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MULTIELEMENT COMPOSITION OF THE CONODONT *ICRIODUS EXPANSUS* BRANSON & MEHL FROM THE UPPER DEVONIAN OF THE CANNING BASIN, WESTERN AUSTRALIA

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The apparatus structure of the conodont *Icriodus expansus* Branson & Mehl is here recognised as consisting of seven element types—I, Ca, Cb, Cc, Cd, Ce and Cf. The apparatus contains one pair of I elements and over 140 associated cone elements. The orientation of the I element is reversed. The study is based on a large collection of fused clusters found in a sample from the Upper Devonian (Frasnian) Napier Formation in the Oscar Range of the Canning Basin, Western Australia.

Introduction

Collection of conodont-bearing limestone samples from the early Late Devonian Napier Formation at the margin of a small leucite lamproite plug (Nicoll, 1981) in the Oscar Range, Canning Basin, of Western Australia (Fig. 1) in 1978 produced one sample (WCB 804/5) that contained about 100 fragments of fused conodont clusters belonging to the genera *Icriodus* and *Polygnathus*. Recollection from the sample site in 1980 has resulted in a collection of over 1000 clusters or cluster fragments and several thousand discrete elements from 25 kg of limestone. All the conodont elements have a conodont colour alteration index of five (CAI 5).

Specimens contained in the clusters and in the associated discrete element fauna are assigned to three multielement taxa: *Icriodus expansus* Branson & Mehl, 1938; *Polygnathus xylus xylus* Stauffer, 1940; and *Ozarkodina brevis* (Bischoff & Ziegler, 1957). *I. expansus* is the most abundant with more than 850 clusters recovered. *P. xylus xylus* is represented by over 200 clusters and *O. brevis* by only 10 clusters. In no case is there any indication of mixing of the three species in any of the clusters. The abundance of clusters accurately mirrors the abundance of discrete elements. Description of *P. xylus xylus* and *O. brevis* will follow in a later paper.

The indicated age range of the three species recovered from the cluster bed is Middle to Late Devonian (Givetian to Frasnian). *P. xylus xylus* is supposed to range as high as the Lower *asymmetricus* Zone (Klapper & Ziegler, 1979) or Upper *asymmetricus* Zone (Seddon, 1970). A sample collected from traverse section (WCB 318), part of a study of the Oscar Range-Napier Range Devonian conodonts, contains *Ancyrodella lobata* (sample WCB 318/11) and is located stratigraphically below the cluster bed. This would indicate an age no older than the Middle *asymmetricus* Zone and would thus suggest that the age

