown in Figure 3Fb. The cavity of the Sc element lies parallel to the axis of the element, but the cavity of the Sb element has a strong inwardly developed lip, similar to the Sd element.

Despite this physical similarity, the absence of an Sd element in the several well-preserved clusters would seem to indicate that the Sd element is not a part of the primary discernens elements structure.

Contundens elements (Pb, Pa)

As in *Oulodus*, the Pb and Pa elements appear to be closely associated in *Polygnathus*. There are several examples of clusters composed only of pairs of either Pa or Pb elements, as well as a number where both Pa and Pb elements are located in

the same cluster (Fig. 4). From this study it appears that the condont organism must have contained only one pair each of the Pa and Pb elements. In those clusters where Pb and Pa elements are found together, both element types appear to be at a similar stage of development. A similar stage of development is also found in each element of all pairs of either Pa or Pb elements. There is thus no indication of late addition or replacement of Pa elements by the condont animal.

Figure 4J shows a partial cluster that contains at least 10 elements, including one pair each of juvenile Pa and Pb elements, one pair of M elements, and at least four S elements. The Pa element pair shows typical juvenile features – well-developed blade and carina, the blade length being roughly the length of an adult blade, a large basal cavity, and a very small platform. The Pb elements, mostly obscured by the Pa elements, show a much more pronounced basal cavity when compared with the adult element. The M and S elements appear morphologically mature except for the anterior process of the M element, which lacks denticles, and the generally angular nature of the denticles.

The orientation of the Pa and Pb elements in the living animal appears to have been with denticles pointing towards each other, basal cavities being directed outward. The upper surfaces of the platforms of Pa elements are frequently found touching (Fig. 4C, F, I). The Pa elements, where found with Pb elements in clusters, are always located with the blades on the concave side of the slightly bowed Pb elements (Fig. 4D). This would seem to indicate that the paired Pa elements lay partially on top of or underneath the Pb elements, depending on whether the function of these elements was to scoop particles up or down.

Systematic palaeontology

Genus *Polygnathus* Hinde, 1879

Type species. *Polygnathus dubius* Hinde, 1879

Polygnathus xylus xylus Stauffer, 1940

Figures 1–5

Synonymy.

Pa element.

1940 *Polygnathus xylus* n.sp.; Stauffer, p.430, Pl. 60, Figs. 54, 60, 72–74 (only).

1970 *Polygnathus xylus* Stauffer; Klapper & others, p. 659, Pl.1, Figs. 4–6, 11; Pl.2, Figs. 4,5,7–12, 16–18.

1978 *Polygnathus xylus* Stauffer; Uyeno, p.17, Pl.4, Figs. 1–3, 5–14 (non Fig 3).

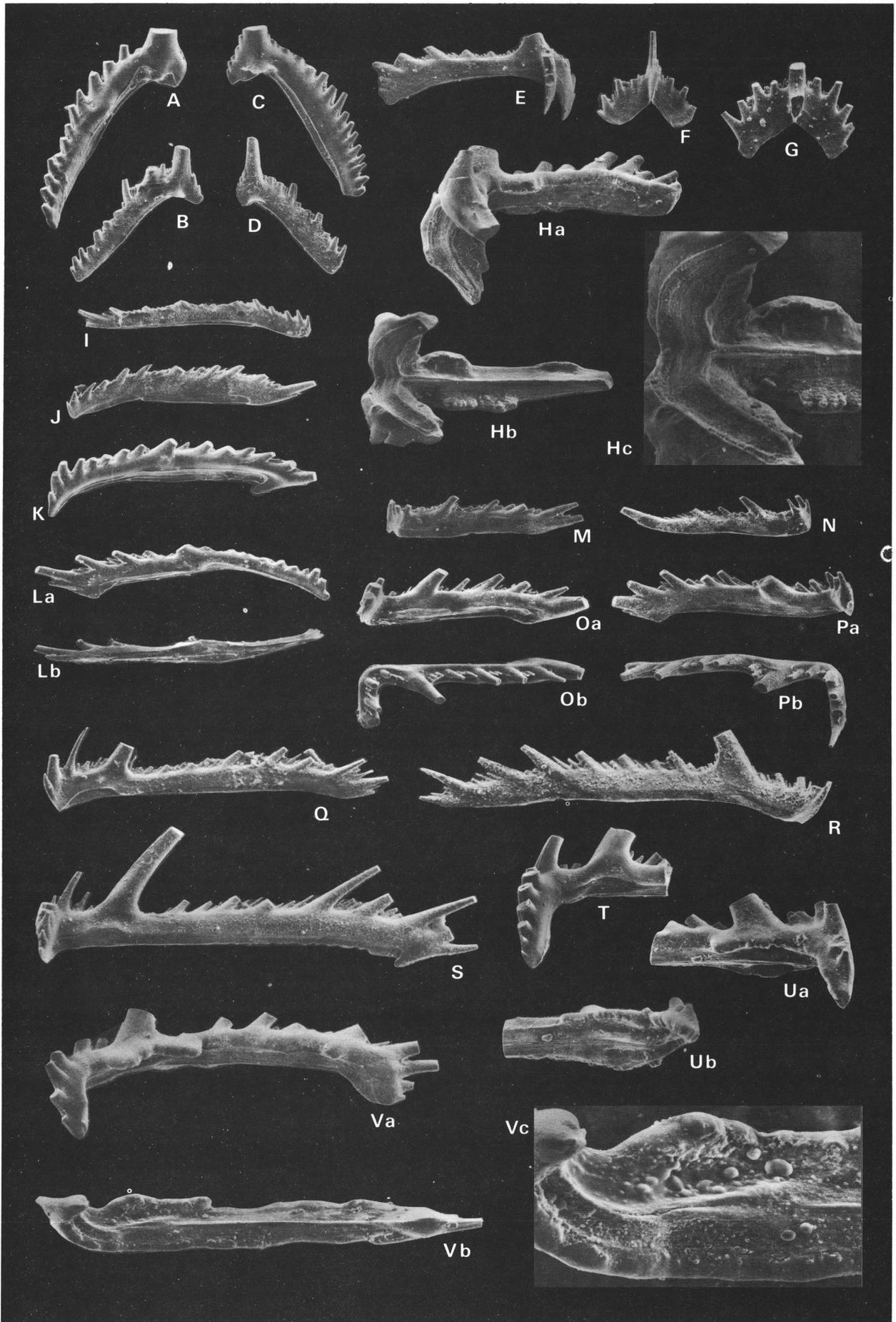
Pb element.

1940 cf. *Ctenognathus elegans* Stauffer; Stauffer, p.422, Pl.59, Figs. 3–5 8.

Material studied. In this study, 1300 discrete elements and about 200 clusters have been examined from sample WCB 804/5. The discrete specimens represent complete or nearly complete elements; broken material was not included. Addi-

Figure 1. *Polygnathus xylus xylus*, discrete elements.

All figs x50 except as noted. A–D, M elements. A, gerontic element (CPC25133), posterior view. B, mature element (CPC25134), posterior view. C, gerontic element (CPC25135), posterior view. D, mature element (CPC25136), posterior view. E–H, Sa elements. E, mature element (CPC25137), lateral view. F, mature element (CPC25138), posterior view. G, mature element (CPC25139), posterior view. H, gerontic element (CPC25140): Ha, lateral view (x60); Hb, basal view (x60); Hc, enlargement (x105) of basal view, showing basal cavity. I–L, Sb elements. I, mature element (CPC25141), lateral view. J, mature element (CPC25142), lateral view. K, gerontic element (CPC25143), lateral view. L, gerontic element (CPC25144): La, lateral view; Lb basal view. M–P, Sd elements (all x60). M, mature element (CPC25145), lateral view. N, mature element (CPC25146), lateral view. O, gerontic element (CPC25147): Oa, lateral view; Ob, oral view. P, gerontic element (CPC25148): Pa, lateral view; Pb, oral view. Q–V, Sc elements (all x60 except as noted). Q, mature element (CPC25149), lateral view. R, mature element (CPC25150), lateral view. S, mature element (CPC25151), lateral view. T, broken mature element (CPC25152), lateral view. U, broken gerontic element (CPC25153): Ua, lateral view; Ub, basal view. V, gerontic element (CPC25154): Va, lateral view; Vb, basal view; Vc enlargement of basal view (x140), showing basal cavity.



