

APPARATUS COMPOSITION, GROWTH, AND  
SURVIVORSHIP OF THE LOWER ORDOVICIAN  
CONODONT *PARACORDYLODUS GRACILIS*  
LINDSTRÖM, 1955

by TANIA YU. TOLMACHEVA *and* MARK A. PURNELL




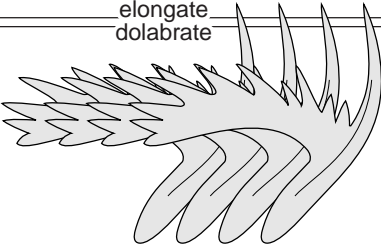
**ABSTRACT.** Analysis of numerous conodont element clusters from the Lower Ordovician cherts of the Burubaital Formation in central Kazakhstan reveals that the apparatus of *Paracordylodus gracilis* Lindström, 1955 consisted of 15 elements: two M elements, nine S elements (including 1 S<sub>0</sub>), and four P elements (2 P<sub>1</sub>, 2 P<sub>2</sub>). The clusters probably originated as faecal pellets, but the best preserved indicate that the architecture of the apparatus of *P. gracilis* was comparable to that of ozarkodinid conodonts, providing strong support for the hypothesis that the 15-element 2M-9S-4P apparatus plan was plesiomorphic for conodonts with morphologically complex elements.

All the elements within the *P. gracilis* clusters appear to be at a similar stage of ontogeny, and there is no evidence for late addition or replacement of elements. Analysis of element growth suggests that the relative dimensions of some elements changed during ontogeny, but the available data support the hypothesis that the growth of the apparatus as a whole was isometric. The size distribution of *P. gracilis* in the Burubaital Formation suggests that individuals in a particular size range were preferentially selected for consumption by predators. The identity of these predators is unknown, but they may have included other *P. gracilis*.

**KEY WORDS:** conodont, apparatus, skeleton, Ordovician, Kazakhstan, growth, survivorship.

RECENT years have seen renewed interest in natural assemblages of conodont elements (e.g. Nicoll 1977, 1985; Aldridge *et al.* 1987, 1995; Nicoll and Rexroad 1987; Smith *et al.* 1987; Purnell 1993a; Sansom *et al.* 1994; Purnell and Donoghue 1997, 1998; Orchard and Rieber 1999). Natural assemblages take the form of diagenetically fused clusters of elements or associations of elements on bedding planes which preserve together elements that originally formed the oropharyngeal skeletal array of an individual conodont. Natural assemblages are significant because they provide unique information of fundamental importance in conodont taxonomy, systematics, functional morphology and evolution. However, with the notable exception of numerous natural assemblages of the giant prioniodontid *Promissum pulchrum* from the Ordovician of South Africa (Theron *et al.* 1990; Aldridge *et al.* 1995; Gabbott *et al.* 1995) almost all known conodont natural assemblages belong to taxa assigned to the Order Ozarkodinida (for reviews, see Purnell and Donoghue 1998, and Purnell *et al.* 2000). In terms of the numbers of taxa preserved as natural assemblages other orders are very poorly known. This is especially true of early members of the Conodonta, so the numerous clusters representing a range of species from the Upper Cambrian and Lower Ordovician radiolarian cherts of central Kazakhstan (Tolmacheva 1996) are of particular importance and will result in significant revisions in the understanding of Cambrian and Ordovician conodonts. Here we describe the apparatus composition and skeletal plan of *Paracordylodus gracilis* Lindström, 1955 as revealed by analysis of element clusters. These clusters also yield information regarding apparatus ontogeny and possible selective predation upon *P. gracilis*.

*Paracordylodus gracilis* is geographically widespread and represents one of the most distinctive of the Early Ordovician taxa which characterize the North Atlantic conodont Province (Ethington 1972; Sweet and Bergström 1972; Barnes and Poplawski 1973; McTavish 1973; Stouge and Bagnoli 1988; Löfgren 1993). In some localities elements of *P. gracilis* dominate the conodont fauna, and may represent 50–99 per cent of the total number of conodont elements in a sample (Löfgren 1994). The development of ideas

morphological description used in text	abbreviated dolabrate		elongate dolabrate		geniculate
					
Lindström 1955	—	—		<i>Paracordylodus gracilis</i>	—
Ethington 1972				cordylodiform	oistodiform
Sweet and Bergström 1972	—	—	—	<i>Paracordylodus gracilis</i>	<i>Oistodus gracilis</i>
van Wamel 1974	cordylodiform	—	—	paracordylodiform	oistodiform
Barnes and Poplawski 1973	cyrtioniodiform	—	—	cordylodiform	oistodiform
Löfgren 1978	cyrtionodontiform	—	—	paracordylodontiform	oistodontiform
Barnes <i>et al.</i> 1979	f	—	—	a, b, c (transition series)	e
Bergström 1981	?	—	—	dolabrate	geniculate
Stouge and Bagnoli 1988	P	—	—	S	M
Löfgren 1993	cyrtionodontiform	—	—	paracordylodontiform	geniculate
Albanesi 1998	P	—	—	S	M
Tolmacheva and Löfgren 2000	P <sub>b</sub>	P <sub>a</sub>	S <sub>a</sub>	S	M
This paper	P <sub>1</sub>	P <sub>2</sub>	S <sub>0</sub>	S <sub>1-4</sub>	M

TEXT-FIG. 1. *Paracordylodus gracilis* as perceived by various authors. The figure shows the elements that have been assigned to the species, their morphology, and the names and element notation that have been applied to them. Relative sizes of elements derived primarily from cluster specimen NMW 98.70G.3. See text for details; for element descriptions, see e.g. Lindström (1955), van Wamel (1974), Bergström (1981), and Tolmacheva and Löfgren (2000).

concerning the composition of *P. gracilis* is summarized in Text-figure 1. The authors of the first multielement interpretations of *P. gracilis* (Ethington 1972; Sweet and Bergström 1972) noted that, although the structure of the apparatus was not definitely known, elements assigned to '*P. gracilis*' (relatively elongate dolabrate elements with a pronounced anticusp and with a posterior process generally longer than the cusp) and geniculate elements assigned to '*Oistodus gracilis*' were consistently associated

and may have been part of the same apparatus (note that use of inverted commas to indicate obsolete taxonomic concepts follows Jeppssen and Merrill 1982). Based on their relative abundances, Ethington (1972) speculated that elongate dolabrate elements outnumbered geniculate elements by 3:1 in the apparatus. Later, a third element type was included in the apparatus (Barnes and Poplawski 1973; van Wamel 1974), an abbreviated dolabrate element without a pronounced anticusp, referred to as cyrtoniodontiform or cordylodiform. Stouge and Bagnoli (1988) were the first to apply P, M, S notation to the elements, based partly on the relative position of elements in a single fused cluster of *P. gracilis* (Stouge and Bagnoli 1988, pl. 8, fig. 17A–B).

Prior to Stouge and Bagnoli (1988), the only record of *P. gracilis* preserved as element clusters was provided by Barskov and Novikov (1984) who described and illustrated schematically two incomplete clusters from the siliceous deposits of central Kazakhstan. These clusters included one P element, one M element and five S elements. Subsequent studies of these early Palaeozoic radiolarian cherts from central Kazakhstan (e.g. Tolmacheva 1996) have demonstrated that they represent an important source of element clusters, including numerous clusters of *P. gracilis*.

#### MATERIAL AND METHODS

The results presented here are based on the study of more than 150 clusters and numerous isolated elements of *P. gracilis*. They represent part of an extensive collection of conodont elements and clusters from the radiolarian cherts of the Upper Cambrian–Middle Ordovician Burubaital Formation in south-central Kazakhstan.

All illustrated specimens are deposited in the collection of the National Museum of Wales, Cardiff (NMW). Element locational notation and terms for orientation follow Purnell *et al.* (2000). Conventional, arbitrary terms for orientation are enclosed in inverted commas to distinguish them from biological orientations.