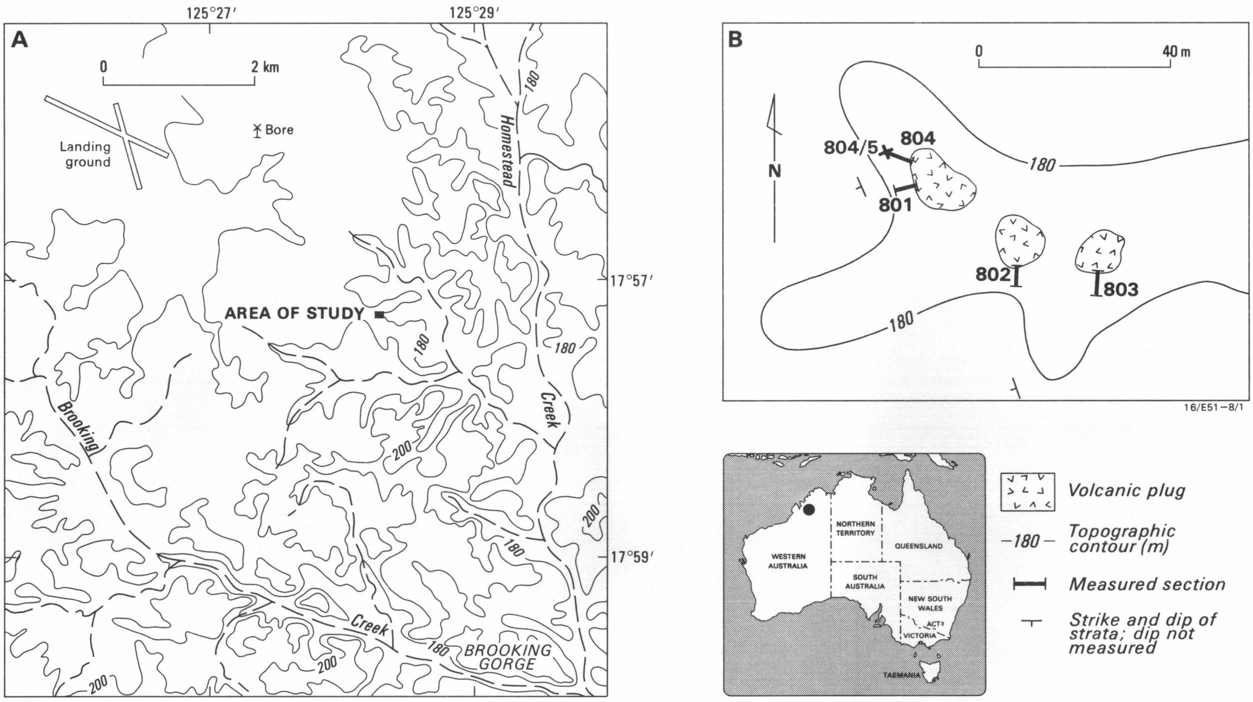
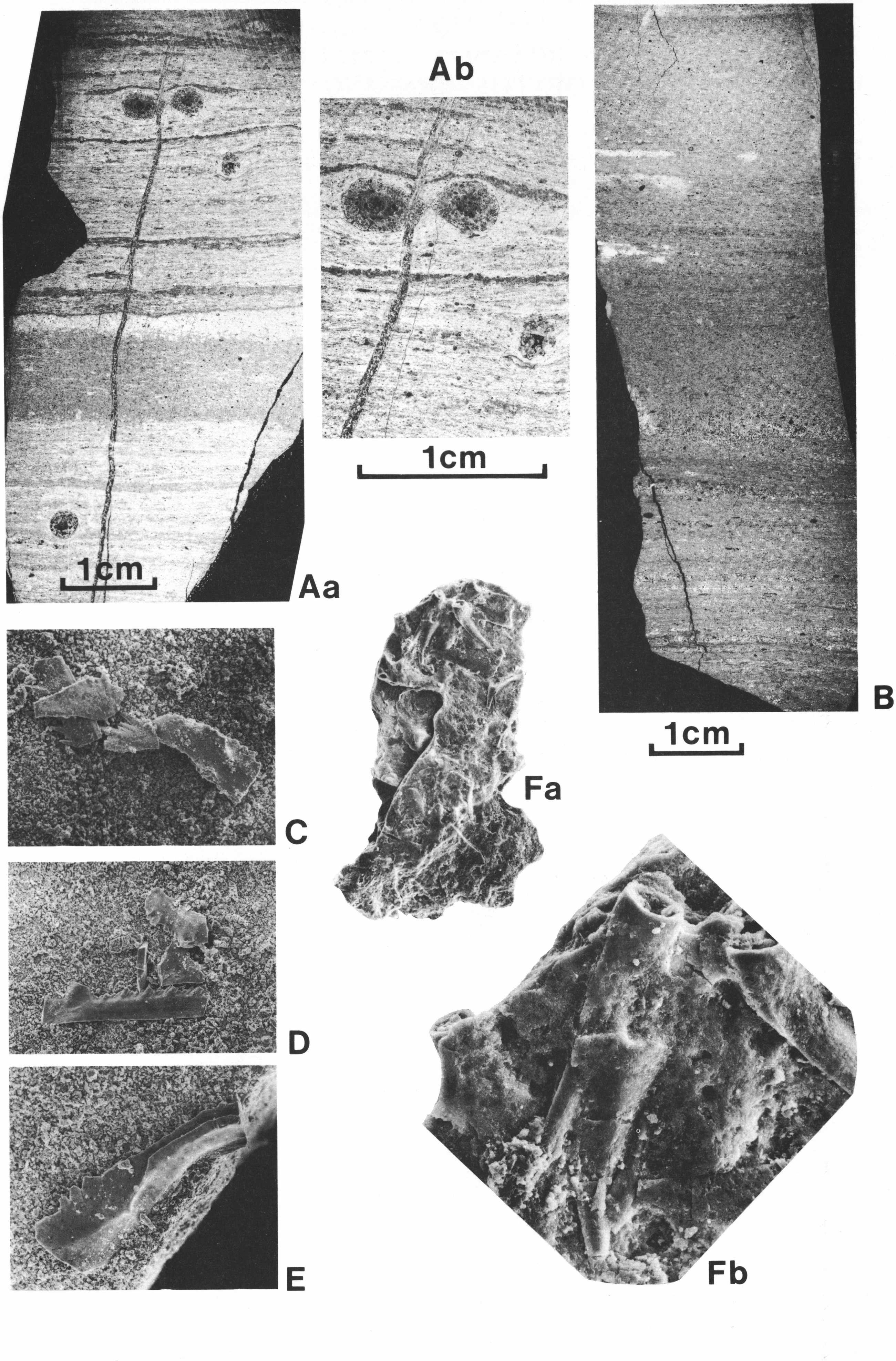