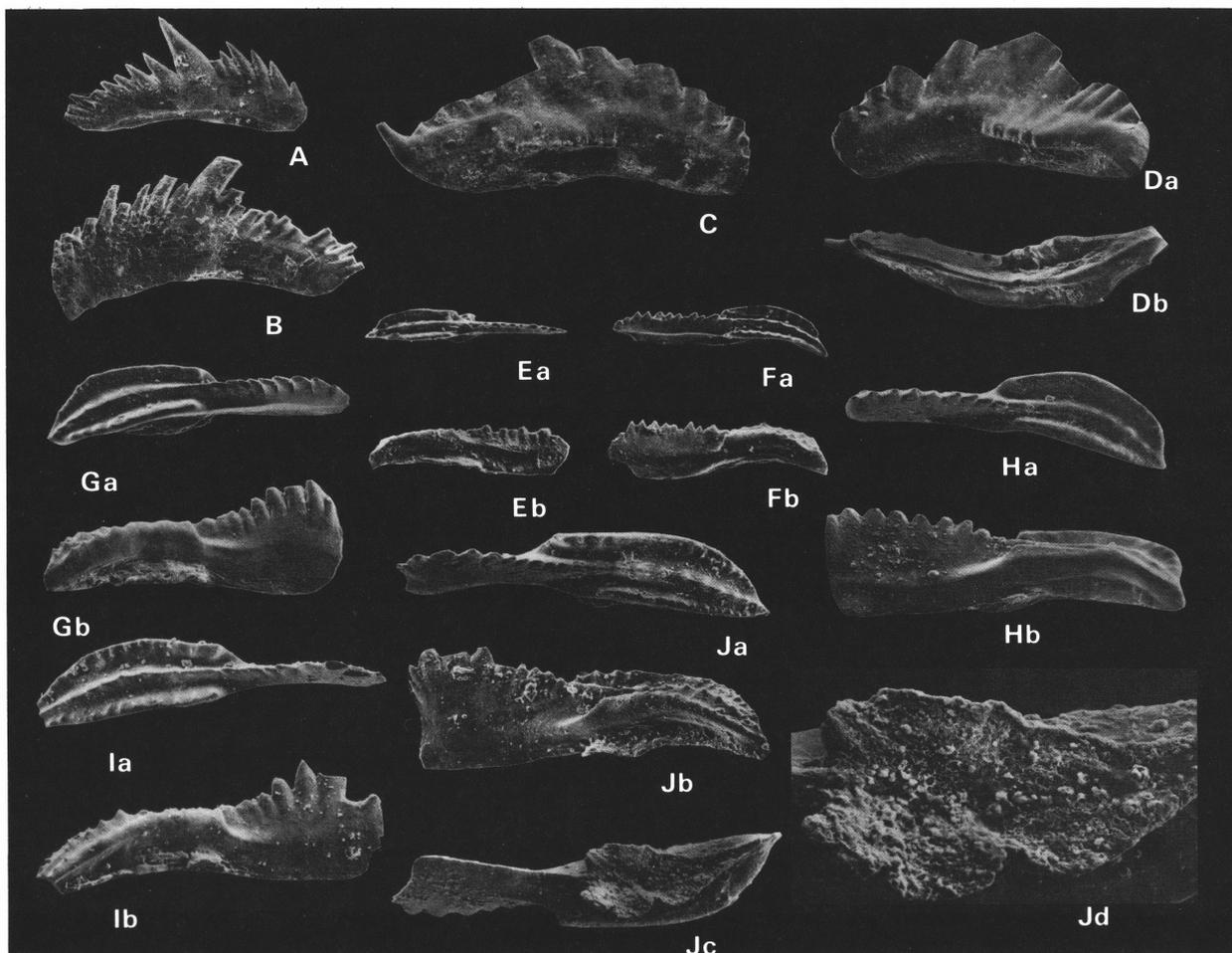


Figure 2. *Polygnathus xylus xylus*, discrete elements.

All figures x55 except as noted. A–D, Pb elements. A, mature element (CPC25155), lateral view. B, mature element (CPC25156), lateral view. C, gerontic element (CPC25157), lateral view. D, gerontic element (CPC25158): Da, lateral view; Db, basal view. E–J, Pa elements. E, small mature element (CPC25159): Ea, oral view; Eb, lateral view. F, small mature element (CPC25160): Fa, oral view; Fb, lateral view. G, mature element (CPC25161): Ga, oral view; Gb, lateral view. H, mature element (CPC25162): Ha, oral view; Hb, lateral view. I, large mature/gerontic element (CPC25163): Ia, oral view; Ib, lateral view. J, large mature/gerontic element (CPC25164): Ja, oral view; Jb, lateral view; Jc, basal view, showing basal plate; Jd, enlargement (x170) of basal plate.

tional discrete elements remain in the residue, but all clusters have been recovered. Distribution of element types is shown in Table 1.

Table 1. Distribution of element types of *P. xylus xylus* from sample WCB 804/5, which form the basis for this study.

	Element type							Total
	M	Sa	Sc	Sb	Sd	Pb	Pa	
Right elements	108		81	35	18	126	212	580
Symmetrical element		109						109
Left elements	110		73	48	25	137	218	611
Total	218	109	154	83	43	263	430	1300

Diagnosis. Multielement taxon with apparatus consisting of 15 elements of seven element types – M (2), Sa (1), Sc (4), Sb (2), Sd (2), Pb (2) and Pa (2). The M elements are dolabrate; the Sa element is alate; the Sc, Sb, and Sd elements are bipennate; the Pb elements are angulate; and the Pa elements are carminiplanate.

The Pa element platform may be smooth or have subdued marginal nodes. The carina usually consists of a series of low but discrete nodes, but these may become prominent and coalesce in larger gerontic specimens. The posterior tips of the platform are bent slightly downward. The geniculation points are opposite.

Remarks. *Polygnathus xylus xylus* is part of a complex of closely related late Middle Devonian–early Late Devonian species of *Polygnathus*, which includes species such as *P. decorosus*, *P. pseudofoliatus*, *P. webbi*, *P. varcus*, *P. dubius*, and others (Huddle, 1970), and species assignment of the Pa element of some of these forms is difficult, especially where populations appear to represent evolving or intermediate morphologies.

The Pa element of *P. xylus xylus* has been adequately illustrated, and does not need to be described here. Other elements of the apparatus are not well described or their relationship to the Pa element has not been recognised, although Uyeno (1978) has illustrated or described most of the elements of the apparatus. Uyeno (1978) thought that the Pb (O₁) element of *P. xylus* was represented by a form similar to *Spathognathodus planus* Bischoff & Ziegler. In this study, the lack of forms similar to *S. planus* in either the discrete elements or the clusters rules out that morphology as the Pb element. The Pb element (Figs. 1B, 4A) is, in fact, similar to that illustrated by Klapper & Philip (1971, Fig. 12) as part of the *P. dubius* apparatus. It is characterised by an enlarged cusp, uniform denticles, and a low to moderate arch.

The ramiform elements of *P. xylus xylus* are generally similar to those of the closely related *Polygnathus* species. In many cases it may be impossible to distinguish the species assignment of the ramiform elements if more than one type of *Polygnathus* Pa

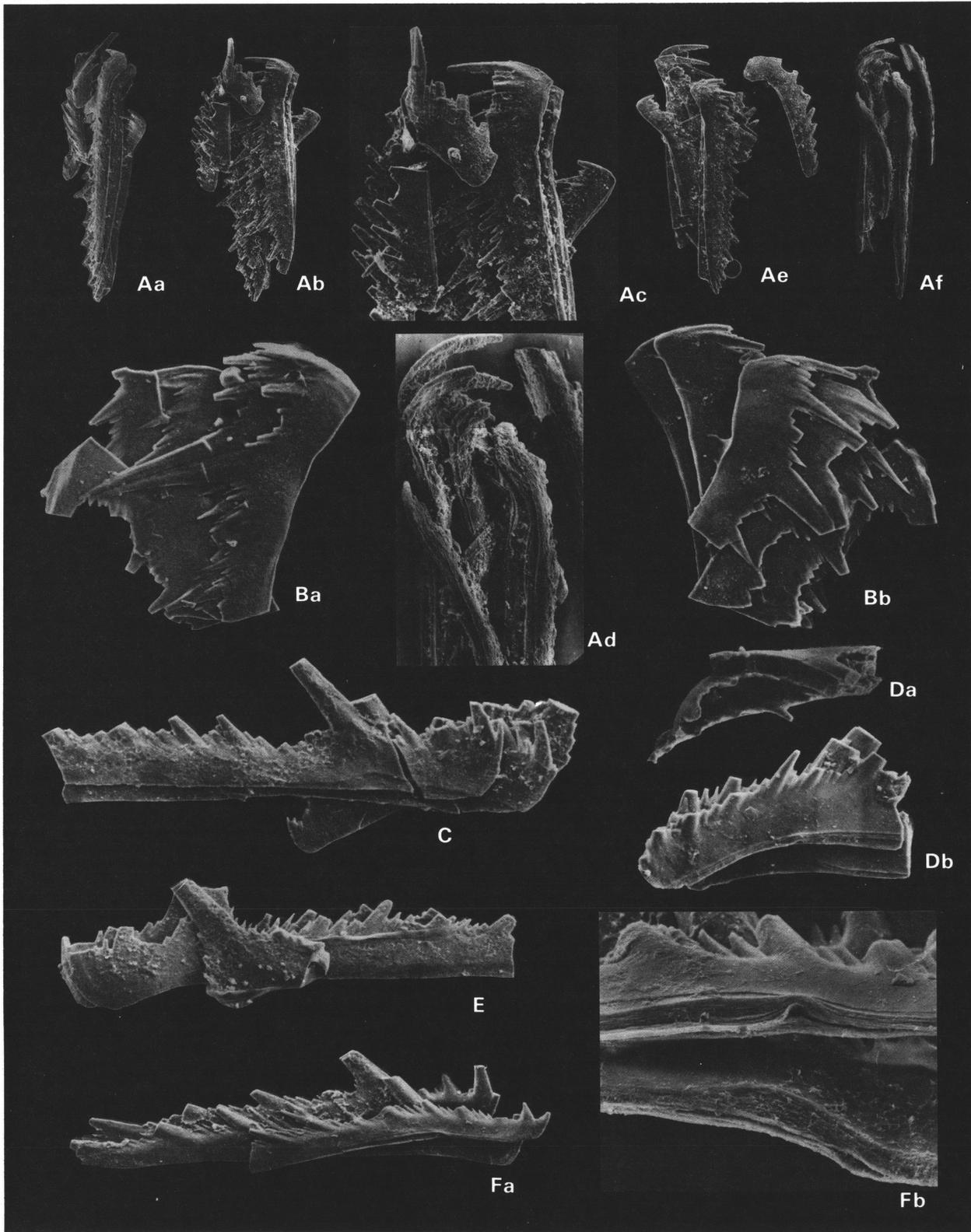


Figure 3. *Polygnathus xylus xylus*, clusters of ramiform elements.