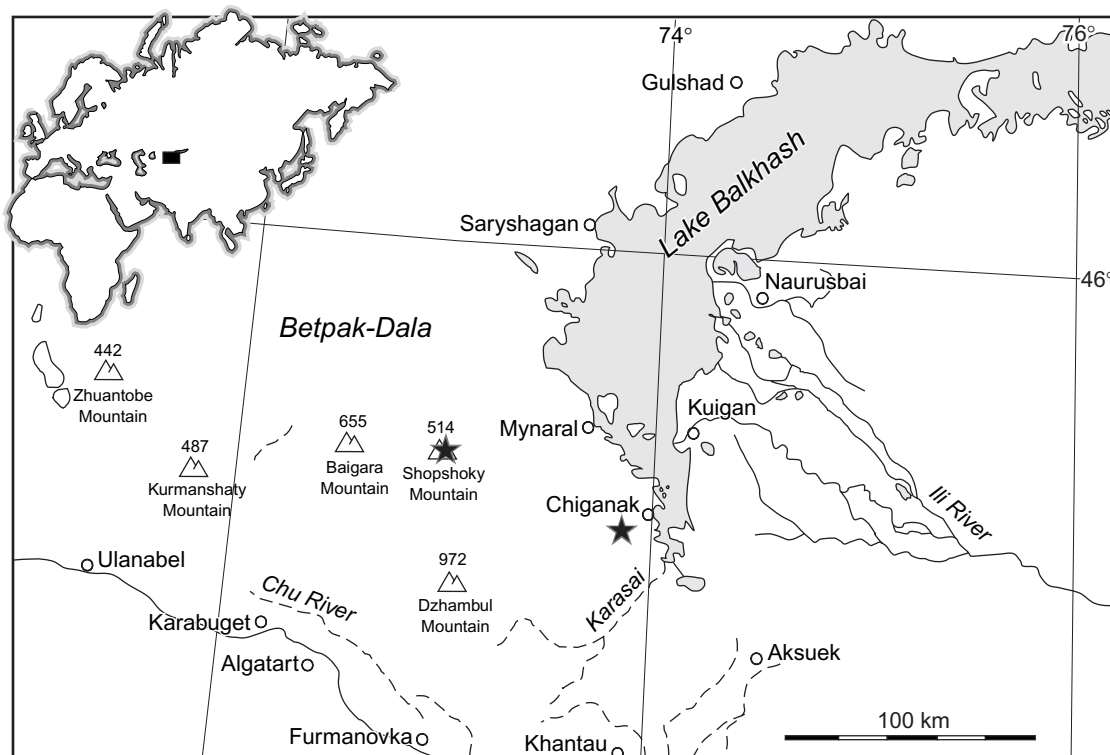
#### *Localities and geological setting*

The cherts of the Burubaital Formation are part of an Early Palaeozoic ophiolite assemblage and represent altered radiolarian oozes deposited on an abyssal plain (Popov and Tolmacheva 1995). The *P. gracilis* clusters come from two localities. Locality 8927 (Shopshoky Section) is situated along a trail on a ridge located about 1.5 km east of the 514-m-high Shopshoky Mountain (Text-fig. 2). *Paracordylodus gracilis* ranges from the late Tremadoc to the early Arenig, and in this continuously exposed 45-m section of radiolarian cherts it has been found to range from the *Prioniodus adami* Zone to the *Oepikodus evae* Zone (Text-fig. 3). *Paracordylodus gracilis* is most abundant in samples from the lower part of the *P. elegans* Zone where it comprises 90–99 per cent of the total number of conodont elements. Samples from the *P. adami* and *O. evae* zones contain 1–20 per cent *P. gracilis* elements. Almost all the clusters of *P. gracilis* in this study were recovered from 10 samples collected from an interval of about 10 m in the lower part of the *P. elegans* Zone.

Locality 9740 is situated west of Lake Balkhash, south-west of Chiganak (Text-fig. 2) on a southward extension of a pronounced ridge on the right bank of the Kaib dry stream. An unnamed hill marked as a 497-m spot height on the 1:50,000 map of the area is situated about 2 km to the north-west. This locality represents a small isolated exposure of cherts of the Burubaital Formation, and 25 clusters of *P. gracilis* associated with an assemblage of isolated elements assignable to the *Prioniodus elegans* Zone were obtained from one sample. At this locality, conodonts are quite abundant in the lower part of the *P. elegans* Zone. The cherts usually contain about 1000–20,000 elements per m<sup>2</sup> but *P. gracilis* is mostly represented by isolated elements. Elements preserved within clusters constitute less than 0.01–0.1 per cent of the total number of elements in a sample.

#### *Methods*

Because of their mode of preservation thin sections represent the only practicable method of studying the clusters. Isolated elements and clusters were photographed and measured under incident and transmitted



TEXT-FIG. 2. The southern part of central Kazakhstan, with stars indicating the two localities from which the clusters of *Paracordylodus gracilis* were obtained. Dashed lines indicate dry river beds.

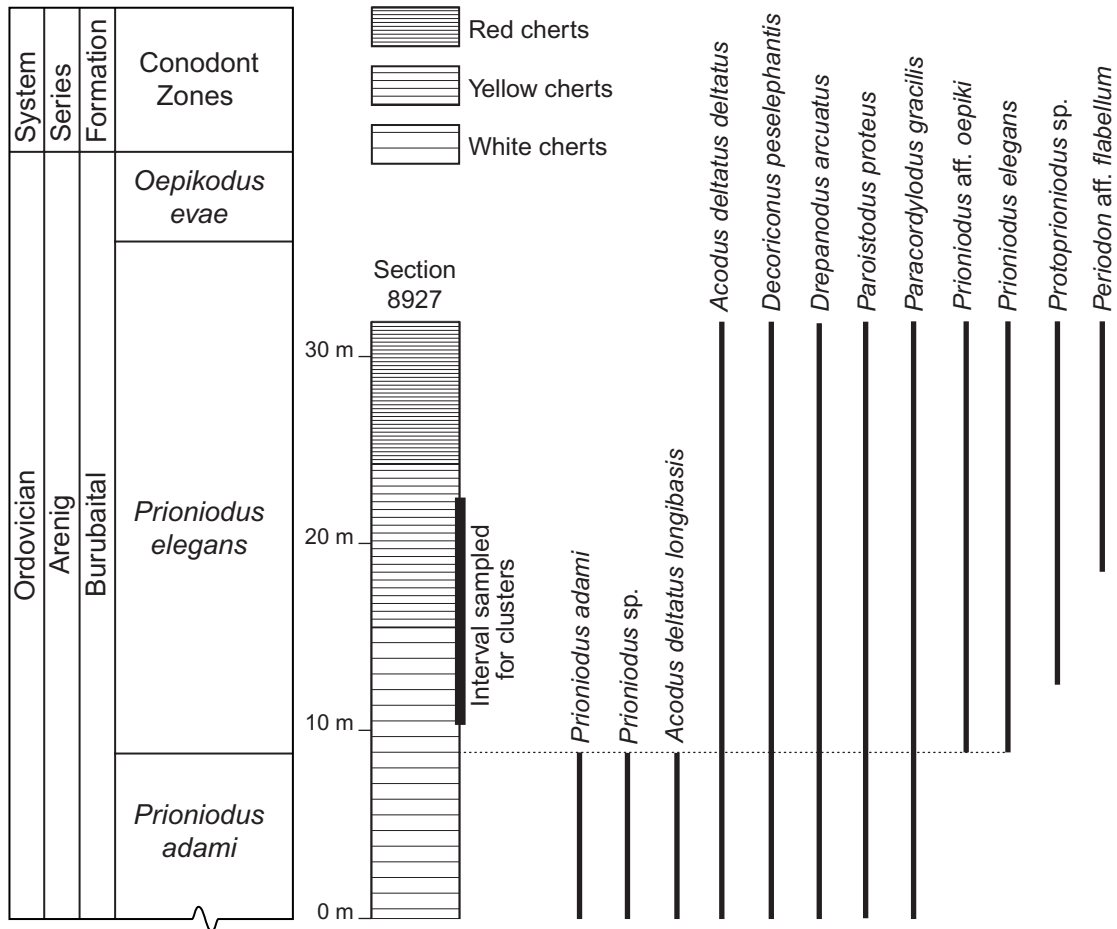
light on a Leitz 2000 microscope. Interpretative drawings were prepared using a paper grid and an eyepiece graticule with a square grid. Element dimensions were measured using an ocular micrometer, and repeat measurements indicate that operator error in measurement was generally less than  $10\ \mu\text{m}$ . Details of the methods used in analysis of ontogeny and survivorship are discussed below under the heading of numerical methods.

Photographic illustrations were produced by traditional photographic methods except that 35 mm negatives were scanned and manipulated digitally using Adobe Photoshop 5.0.2. In most cases, image clarity was improved by removing scratches (mostly a result of the process of preparation of the cherts) using a 'dust and scratches' filter (radius 2 or 3, threshold 0). Grey levels were adjusted to optimise the contrast between the elements of the cluster and the background; in several cases this involved independent adjustments to specific portions of the image.

#### *Preservation of clusters*

There is no evidence of tectonic deformation of the cherts or the clusters of *P. gracilis*. A few elements exhibit slight fracturing and some stretching, but most elements are preserved without significant distortion. There is no evidence for significant compression of the cherts; radiolarians preserved with the clusters are spherical or close to spherical in shape. All studied and illustrated clusters were oriented parallel to bedding.