Figure 1. Locality maps.
A—Study area near the eastern end of the Oscar Range, Leopold Downs 1:100 000 topographic map, grid reference 3962-618132.
B—Location of *Icriodus*-bearing material (sample 804/5).


Ab
1cm
1cm
Aa
1cm
B
C
Fa
D
E
Fb

range of both *O. brevis* and *P. xylus xylus* could be as high as the Upper *asymmetricus* Zone, as was indicated by Seddon (1970). The age of the cluster bed fauna is thus Late Devonian (Frasnian) and more specifically, Middle *asymmetricus* Zone.

The limestone bed containing the conodont clusters is a micrite about 10 cm thick. The composition and texture of the bed (Fig. 2 A,B) are not uniform, but show a distinct layering, in part, owing to the distribution of small fossils. The fossils are mostly ostracods, some small gastropods, a few small brachiopods, and what may be a calcareous sponge. One acid-etched surface contained a small echinoid spine. Burrows, up to 5 mm in diameter, found mostly in the upper half of the bed, are generally in the plane of the bedding and filled with sparry calcite.

To determine the distribution and relationship of conodont elements in the bed, a series of slabs, each about 10 mm thick, was cut parallel to the bedding and then partly etched with acid. Conodonts, as discrete elements or clusters, were found on the slab surfaces throughout the bed and do not appear to be related to any lithology or level within the bed.

Eighteen discrete elements or clusters were observed on the 0.3 m^2 of etched slab surface. None of the elements were observed either within the burrows or along the margin of the burrow structures. The distribution of conodonts appears to be random within the bed and not related to any variation of microfacies of the bed. Elements appear as single discrete elements (Fig. 2E), fused clusters (Fig. 2C), and as related elements in close proximity (Fig. 2D). No other skeletal phosphatic material is associated with the elements.

Processing of samples to obtain the clusters was done using acetic acid on lumps of rock 5-10 cm across. Acid was changed daily and the residue washed by decanting. This last step was taken because the cone elements of the *Icriodus* apparatus are so small that they would have been lost through standard sieves. Some specimens may have been lost, owing to surface tension during decanting of excess water, but virtually all conodont elements in the rock were recovered.