All figures x135 except as noted. A, cluster of ramiform elements (CPC25165), includes M (2), Sa (1), Sc (4), & Sb (2) elements: Aa, basal view (x40); Ab, lateral view (x40); Ac, enlargement (x80) of anterior part of cluster, broken posterior process near left margin is an M element; Ad, enlargement (x95) of anterior part of cluster, showing diagonal position of broken posterior process of Sa element flanked on either side by a single Sb element and two Sc elements; Ae, lateral view of reverse side (x40), M and Sa elements detached; Af, basal view of reverse side (x40). B, two lateral views, Ba and Bb, of cluster of ramiform elements (CPC25166), including Sa (1), Sc (4) and Sb (2) elements; Sa element with missing lateral processes in centre and flanked by single Sb and two Sc elements on either side. C, cluster of two Sc elements with single M element on outer side (CPC25167), inner lateral view. D, cluster of two Sc elements with Sb element on inner side (CPC25168): Da, oral view; Db, inner lateral view. E, cluster of two Sc elements with single M element on outer side (CPC25169), outer lateral view (x100). F, cluster of two Sc elements with single Sb element on inner side (CPC25170): Fa, inner lateral view (x85); Fb, enlargement (x400) showing basal cavity morphology of Sb (upper) and Sc (lower) elements.

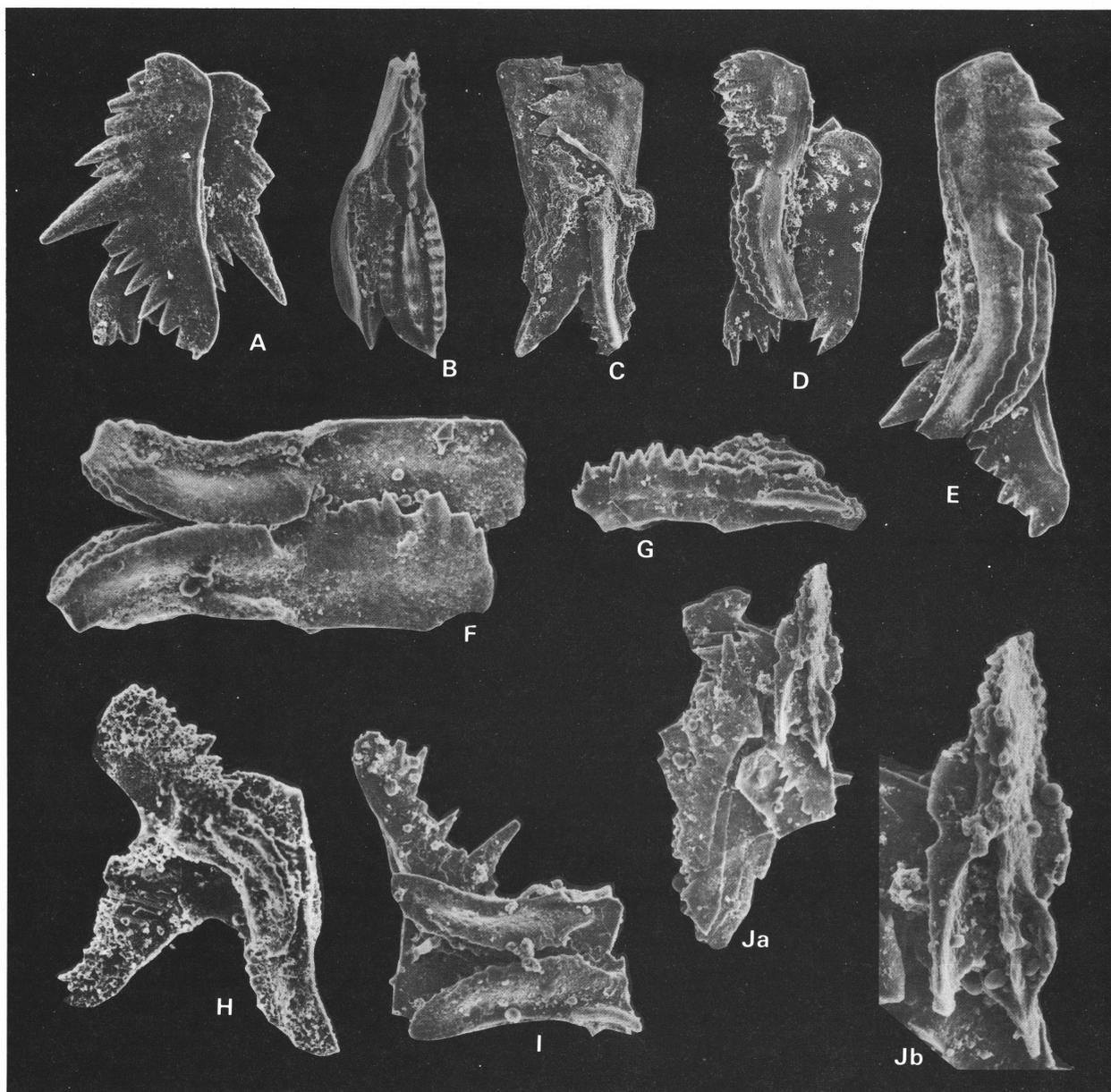


Figure 4. *Polygnathus xylus xylus* clusters.

All figures x100 except as noted. A, cluster of two overlapped Pb elements, basal cavities directed outward (CPC25171). B, cluster of two overlapped Pa elements, oral surfaces not intermeshed (CPC25172). C, cluster of two Pa elements (x60) in presumed functional orientation with oral surfaces intermeshed (CPC25173). D, cluster of two Pb elements and single Pa element (x60); Pb elements overlapped with basal cavities directed outward (CPC25174). E, cluster with single Pa and Pb elements (CPC25175). F, cluster of two Pa elements, oral surfaces intermeshed (CPC25176). G, cluster of two juvenile Pa elements, oral surfaces both facing in same direction (CPC25177). H, cluster of two Pa elements and single Pb element (x120); Pa elements not intermeshed, but with basal cavities facing outward (CPC25178). I, cluster of two Pa elements and single Pb element (x120); Pa elements with oral surfaces intermeshed (CPC25179). J, cluster of juvenile elements containing two Pa, two Pb, two M and an indeterminate number of S elements (CPC25180): Ja, view of cluster (x120); Jb, enlargement of cluster, showing pair of juvenile Pa elements (x250).

element is present in the fauna. For this reason, I have not attempted to sort out and apply full synonymies of all the elements of *P. xylus xylus*. However, it is possible to give form-species names to representative morphologies of each of the element types. The M element is of the *Neoprioniodus* (*Synprioniodina*) *forsenta* Stauffer, 1940, type; the Sa element is of the *Hibbardella alternata* Branson & Mehl, 1934, type; the Sc element is of the *Hindeodella subtiles* Bassler, 1925, type; the Sb element is of the *Hindeodella compressa* Huddle, 1934, type; and the Sd element is of the *Hindeodella uncatata* (Hess, 1959) type.

The Sd element, the only element type not previously associated with multielement reconstructions of *Polygnathus*,

is generally morphologically similar to the Sc and Sb elements. The major morphologic distinction of the Sd element is that the anterior process is turned inward at a right angle to the axis of the posterior process.

An observation with important implications for loss or retention of ramiform elements in 'mature' or 'gerontic' conodonts can be made in this study. A number of specimens in the fauna show a marked thickening of the elements (Figs. 1, 2). At first, I considered this might represent another species in the fauna, but the restriction of this morphology to larger specimens seems to indicate that it represents a mature or gerontic modification of *P. xylus xylus*. It has been observed in all elements.

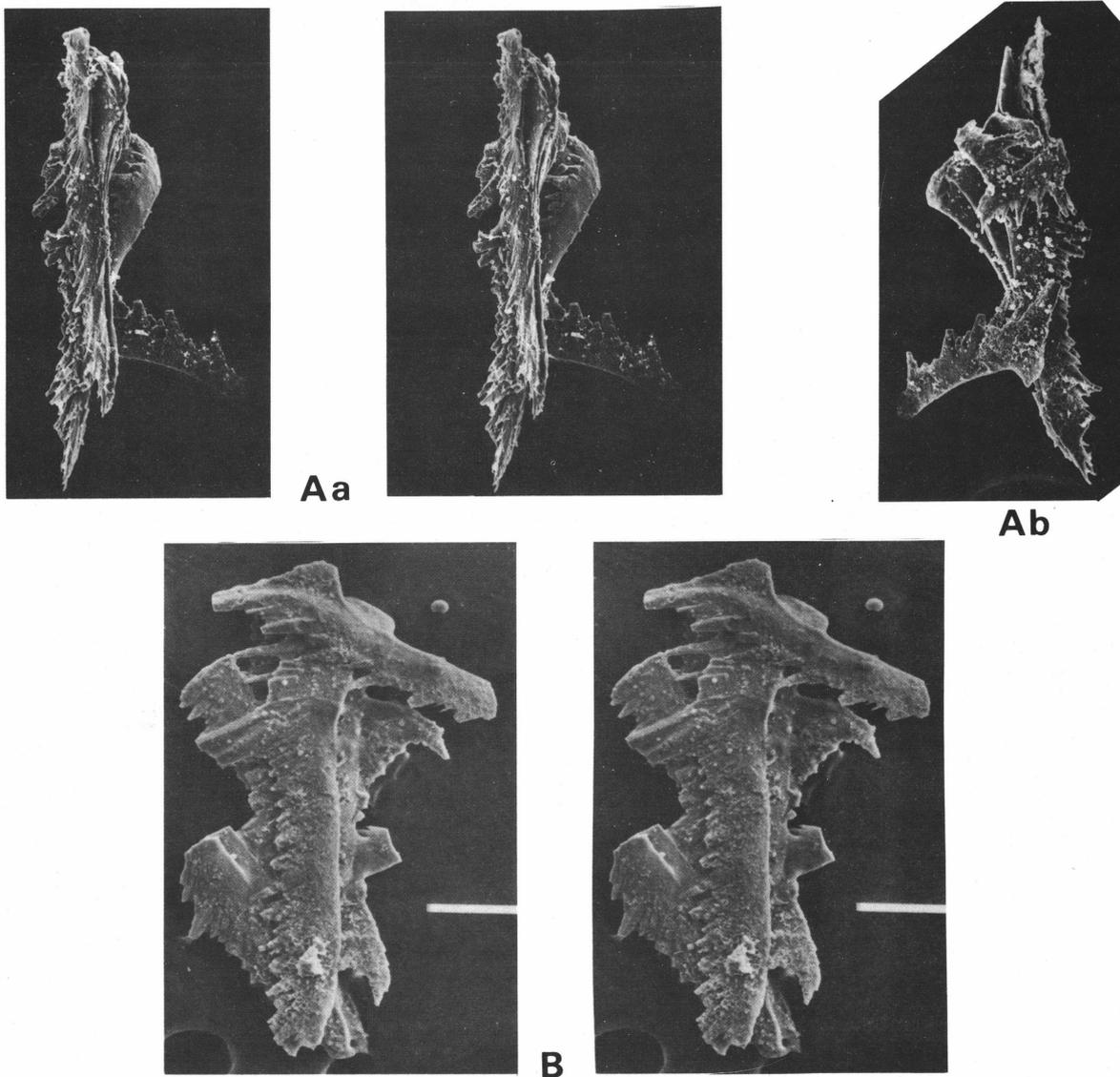


Figure 5. *Polygnathus xylus xylus* clusters.

