

## Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia

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Conodont elements recovered from the gut region of a palaeoniscoid fish from the Gogo Formation, Upper Devonian (Frasnian), of the Canning Basin, Western Australia, are assigned to two multielement taxa. The complete apparatus of *Oulodus angulatus* (Hinde) has 15 elements, most of which have excellent preservation of the basal plate. An additional 13 elements are assigned to the *Icriodus brevis* apparatus which is not a complete apparatus.

The term 'crown' is introduced for the upper part of the conodont element. A conodont element, or element, is thus composed of two parts, the upper part or crown, and the lower part or basal plate. Four new terms—boss structure, prong, furrow and notch—are introduced to describe features of the basal plate.

### Introduction

Examination of a limestone nodule collected by the author in 1972, from the Gogo Formation (Upper Devonian) of the Canning Basin (Fig. 1), Western Australia, has revealed the presence of conodont elements located in the gut region of a stegotrachelid palaeoniscoid fish. The fish has not yet been prepared or identified, but probably can be referred to one of three monotypic genera of palaeoniscoid fish that have been recovered from the Gogo Formation (Gardiner, 1973; Gardiner & Miles 1975), and are now being studied by Brain G. Gardiner of Queen Elizabeth College, University of London.\*

The nodule, 115 mm long and 82 mm wide, was split along the axial plane of the fish with part of the fish adhering to each half of the nodule (Fig. 2). The fish is slightly more than 100 mm in length and has only the tip of the caudal fin missing. Preservation of the palaeoniscoid fish is excellent with intact scale layers and bone structure of the head region. Directly under the scale layer throughout much of the body region is a fibrous white layer (Fig. 3E, F) that may represent mineralisation of the muscle tissue of the fish. The gut region is delineated by the presence of sparite and silty looking material between the scale layers. There are also patches of dark organic material concentrated in the gut region of the fish.

Broken edges of conodont elements (Fig. 3A), subsequently identified as belonging to the multielement genus *Oulodus*, Sweet & Schonlaub (1975), were observed on the right half of the nodule. After initial photography a 10 percent solution of acetic acid was applied, drop by drop, to a small region surrounding the conodonts. The process was observed under the microscope and a series of photographs, Fig 3B-F, was taken at several stages. When the last of the conodont elements had been removed a cavity about 7 mm in diameter and 2 mm deep had been etched in the fish, and had extended slightly into the calcareous siltstone matrix of the nodule.

As the etching process progressed it became apparent that the elements represented a complete and intact apparatus with exceptional preservation of the basal plates. Some of the elements of the apparatus were broken when the nodule was originally split, but all elements within the right half of the nodule were unbroken. No elements were

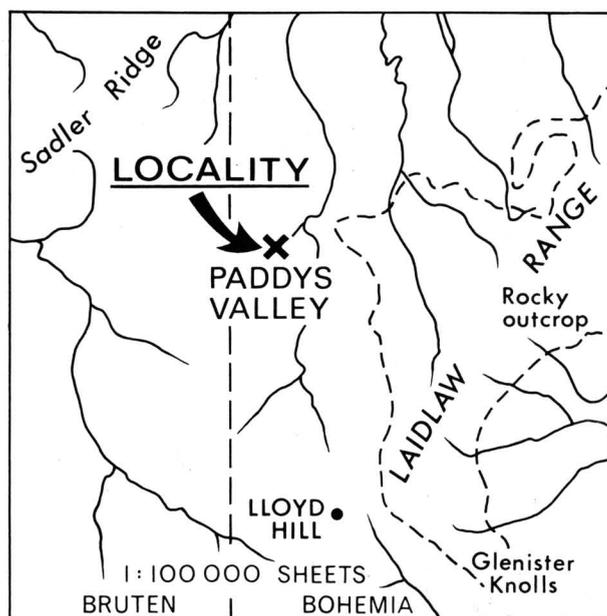


Figure 1. Locality map.

observed on the left half of the nodule and it is assumed that a thin sliver of material was lost when the nodule was split.

Study of the complete elements of the *Oulodus* apparatus has presented a problem of terminology. The majority of previous workers have applied the term conodont or conodont element to the laminated, denticulate structure which may or may not have had a basal plate attached to the 'lower' surface. Other workers, most recently Muller & Nogami (1971, 1972), have restricted the term conodont to the upper part of the element. The majority of present workers apply the terms conodont element or element to the entire structure of each individual part of an apparatus, that is the upper part and the basal plate. Because there is no unambiguous term for the upper part of the element it is suggested that the crown be applied to the upper part of the conodont element. Thus a conodont element would be

\* Since this paper went to press, two stegotrachelid palaeonisciform fish from the Gogo Formation have been described by Gardiner & Bartram (1977). These are *Mimia toombsi* and *Moythomasia durgaringa*. The specimen from this study probably belongs to one of these species, but until the fish is prepared, identification is not possible.

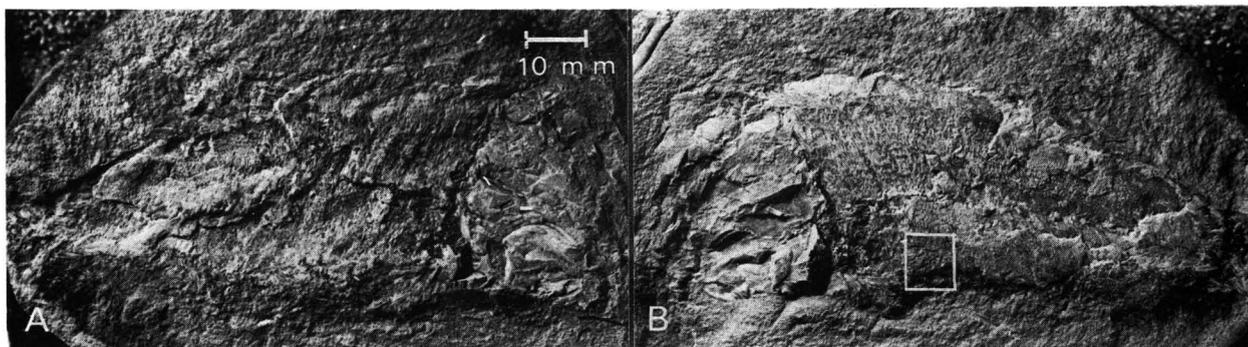


Figure 2. Left and right halves, respectively, of the limestone nodule containing the palaeoniscoid fish and conodont apparatuses. The square on Figure 2B outlines the area shown in Figure 3A-F.