The clusters differ significantly in their completeness, structural integrity, and the degree to which they preserve the original juxtaposition of elements (see Text-figs 4–7). Elements in some clusters are closely

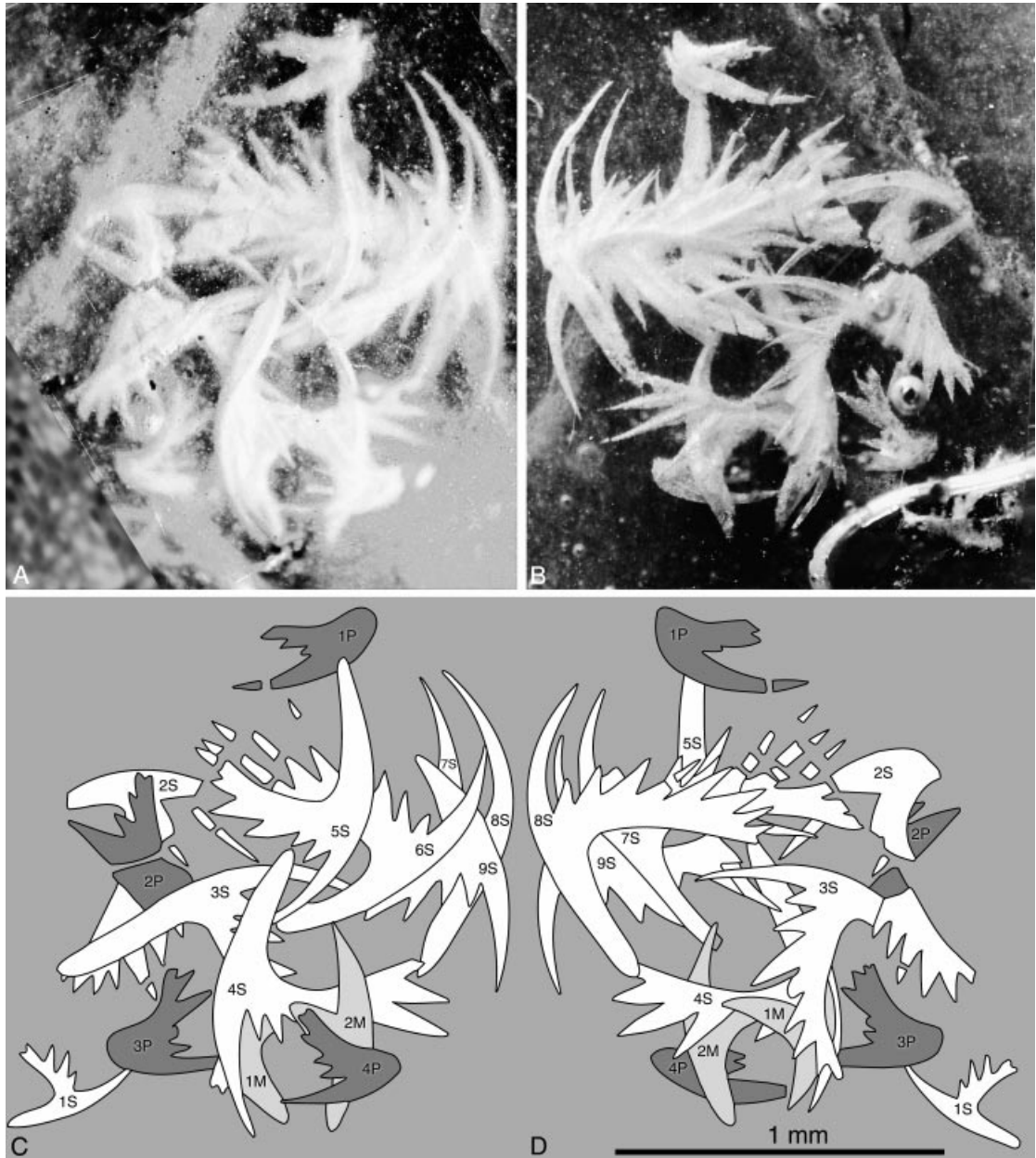


TEXT-FIG. 3. Stratigraphic distribution of selected conodonts in the section through the Lower Ordovician Burubaital Formation exposed near Shopshoky Mountain (locality 8927). The interval sampled for *Paracordylodus gracilis* clusters is indicated by the thick black line; conodont zones after Stouge and Bagnoli (1988).

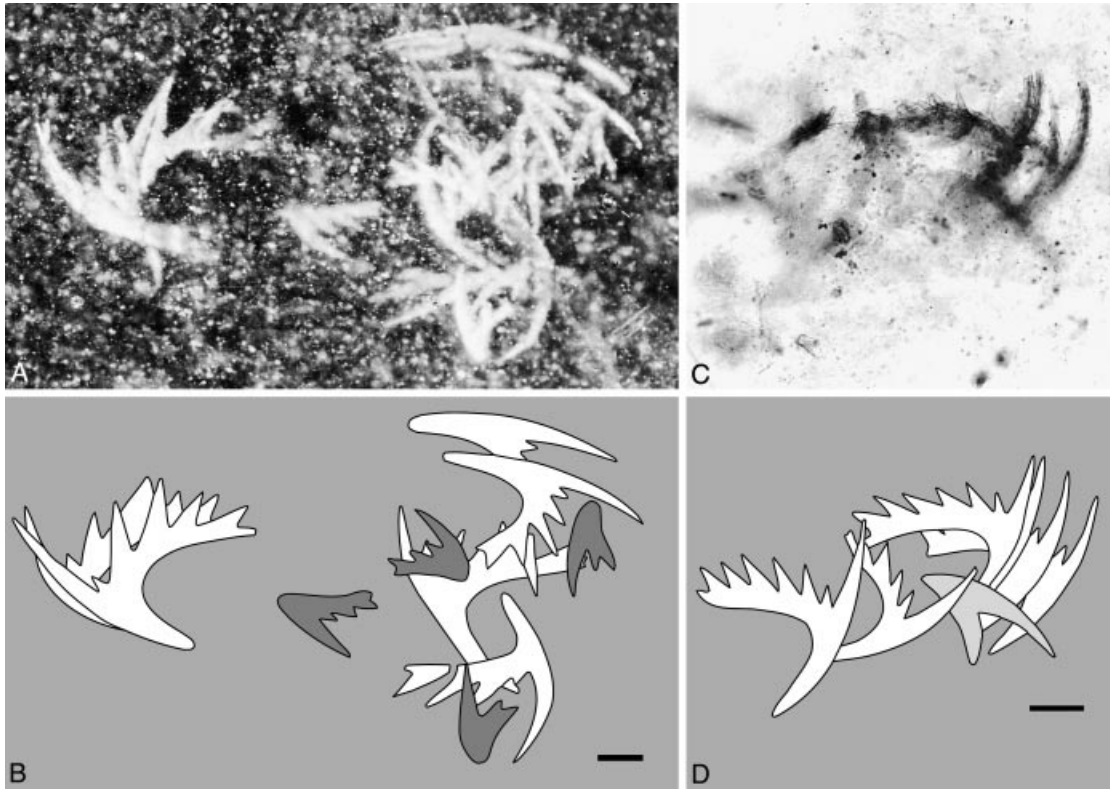
superposed and lie in contact with one another, but a large number of clusters consist of elements that are not in contact and lie at some distance apart. Depending on the size and the number of elements they contain the clusters vary in size between 0.2 mm and 2 mm. Most of the clusters contain very few elements and clusters representing the complete apparatus of *P. gracilis* are rare: fewer than 40 per cent of the studied clusters consist of more than six elements. The arrangement of elements in the majority of clusters is chaotic but in several clusters a few elements have retained something of their original symmetrical disposition about the axis of the apparatus.

Thus, the clusters are all disrupted to some extent, and most are incomplete. Given that the chert deposits in which they are found come from an ophiolite sequence deposited in an abyssal setting, post-mortem disruption of apparatuses on the sea floor by current activity or bioturbation can be effectively ruled out. It is, therefore, unlikely that clusters represent the remains of carcasses that fell to the sea floor, yet the elements are preserved together. We interpret them as having been formed by the passage of conodonts through the gut of a predator. That is, most or all of the clusters originated as faecal pellets.

It seems that the conodont apparatuses underwent considerable disruption in the stomachs of predators or as a result of being squeezed together during formation of faecal pellets, resulting in destruction of the



TEXT-FIG. 4. Element cluster preserving complete apparatus of *Paracordylodus gracilis* (specimen NMW 98.70G.3);  $\times 47$ . A and B are views of each side of the cluster; C and D are interpretative drawings of A and B respectively. Elements are interpreted as follows: 1P, P<sub>1</sub> element; 2P, P<sub>1</sub> element; 3P, P<sub>2</sub> element; 4P, P<sub>2</sub> element; 1S, ?S<sub>0</sub> element; 2S—8S, S elements  $\times 8$ ; 1M, M element; 2M, M element.