All figures x60. A, two views of cluster containing one M, one Sa, four Sc, and two Sb elements (CPC 25181): Aa, stereo pair emphasising basal view of a triplet of one Sb and two Sc elements; Ab, view showing Sa element with broken but attached posterior process, flanked by a triplet of one Sb and two Sc elements. B, stereo pair (x120) of cluster containing nine elements (CPC25182): M element at top covers two Sc elements; exact identification of the remaining elements is not definite.

Genus *Ozarkodina* Branson & Mehl, 1933

Type species. *Ozarkodina confluens* (Branson & Mehl, 1933)

Ozarkodina brevis (Bischoff & Ziegler, 1957)
 Figures 6–9.

Synonymy.

- 1957 *Spathognathodus brevis* n.sp.; Bischoff & Ziegler, pp.116–117, Pl. 19, Figs. 24, 27–29.
- 1977 *Ozarkodina brevis* (Bischoff & Ziegler); Klapper in Ziegler, p.263, Pl. Oz3, Figs. 9,11 (includes synonymy).
- 1982 *Ozarkodina brevis* (Bischoff & Ziegler); Uyeno in Norris & others, p.77, Pl. 32, Figs. 23, 24, 29–38. (includes synonymy).

Material studied. *O. brevis* is not abundant in sample WCB-804/5, from which only five clusters and two discrete Pa elements were recovered. To supplement this limited fauna, ten

samples have been included from an additional locality, WCB-811 (Nicoll, in press), which does contain abundant *O. brevis* (Table 2).

Table 2. Distribution of *O. brevis* element types in samples from depth study section WCB-811, McWhae Ridge, Canning Basin

Sample	Element type							Total
	Pa	Pb	M	Sa	Sb	Sc	Sd	
1A	24	4	4	6	3	9	2	52
1B	35	7	2	4	2	11	0	61
2A	41	8	1	3	5	9	0	67
2B	61	38	5	9	7	7	0	127
3A	44	8	3	2	2	18	0	77
3B	59	23	2	1	8	1	0	94
4A	8	11	0	4	3	3	0	29
4B	18	2	0	2	2	2	0	23
5A	0	0	0	0	0	0	0	0
5B	0	0	0	0	0	0	0	0
Total	287	101	17	31	32	60	2	530

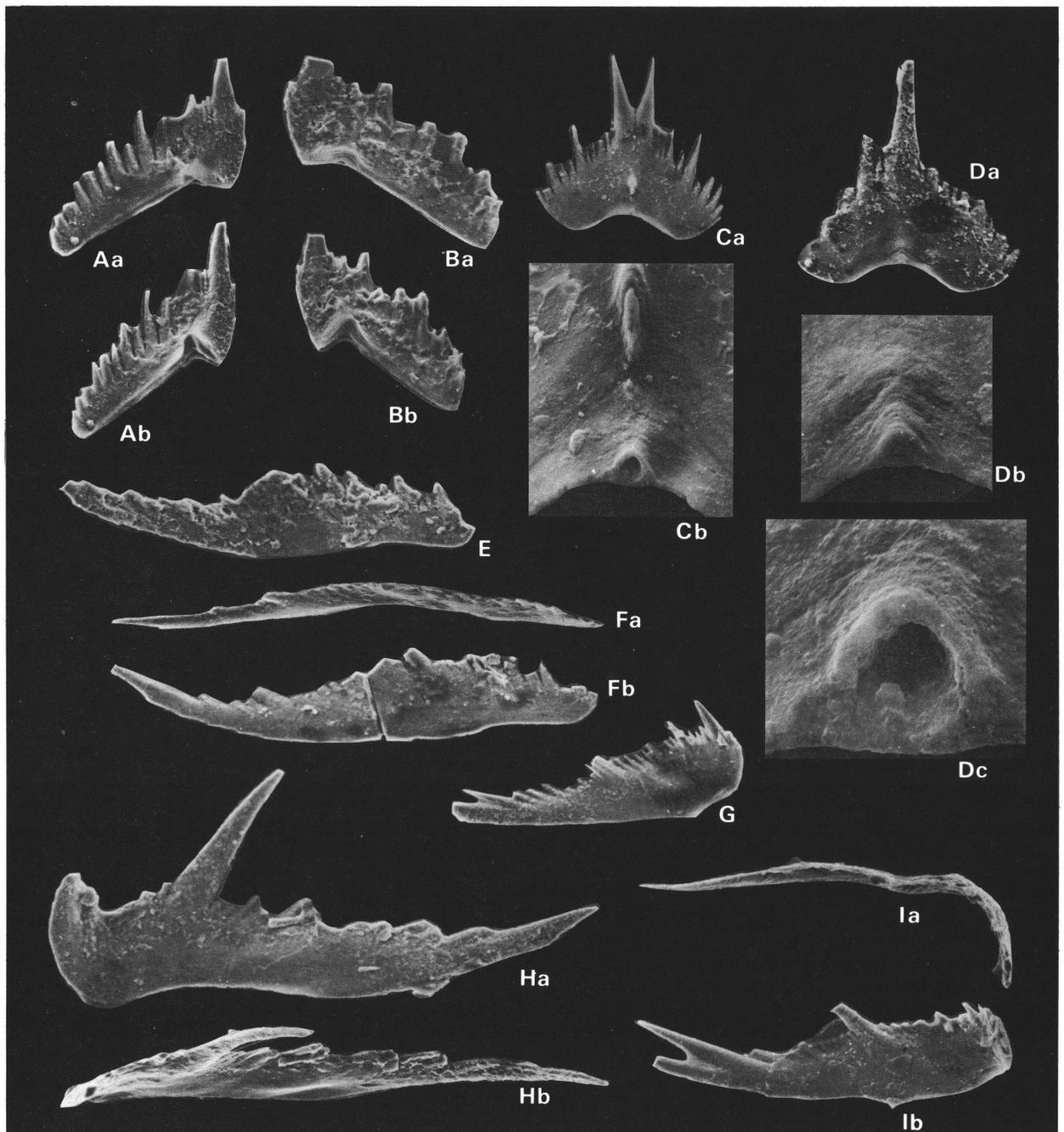


Figure 6. *Ozarkodina brevis*, discrete elements.

All figures x135 except as noted. A, M element (CPC25183): Aa, posterior view; Ab, posterior basal view. B, M element (CPC25184): Ba, posterior view; Bb, posterior basal view. C, Sa element (CPC25185) with bifid cusp and protrusion indicating possible site of a posterior process. Specimen probably a pathologic freak. Ca, posterior view; Cb, enlargement (x450) of basal cavity area. D, Sa element (CPC25186): Da, posterior view; Db, enlargement (x450) of basal cusp area; Dc, enlargement (x1800) of basal cusp. E, Sb element (CPC25187): inner lateral view. F, Sb element (CPC25188): Fa, oral view; Fb, inner lateral view. G, Sc element (CPC25189): inner lateral view. H, Sc element (CPC25190): Ha, inner lateral view; Hb, oral view. I, Sd element (CPC25191): Ia, oral view; Ib, inner lateral view.

Diagnosis. Multielement taxon consisting of 15 elements of seven element types – M (2), Sa (1), Sc (4), Sb (2), Sd (2), Pb (2) and Pa (2). The M elements are dolabrate; the Sa element is alate; the Sc, Sb, and Sd elements are bipennate; the Pb elements are angulate; and the Pa elements are segminate or carminate. The ovoid basal cavity of the Pa element is at the posterior end of the element, and there is no indication of a groove on the posterior inner margin. Up to three denticles may be located posteriorly to the cusp of the Pa element.

Description. All the elements of *Ozarkodina brevis* are smaller than the normal size range of mature conodont elements. The

elements are also thin and hence fragile, and tend to break easily. The larger denticles, including the cusps, of all element types have well-developed, relatively coarse striations.