A number of the figured specimens were lost or damaged when two SEM stubs were dropped during photography. In addition, some of the most delicate clusters, most notably the fused juvenile I elements shown in Figure 9, disintegrated while being removed from the stubs. The specimens from this study are lodged in the Commonwealth Palaeontological Collection (CPC) at the Bureau of Mineral Resources in Canberra.

Multielement *Icriodus*

The first documented interpretation of the multielement structure of *Icriodus* was by Lange (1968) on material that he considered to be of probable coprolitic origin. Lange assigned his material to *I. alternatus* and recognised an assemblage consisting of a single pair of I elements in association with an indeterminate number, 30 to 56, of acodinan cone elements. Lange's line drawings (1968, pl. 6) show some differentiation of the cone elements, but do not have sufficient detail to allow comparison with the cone element types recognised in the present study.

Klapper & Philip (1971, 1972) described the apparatus structure of *Icriodus* as well as *Pelekysgnathus* and *Pedavis*. At that time they thought that *Icriodus* consisted of only two element types, the I and the acodinan S_2 elements. Later, Klapper & Ziegler (1975) recognised that *Icriodus* might also contain an M_2 element.

Other workers, most notably Bultynck (1972) and van den Boogaard & Kuhry (1979) have argued that the *Icriodus* apparatus lacked cone elements. These authors cited the low levels of occurrence together of I and cone type elements in samples as the principal reason for rejecting an *Icriodus* plus cone apparatus structure.

In 1977, I recognised an *Icriodus* apparatus structure consisting of I, M_2 and S_2 elements (Nicoll, 1977). At the time, I speculated that, on the basis of a size-graded series of four I elements, the *Icriodus* apparatus might contain as many as four pairs of I elements. The present study has not substantiated that speculation, but it should be noted that the former material represented a different *Icriodus* species.

Several recent studies have tended to support the multielement composition of genera in the family Icriodontidae. Uyeno & Klapper (1980) have defined an apparatus structure of I, S_2, and M_2 elements in *Steptotaxis* and recognised three types of S_2 elements in *S.* n.sp. A and *S.* n.sp. B. Uyeno (*in* Norris & Uyeno, 1981) has recognised three acodinan cone element types (S_{2a}, S_{2b}, S_{2c}) in association with *Icriodus subterminus*. Johnson & Klapper (1981) have established statistically the presence of both S_2 and M_2 elements associated with I elements in *Icriodus nevadenis* and *T. trojani*.

Notation applied to elements

As the number of element types recognised as part of the *Icriodus* apparatus has changed over the years, there has been established a patchwork notational scheme modified from that originally proposed by Klapper & Philip (1971). This has meant that the notational scheme has grown without an overall plan

Figure 2. Thin sections of cluster bed (A,B), three examples of conodont elements from acid-etched surfaces of limestone slabs, (C-E) and phosphatic chips (F).
A—Thin section (Aa) of cluster bed and enlargement of burrows (Ab) showing microfacies variation; circular features near top and bottom are cross sections of burrows and are about 3 mm in diameter; CPC 22459. B—Thin section from another specimen, showing the degree of lateral variation of microfacies; CPC 22460. C—*Polygnathus xylus xylus;* Pa element and broken S elements; (56x) CPC 22461. D.—*Polygnathus xylus xylus;* broken Sa and Sc elements; (40x) CPC 22462. E. *Polygnathus xylus xylus;* single Pa element; (65x) CPC 22463.
A number of thin phosphatic chips were recovered in the residue and many of these contained conodonts, both *Icriodus expansus* and *Polygnathus xylus xylus*. As in the other clusters, there is no mixing of taxa on the chips. F—Cone elements of *I. expansus* in phosphatic chip. CPC 22464. Fa—view of chip (65x) and Fb—enlargement of cones (330x).

and that there is no unity between schemes that have been applied to different genera of the Icriodontidae. In an attempt to resolve some of the these problems I suggest a new notational scheme that can be applied to all the Icriondontidae.