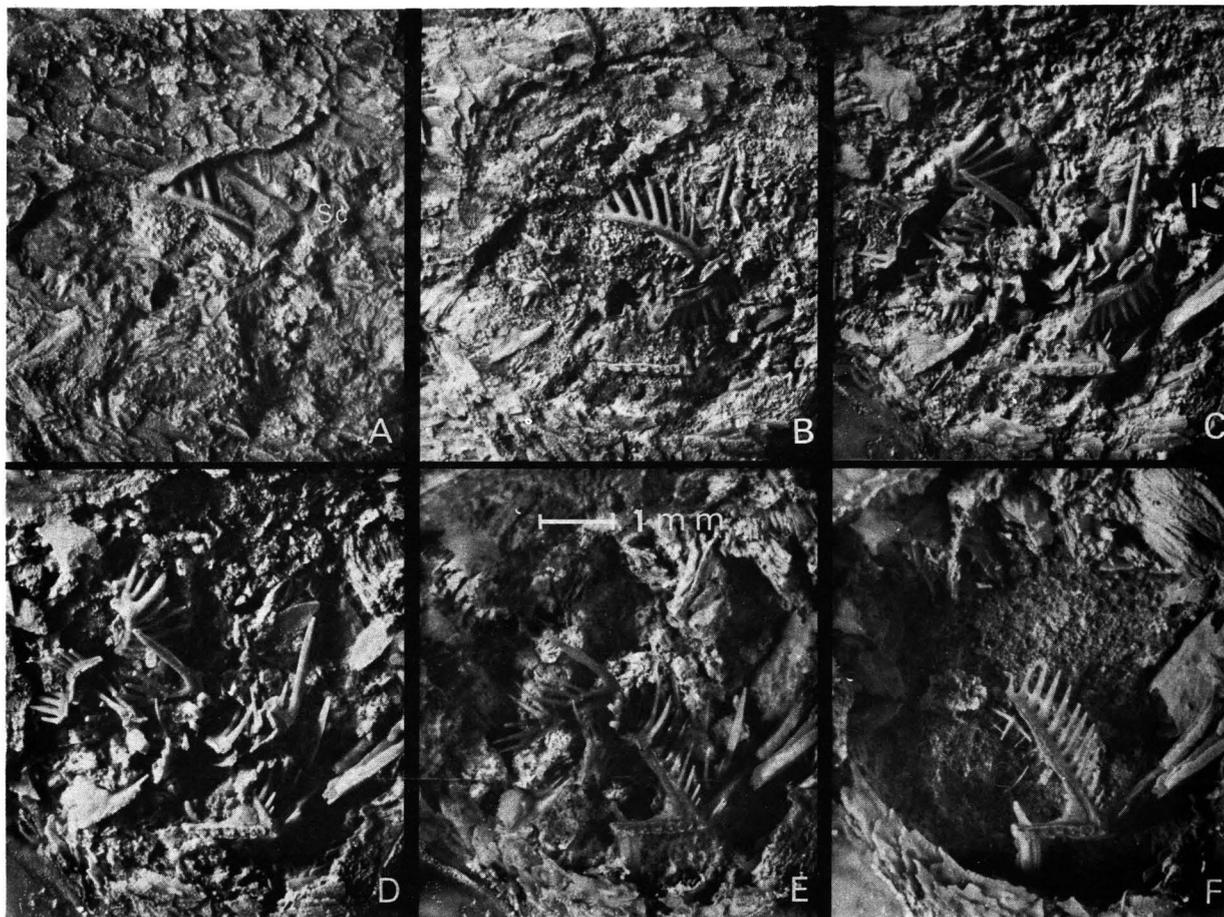


Figure 3. Sequence showing the area containing the conodont apparatuses at different stages of the acidization process. 3A—prior to etching, note impression of Sc element (CPC 17195). 3B—early etching stage. 3C—note I element of *Icriodus brevis* apparatus (circled). 3D, E—later stages of etching, note probable mineralized muscle fibres in upper right corner. 3F—Sa element with floor of cavity showing matrix and sponge spicules underlying fish.

composed of two parts, an upper part termed the crown and a lower part termed the basal plate.

### Locality and specimen data

The limestone nodule containing the fish and the conodont elements was collected from an exposure of the Gogo Formation, Upper Devonian (Frasnian), in Paddys Valley, between the Laidlaw Range and Sadler Ridge, grid ref. 4160-840360, Bohemia 1:100 000 topographic map.

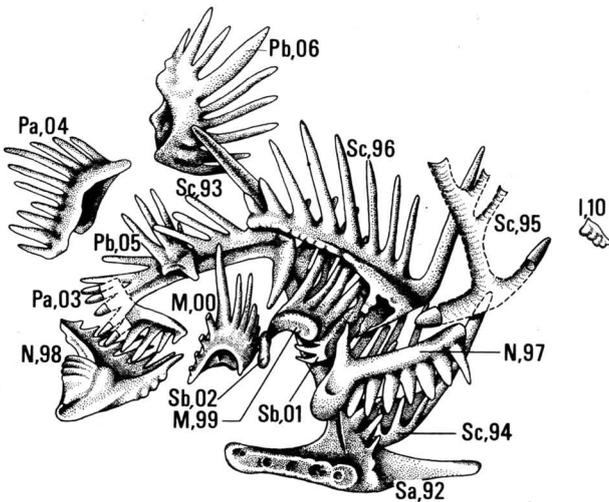
The material from this study has been assigned the following CPC numbers. Elements of the *Oulodus angulatus* apparatus—CPC 17192-17206. Elements of the *Icriodus brevis* apparatus—CPC 17202-17210. The faunal

slide containing the discrete conodont elements enumerated in Table 1—CPC 17221. The two halves of the nodule containing the fish—CPC 17220. In addition one faunal slide that contains the insoluble residue from around the conodont elements within the fish—CPC 17222, and a faunal slide that contains fish fragments, sponge spicules and one fragment of crustacean exo-skeleton from the 297 g of dissolved nodule—CPC 17223.

### Conodont elements recovered

In all, 15 elements representing a complete *Oulodus* apparatus and 13 elements of an *Icriodus* apparatus were recovered from the cavity dissolved in the gut region of the

fish. All elements of the *Oulodus* apparatus were observed in situ (Fig. 4), and comments will be made on the nature and function of the apparatus. Only one I element (Fig. 7N-Q) of the *Icriodus* apparatus was observed in situ (Fig. 3C) and the rest of the elements of this apparatus were recovered from the insoluble residue of the cavity.



**Figure 4.** Drawing showing relative positions of the elements of the *Oulodus* apparatus and the single I element of the *Icriodus* apparatus prior to their removal from the nodule. The number is the last two digits of the CPC accession number. Symmetrical element: Sa-92. Left elements: Sc-93, 94; N-97; M-99; Sb-01; Pb-05; Pa-03. Right elements: Sc-95, 96, N-98; M-00; Sb-02; Pb-06; Pa-04.

An additional 37 discrete elements were recovered from a slab cut from the outer edge of the right half of the nodule (Table 1). The slab, was processed without crushing, and the residue collected by decanting. A number of elements belonging to the *Icriodus brevis* (14) and *Oulodus angulatus* (2) apparatuses were recovered along with 21 elements that were assigned only to form taxa or left in open nomenclature.

The number and types of discrete elements recovered from the slab suggest that the *Icriodus brevis* and *Oulodus angulatus* apparatuses recognised from the body cavity are

not representative of the random distribution of elements in the associated matrix material.

The composition and function of the *Oulodus* and *Icriodus* apparatuses discussed in the following sections is based only on the elements recovered from the gut region of the fish.

### The *Oulodus* apparatus

Sweet & Schonlaub (1975) recognised the multielement genus *Oulodus* as an apparatus composed of six distinct morphologic types and placed in synonymy the multielement taxa *Delotaxis* Klapper & Philip, and *Ligonodina* Bassler *sensu* Jeppsson that were thought to contain only five element types. In the present study the apparatus assigned to the multielement genus *Oulodus* has seven element types.