Pa element (Fig. 7C–G) – This segminate or carminate element has an irregular, usually slightly asymmetrical, ovoid basal cavity that is rounded posteriorly and narrows anteriorly to a groove under the blade. The cusp is developed over the basal cavity and may be twice as large as the adjacent denticles. The denticles are laterally compressed, and decrease in size toward the anterior end of the blade, but the total height of the blade re-

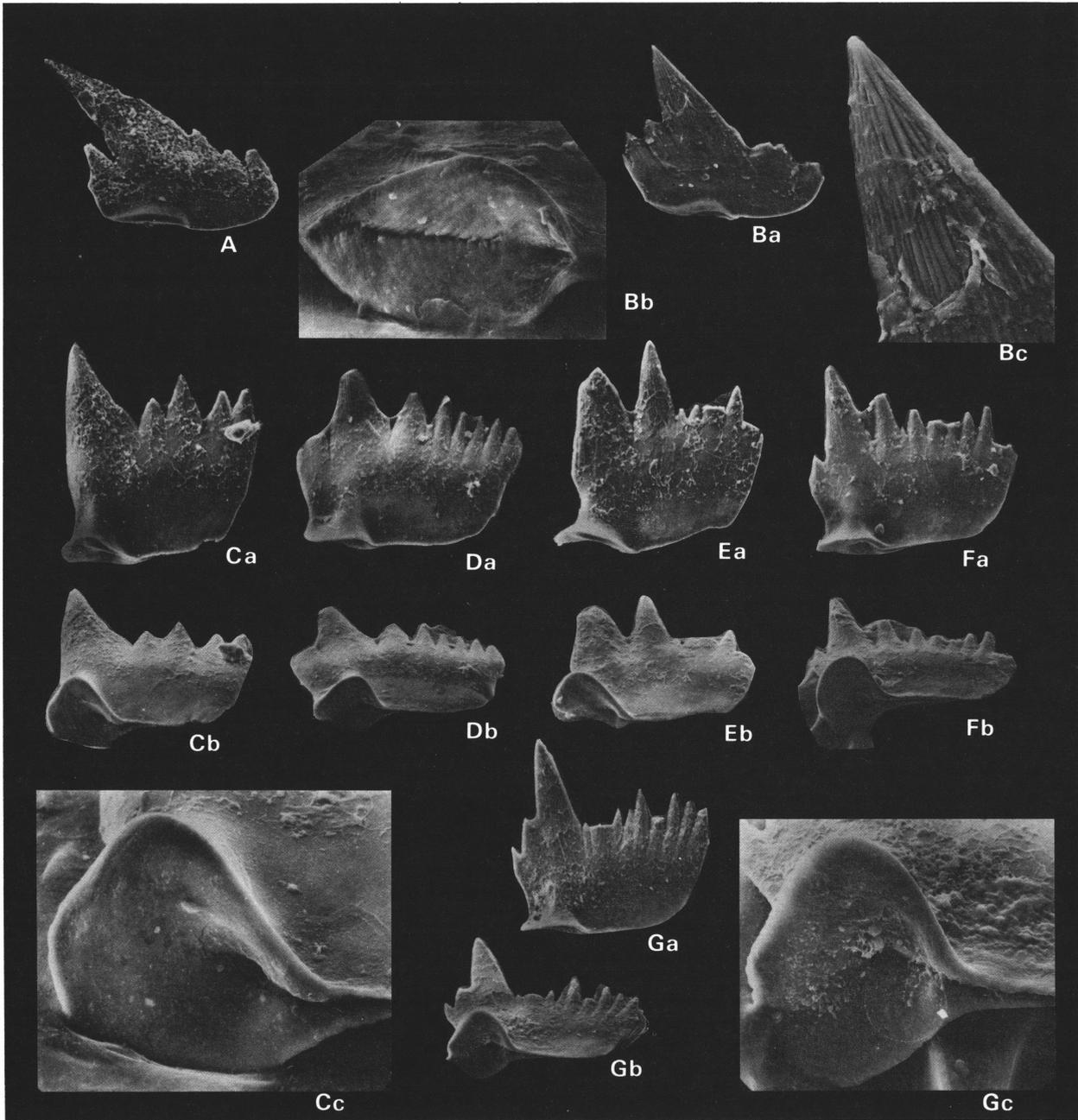


Figure 7. *Ozarkodina brevis*, discrete elements.

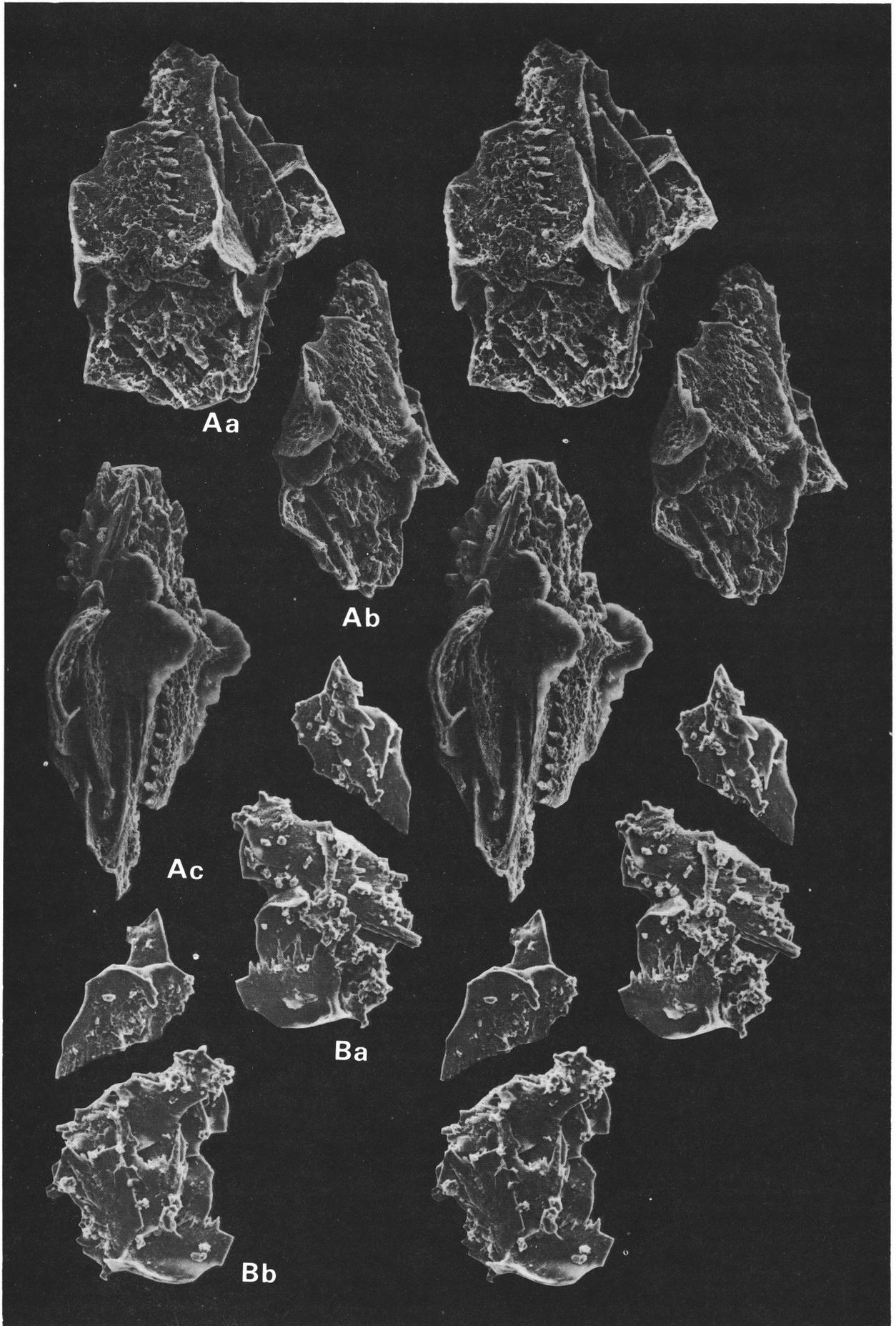
All figures x120 except as noted. A, Pb element (CPC25192), lateral view. B, Pb element (CPC25193): Ba, lateral view; Bb, enlargement (x550) of basal cavity; Bc, enlargement (x550) of cusp, showing striations. C, Pa element (CPC25194): Ca, lateral view; Cb, oblique basal view; Cc, enlargement of basal cavity (x500). D, Pa element (CPC25195): Da, lateral view; Db, oblique basal view. E, Pa element (CPC25196): Ea, lateral view; Eb, oblique basal view. F, Pa element (CPC25197): Fa, lateral view; Fb, oblique basal view. G, Pa element (CPC25198): Ga, lateral view; Gb, oblique basal view; Gc, enlargement of basal cavity (x400).

mains roughly uniform. Elements are usually straight with little, if any, lateral bow.

Table 3. Numbers of anterior and posterior blade denticles on the Pa element of *O. brevis* in samples from depth study section WCB-811

Posterior denticles	Anterior blade denticles									Total
	4	5	6	7	8	9	10	11	Indt.	
0	8	10	23	23	16	10	7	0	35	132
1	1	4	13	26	16	8	5	2	31	106
2	0	1	13	9	10	4	0	0	7	44
3	0	2	0	0	1	0	0	1	1	5
Total	9	17	49	58	43	22	12	3	74	287

Table 3 shows the abundance of anterior and posterior denticles of the 287 Pa elements studied from samples at McWhae Ridge (Nicoll, in press). Two basic morphologies, i.e. those with and without post-cusp denticles, have previously been referred to the discrete element taxon *Spathognathodus brevis*. Those elements lacking blade denticles behind the cusp have usually been referred to *S. brevis* ss., and those elements with one or more denticles posterior to the cusp have frequently been referred to *S. cf. S. brevis* (see Druce, 1976). In this study, 132 specimens lack denticles posterior to the cusp and 155 specimens have from one to three denticles posterior to the cusp. There is a slight tendency for more blade denticles in elements with post-cusp denticles (Table 3). Thus, the specimens with post-cusp denticles may represent more mature animals, although the