The notational scheme devised by Klapper & Philip (1971) for their type 4 apparatuses (I, S & M) is too tied to form-element nomenclature to be used in the present situation, where six distinct cone element types are recognised in the *Icriodus* apparatus.

Barrick (1977) has applied the Sweet & Schonlaub (1975) notational system to his simple-cone element apparatuses. I feel it is improbable that there is either a close positional or functional analogue between the simple cone elements M and Sb-Sd, as used by Barrick, and the platform-ramiform elements to which Sweet & Schonlaub applied the original notation scheme. If this contention is accepted, then the forcing of cone elements into a platform-ramiform notational scheme is not relevant when a functional and positional interpretation is applied to the analysis of the elements.

I also find the letter-code system applied by Barnes & others (1979) to simple cones difficult to apply to the style of morphologic variation found in *Icriodus* elements, especially as the *Icriodus* apparatus does not fit any of their categories of apparatus type.

For the above reasons I will here apply yet another notational scheme, specifically to the genus *Icriodus*, but which is also probably relevant to related taxa (e.g. *Pelekysgnathus, Pedavis, Steptotaxis*). The notation of the *Icriodus* apparatus is I, Ca, Cb, Cc, Cd, Ce, and Cf. The notation I is applied to the platform element and is used as originally defined by Klapper & Philip (1971). All cone elements are described by an upper case C and the lower case letters a-f. The notations Ca to Cf are applied to distinct element morphologies and do not imply a symmetry transition series with morphologic or functional intergradation between element types. As a general statement the cone element types Ca-Cd are comparable to the Klapper & Philip S_2 acodinan element. The cone elements Ce and Cf are analogous to the M_2 element of other authors.

Orientation of I element

Branson & Mehl (1934, 1938) in their original description of the genus *Icriodus* oriented the specimens with the tips of the basal cavity posterior and the three-rowed process anterior. This orientation has been followed by most subsequent workers (Klapper & Ziegler, *in* Ziegler, 1975). The direction of curvature of the tips of the basal cavity has been cited as confirming the validity of this orientation (Lindstrom, 1964).

From this study, it is apparent that this orientation of the I element of the genus *Icriodus*, and thus all members of the family Icriodontidae, should be questioned. I propose that the correct orientation of the I element of the genera *Icriodus*, *Pelekysgnathus*, *Pedavis*, and *Steptotaxis*, is with the dual-tipped basal cavity anterior and the platform-like denticle supporting structure posterior. This proposal is based on the interpretation of a number of morphologic features shown by the *I. expansus* material from this study, including: (1) the origin of the dual-tipped basal cavity; (2) the shape of the basal cavity; (3) the growth pattern of the upper surface.

The apparent pattern of growth of the Pa element of many genera, such as *Polygnathus, Gnathodus*, and *Siphonodella*, is for the anterior blade to be well