Sweet & Schonlaub (1975, p. 42) recognised the six components of their *Oulodus* apparatus on the basis of similar morphologic features of the elements. However it is now apparent that gross morphologic similarity of all types of elements within an apparatus is not necessarily a fact. In the *Oulodus* apparatus recovered in this study the denticles and general morphology of the N element are different from those of all other elements of the apparatus.

In the following section the letter designations of elements suggested by Sweet & Schonlaub (1975) are followed except that the neoprioniodontiform element, not recognised by Sweet & Schonlaub, is designated by the letter N.

#### Systematic description

##### Genus *Oulodus* Branson & Mehl, 1933

Type species: *Cordylodus serratus* Stauffer, 1930 (= senior subjective synonym of *Oulodus mediocris* Branson & Mehl, 1933, the originally designated type species).

##### *Oulodus angulatus* (Hinde, 1879)

(Figs. 5, 6)

#### Sa element

- 1879 *Prioniodus angulatus* Hinde, p. 360, pl. 15, fig. 17.
- 1933 *Hibbardella angulata* (Hinde), Branson & Mehl, p. 141, pl. 11, fig. 16.
- 1968 *Hibbardella angulata* (Hinde), Huddle, pl. 14, pl. 8, figs. 2, 7; pl. 9, fig. 3 (with synonymy).
- 1970 *Hibbardella* sp. cf. *H. angulata* (Hinde), Seddon, pl. 15, figs. 13, 16.

#### Sc element

- 1879 *Prioniodus panderi* Hinde, p. 361, pl. 16, fig. 4.
- 1926 *Ligonodina panderi* (Hinde), Ulrich & Bassler, p. 13, pl. 2, figs. 1, 2.
- 1968 *Ligonodina panderi* (Hinde), Huddle, p. 19, pl. 9, fig. 11, pl. 10, figs. 1-8, 11 (with synonymy).
- 1970 *Ligonodina panderi* (Hinde), Seddon, pl. 15, figs. 8, 10.

#### N element

- 1879 *Prioniodus? alatus* Hinde, p. 361, pl. 16, fig. 5.
- 1957 *Neoprioniodus alatus* (Hinde), Hass in Cloud, Barnes & Hass, p. 809, pl. 4, fig. 3.
- 1968 *Neoprioniodus alatus* (Hinde), Huddle, p. 25, pl. 6, figs. 1, 2 (with synonymy).
- 1970 *Neoprioniodus alatus* (Hinde), Seddon, pl. 15, figs. 12, 14.

Element type	Number of elements
<i>Icriodus brevis</i>	
I element	12
S <sub>2</sub> element	2
<i>Oulodus angulatus</i>	
M element	1
Pb element	1
Pa elements	
<i>Polygnathus xylus</i>	4
<i>Spathognathodus brevis</i>	1
Pb elements	
ozarkodinian	2
N elements	
neoprioniodontan	1
Sa (A <sub>3</sub> , B <sub>3</sub> ) elements	
hibbardellan	1
Sb (A <sub>2</sub> , B <sub>2</sub> ) elements	
angulodontan	2
lonchodinian 'a'	1
lonchodinian 'b'	1
Sc (A, B) elements	
hindeodellan 'a'	2
hindeodellan 'b'	3
hindeodellan 'c'	1
ligonodinian 'a'	1
ligonodinian 'b'	1
	37

**Table 1** Disjunct elements recovered from nodule.

*Pa element*

1970 *Prioniodina?* Seddon, pl. 15, fig. 9.

The above are the only elements that have been positively identified from the literature. The lonchodiniiform elements (M, Sb and Pb) are highly variable and no attempt was made to develop synonymies for these elements.

*Diagnosis:*

An apparatus of 15 elements with 7 morphologic types represented as Pa (2), Pb (2), Sa (1), Sb (2), Sc (4), M (2) and N (2). The Pa element is prioniodiniiform, Pb element is lonchodiniiform, Sa element is hibbardelliiform, Sb element is lonchodiniiform, Sc element is ligonodiniiform, M element is lonchodiniiform, and the N element is neoprioniodontiiform.

*Description:*

The 15 elements of the *Oulodus* apparatus form three groups based on the morphology of the crown and the basal plate. The first group has three element types (N, Sa, Sc), and 7 elements. The members of this group are characterised by long posterior processes and shorter downward directed anterior or anterior-lateral processes.

The second group contains 2 element types, Sb and M, and 4 elements. Members of this group have processes of similar length with a tendency for the anterior process to be the longest. The third group also contains 2 element types, Pa and Pb, and has 4 elements.

Four new terms are applied to features found on the basal plate: these are boss structure, prong, furrow and notch. Boss structures (Fig. 5X-CC) are small raised features distributed over part of the upper surface of the basal plate; most have an oblong outline and at high magnification (Fig. 5AA) have a rough surface texture. There is no preferred orientation of the long axis of the structure.

Prongs are projections on the margin of the basal plate. These are best developed on the N and M elements (Figs. 5F-H, 6J & K), but are also found on other elements. Furrows are grooves on the upper surface of the basal plate. The furrows may radiate from the vicinity of the contact between crown and basal plate to the margin of the plate, as in the N and M element (Figs. 5F & I, 6L), or show a complex of radiate and parallel pattern as in the Sc element (Fig. 5X). The notch is a deep indentation of the margin of the basal plate. This feature is developed on the inner lateral margin of M and Sb elements (Fig. 6L, N, & V) and on the outer lateral margin of the Pa and Pb elements (Fig. 6T & BB). The notch is interpreted as an accommodation by the basal plate to a T or L-shaped ridge in the soft anatomy of the organism to which the element was attached. The Sc and Sa elements have an elongated posterior process that is attached to this ridge with short lateral processes that are transverse to the long ridge, and

presumably follow the axis of a short transverse ridge. The elements of Groups 2 and 3, lacking posterior processes, are located on the short transverse ridge; the notch accommodates the long ridge which is not covered the element.

*Group 1:*

The Sa element is hibbardelliiform with prominent downwardly directed lateral processes and a long, well-developed posterior process on which the denticle size increases posteriorly towards the end of the bar. The basal plate is developed as a web linking the posterior and lateral processes and narrows toward the tip of the posterior process.

The Sc element is ligonodiniiform and the four elements represent two left-right pairs. The three elements that were recovered intact are morphologically similar but are not identical. It is impossible to conclusively pair the well-preserved left element with either of the right elements to establish a direct mirror image pair due to the minor morphologic variation that is expected between paired elements.

The N element has denticles that are laterally compressed, and the lower part of each denticle is fused to the adjacent one. The crown has a prominent anticusp and a large flange on the lower inner margin of the cusp denticle. The basal plate is largest under the cusp and narrows toward the anticusp and the end of the posterior process.

The N element is placed in group 1 because it has a long posterior process (conventional orientation), but this element type differs from all other elements in the cross-sectional profile of the denticles. All other element types have discrete denticles with a small ridge or flange on the margin of the denticle. Denticles of the N element lack this flange and are fused with adjacent denticles near the bar.