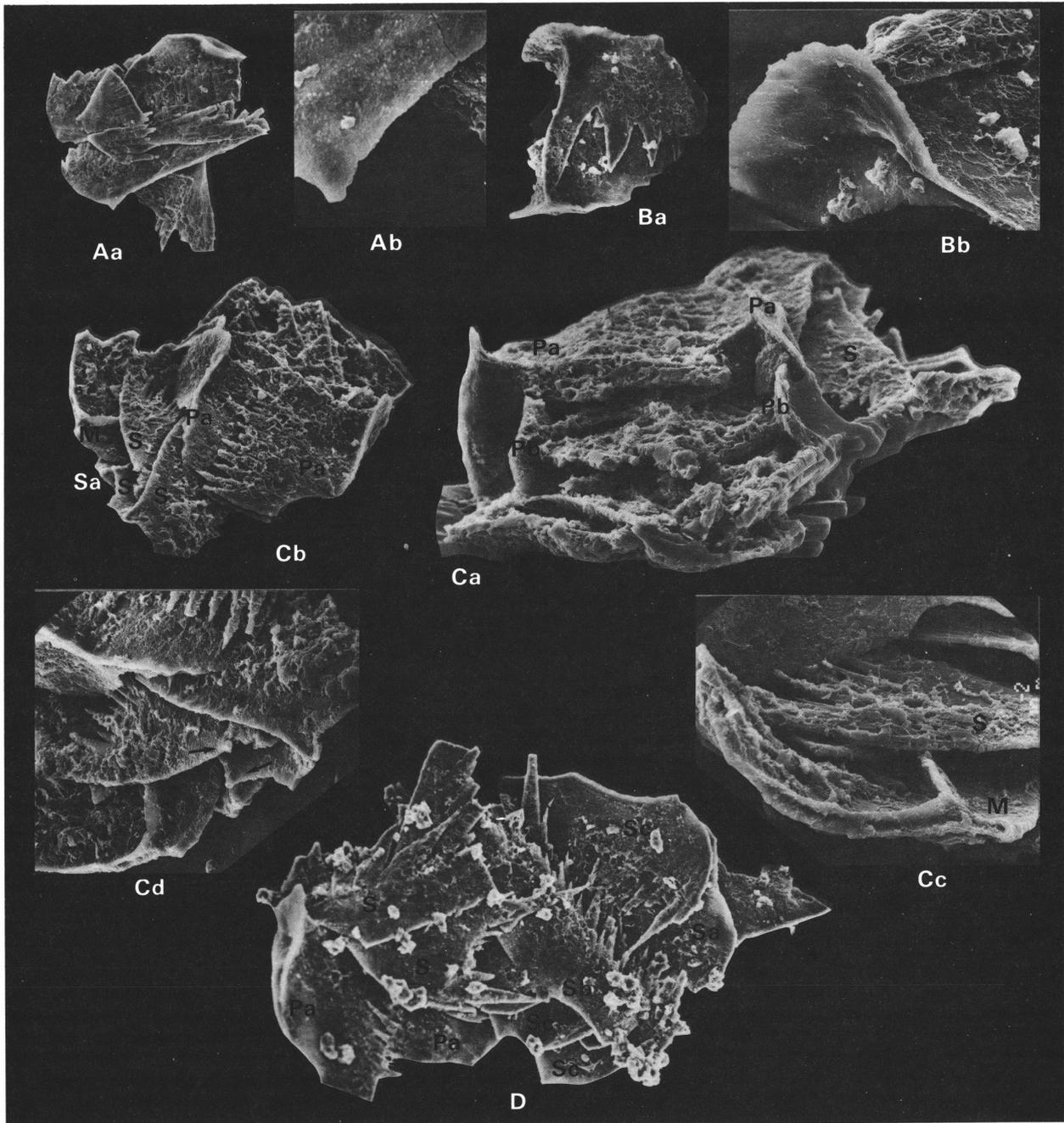


Figure 9. *Ozarkodina brevis*, clusters.

A, clusters containing 5 or 6 elements, including one Pa and one Sc element (CPC25201): Aa, view of cluster (x150); Ab, enlargement showing basal cavity projection of Sc element (x750). B, cluster containing one pair of Pa elements (CPC25202): Ba, lateral view (x100); Bb, enlarged basal view of one element (x175). C, enlargements of cluster shown in Figure 8A (CPC25199): Ca, view of posterior of paired Pa elements on top of paired Pb elements (x400); Cb, anterior view of paired Pa elements on top, M element on bottom left (x240), S elements between; Cc, enlargement of base of M element, showing squashed basal cavity (x650); Cd, enlargement showing projecting basal cavity (x370). D, enlargement (x200) of cluster shown in Figure 8B (CPC25200).

population may be too small for this difference to be statistically significant. There seems to be no justification for recognition of separate species based on the presence or absence of denticles located posterior to the cusp.

Pb element (Fig. 7A–B) – This angulate element has a large laterally compressed cusp, which may be as much as one-third of the total length of the element. The anterior process has three to eight denticles and the posterior process has one to four den-

ticles. The basal cavity opens abruptly from the enlarged groove along the base of the anterior process and then tapers to the posterior tip.

M element (Fig. 6A, B) – The M element is dolabrate with one or more denticles on the inner side of the cusp. The basal cavity has a well-developed, posteriorly directed flange, and a prominent basal groove along the entire margin.

Figure 8. *Ozarkodina brevis*.

A, stereo pairs of cluster (CPC25199) containing at least 13 elements, including two Pa, two Pb, two M, and one Sa elements, and six unidentified Sc-Sb-Sd elements: Aa, lateral view with Pa element pair on top (x220); Ab, edge view, same orientation as Aa (x220); Ac, edge view of inverted cluster (x270). B, stereo pairs of cluster (CPC25200) containing at least 11 elements, including two Pa, two M, two Sc, and one Sa elements. Ba and Bb are reverse sides. Sa element is second element from top in Ba and is partly covered by an Sc element. Pa element pair at bottom of both Ba and Bb (x120).

Sa element (Fig. 6C, D) – The Sa element is alate, but lacks a posterior process. The lateral processes are bent slightly anteriorly, and have eight to twelve denticles on each bar. The basal cavity consists of a small semi-circular raised lip with a central depression. It is located on the posterior side of the element.

Sc, Sb & Sd elements – The Sc (Fig. 6G, H), Sb (Fig. 6E, F), and Sd (Fig. 6I) elements are bipennate with posteriorly inclined denticles. The posterior end of these elements is usually composed of one or two large denticles that are inclined with their long axis almost parallel with the long axis of the element. The lower margin of these denticles may bear a number of small subdenticles. The lower margin is knife-like, with no groove or basal cavity apparent in discrete elements. The elements do have a basal cavity, the morphology of which, to my knowledge, is unique among ramiform elements. It consists of a short round projection extending down from the basal margin of the element. There is a central depression in the tip of this projection that is similar to the cavity of the Sa element. None of these basal cavity projections was observed on the discrete elements in this study, and I suspect that this structure is so fragile that it has broken off most, if not all, discrete elements.

The anterior process of the Sc element is high and bent slightly inward, and the anterior margin is curved upward. The Sb element has an anterior process that is inclined slightly inward and downward. The Sd element has the anterior process bent inward at 90 degrees from the axis of the posterior process.

Remarks. The small size of most, if not all, illustrated examples of *O. brevis* may indicate that this species represents a 'dwarfed' conodont animal. It is unlikely that all the specimens examined in this and other studies represent juvenile material, and, hence, the small size of the adult conodont element probably also reflects a smaller than average size of the *O. brevis* animal.

Klapper & Barrick (1983) have described a new species *Ozarkodina raaschi*, which appears to be very closely related to *O. brevis*. As noted by them, the only significant difference in the two species appears to be in the morphology of the Pa element. It seems probable that *O. brevis* has evolved from *O. raaschi*. The morphology of the basal cavity of the Pa element of *O. raaschi*, which has a groove at both the anterior and posterior margins, is closer to that of most species of *Ozarkodina* than is the cavity of *O. brevis*.

Five clusters of *O. brevis* were recovered from sample WCB-804/5. Preservation of the clusters is variable and none is thought to contain all 15 elements of the apparatus. Most clusters are partly obscured by apatite crystal overgrowth and, thus, element identification and exact counts are difficult. Elements are also partly or almost completely obscured by their stacked nature in most of the clusters, and this has made it impossible to be completely sure of distinguishing Sc, Sb, and Sd elements in some of the clusters.

The simplest cluster (Fig. 9B) consists of only a single pair of Pa elements. The cluster shown in Figure 9A contains a single Pa element and five S elements, two of which appear to be Sc elements. These elements show the projecting basal cavity (Fig. 9Ab).

The elements in the two views of the cluster shown in Figures 8B and 9D are very much obscured by apatite overgrowth. However, at least eleven elements can be distinguished, including a pair of Pa elements, probably two M elements and possibly two Sc elements.

The best preserved cluster is shown in Figures 8A and 9C. This cluster contains at least 13 elements, which are partly obscured by apatite overgrowth. Seven elements have been positively identified and these comprise one pair each of Pa, Pb, and M elements and a single Sa element. The additional six elements are of the Sc–Sb–Sd types, but cannot be positively differentiated in the cluster because they are broken or obscured by other elements.

Morphology and function: an interpretation of the conodont apparatus.

The recent discovery by Briggs & others (1983) of the impression of a conodont animal and the well-preserved clusters of this study allow an interpretation of the arrangement and function of the apparatus elements within the conodont organism.

Previously published examples of bedding-plane assemblages (Schmidt, 1934; Scott, 1934; Dubois, 1943; Rhodes, 1952) and Devonian or Carboniferous fused clusters (Lange, 1968; Austin & Rhodes, 1969; Higgins, 1975; Nicoll, 1977) have not shown the element relationships as well as the fused clusters of this study or the bedding-plane assemblage of Briggs & others (1983). The element-distribution pattern determined from the fused clusters of this study (Fig. 10) is essentially the same as that suggested by Briggs & others (1983). It is also nearly identical, with the exception of the addition of the Sd elements, to the reconstruction of the apparatus proposed by Jeppsson (1971).

Unfortunately, there is not much fine detail preserved in the head region of the conodont animal illustrated by Briggs & others (1983, fig. 3). However, it is clear from their illustrations that the elements are located within the body of the animal, on or about the midline, and near the anterior end. The elements are certainly not located externally, as suggested by Lindstrom (1972, 1974).