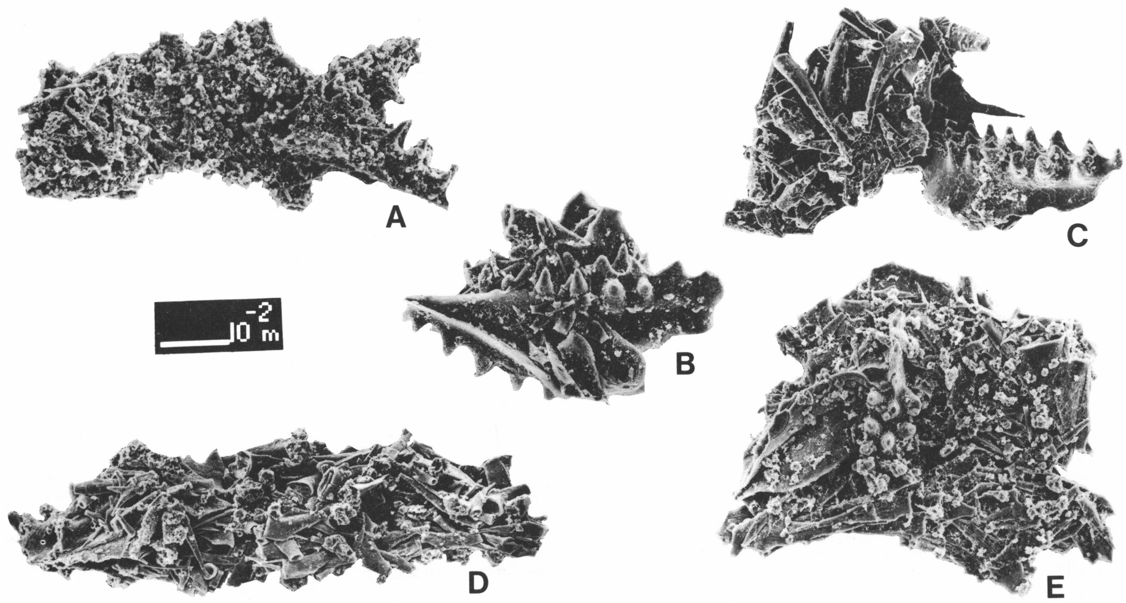


Figure 3. *Icriodus expansus* **clusters (all specimens 115 x).**
A—Cluster with one pair of I elements and an indeterminate number of cone elements; I elements configuration anterior-anterior, bases outward; CPC 22465. B—Cluster with one pair of I elements and more than 30 cone elements; I element configuration anterior-anterior, bases outward; CPC 22466. C—Cluster with single I element and more than 60 cone elements; CPC 22467. D—Cluster with single I element and 130 cone elements counted from exposed view; one Ca element is located almost touching anterior end of I element; CPC 22468. E—Cluster with one pair of I elements and 105 cone elements counted on exposed view; I element configuration anterior-anterior, bases outward; CPC 22469.

formed at a very early growth stage. This does not necessarily mean that additional denticles will not be added to the anterior margin of the blade as the specimen matures, but that, by comparison with the platform, the blade attains a mature morphology at an early stage. Subsequent major growth modification of most platform elements takes place as a modification of the platform, principally by its posterior and lateral expansion. By orienting the *Icriodus* I element with the three-row platform posterior, a similar growth pattern is observed.

The outline shape of the basal cavity of the I element, when conventionally oriented, is not the shape displayed when most Pa elements with enlarged basal cavities are oriented with the blade anterior. The morphology of the basal cavity of genera such as *Gnathodus*, *Clydagnathus*, and *Polygnathus* is for the cavity to open laterally, very abruptly, at or near the posterior end of the blade and to then gradually taper posteriorly. If *Icriodus* is oriented with the rounded, dual-tipped lip of the basal cavity anterior, then the outline of the basal cavity is similar to that of other genera. The outline of the cavity reflects the morphology of the surface to which the conodont element is attached, and one would not expect the attachment structure of *Icriodus* to be the reverse of that of other conodont organisms.

The mode of origin of the dual-tipped basal cavity suggested below, that is the fusion of a cone element to the margin of the I element, is only possible if the margin is the anterior margin. If the I element of *Icriodus* is analogous to the Pa element of genera such as *Polygnathus* or *Ozarkodina*, then the position of the I element is at the posterior end of the element sequence, assuming a linear rather than radial pattern (Nicoll, 1977). There would thus have been no cone elements located behind the I element to fuse with it, if the previously accepted element orientation is used.

I conclude, therefore, that, for the family Icriodontidae, the dual-tipped basal cavity is located at the anterior rather than the posterior margin of the I element. An analogy between platform type Pa elements and the I element can be made; the I element has a short anterior blade, usually no more than two or three denticles, located in front of a platform composed of three rows of denticles

In members of the *Icriodus latericrescens* group the lateral process is anteriorly directed, but the spurs and lateral processes of *Icriodus* and *Pedavis* species are posteriorly directed.