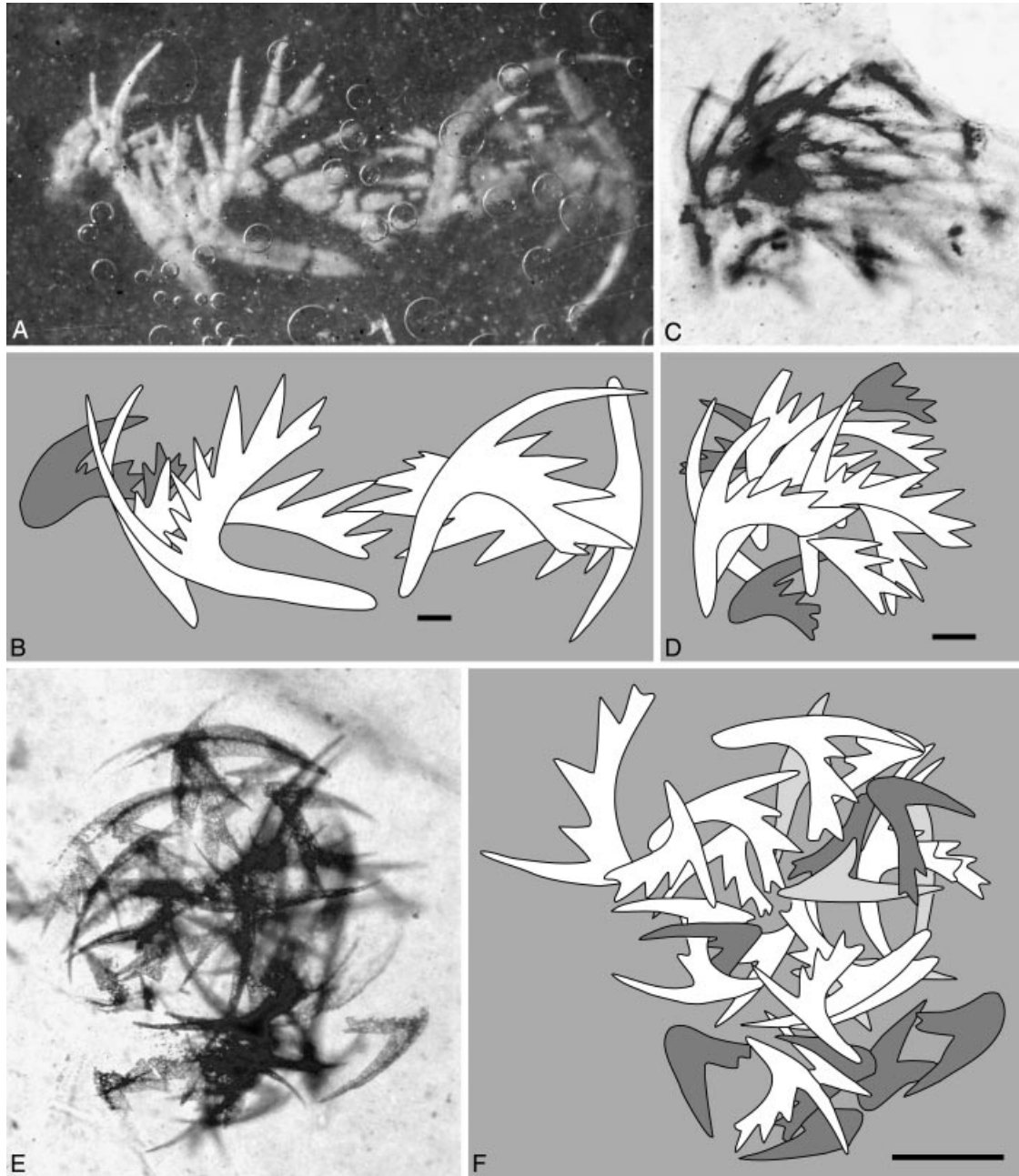
TEXT-FIG. 5. Element clusters preserving partial apparatuses of *Paracordylodus gracilis*. A, specimen NMW 98.70G.8, incident light;  $\times 60$ . B, interpretative drawing of specimen shown in A; cluster comprises six S elements (white) and two pairs of P elements (dark grey), the pair of shorter P elements with fewer denticles are interpreted as  $P_1$  elements, the other pair are  $P_2$  elements; see text for explanation. C, specimen NMW 98.70G.15, transmitted light;  $\times 70$ . D, interpretative drawing of specimen shown in C; cluster comprises six S elements (white) and one M element (pale grey); the close spacing and alignment of several S elements suggest that they retain some evidence of primary architecture. Scale bars represent  $100\ \mu\text{m}$ .

primary architecture and loss of elements. As a result of these processes, in some clusters it is impossible to count the exact number of elements or identify them precisely (e.g. Text-fig. 6E-F). Element superposition in other clusters prevents examination of the overlapping elements (e.g. Text-fig. 7A). Consequently, the element identifications, measurements, and analyses presented here are actually based on only 80 per cent of the total number of clusters studied.

In 92 element clusters with identifiable elements nine or fewer of the elements are elongate dolabrate elements. Of these clusters, 39 per cent contain elongate dolabrate elements only (e.g. Text-fig. 7), and 19 per cent contain all of the three element types of *Paracordylodus* (e.g. Text-fig. 4). Twenty-four per cent contain elongate dolabrate elements together with four or fewer abbreviated dolabrate elements (e.g. Text-figs 5A-B, 6A-D) and 14 per cent contain elongate dolabrate elements with one or two geniculate elements (e.g. Text-fig. 5C-D). Clusters containing only abbreviated dolabrate elements are rare (3 per cent).

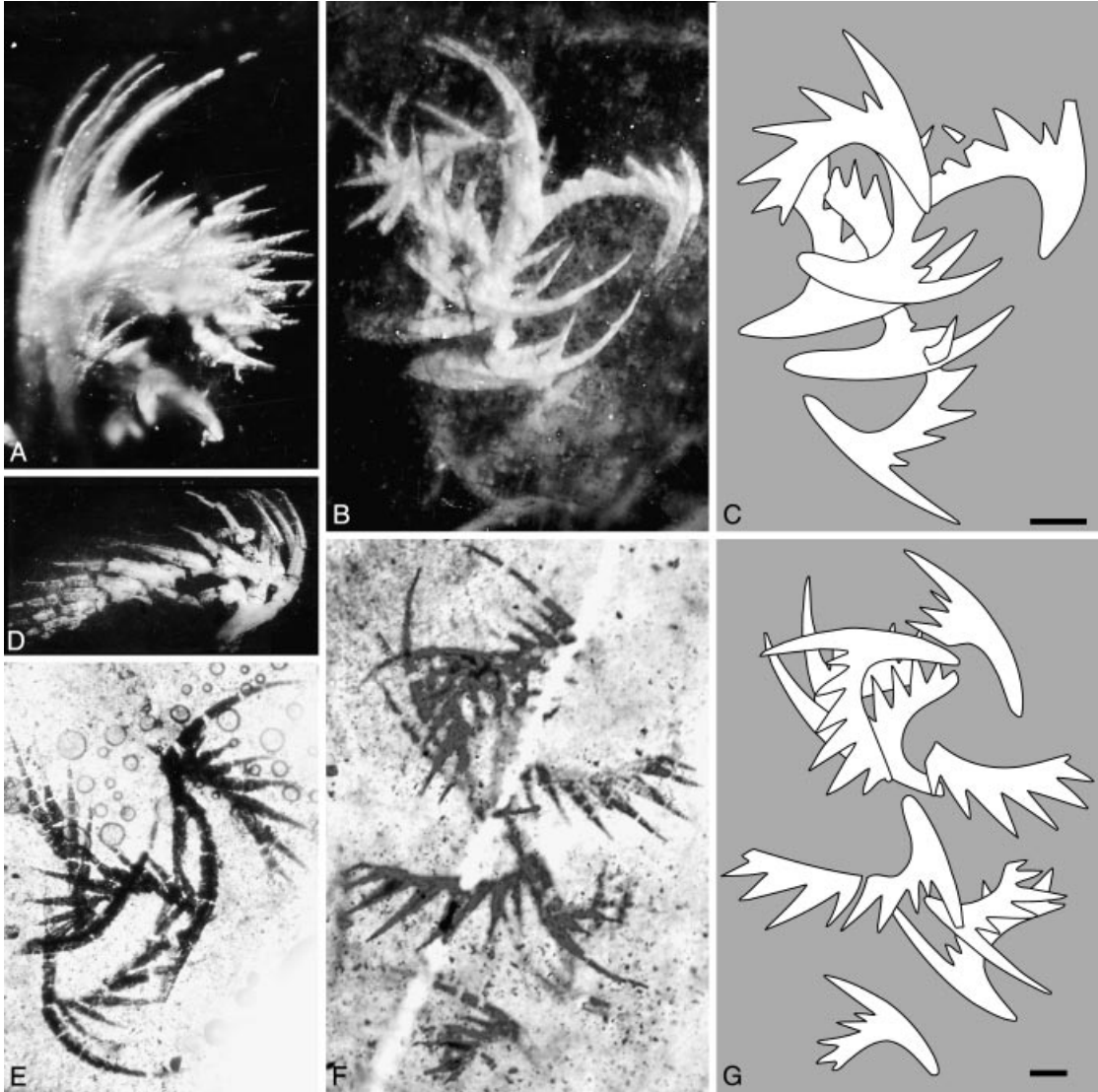
#### APPARATUS COMPOSITION, ELEMENT LOCATION, NOTATION AND HOMOLOGIES

Specimen NMW 98.70.G3 (Text-fig. 4) comprises 15 elements: nine elongate dolabrate elements (all, except one, of closely similar size), a pair of geniculate elements, and two pairs of abbreviated dolabrate



TEXT-FIG. 6. A, element cluster preserving partial apparatus of *Paracordylodus gracilis* (specimen NMW 98.70G.9), incident light;  $\times 60$ . B, interpretative drawing of specimen shown in A; cluster comprises four S elements (white) and two P elements (dark grey); postmortem extension and fracturing has distorted element proportions. C, element cluster preserving partial apparatus of *Paracordylodus gracilis* (specimen NMW 98.70G.13), transmitted light;  $\times 63$ . D, interpretative drawing of specimen shown in C; cluster comprises a closely juxtaposed suite of five S elements (white) and three P elements (dark grey); the P elements lie on either side of the S suite. E, element cluster preserving remains of two individuals of *Paracordylodus gracilis* (specimen NMW 98.70G.10), transmitted light;  $\times 162$ . F, interpretative drawing of specimen shown in E; cluster comprises 17 or 18 S elements (white), eight P elements (dark grey) and four M elements (light grey). Scale bars represent  $100\ \mu\text{m}$ .