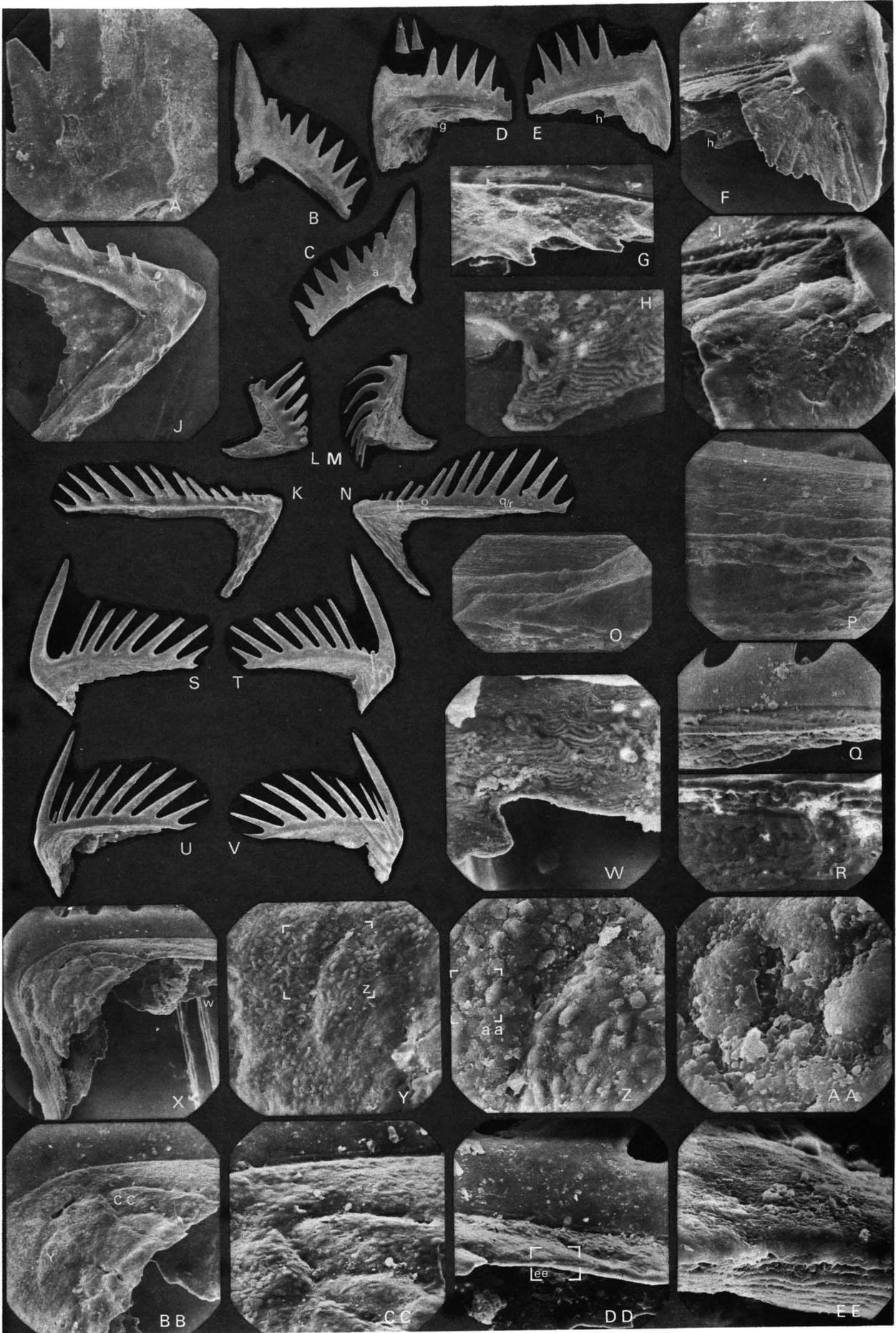
The inner surface of the basal plate of group 1 elements shows parallel ribs along the portion of the plate that extends along the posterior process. However under the cusp the ribs give way to a pattern of intersecting ridges (Fig. 6A, B). The ribs probably continue under the reticulate pattern.

*Group 2:*

The M and Sb elements of this group are characterised by similar lengths of the processes, with the anterior process slightly longer, and a large notch in the inner lip of the basal plate.

The M element is lonchodiniiform. The anterior process has 5 to 7 denticles, the posterior process 4 to 5. The cusp is slightly offset to the inner side and all denticles are posteriorly directed. The two denticles just anterior to the cusp are joined slightly above the process. The inner lip of the basal plate is broader than the outer lip, but it has a large notch located below the cusp that is not found on the

**Figure 5.** *Oulodus angulatus* apparatus. Small letters on photos indicate location of areas shown in enlargements. A-C, N element, CPC 17197. A. enlargement of etched outer lateral surface (100X). B. inner lateral view (20X). C. outer lateral view (20X). D-I, N element, CPC 17198. D. outer lateral view (23X). E. inner lateral view (23X). F. view of basal plate below cusp showing deep furrow structures (100X). G. outer view of prongs developed on margin of basal plate (85X). H. inner view of the posterior of the two prongs in G (350X). I. view of the outer surface of the basal plate showing the contact of the basal plate and the crown, furrows, and boss structures (230X). J-R, Sa element, CPC 17192. J. anterior part of element showing basal plate web developed between the posterior and lateral processes (42X). K. oral view (16X). L. oral view of broken left lateral process (16X). M. aboral view of broken left lateral process (16X). N. aboral view (16X). O. aboral view of left margin of basal plate showing basal plate (broken margin) and ridged under lip of the crown (300X). P. aboral view of left margin of basal plate showing transect from ribbed under lip of crown, broken attachment area of basal plate to crown, and part of the aboral surface of the basal plate (300X). Q. aboral-lateral view of part of the posterior process showing ribbed pattern and irregular grooves (72X). R. aboral view of area shown in Q ( X). S-T, Sc element, CPC 17194. S. outer lateral view (14X). T. inner lateral view (14X). U-EE, Sc element, CPC 17193. U. outer lateral view (13X). V. inner lateral view (13X). W. aboral view of basal plate showing contortion of ribs (280X). X.-AA. progressive enlargement of outer lateral basal plate surface to show detail of boss structures and furrows. X (40X), Y (150X), Z (370X), AA (1350X). BB. outer lateral surface of basal plate showing detail of furrows (80X). CC. enlargement of area of branching furrow structures (170X). DD. view showing the relationship of the crown surface, and the oral and aboral surfaces of the basal plate. Note that the boss structures are more prominent toward the crown-plate contact (100X). EE. enlargement of lower edge of the basal plate showing the transition from the ribbed aboral surface to the rough upper surface to the rough upper surface (500X).



outer lip. The edge of the basal plate around the notch is regular and there is no indication that the notch is the result of breakage.

The Sb element is also lonchodiniiform. Only one of the two Sb elements is complete (Fig. 6V-Y)—the second is represented only by isolated denticles (Fig. 6P). The element has 5 posterior and 4 anterior denticles, but the tip of the anterior process is broken. The cusp is posteriorly directed and both processes are bent slightly posteriorly. As with the M element the outer lip of the basal plate is smaller but continuous, and the inner lip is larger, but interrupted by a large notch.

I have oriented both the M and Sb elements transverse to the long axis of the apparatus (Figs. 9, 10). This is based on the orientation of the elements when found (Figs. 3E, 4), and the attitude of the denticles.