I have made several assumptions in this reconstruction and analysis of the conodont apparatus. The first is that the working surface of the conodont element was covered by tissue that was probably ciliated, enabling the tissue both to secrete the layers of the crown and, with its outer ciliated surface, move water or particulate matter. It is improbable that the lateral spacing of the elements would have allowed them to have been retracted into a tissue fold where secretion of the element could have taken place in the manner suggested by Bengtson (1976).

I have also assumed that the conodont elements were located in a structure on the ventral surface of the organism. It seems logical (see below) that the feeding structure, of which the preserved elements were a part, would have functioned more effectively on the ventral rather than the anterior or dorsal surfaces of the organism.

The sequence of anterior ramiform elements followed by paired Pb and then Pa elements confirms the general sequence suggested by Jeppsson (1971) and Nicoll (1977), rather than the reverse sequence suggested by Rhodes (1952), which Hitchings & Ramsay (1978) used as a model for their interpretation of the apparatus function.

From the element relationships indicated by the clusters of this study, the morphology of the individual elements, and the outline of the organism illustrated by Briggs & others (1983), I have attempted, using *Polygnathus xylus xylus* as the model, to show the relative positions of the elements in the conodont animal (Fig. 10). As can be seen in the reconstruction, the elements have been separated into three groups, based on the

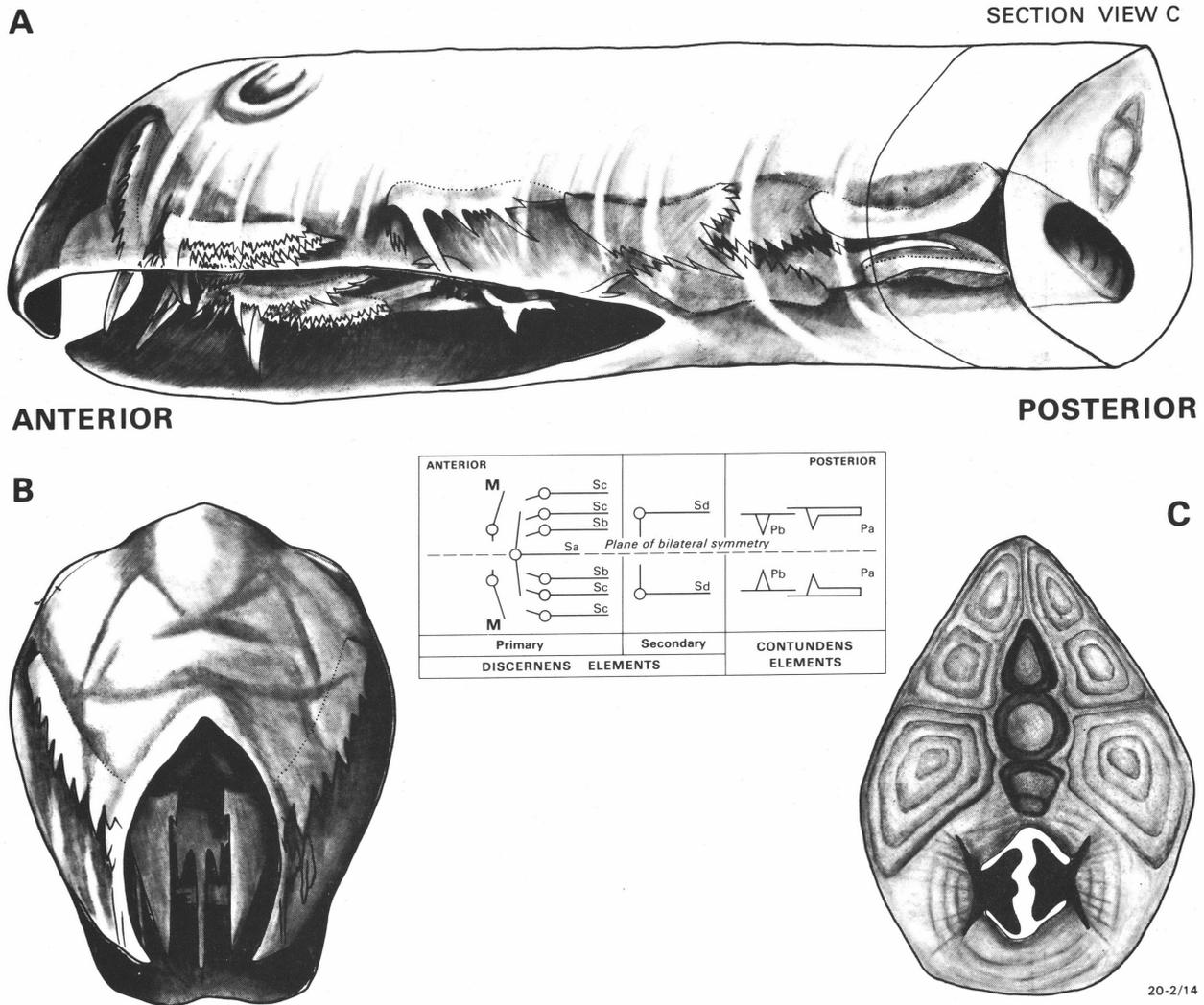


Figure 10. Artist's impression of the head region of a conodont animal, based on the specimen illustrated by Briggs & others (1983) and the *Polygnathus xylus xylus* clusters of this study.

View A shows a lateral projection of the animal with the elements in position along the food groove. B is an anterior view, showing the lateral flaps in a half-closed position. C is a cross-section through the Pa elements.

relationship of the elements in the clusters. Discernens elements are anteriormost in the sequence. The denticles of this group are directed ventrally and are slightly recurved posteriorly. The M elements have the long axis of the 'posterior' process located transversely to the long axis of the rest of the S elements, but parallel to the lateral processes of the Sa element. The cusps of the M, Sa, Sc, and Sb elements project well below the rest of the minor denticles of these elements. As the cusp denticles are significantly bigger than any of the adjacent denticles, they must have served a slightly different function. The parallel posterior processes of the Sa, Sc, and Sb elements provide a massive surface area, which, if covered with ciliated tissue, should have been very effective in the movement of water currents and particulate matter.

The function of the primary discernens elements is thus interpreted as that of a sieve for the initial sorting of food particles at the anterior end of the food groove. The transverse M elements at the front would have served as the initial deflectors, and the triangular cross-section of the large cusps of these, being structurally very strong, would have taken the brunt of the impact of large particles. The cusps of the Sa, Sc, and Sb elements would also have served to deflect larger particles away from the food groove. The smaller denticles with their ciliated surfaces would have set up a current action to carry food particles along the

food groove toward the mouth. These elements would probably have been located in a food groove that was open ventrally, but would have been protected laterally by soft tissue to at least the height of the cusps. The lateral flap-like features on either side of the anterior end of the conodont animal (Briggs & others, 1983) could have served to help direct particulate material toward the entrance of the food groove.

It is interesting to note here that most examples of element breakage and regrowth involve the cusps of S-type elements. These large projecting denticles, with the function of deflecting large particles, would have been subjected to much greater stress than the shorter, smaller denticles.

Behind the primary discernens elements are the two Sd elements, the only secondary discernens elements. The Sd element has not been recognised in most of the reconstructed apparatus structures. However, in studies of Late Devonian and Early Carboniferous conodont faunas, representing a wide variety of genera, I have been able to assign an element to the Sd position. In many species, the Sd element is characterised by an antero-lateral process that is directed inward at about 90 degrees from the posterior process.

The function of the secondary discernens elements must be similar to that of the primary discernens elements, because they

share a very similar basic morphology. In fact, it is the close similarity of the Sb and Sd elements that has caused the Sd element to be unrecognised in so many apparatus reconstructions. On the basis of the transverse nature of the relatively large antero-lateral process and the generally greater number of long, large denticles of this element, I would suggest that this element served as the final filter of particles unacceptable to the conodont animal. If this was the case, the Sd elements would also have been located above a ventrally open groove so that the rejected particles could have been expelled.

The final elements of the apparatus, and of the food groove, are the paired Pa and Pb elements that form the contundens elements. These are usually completely different, morphologically, and, thus, functionally, from the discernens elements. There is an indication from the preservation of fused Pb and Pa elements from this and other studies (Rexroad & Nicoll, 1964; Pollock, 1969) that these elements were oriented with the upper surfaces of paired elements facing each other rather than side by side. This orientation is frequently preserved in fused clusters (Figs. 4, 8), and I believe it to represent the life position of the elements, rather than a post-mortem position.

The result of this orientation can be seen when pairs of Pa elements of many Devonian and Carboniferous species are examined. This is especially true of species with asymmetric pairs, those representing Lane's Class IIIb symmetry (Lane, 1968). The lateral offset of blades and platforms common in these species is an adaptation to allow them to intermesh. This can also be seen in several species of *Polygnathus*, where the morphology of the opposing platforms is modified so that raised platform margins will fit into depressions in the opposing element. An excellent example of this is seen in *Polygnathus inornatus nodulatus* Druce and *P. siphonellus* Druce, where the right and left elements have been identified as separate species (right = *P. inornatus nodulatus*, left = *P. siphonellus*).

The function of Pb and Pa elements is difficult to determine just from element morphology, but, because some or many of the Pa elements show morphologic modification to allow the blades and platforms to intermesh, this must indicate that these elements touched or nearly touched.

The interpretations of the relationships, function, and morphology of the conodont elements examined in this study have a number of important implications for the biology and ecology of conodonts. Some of these interpretations may be applied to all conodont species, but others may be limited to only a few taxa.

The gerontic modification seen in *P. xylus xylus* shows that, at least under favourable ecologic conditions, all elements of the apparatus were retained in the organism, probably for its entire life. A corollary of this is that the imbalance of ramiform-pectiniform elements in many conodont samples cannot be explained by the shedding of ramiform elements.