TEXT-FIG. 7. Element clusters preserving partial apparatuses of *Paracordylodus gracilis*; all preserve S elements only. A, specimen NMW 98.70G.4, closely juxtaposed suite of six S elements, incident light; composite image combining two photographs to increase depth of specimen in focus;  $\times 120$ . B, specimen NMW 98.70G.2, cluster of six S elements, incident light;  $\times 73$ . C, interpretative drawing of specimen shown in B. D, specimen NMW 98.70G.6, cluster of three S elements, distorted by post-mortem extension and fracturing, incident light;  $\times 20$ . E, specimen NMW 98.70G.7, cluster of four S elements, transmitted light;  $\times 30$ . F, specimen NMW 98.70G.11, cluster of nine S elements, transmitted light. G, interpretative drawing of specimen shown in F; the smaller element towards the bottom of the drawing is interpreted as  $S_0$ . Scale bars represent  $100 \mu\text{m}$ .

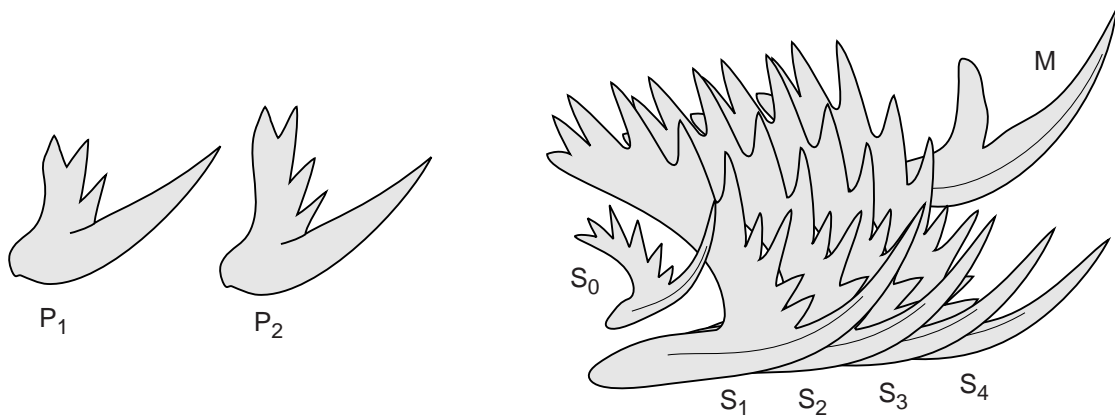
elements, one pair of which is shorter than the other pair. This is a highly significant association of elements, as it is exactly what would be expected of an apparatus conforming to the 15 element skeletal plan as exhibited by members of the well-known Ozarkodinida (see e.g. Purnell *et al.* 2000 for discussion). The alternative interpretation of this cluster, that it represents a fortuitous association of exactly the right

number of each type of element, cannot be ruled out entirely, but it seems unlikely. Additional evidence comes from specimen NMW 98.70G.10 (Text-fig. 6E-F). Unfortunately, the elements in this cluster are small and closely spaced, making it difficult to count and to identify some of them. However, this cluster contains at least 17 elongate dolabrate elements, four geniculate elements, and eight abbreviated dolabrate elements (these elements differ slightly in their size and the number of denticles, four having two denticles, the other four having three). The number of elements in the cluster is thus double the number of elements in specimen NMW 98.70.G3, and the most parsimonious interpretation is that the cluster comprises the remains of two individuals, each of which bore a 15-element apparatus. Furthermore, of 92 clusters in which elements could be identified most contain fewer than 15 elements, and in no case did a cluster with nine or fewer elongate dolabrate elements contain more than four abbreviated dolabrate elements or more than two geniculate elements.

Thus, the clusters reveal that the apparatus of *P. gracilis* contained 15 elements conforming to three basic morphologies: nine elongate dolabrate elements, two geniculate elements, and four abbreviated dolabrate elements (see Text-fig. 1). Several clusters (e.g. Text-figs 4, 6A-B) indicate that the abbreviated dolabrate elements occur in two forms: all four elements are similar in cusp height, but two have a shorter 'posterior' process bearing fewer denticles. The questions of how these 15 elements were arranged in the apparatus and whether topological homologies can be drawn between the apparatus of *Paracordylodus* and that of ozarkodinid conodonts (see Purnell *et al.* 2000) are more difficult to answer. Because the clusters probably represent faecal remains, direct evidence for primary architecture is limited, but several of the clusters (e.g. Text-figs 5D, 6C, 7A, D) and the fused cluster illustrated by Stouge and Bagnoli (1988, pl. 8, fig. 17) preserve as many as six elongate dolabrate elements in closely aligned juxtaposition. Taking this together with the evidence that the apparatus contained nine of these elements, one of which was morphologically distinct, provides almost unequivocal support for the hypothesis that these elements are homologous to the S elements of the ozarkodinid apparatus and occupied S<sub>0</sub> and S<sub>1-4</sub> positions. This interpretation and the evidence that the apparatus of *Paracordylodus* contained 15 elements in total provide strong support for the hypothesis that the apparatus conforms to the 2M-9S-4P skeletal template.

Evidence for the positions occupied by the two geniculate and the four abbreviated dolabrate elements is slightly more equivocal and two alternative hypotheses are possible: either the M positions were occupied by one pair of the abbreviated dolabrate elements, and the four P positions were occupied by the remaining pair of abbreviated dolabrate elements and the pair of geniculate elements, or the M positions were occupied by the geniculate elements, and the four P positions were occupied by the four abbreviated dolabrate elements. Other interpretations require that abbreviated dolabrate elements were paired with geniculate elements, but there is no evidence in any natural assemblage or cluster of any taxon that P or M element-pairs exhibited this degree of asymmetry; these hypotheses of asymmetry are not considered further. The relative frequency with which elements co-occur in clusters of *Paracordylodus* (see above) provides evidence which bears directly on this question, and it is pertinent to note that, although clusters comprising only four or fewer abbreviated dolabrate elements are rare (3 per cent), clusters composed of only abbreviated dolabrate elements and geniculate elements are unknown. This is consistent with the hypothesis that M positions were occupied by geniculate elements, and P positions by abbreviated dolabrate elements. Additional support comes from the cluster of six S elements and a geniculate element illustrated in Text-figure 5C-D. The geniculate element lies close to the cusps of four aligned S elements preserved in a close juxtaposition, which probably reflects their primary architectural arrangement. Perhaps the best evidence comes from the partial apparatus of *P. gracilis* described and illustrated by Stouge and Bagnoli (1988, pl. 8, fig. 17). According to these authors, this cluster comprises five aligned S elements with a geniculate element fused by its inner face to the outer side of the outermost S element. It is possible that all these associations are fortuitous, but a more parsimonious interpretation of the available data is that the geniculate elements occupied the M positions in the apparatus.

The only remaining question concerns which of the two types of abbreviated dolabrate element occupied which of the four P positions. Here there are three alternative hypotheses to consider: hypothesis 1, symmetrical pairing, with the shorter elements occupying the P<sub>1</sub> positions, the longer elements the P<sub>2</sub>; hypothesis 2, symmetrical pairing, with the longer elements occupying the P<sub>1</sub> positions, the shorter the P<sub>2</sub>; hypothesis 3, asymmetrical pairing. Hypothesis 3 would require *Paracordylodus* to have had P elements of



TEXT-FIG. 8. Architectural reconstruction of the apparatus of *Paracordylodus gracilis*. Only the  $S_0$  and sinistral half of the apparatus are shown; the number of elements is based on the clusters described in this paper, their relative positions and application of positional notation are based on the topological homologies with the apparatus of ozarkodinid conodonts discussed in the text. The angle of inclination of the S and M elements is conjectural; the occupants of  $S_1$ – $S_4$  positions are morphologically similar.

significantly different length opposed across the sagittal plane. This situation is unknown in any taxon preserved as a natural assemblage, and for this reason we reject this hypothesis. Of the two remaining hypotheses, it is difficult to be certain which of the P element pairs occupied which element positions, but in specimen NMW 98.70.G3 six of the nine S elements (1S, 5S, 5S, 7S, 8S, and 9S in Text-fig. 4) have their 'posterior' process directed in the same general direction. Taking this to indicate the caudal end of the apparatus, then the P element pair with the shorter posterior process (i.e. 1P and 2P) lie caudally relative to the longer P pair (3P and 4P). Similarly, of the four P elements preserved in cluster NMW 98.70G.8 (Text-fig. 5A–B) the shorter pair of P elements are towards the edge of the cluster that S element orientation suggests is more caudal. This hypothesis of apparatus configuration and arrangement is summarized diagrammatically in Text-figure 8.