The basal plate of the M and Sb elements is not as well preserved as those in group 1. However they show similar furrows and boss structures on the upper surface. The lower surfaces have parallel ribs developed under the lateral processes and the over-coating of smooth or reticulate pattern under the cusp (Fig. 6J).

### Group 3:

The Pa and Pb elements are the most posterior elements of the apparatus. I have shown them surrounding the mouth area in the reconstructed apparatus (Fig. 10).

The Pb element is lonchodiniiform, with 5 denticles on the anterior process, and 3 denticles on the posterior process. The element is slightly bowed and arched with the denticles curved posteriorly and slightly inward. There is a prominent notch below the cusp on the outer lip of the basal plate. The inner lip of the basal plate is broken, and it is not clear if there was a notch on the inner side.

The Pa element is prioniodiniiform with 6 anterior and 4 posterior denticles. Denticles of this element are erect, the element is bowed outward, and the posterior process is bent slightly down. There is a notch in the outer lip of the basal plate but, again, the inner lip is broken and no notch can be seen.

Unlike the elements of group 2, the elements of group 3 have a notch on the outer lip of the basal plate. This is taken to indicate a more normal orientation for these elements. The ridges of soft tissue of the group 3 element could have been roughly parallel to the tissue ridges of groups 1 and 2. Boss structures and shallow furrows are present on the outer surfaces of the basal plates.

## The *Icriodus* apparatus

The *Icriodus* apparatus was shown by Klapper & Philip (1971) to consist of two element types, I and S<sub>2</sub>. Later Klapper & Ziegler (1975, p. 67) suggested that the *Icriodus* apparatus might also contain a M<sub>2</sub> element. The present

study confirms the presence of an M<sub>2</sub> element in the apparatus.

A total of 13 elements of an *Icriodus* apparatus were recovered from the body cavity of the fish. There were 4 I elements, 6 S<sub>2</sub> elements and 3 M<sub>2</sub> elements. Only one, an I element, was observed in situ (Fig. 3C) during the etching process and the rest were picked from the residue.

### Systematic description

Genus *Icriodus* Branson and Mehl, 1938

Type species: *Icriodus expansus* Branson and Mehl, 1938;  
*Icriodus brevis* Stauffer, 1940

Fig. 7

### Synonymy:

#### I Element

1940 *Icriodus brevis* Stauffer, p. 424, pl. 60, figs. 36, 43, 44, 52.

1975 *Icriodus brevis* Stauffer, Klapper, p. 89, pl. 3, figs. 1-3 (with synonymy).

#### S<sub>2</sub> Element

Stauffer (1940) described several species of *Acodina* from Austin, Minnesota. Several of them appear from the illustrations to be within the range of variation of the S<sub>2</sub> elements recovered in this study. The species of *Acodina* include *A. velva*, *A. concava* and *A. cuspidata*. Without an examination of both original and topotypic material to establish its variability, it is impossible to assign the specimens from this study to a form species. It is probable that all three species of *Acodina* named above were associated with the *I. brevis* apparatus.

#### M<sub>2</sub> Element

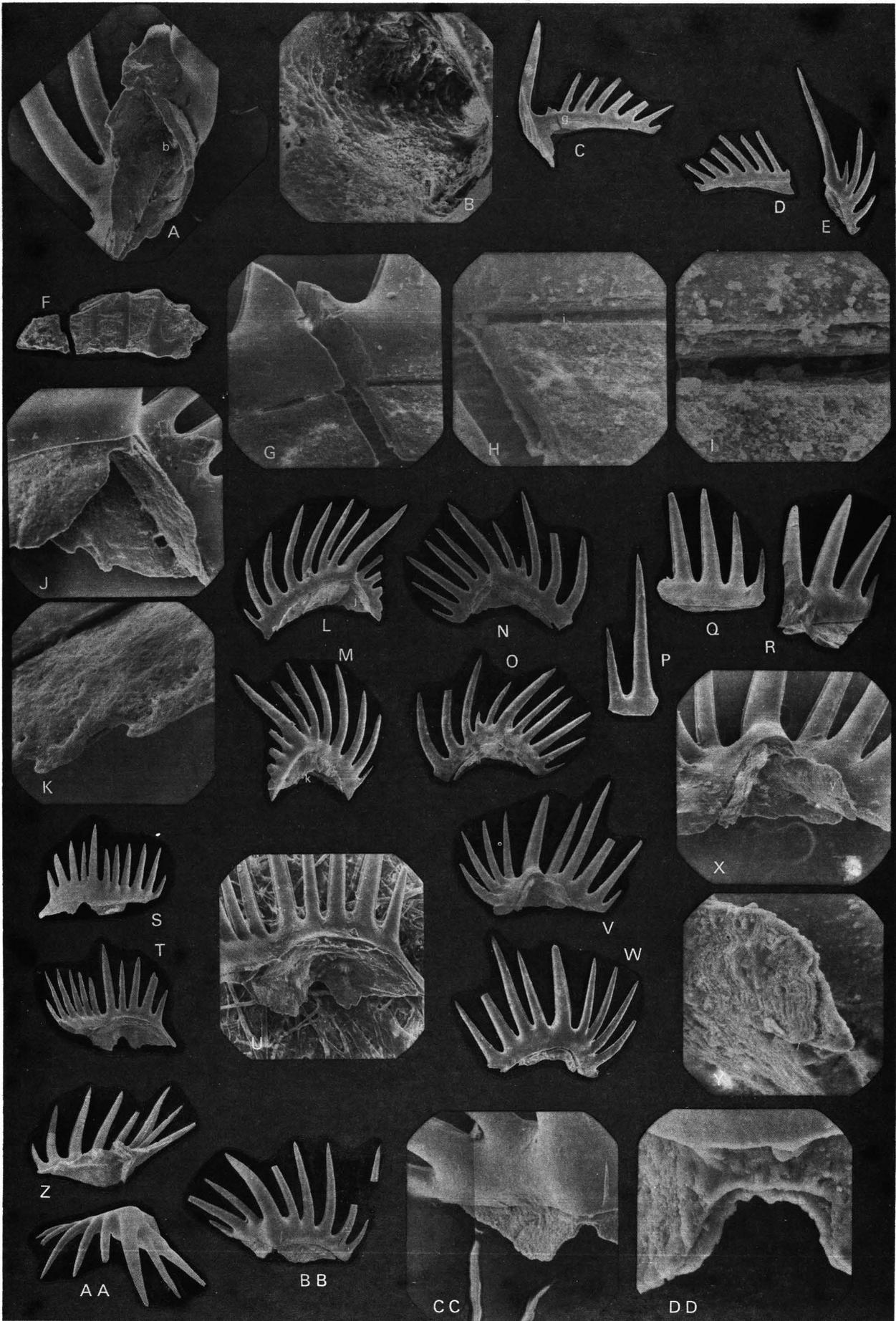
Stauffer does not appear to have recognised any M<sub>2</sub> elements.

### Remarks:

Four I elements were recovered. These show a size gradation from the smallest with only one pair of lateral row denticles to, the largest specimen with 4 pairs of lateral row denticles. The lateral denticles are curved outward and upward, and there is no ridge between them and denticles of the middle row. The posterior denticle is the largest denticle and is morphologically very similar to the S<sub>2</sub> element. In the smallest specimen (Fig. 7A-E) the posterior denticle is striated. Middle row denticles range from 3 to 7 in number.