The interpretation of grouping and function of the different elements in the conodont may begin to explain some trends in morphology seen in evolutionary sequences of some conodont taxa. For example, the M elements of early Ordovician genera such as *Prioniodus* or *Bergstroemognathus* are morphologically very similar to the M elements of Devonian or Carboniferous genera, such as *Polygnathus* or *Gnathodus*. This general stability of morphology of the ramiform elements probably reflects, in part, their function of filtering and directing particulate matter, rejecting the non-food matter, and moving the food particles toward the mouth. This is not to say that all conodont genera have this morphologic similarity: for example, *Icriodus* or *Panderodus* are not very similar to the Polygnathidae.

The opposed pectiniform elements, especially the Pa elements, show a great deal of basic morphologic variation, which must reflect a continual attempt to improve some specialised function of the apparatus structure. Some genera, such as *Ozarkodina*, appear to be relatively conservative, but are also the root stock of many more highly specialised platform elements, of which *Polygnathus*, *Gnathodus* and *Pseudopolygnathus* are only three of many examples.

The exact function of the Pa element is not known, but the closeness of the surfaces of the opposing elements, interpreted from their morphologic modifications, and their interpreted tissue cover suggest that they served to gently squash soft food particles being eaten by the animal. Where the Pa element did not develop a platform, the same function could have been performed by a shearing action between the opposed lateral surfaces of the elements.

The abrupt bend of the posterior tip of the platform of some Pa elements, such as *Polygnathus linguiformis*, must also have had some important function, but none that can be clearly demonstrated from this study. To be very speculative, it almost appears as a depressor to keep the inside of the upper end of the gut tube wide open, as one might hold open the end of a rubber tube with a pair of forceps inserted into the opening.

The interpretation of the ramiform elements having the points of their denticles directed ventrally is the result of several lines of evidence. If the elements, as seems clear from the *Polygnathus* clusters, were aligned parallel, side by side and in a single plane, then they must have been oriented with the denticles pointed either dorsally or ventrally. If they pointed dorsally, then they were probably located internally, in the mouth. But because they were not opposed, they would not have had a tooth-like function. If, however, we orient the denticle tips toward the ventral surface, and leave that surface open, as in a food groove, then the denticles of the ramiform elements could have a number of functions. I suggest, as have others previously (Lindstrom, 1974), that the elements were tissue covered, that the tissue was probably ciliated, and that the function of the elements was to sort particulate matter into food particles, which were moved by the cilia toward the gut opening, the non-food particles being expelled downward through the open groove.

The flap-like structures located at the anterior end of the specimen illustrated by Briggs & others (1983) would have served to help direct food particles ahead of the animal into the food groove as it swam along with the flaps spread open. For faster swimming or when the animal was not specifically feeding, the flaps could have been closed, thus blocking the entrance to the groove.

We now have a picture of the conodont animal as one who consumed particulate matter by swimming through the water with its mouth open. It was thus a nektonic or nektobenthonic organism, free to go where there was appropriate food, which may have been near the surface or at some depth. It is unlikely that the animal was exclusively a bottom feeder or that it burrowed in sediment.

I have pointed out elsewhere (Nicoll, in press) that I believe that conodonts were an ideal food source for many contemporary marine animals, and that this may explain why relatively few very large conodont elements are found. The extremely large conodonts reported by Sandberg (personal communication, 1983) from sandstones show that the conodont animal may have grown to a very large size under low predation conditions. It would thus appear that most conodont animals were probably eaten by some predator before they reached a state that

could be considered as 'old age'. It could also be that body size of conodonts was indeterminate rather than determinate, and that conodont animals, as reflected by the elements, continued to grow until death.

The apparent success of the conodont animal, as reflected by its abundance, despite the speculated high predation levels, could indicate that the animal may have reached sexual maturity before it reached the size normally associated with 'mature' or 'adult' conodont elements.

Conclusions

From this study it should be clear that the apparatus structures of a diverse group of conodont genera, *Icriodus*, *Polygnathus*, and *Ozarkodina* are similar in terms of numbers of element types. All three have seven types of elements. It is also clear that *Polygnathus* and *Ozarkodina* have apparatus structures composed of 15 elements divided into M (2), Sa (1), Sc (4), Sb (2), Sd (2), Pb (2), and Pa (2) element types.

Using the specimen described by Briggs & others (1983) as a model, I have shown (Fig. 10) what the anterior end of the conodont animal might have looked like with all its elements in place. While the appearance of the animal is speculative, the arrangement of the elements is not, and the anterior ramiform-posterior pectiniform sequence is supported by both this study and the location of elements in the animal figured by Briggs & others (1983).

The function of the ramiform elements appears to have been to sort particulate matter. The exact function of the pectiniform elements is not clear, but it is possible that they served to gently mash food.

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References

- Austin, R.L., & Rhodes, F.H.T., 1969 - A conodont assemblage from the Carboniferous of the Avon Gorge, Bristol. *Palaentology*, 12, 400-405.
- Baesemann, J.F., 1973 - Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. *Journal of Paleontology*, 47, 689-710.
- Bengtson, S., 1976 - The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. *Lethaia*, 9, 185-206.
- Briggs, D.E.G., Clarkson, E.N.K., & Aldridge, R.J., 1983 - The conodont animal. *Lethaia*, 16, 1-14.
- Chatterton, B.D.E., 1974 - Middle Devonian conodonts from the Harrogate Formation, southeastern British Columbia. *Canadian Journal of Earth Science* 11, 1461-1484.
- Druce, E.C., 1976 - Conodont biostratigraphy of the Upper Devonian reef complexes of the Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Bulletin* 158.
- Dubois, E.P., 1943 - Evidence on the nature of conodonts. *Journal of Paleontology*, 17, 155-159.
- Higgins, A.C., 1975 - Conodont zonation of the late Visean-early Westphalian strata of the south and central Pennines of northern England. *Geological Survey of Great Britain, Bulletin* 53.
- Hitchings, V.H., & Ramsay, A.T.S., 1978 - Conodont assemblages: A new functional model. *Palaeoecology, Palaeoecology*, 24, 137-149.
- Huddle, J.W., 1970 - Revised descriptions of some Late Devonian polygnathid conodonts. *Journal of Paleontology*, 44, 1029-1040.
- Jeppsson, L., 1971 - Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. *Lethaia*, 4, 101-23.
- Klapper, G., & Barrick, J.E., 1983 - Middle Devonian (Eifelian) conodonts from the Spillville Formation in northern Iowa and southern Minnesota. *Journal of Paleontology*, 57, 1212-1243.
- Klapper, G., & Philip, G.M., 1971 - Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia*, 4, 429-52.
- Klapper, G., & Philip, G.M., 1972 - Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaentologica*, SBI, 97-114.
- Lane, H.R., 1968 - Symmetry in conodont element-pairs. *Journal of Paleontology*, 42, 1258-1263.
- Lange, F.G., 1968 - Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. *Geologica et Palaentologica*, 2, 37-57.
- Lindstrom, M., 1973 - On the affinities of conodonts. In Rhodes, F.H.T. (Editor), Conodont paleozoology. *Geological Society of America, Special Paper* 141, 85-102.
- Lindstrom, M., 1974 - The conodont apparatus as a food-gathering mechanism. *Palaentology*, 17, 729-44.
- Nicoll, R. S., 1977 - Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics*, 2, 217-28.
- Nicoll, R.S., 1980 - The multielement genus *Apatognathus* from the Late Devonian of the Canning Basin, Western Australia. *Alcheringa* H, 133-152.
- Nicoll, R.S., 1981 - Conodont colour alteration adjacent to a volcanic plug, Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics*, 6, 265-7.
- Nicoll, R.S., 1982 - Multielement composition of the conodont *Icriodus expansus* Branson & Mehl from the Upper Devonian of the Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics*, 7, 197-213.
- Nicoll, R.S., in press - Conodont distribution in the marginal-slope facies of the Upper Devonian reef complex, Canning Basin, Western Australia.
- Pollock, C.A., 1969 - Fused Silurian conodont clusters from Indiana. *Journal of Paleontology*, 43, 929-935.
- Rexroad, C.B. & Nicoll, R.S., 1964 - A Silurian conodont with tetanus? *Journal of Paleontology*, 38, 771-773.
- Rhodes, F.H.T., 1952 - A classification of Pennsylvanian conodont assemblages. *Journal of Paleontology*, 26, 886-901.
- Schmidt, Hermann, 1934 - Conodonten-Funde in ursprunglichen Zusammenhang. *Palaentologische Zeitschrift*, 16, 76-85.
- Scott, H.W., 1934 - The zoological relationships of the conodonts. *Journal of Paleontology*, 8, 448-55.
- Sparling, D.R., 1981 - Middle Devonian conodont apparatuses with seven types of elements. *Journal of Paleontology*, 55, 295-316.
- Stauffer, C.R., 1940 - Conodonts from the Devonian and associated clays of Minnesota. *Journal of Paleontology* 14, 417-35.
- Uyeno, T.T., 1978 - Some Late Middle Devonian (*Polygnathus varcus* Zone) conodonts from Central Mackenzie Valley, District of Mackenzie. *Geological Survey of Canada, Bulletin* 267, 13-23.
- Uyeno, T.T., 1982 - Systematic conodont paleontology. In Norris, A.W., Uyeno, T.T., & McCabe, H.R. - Devonian rocks of the Lake Winnipegosis-Lake Manitoba outcrop belt, Manitoba. *Geological Survey of Canada, Memoir* 392.
- Van Den Boogaard, M., & Kuhry, B., - Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric, and specific level. *Scripta Geologica*, 49, 1-57.
- von Bitter, P.H., 1976 - The apparatus of *Gondolella sublancoolata* Gunnell (Conodontophorida, Upper Pennsylvanian) and its relationship to *Illinella typica* Rhodes. *Royal Ontario Museum Life Sciences Contribution*, 109, 1-44.