#### AFFINITIES OF *PARACORDYLODUS* AND THE QUESTION OF THE PLESIOMORPHIC CONODONT APPARATUS

To date, *Paracordylodus* is the earliest conodont taxon for which we have direct evidence for the possession of the 15 element 2M-9S-4P skeletal plan. It thus provides a potential test of Purnell and Donoghue's (1998) hypothesis that this architectural template represents the plesiomorphic condition for conodonts with apparatuses composed of morphologically complex elements (i.e. Ozarkodinida, Prioniodinida and Prioniodontida). Testing this hypothesis, however, requires a phylogenetic framework within which to assess whether *Paracordylodus* is plesiomorphic or derived with respect to other taxa for which apparatus configuration is known. Unfortunately, hypotheses of relationships among conodonts are not well resolved at present, and although work is ongoing (Donoghue *et al.* in manuscript) a rigorous cladistic analysis of relationships between taxa currently assigned to the major groups of conodonts with apparatuses composed of complex elements has yet to be published. At the present time, therefore, we can do little more than simply consider the implications of the alternative hypotheses for the affinities of *Paracordylodus* that have been proposed. With few exceptions these hypotheses have not been expressed in terms of sister group or even ancestor-descendant relationships, but as groupings of genera into higher taxa.

Without doubt the most widely used classification of conodonts is that of Sweet (1988). This scheme is not perfect (for discussion, see Aldridge and Briggs 1990; Smith 1990; Aldridge and Smith 1993) but it is linked to hypotheses of relationship which are, in theory, open to testing. For this reason, and because it has

achieved such widespread usage and is familiar to many conodont workers, we use Sweet's scheme here as a convenient framework for discussion. Unfortunately, *Paracordylodus* is among a number of taxa which Sweet (1988) did not mention.

Most opinions concerning the affinities of *Paracordylodus* favour a close relationship with taxa considered by Sweet (1988) to be among the early offshoots of the core lineage of the Order Prioniodontida (i.e. a relatively plesiomorphic member of a clade made up largely of paraphyletic groupings designated by Sweet as families). For example, Barnes and Poplawski (1973, p. 779) considered *P. gracilis* to be 'certainly primitive', possibly an early relative or ancestor of *Periodon flabellum*; Löfgren (1978) suggested that a relationship with *Oepikodus*, or possibly with *Protoprioniodus*, was more likely; Barnes *et al.* (1979) considered *Paracordylodus* to be most closely related to *Oepikodus* and '*Acodus*' *deltatus*. Bergström (1981) simply assigned *Paracordylodus* to the monotypic family Paracordylodontidae of the Superfamily Prioniodontacea, the latter being more or less equivalent to Sweet's (1988) Order Prioniodontida. In Fähræus's (1984) modified classification of the Prioniodontacea *Periodon*, *Microzarkodina*, *Protoprioniodus* and *Acodus* were added to the Paracordylodontidae to form a paraphyletic group of plesiomorphic prioniodontids. After Sweet's (1988) omission, Aldridge and Smith (1993) resurrected the Paracordylodontidae as a family of Prioniodontida, and included *Fahraeusodus* and *Protoprioniodus* within the group. In similar vein, Albanesi (1998) allied *Paracordylodus* with *Fahraeusodus* and *Protoprioniodus* within the Family Paracordylodontidae, but he assigned this family to the Superfamily Oistodontacea which, following the classification scheme of Dzik (1991), he included within the Suborder Plectodinina, Order Ozarkodinida.

In marked contrast to all these opinions, stand those of Dzik (1991). He assigned *Paracordylodus*, albeit with some equivocation, to the Family Cordylodontidae, Superfamily Cordylodontacea, Order Panderodontida. His reasoning is not explicitly stated, but it seems probable that he did this because he thought it possible that the apparatus of *Paracordylodus* did not include a medial (i.e.  $S_0$ ) element (Dzik 1991, p. 289). Of all the higher taxa included in his study, Dzik (1991, fig. 18) seems to have considered Cordylodontidae to be the most plesiomorphic.

If, as the majority of authors have suggested, the affinities of *Paracordylodus* prove to lie among the Prioniodontida, this will support the hypothesis that the 15 element apparatus arose early in the evolution of the Prioniodontida. As we note above, the relationships between the major groupings of conodonts are not known with certainty at present, but the evidence from Prioniodontida combined with that from Ozarkodinida and Prioniodinida supports the hypothesis that the standard 2M-9S-4P apparatus evolved before the common ancestor of these three major groups, i.e., that this plan is plesiomorphic for conodonts with apparatuses composed of morphologically complex elements (Purnell and Donoghue 1998).

The implications of Dzik's opinions concerning *Paracordylodus* are highly significant in the context of this discussion; in terms of Sweet's (1988) classification, Dzik's (1991) hypothesis that *Paracordylodus* was most closely related to *Cordylodus*, *Euconodontus*, *Iapetognathus* and *Cambroistodus* would make it part of the so-called '*Proconodontus* lineage' (Miller 1980, 1984; Sweet 1988). All other euconodonts are thought to be part of the entirely separate '*Teridontus* lineage' (Sweet 1988), the two clades sharing a common ancestor among paraconodonts. If this hypothesis of a polyphyletic Euconodontia is valid, then the most parsimonious interpretation resulting from Dzik's hypothesis that *Paracordylodus* is most closely related to taxa of the *Proconodontus* lineage is that the 2M-9S-4P apparatus arose within paraconodonts before the origins of euconodonts. However, although popularity is not a useful criterion for accepting or rejecting hypotheses of relationship, Dzik's view stands alone, and if his primary criterion for assigning *Paracordylodus* to his concept of Panderodontida was the possible absence of an axial element, then our reconstruction of *Paracordylodus* raises further doubts about his hypothesis.

#### ELEMENT AND APPARATUS GROWTH AND SURVIVORSHIP ANALYSIS

In addition to revealing apparatus composition, structure, and homologies with other taxa, the preservation of numerous elements and clusters of *Paracordylodus* make possible a number of quantitative analyses. To

this end, more than 300 isolated elements and 500 elements from 90 clusters of *P. gracilis* were measured. In terms of general element size within clusters,  $P_1$  elements are shorter and have fewer denticles than  $P_2$  elements, but the length of the cusp of all P elements in the same cluster is equal. Measurements of elements from clusters show that morphological variation of  $S_{1-4}$  elements in a single apparatus is minimal, with the number of denticles in all S elements within the same cluster differing by not more than one. This does not apply to the  $S_0$  element, which is smaller and has fewer denticles, but because of deformation of the cherts during diagenesis and the vagaries of element preservation  $S_0$  elements can be recognized in only a few clusters (e.g. Text-fig. 7G).

#### Numerical methods

The overall proportions of the elements were approximated by measuring three variables: *h*, the height of the cusp; *l*, the length of the posterior process of S elements, or the length of the aboral surface of P and M elements; and *nd*, the number of denticles on the posterior processes (Text-fig. 9). Data for each element reveal that the linear dimensions and number of denticles exhibit considerable variation but are nonetheless strongly correlated. (It is worth noting that the relationship between linear dimensions and the number of denticles in P elements may be obscured somewhat because the data include measurements of both  $P_1$  and  $P_2$  elements.) However, owing to the difficulties of measuring elements within chert, the number of each type of element for which complete data are available is limited, and although analysis of the growth of elements is possible, the significance that can be placed in the results is, in some cases, limited.

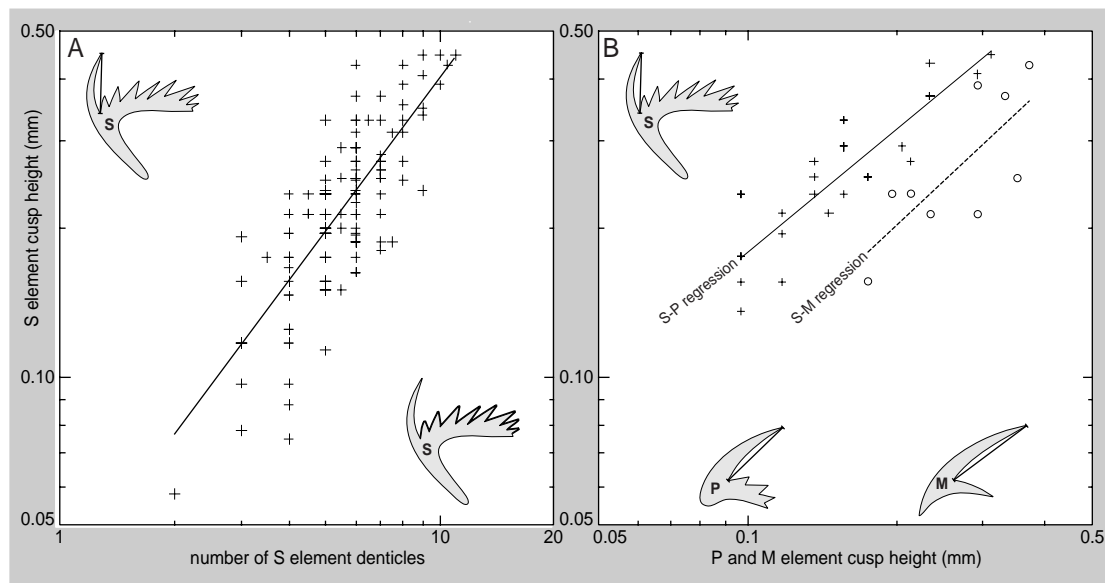
Element growth was investigated using the power function, or allometric equation,  $y = ax^b$  and its log transformation  $Y = bX + A$ . We undertook two different analyses. Firstly, relationships between elements dimensions during growth were investigated by fitting a Reduced Major Axis (RMA) through log-transformed data. Secondly, linear regression was used to provide a numerical model from which S cusp height (*Sh*, the unknown variable, *y*) could be predicted from other variables (*Snd*, S denticle number; *Ph*, P cusp height; and *Mh*, M cusp height). For computational details and discussion of reduced major axis and linear regression in analyses of ontogeny see, for example, Imbrie (1956), Hayami and Matsukuma (1970), Rayner (1985), and Hofman (1988). The data are included in the Appendix.