The 6 S<sub>2</sub> elements recovered show a range of morphology. All are laterally compressed with a slight flare of both the anterior and posterior margins a short distance above the base of the crown. Two of the specimens (Fig. 7V, W, Z-CC) were joined by the basal cone when found; however in moving them on the SEM stub the elements separated. The two elements are recurved posteriorly, and the axial plane slightly twisted so that there is a slight en echelon arrangement. The tips of these elements are striated.

**Figure 6.** *Oulodus angulatus* apparatus. A-E, G-I. Sc element, CPC 17196. A. posterior view of broken anterior end showing relationship of basal plate to crown (85X). B. enlargement of the apex of the aboral surface of the basal plate (290X). C. inner lateral view (13X). D. outer lateral view of posterior process (13X). E. anterior view (13X). G. enlargement of break in posterior process (120X). H. junction of basal plate and crown showing ridged surfaces of both parts and the narrow solid connection (250X). I. closeup of area outlined in H showing ridged surfaces of crown and basal plate (500X). F. Sc element, CPC 17195. part of posterior process adhering to the inner surface of fish-scale layer (20X). J-M, M. element, CPC 17200. J. enlarged inner lateral view showing notch and prongs on outer lateral margin (100X). K. enlargement of outer lateral margin of basal plate showing prongs (220X). L. inner lateral view, note notch (22X). M. outer lateral view, note lack of notch (22X). N, O, M element, CPC 17199. N. inner lateral view (22X). O. outer lateral view (22X). P. Sb element, CPC 17202. fragment of posterior process (50X). Q. Pa element, CPC 17203. fragment of anterior process (50X). R. Pb element, CPC 17205. fragment of posterior process (50X). S-U, Pa element, CPC 17204. S. outer lateral view, note notch in basal plate (22X). T. inner lateral view (22X). U. enlargement of basal plate area, note notch on outer margin of basal plate (50X). V-X, CC. Sb element, CPC 17201. V. inner lateral view (26X). W. outer lateral view (26X). X. enlarged inner lateral view showing notch area (65X). Y. enlargement of margin of basal plate showing edge and laminae (130X). Z-DD, Pb element, CPC 17206. Z. aboral view (17X). AA. oral view (17X). BB. outer lateral view (17X). CC. enlarged outer lateral view showing notch development (29X). DD. enlargement of area shown in AA to show tip of notch (160X).





Only three  $M_2$  elements were recovered. Two were adhering to the side of the largest I element (Fig. 7P), and the third was free in the sediment. The elements have sub-rounded cross sections of the lower part of the crown, and the basal cone continues this outline. The crown is striate for most of its length.

Lange (1968) assumed a model of 1 pair of I elements to 30 cone elements for the *Icriodus* apparatus. Bultynck (1972) however has argued that the I element was not associated with any cone element. From this study it appears that the *Icriodus* apparatus has at least three distinct morphologic elements; the I element, a laterally compressed  $S_2$  element, and a rounded  $M_2$  element. All element types show a broad range of morphologic variation. There were at least 4 I elements, 6  $S_2$  elements and 3  $M_2$  elements in the *Icriodus brevis* apparatus. As none of the I elements is paired it is probable that there were at least 8 I elements, i.e. 4 pairs, in the original organism, and an undetermined number of  $S_2$  and  $M_2$  elements.

### Interpretation of the conodont elements

#### *Oulodus apparatus*

The elements of the *Oulodus angulatus* apparatus allow an interpretation of the position of elements within the conodont organism and of their possible function. This interpretation is based on the complete or nearly complete basal plates found on all elements of the apparatus, as well as the morphology of the crown and the relative position of the elements.

The elements assigned to the *Oulodus angulatus* apparatus represent the only hard parts of that conodont organism. Despite the presence of what is thought to be post-mortem mineralisation of the muscle tissue of the fish, there were no structures observed during the etching process that could be related to the elements. This is a clear indication that the conodont organism was, with the exception of the elements, composed only of non-mineralised tissue. The conodont elements must have been attached to soft tissue.

Three distinct tissue types were in contact with different surfaces of the element (Fig. 8). These are the smooth crown surface, the rough boss-covered upper basal plate surface, and the parallel ribs of the aboral basal plate surface. Functionally the ribbed surface of the lower part of the basal plate would have been excellent for attachment of the element to the supporting tissue of the organism because of the greatly increased area of the attachment surface. The surface of the crown is smooth when compared with the upper surface of the basal plate that is marked with boss structures. The upper surface of the basal plate was probably embedded in supporting tissue—which may have included muscle fibres, regulating the fine movement of the element, that were attached to the boss structures.

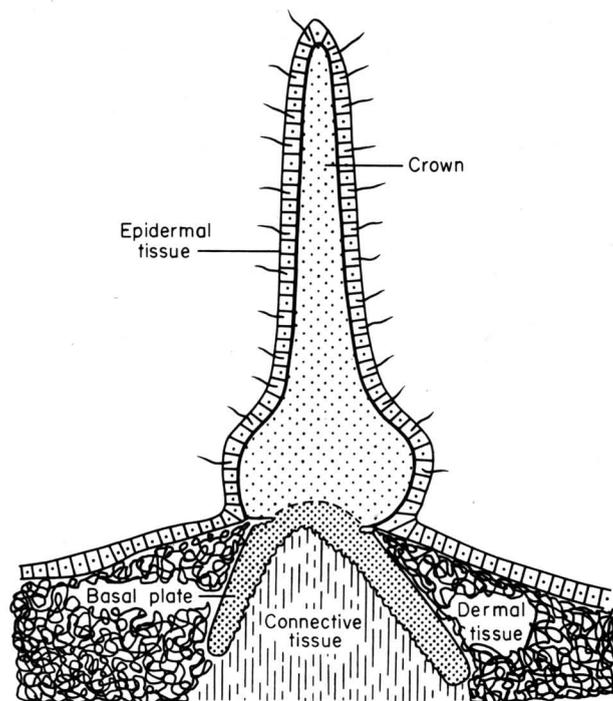


Figure 8. Cross-section of element showing hypothetical soft tissue relationships.

Bengtson (1976, 1977) suggested that the crown was not tissue-covered, and that growth took place when the element was withdrawn into a pocket while not functioning. I disagree with Bengtson and believe that the crown surface was tissue-covered, and that growth took place by precipitation from the inner surface of this tissue layer. Lindstrom (1973, 1974) has argued this to be the case, and Morris (1976) suggests that the 'teeth' of *Odontogriphus omalus*, which may be conodont elements, were covered by tentacles. Conceptually it is hard to envisage the growth of the more complex platform elements by the process put forward by Bengtson.

The furrow structures on the basal plate surfaces may be the impression of nerve or circulatory pathways. Similar features are common on vertebrate bones, especially those of the head region.

#### *Icriodus apparatus*

Two aspects of the *Icriodus* apparatus require comment. One is the pair of  $S_2$  elements (Fig. 7W) that were fused by the basal cones, the other is the size disparity shown by both the  $S_2$  and I elements.

As stated earlier the basal cones of two of the  $S_2$  elements (Fig. 7Z, BB) were fused when first observed (Fig. 7V, W). The crown portions of these elements had a slight echelon arrangement. After separation it can be seen that the basal cone of the left element (Fig. 7AA) is modified to fit over the leading edge of the basal cone of the right element

Figure 7. *Icriodus brevis* apparatus. A-F, I element, CPC 17207. A. enlargement of ribbed posterior denticle (270X). B. right-lateral view (185X). C. posterior view (250X). D. left-lateral view (215X). E. oral view (200X). F. oblique-aboral view (225X). G-J, I element, CPC 17208. G. oblique right-lateral view (110X). H. posterior view (110X). I. oblique left lateral view (110X). J. oral view (110X). K-M, I element, CPC 17209. K. oblique left-lateral view (90X). L. oblique right-lateral view (90X). M. oral view (110X). N-Q, I element, CPC 17210. N. oral view, the  $M_2$  elements CPC 17216 is located near the posterior denticle; the  $S_2$  element CPC 17218 is located on the large posterior left denticle; and the  $S_2$  element CPC 17215 is located between the second pair of lateral row denticles (105X). O. right-lateral view (90X). P. oblique left-lateral view (120X). Q. oblique posterior view (120X). R.  $S_2$  element, CPC 17215. lateral view (390X). S-U,  $M_2$  element, CPC 17216. S. lateral view (240X). T. enlargement of basal cone and adjacent part of crown (375X). U. aboral view of tube-like structure inside the basal cone (400X). V, W, Z-CC,  $S_2$  elements; CPC 17211 and 17212. V. enlarged view of base of fused elements (350X). W. lateral view (140X). CPC 17211. Z. lateral view (165X). AA. enlargement of basal cone (600X). CPC 17212. BB. lateral view (160X). CC. enlargement of crown and basal cone (360X). X, probable  $M_2$  element, CPC 17219, element lying partly across  $M_2$  element CPC 17216 and attached to I element CPC 17210 (400X). Y.  $S_2$  element, CPC 17218. very small element attached to posterior left-lateral denticle of I element CPC 17210 (680X). DD.  $S_2$  element, CPC 17213. lateral view (140X). EE.  $S_2$  element, CPC 17214. lateral view (145X). FF.  $M_2$  element, CPC 17217. lateral view (250X).

(Fig. 7CC). The relationship of these cone elements is similar to specimens illustrated by Walliser (1964, text fig. 2; plate 10, figs 1-4, *non* fig. 9).

The relationship of the two  $S_2$  elements may indicate that rather than functioning as discrete elements within the apparatus, several  $S_2$  elements formed an elongate structure. This format would mean that cone elements, for some apparatuses, had a similar function to bar-type elements. I do not, however, think that these bar-type structures are similar to those described by Bischoff (1973) as conodont-supporting elements.

This fused relationship may also have a bearing on the origin of the double tip of the basal cavity that has been observed in most I elements. There is a close similarity between the morphology of the large posterior denticle of the I element and the associated  $S_2$  element. In some cases the I element is constricted between the ultimate and penultimate denticles (Fig. 7F). This may be an ontogenetic demonstration of the fusion of an  $S_2$  element to the I element at some point in the early phylogeny of the genus *Icriodus*. This view may be supported by the lack of lateral denticles associated with the posterior denticle of many I elements.

Both the I and  $S_2$  elements show a considerable size range. The I elements also show progressive addition of middle and lateral row denticles. This is in marked contrast to the relatively uniform size and appearance of the elements of the *Oulodus* apparatus. The size range and denticle addition may indicate that elements are progressively added to the *Icriodus* apparatus during the ontogeny of the organism, or at least until maturity is reached. Thus a juvenile specimen of *Icriodus* might have only one pair of I elements, and a mature specimen could have 4 or more pairs of I elements. A similar addition of  $S_2$  and  $M_2$  elements would be expected.

### Arrangement of elements in the *Oulodus* apparatus

There have been two basic models of the arrangement of the elements in this apparatus. Early reconstructions by Schmidt (1934), and studies by Scott (1934), and Rhodes (1952), indicated an elongated, bilaterally symmetrical arrangement of the elements. Later studies, such as those of Lange (1968), Jeppsson (1971), and Mashkova (1972), have tended to confirm the above interpretation. Lindstrom (1964, 1973, 1974) has proposed a number of models of the arrangement which culminated in his 1974 paper, in which he presented a hypothetical reconstruction of the conodont animal with the elements, supporting a lophophore, located externally and radially about an anterior mouth.

The *Oulodus angulatus* apparatus is best interpreted as an elongated, bilaterally symmetrical arrangement (Figs. 9, 10). Supporting this interpretation are the numerous occurrences of clusters of elements that have been recovered on rock surfaces, especially those of Scott (1934), Schmidt (1934) and Rhodes (1952), that have this basic linear arrangement. A linear arrangement of structures associated with ingestion of food particles in bilaterally symmetrical organisms, as we believe the conodont to have been, is the norm in the modern biological world. No living organism resembles the Lindstrom's hypothetical reconstruction.

In this study only the *Oulodus angulatus* apparatus has contributed information concerning the arrangement and function of the conodont organism. There is a basic linear arrangement of the elements (Fig. 4), although some of the elements have been skewed relative to their original orientation.

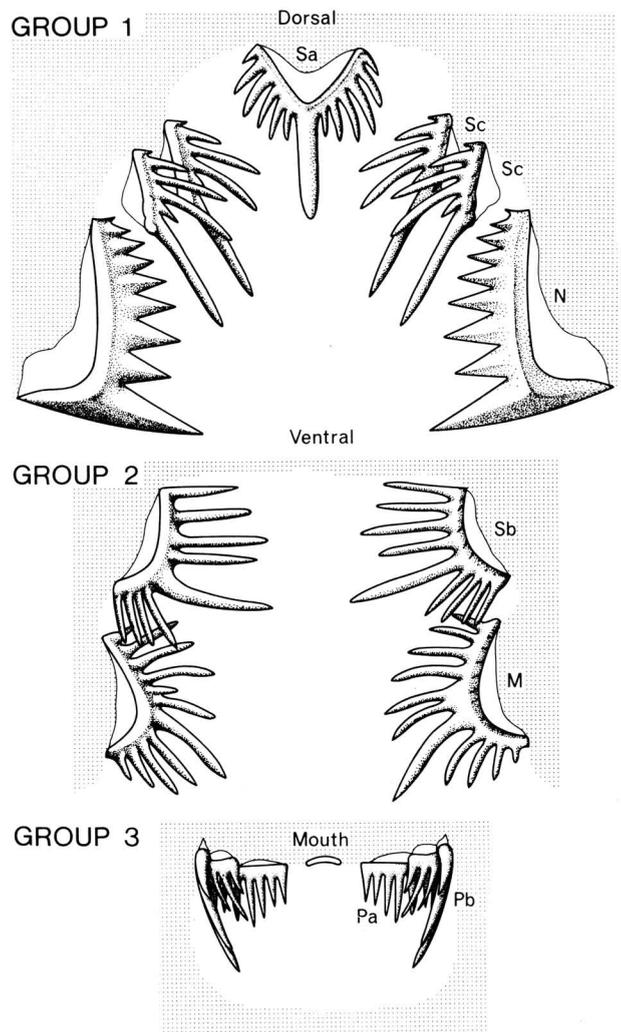


Figure 9. Hypothetical reconstruction showing the anterior views of the three groups of elements of the *Oulodus angulatus* apparatus.