In RMA analysis of the growth of elements, hypotheses of positive and negative allometry were tested statistically by comparing calculated growth exponents (*b*) with isometric values using *Z* tests (Hayami and Matsukuma 1970). Isometry was taken to be growth throughout which proportions remain constant, such that when *x* and *y* are both linear dimensions (as is the case in this study) growth exponents (*b*) have a value of 1.

In analysis of survivorship in *P. gracilis*, S cusp height was taken as a proxy for age at death of the animal to which the element belonged. Although data are limited, the known specimens preserving conodont body traces indicate that larger conodonts bore larger elements (Purnell 1994). Recent work (Donoghue and Purnell 1999) supports the validity of the assumption that conodont element size can be taken as a proxy for age and confirms that elements were not shed. Because of the imperfect nature of preservation of the elements and because elements in clusters often obscure other elements, the height of the cusp of the S elements in some clusters was calculated using the linear regressions derived from analyses of element and apparatus growth.

#### Analysis of element ontogeny

Reduced Major Axis analysis of the log transformed data using the allometric equation ( $y = ax^b$ ) suggests that element dimensions increased isometrically during growth. None of the calculated growth exponents (*b*) differs significantly from isometry ( $b = 1$ ) (*Sh* onto *Sl*:  $y = 0.98x^{0.98}$ ,  $n = 18$ ,  $r = 0.90$ ,  $z = -0.22$ ; *Ph* onto *Pl*:  $y = 1.035x^{1.01}$ ,  $n = 19$ ,  $r = 0.93$ ,  $z = -0.11$ ; *Mh* onto *Ml*:  $y = 0.96x^{1.07}$ ,  $n = 13$ ,  $r = 0.89$ ,  $z = 0.525$ ). However, analysis of a larger data set derived from discrete elements in collections from Sjurberg, Sweden (data from Tolmacheva and Löfgren 2000) does not yield the same results. Reduced Major Axis analysis of these data confirms that, as with the cluster data, the hypothesis that S element growth is isometric

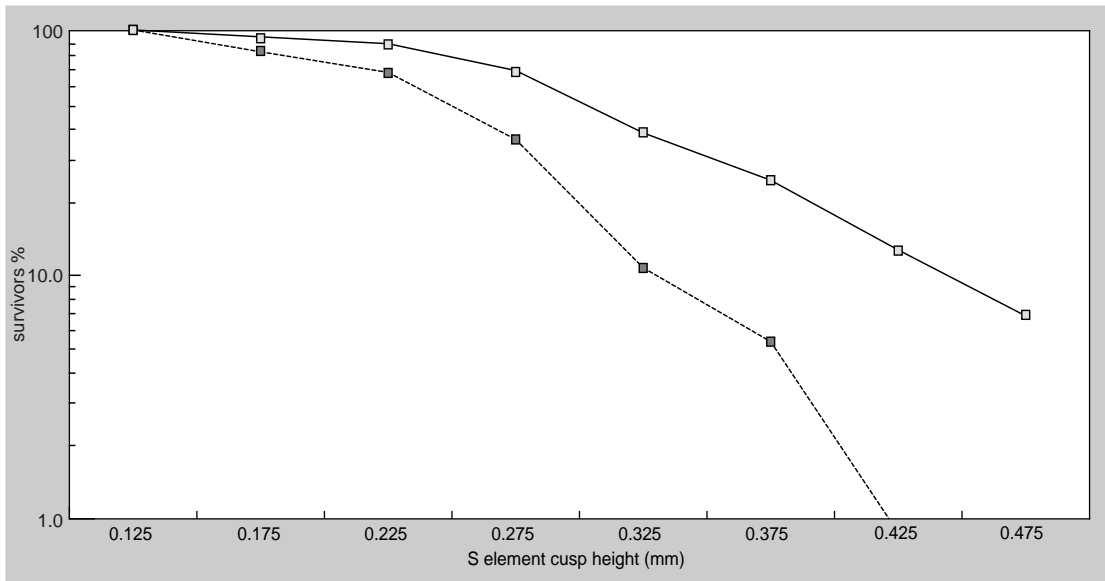


TEXT-FIG. 9. A, scatter plot of S element cusp height onto S element denticle number. Line  $y = 0.037 x^{1.029}$  ( $r = 0.78$ ;  $n = 128$ ) fitted by linear regression of log data. Data from isolated elements and clusters from Burubaital Formation; see Appendix. B, scatter plots of S element cusp height onto P element cusp height and M element cusp height, lines fitted by linear regression of log data, S-P regression  $y = 1.18 x^{0.82}$  ( $r = 0.89$ ;  $n = 23$ ), S-M regression  $y = 0.92 x^{0.94}$  ( $r = 0.73$ ;  $n = 9$ ). Data from clusters from Burubaital Formation; see Appendix.

cannot be rejected ( $P = 0.05$ ; regression of Sh onto Sl:  $y = 1.40x^{1.27}$ ,  $n = 38$ ,  $r = 0.67$ ,  $z = 1.79$ ), but the hypothesis of isometry can be rejected for M elements ( $P = 0.05$ ; regression of Mh onto Ml:  $y = 0.72x^{0.82}$ ,  $n = 78$ ,  $r = 0.62$ ,  $z = -2.43$ ) and P elements ( $P = 0.001$ ; regression of Ph onto Pl:  $y = 0.62x^{0.77}$ ,  $n = 163$ ,  $r = 0.76$ ,  $z = -5.99$ ). Thus, according to these data, S element growth was isometric, but P and M elements exhibit significant negative allometry in cusp height relative to element basal length. The differences in the results using the two data sets may have arisen because the Swedish data set is much larger, because of the difficulties in measuring elements in cherts, or because of real differences in relative rates of element growth in *P. gracilis* in these geographically distant populations. Without additional data for elements in chert it is not possible to decide between these alternative explanations. However, for the purposes of the data used in the survivorship analysis presented below it is worth emphasizing that both analyses indicate isometric growth of S elements. Simple regression techniques cannot be used to determine whether the addition of denticles during growth was isometric with respect to linear dimensions because it is not possible to define an isometric value for  $b$ .

#### Analysis of apparatus ontogeny

Uniquely, the data from clusters also allow the relative growth of the different elements in the apparatus of *P. gracilis* to be determined. Observations of the proportions of elements in clusters seem to suggest that P elements become relatively larger during growth, but RMA analysis of the linear dimensions of elements failed to detect any statistically significant difference between element growth rates and isometry (e.g. Sh onto Ph:  $y = 1.48x^{0.94}$ ,  $n = 23$ ,  $r = 0.87$ ,  $z = -0.63$ ; Sh onto Mh:  $y = 1.37x^{1.24}$ ,  $n = 9$ ,  $r = 0.76$ ,  $z = -0.88$ ). The reliability of this result is open to question because of the small size of the samples. However, the values of  $z$  are not even close to the values required for statistical significance at the  $P = 0.05$  level (i.e.  $-1.96 < z < 1.96$ ). The data suggest, therefore, that like all other conodonts that have been subjected to RMA analysis (Purnell 1993b, 1994) apparatus growth in *Paracordylodus* was isometric.



TEXT-FIG. 10. Survivorship curves for *Paracordylodus gracilis* from the Burubaital Formation. Solid curve derived from measurements of discrete elements, dashed curve derived from measurements of elements in clusters. See text for interpretation and Appendix for data.

As noted above, the relationship between cusp height and basal length in isolated P and M elements from the Sjurberg collection is not isometric. Ideally, the hypothesis of isometric apparatus growth in the clusters from the Burubaital Formation should also be tested using length data, but because of preservation and difficulties in measuring elements in clusters there are too few data to perform a meaningful analysis (for SI:PI,  $n = 7$ ; for SI:MI,  $n = 2$ ).

#### *Survivorship analysis and selective predation on Paracordylodus?*

Preliminary observations of the size distribution of the elements in clusters and those found in isolation suggested that there may have been some preferential predation on *Paracordylodus* animals of a particular size, and a survivorship analysis was undertaken to test this hypothesis. As discussed above, in this analysis *P. gracilis* S element cusp height is taken to represent the age at death of the animal to which the element belonged. Where this could not be measured directly, S cusp height was calculated using linear regressions (Text-fig. 9; caption includes results of linear regressions). These data (see Appendix) yield the survivorship curves shown in Text-fig. 10 (for reviews of survivorship curves and their interpretation, see e.g. Hallam 1972; Dodd and Stanton 1990).

In the size range of small animals, with S elements up to 0.275 mm in height, both survivorship curves (Text-fig. 10) are convex towards the top right of the plot, indicating increasing rates of mortality. Mortality rates of the animals represented by clusters (dashed line) increase faster than those of the animals represented by isolated elements (solid line). From this point onwards, however, the patterns of survivorship differ: the apparent mortality rate in animals represented by clusters continues to rise and shows no sign of slowing even in the largest size class, whereas the mortality rate in animals represented by isolated elements becomes constant (i.e. the solid line is straight).