The elements are separated into 3 morphologic groups and, using denticle curvature, the N, Sa and Sc elements are assigned to an anterior position. This group is followed by a transverse-oriented group composed of Sb and M elements. In the last group, the Pa and Pb elements have a posterior position. If the elements are located as shown in Figure 10, then the length of the apparatus, from the N element to the Pa element, must have been between 5.0 and 5.5 mm; this is based on a length of the Sa element of 2.5 mm and of the Pa and Pb elements of about 1.0 mm each. Thus, had the apparatus occupied about 1/10 of the body length, the conodont organism would have been 50 mm long. The Sa element is just over 2.0 mm wide and if it was flanked by the Sc and N elements, the organism was at least 4 mm wide.

### Some speculative comments on the function of the conodont apparatus and the nature of the conodont organism

Association of conodont elements with various types of organisms have still failed conclusively to link the conodont organism with any described animal, vertebrate or invertebrate (Lindstrom, 1973). The proposed conodont-bearing organism of Melton & Scott (1973) is dismissed by Lindstrom (1974), and I concur, as more probably representing an organism that ate conodonts.

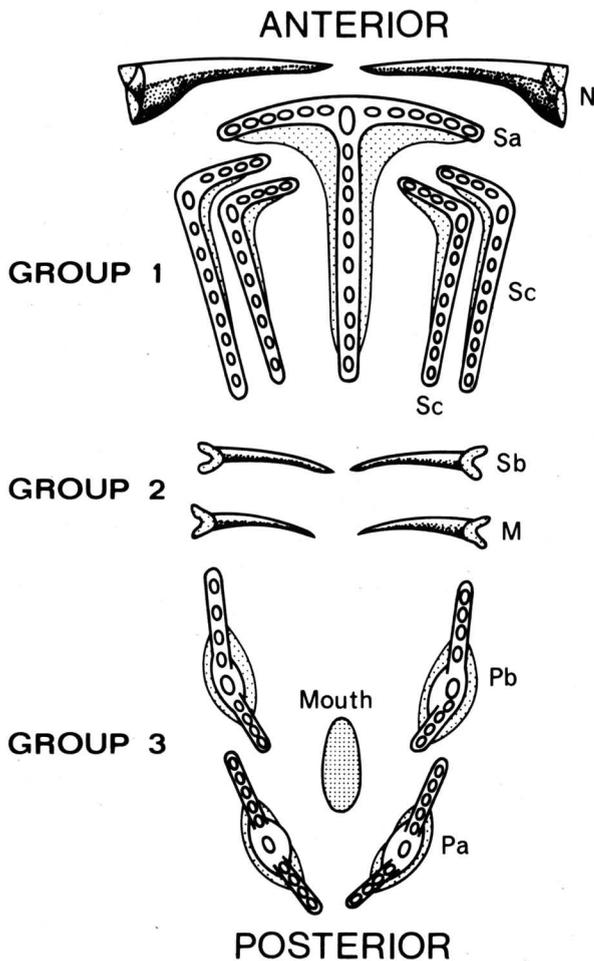


Figure 10. Hypothetical plan view of the elements of the *Oulodus angulatus* apparatus. Overall length is about 5 mm. Elements viewed from ventral surface.

Morris (1976, p. 200) describes his *Odontogriphus omalus* from the Middle Cambrian Burgess Shale as a 'bilaterally symmetrical, dorso-ventrally compressed lophophorate. Body tapering at posterior, head poorly differentiated from the annulated trunk. Head bears double-looped lophophoral apparatus containing tooth-like elements and a pair of lateral palps. Gut straight, mouth ventral, anus probably terminal. Lateral longitudinal muscles running along edges of trunk'.

The lophophore structure of *O. omalus* is poorly preserved but there were about 25 'teeth' that bore a strong resemblance to upper Cambrian cone-type conodont elements. *O. omalus* is about 60 mm in length, and has a width of about 25 mm. *O. omalus* fills most of the theoretical attributes that workers have speculated must be present in the conodont animal: marine, bilaterally symmetrical, lacking in skeletal members except for the conodont elements, and a body length of less than 100 mm.

The mouth or feeding apparatus of most vagrant organisms is located either ventrally or anteriorly. If the conodont organism was either a nektonic or a vagrant benthonic dweller, then the mouth was most probably located near the anterior end of the body and on the ventral surface. A possible reconstruction of the *Oulodus angulatus* apparatus has the elements located in a groove on the ventral surface (Figs. 9, 10). To work effectively elements of group 1 would probably have to have been exposed to the outer surfaces. Elements of group 2 may also

have been exposed, but the elements of group 3 might have been partly covered. It would be interesting to examine regeneration of elements statistically to determine if there is a significant difference between specimens showing regeneration between the three groups.

I suggest that the conodont apparatus operated to pick up food particles and direct them toward the mouth region. The three groups enumerated above for the *Oulodus* apparatus would have performed different functions in the food acquisition process. Elements of group 1 could have specialised in picking up food material. Group 2, with its palmate shape, may have directed a water current toward the mouth, and group 3 directed the food particles into the mouth opening.

The denticles of individual elements may have served as supports for tentacles or have been completely, or partially, covered by cilia. I think that the presence of tentacles is unlikely, because the flexibility usually associated with tentacles would have been limited by the rigidity of the denticle. J. W. Pickett (pers. comm., 1977) has pointed out that organisms with ciliated lophophore structures usually are not associated with the vagrant benthonic organisms whose feeding operations may required the movement of large volumes of silt. This leaves an impasse on the mechanism of operation of the elements.

The conodont animal probably fed mostly on micro-organisms and fine organic detrital material. It has generally been assumed (Lindstrom, 1973) that conodont elements, with some exception, are not robust enough to have been employed in an active food gathering operation. However, it is possible that the elements of group 1 are robust enough to have been used to stir up mud and organic sediments from the bottom, and that these and other element served, at least in part, as filter mechanisms to keep inorganic particles out of the alimentary tract.

I suggest that the conodont organism lived a vagrant benthonic or nektonic existence, feeding on micro-organisms and organic detritus collected by the apparatus, possibly ciliated, located near the anterior end of the ventral surface. The conodont organism probably had a length of 30 to 80 mm. Except for the elements, the organism lacked mineralised structures.

The conodont organism was of sufficient size to have been attractive to a palaeoniscoid fish as food. The recovery of two different types of conodont apparatuses from a single fish may mean that the conodont organism was a choice food for fish in shallow marine seas. No precise information about the local environment has been gained from the fish other than it was a free-swimming type, and probably fed over a considerable depth range. The mouth structure of the fish is probably indicative of an organism that did not feed on muddy bottoms, and thus it is likely that the fish caught the conodont when it was swimming some distance above the sea floor.

### Acknowledgements

I wish to thank Arthur Wilson and Richard Brown for their assistance with the photography. I also wish to thank Dr Peter Jones (BMR) for his critical comment at several stages in the preparation of the manuscript. Drs Brian Chatterton (Univ of Alberta) and John W. Pickett (New South Wales Dept of Mines) have critically read the manuscript. Text figures were drawn by Sue Davidson, and Andrew Retter, Geological Drawing Office, BMR.

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