Interpretation of these differences in survivorship requires a hypothesis of what clusters and isolated elements represent. As noted above (see section on preservation of clusters) the clusters do not preserve intact apparatuses and we interpret them as the remains of faecal pellets. Isolated elements, on the other hand, may have fallen to the sea floor from floating carcasses, the elements being released as the soft

tissues that held them together during life gradually decomposed. They may also represent conodonts that were consumed by predators that produced dispersed faecal material or stomach ejecta, rather than discrete pellets containing closely juxtaposed elements. Because of the abyssal setting of the deposits, the elements are most unlikely to represent the remains of whole carcasses that were disrupted by current activity or bioturbation on the sea floor.

Thus we interpret the clusters as the remains of conodonts that were consumed by predators, and isolated elements as the remains of conodonts that floated as decomposing carcasses, or were consumed by non-pellet forming predators. Based on these interpretations, the survivorship curves suggest that whatever pellet-forming predator or predators were eating *Paracordylodus*, it or they preferred not to eat larger individuals.

Irrespective of the survivorship analysis, the presence of faecal clusters of elements indicates that something was eating *Paracordylodus*, and the obvious question to ask is, what? Other vertebrates certainly existed at this time, but none is demonstrably macrophagous (see Purnell 2001 for a review), and they seem rather implausible candidates for consumers of conodonts. Invertebrate predators, such as arthropods and cephalopods are perhaps more likely to have eaten conodonts, but their remains are unknown in the Burubaital Formation. In fact, the only organism recorded from these deposits that is known to have been macrophagous and probably predatory is conodonts (Purnell 1995; Purnell *et al.* 1995). The possibility that *Paracordylodus* indulged in cannibalism cannot be ruled out.

#### CONCLUSIONS

Clusters of elements of *P. gracilis* from the Burubaital Formation are partially disrupted and mostly incomplete. They probably originated as faecal pellets. Nevertheless, many preserve together elements from the same individual conodont, and this has allowed us to analyze the relative growth rates of different elements of the apparatus. Because of the style of preservation of the clusters only cusp heights of P, M, and S elements can be compared, but these data exhibit isometric growth relationships.

The material also allows the mortality rates of animals preserved as clusters to be compared with animals represented by isolated elements. This survivorship analysis reveals increasing mortality rates in animals represented by clusters (faecal pellets) compared to constant rates in animals represented by isolated elements. This suggests that whatever pellet-forming predator or predators were eating *Paracordylodus*, it or they selected smaller individuals for consumption.

Perhaps most significantly, the clusters preserve direct evidence that *Paracordylodus* bore a 15 element apparatus comprising two M elements, nine S elements ( $S_0$ – $S_4$ ) and four P elements (2  $P_1$ , 2  $P_2$ ) comparable to the apparatus of better known Late Palaeozoic conodonts. Currently, the phylogenetic position of *Paracordylodus* within the conodonts is rather poorly constrained, but depending on the hypothesis of relationship, the evidence from *Paracordylodus* indicates that the 15-element 2M-9S-4P apparatus configuration was either plesiomorphic for conodonts with morphologically complex elements, or arose some time before the origin (or origins) of euconodonts.

*Acknowledgements.* We thank Howard Armstrong and Svend Stouge for helpful comments and a detailed review of the manuscript. Editorial guidance from Dave Harper was also appreciated. TYuT is grateful to L. E. Popov (VSEGEI, St Petersburg), E. V. Alperovich and E. V. Vinogradova ('Didar', Mirnyi) for geological information and assistance in the field. TYuT's work at Uppsala University is supported by a grant from the KVA (Royal Swedish Academy of Sciences); MAP is funded by NERC Advanced Research Fellowship GT5/98/4/ES.

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TANIA YU. TOLMACHEVA

All Russian Scientific Research Geological Institute (VSEGEI)  
Sredni pr., 74  
199016, St. Petersburg, Russia  
e-mail tolma@SV1403.spb.edu.

Current address  
Uppsala University  
Department of Earth Sciences / Hist. Geol. and Pal.  
Norbyvägen 22  
S-75236 Uppsala, Sweden

MARK A. PURNELL

Department of Geology

Typescript received 11 September 2000  
 Revised typescript received 20 March 2001

University of Leicester  
 Leicester LE1 7RH, UK  
 e-mail map2@le.ac.uk

## APPENDIX

*Abbreviations*

Snd, number of S element denticles  
 Sh, S element cusp height  
 Sl, S element posterior process length  
 Ph, P element cusp height  
 Pl, length of aboral surface of P element  
 Mh, M element cusp height  
 Ml, length of aboral surface of M element

*Data for analysis of P, M and S element growth*

Snd	Sh	Ph	Pl	Mh	Ml	Sh	Sl
9	0.238	0.097	0.078	0.195	0.136	0.156	0.175
6	0.238	0.097	0.078	0.175	0.156	0.166	0.166
6	0.163	0.097	0.097	0.175	0.156	0.195	0.195
8	0.250	0.117	0.117	0.175	0.175	0.195	0.234
7	0.281	0.117	0.117	0.195	0.175	0.234	0.214
6	0.163	0.097	0.136	0.214	0.175	0.234	0.234
4	0.088	0.136	0.136	0.351	0.234	0.253	0.244
6	0.225	0.136	0.136	0.292	0.253	0.253	0.292
6	0.188	0.156	0.136	0.312	0.273	0.253	0.331
6	0.238	0.117	0.146	0.351	0.292	0.273	0.273
6	0.250	0.156	0.156	0.370	0.292	0.273	0.312
6	0.194	0.175	0.156	0.292	0.312	0.292	0.195
5.5	0.150	0.175	0.175	0.331	0.370	0.312	0.292
6	0.188	0.175	0.175			0.312	0.331
5	0.150	0.195	0.195			0.429	0.39
9	0.338	0.234	0.234			0.429	0.429
5	0.175	0.234	0.253			0.448	0.448
5	0.113	0.292	0.253			0.448	0.448
5	0.200	0.312	0.273				
7	0.263						
6	0.200						

Snd	Sh	Snd	Sh
4	0.125	4	0.097
5	0.200	2	0.058
6	0.263	3	0.097
5	0.200	4	0.156
7.5	0.188	4	0.166
5.5	0.200	5	0.175
7	0.181	4	0.195
4	0.075	5	0.195
6	0.188	5	0.195
5	0.213	5	0.195
5	0.150	5	0.195
5	0.156	5	0.214
6	0.163	5	0.214
6	0.213	6	0.214
7	0.188	7	0.214
5	0.238	5	0.234
6	0.195	5	0.234
5	0.156	6	0.234
4	0.117	6	0.234
3.5	0.175	5.5	0.253
6	0.175	6	0.253
5	0.234	6	0.253
6	0.312	7	0.253
3	0.117	7	0.253
6	0.253	7	0.263
5	0.195	5	0.273
5	0.251	6	0.273
4	0.175	6	0.273
5.5	0.214	7	0.273
4	0.175	7	0.273
3	0.117	8	0.273
4	0.195	6	0.292
4.5	0.234	6	0.292
4.5	0.214	6	0.292
5	0.234	7.5	0.312
5	0.175	8	0.312
5	0.234	5	0.331
6	0.253	6	0.331
6	0.292	6.5	0.331
5	0.156	7	0.331
4.5	0.214	8	0.331
3	0.156	9	0.351
5.5	0.292	6	0.370
4	0.146	7	0.370
4	0.214	8	0.390
7	0.234	10	0.390
3	0.117	9	0.409
3	0.078	6	0.429
5	0.234	8	0.429
3	0.192	10.5	0.429
8	0.356	9	0.448
6	0.331	10	0.448
4	0.117	11	0.448
4	0.234		

<i>Data for analysis of apparatus growth</i>			
Sh	Ph	Sh	Mh
0.136	0.097	0.156	0.175
0.156	0.097	0.214	0.234
0.156	0.117	0.214	0.292
0.175	0.097	0.234	0.195
0.195	0.117	0.234	0.214
0.214	0.117	0.253	0.351
0.214	0.146	0.370	0.331
0.234	0.097	0.390	0.292
0.234	0.136	0.429	0.370
0.234	0.156		
0.253	0.136		
0.253	0.175		
0.253	0.175		
0.273	0.136		
0.273	0.214		
0.292	0.156		
0.292	0.205		
0.331	0.156		
0.331	0.156		
0.370	0.234		
0.409	0.292		
0.429	0.234		
0.448	0.312		

<i>Survivorship analysis, cluster data</i>			
Sh	Survivors	Deaths	Survivors %
0.125	99	3	100.00
0.175	96	6	96.97
0.225	90	20	90.91
0.275	70	31	70.71
0.325	39	14	39.00
0.375	25	12	25.25
0.425	13	6	13.13
0.475	7	7	7.07

<i>Survivorship analysis, isolated element data</i>			
Sh	Survivors	Deaths	Survivors %
0.125	108	17	100
0.175	91	16	84.26
0.225	75	35	69.44
0.275	40	28	37.04
0.325	12	6	11.11
0.375	6	5	5.56
0.425	1	1	0.93