Table 1. Configuration of I-element clusters of *I. expansus* and associated cone elements

Two-I elements configuration	*Associated cone elements* >10	<10	*Totals*
ant-ant bases opposed	15	23	38
ant-pos bases opposed	1	4	5
ant-ant bases same	6	10	16
ant-pos bases same	5	—	5
other orientations	6	13	19
One-I element & cone element association	92	172	264

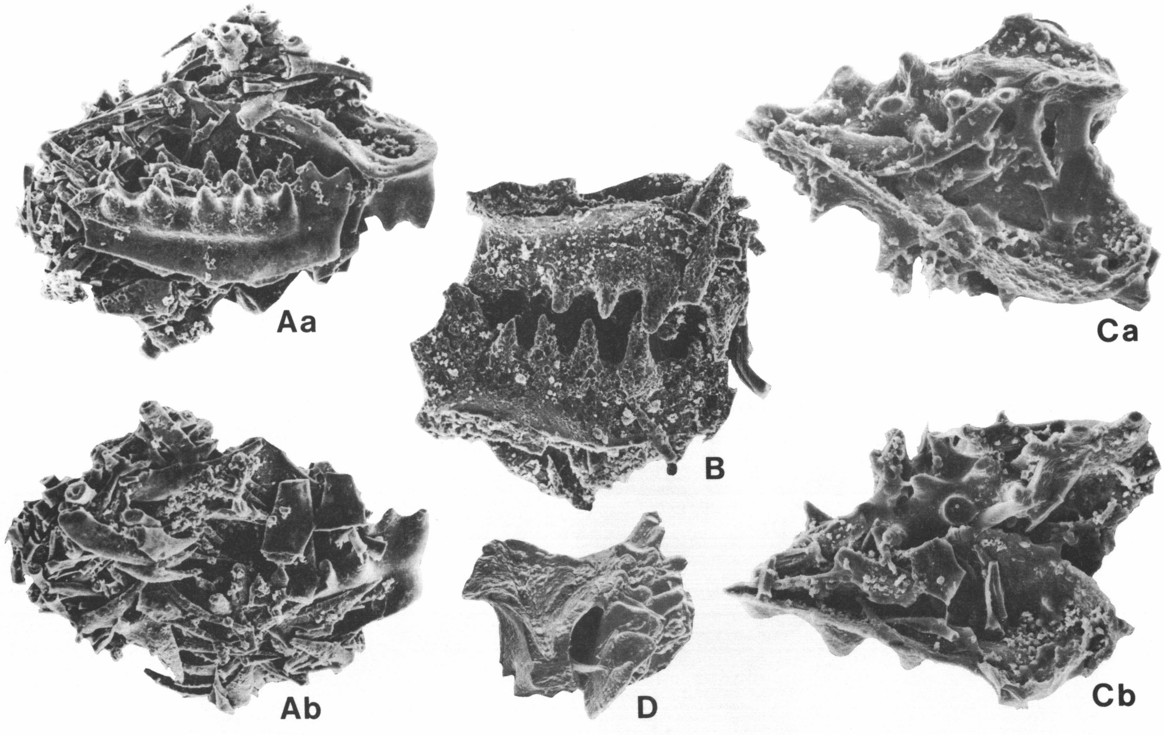


Figure 4. ***Icriodus expansus*** **clusters (all specimens 110x).**
A—Two sides of cluster containing single pair of I elements and at least 140 cone elements. Care was taken in counting the reverse side cone elements not to count any denticle that might have been observable from other side, and thus the denticle count is probably conservative; I elements anterior-anterior, bases outward; CPC 22470. B—Cluster with single pair of I elements and at least 25 cone elements. I element configuration anterior-anterior, upper surfaces touching; CPC 22471. C—Two sides of cluster containing single pair of I elements and at least 40 cone elements; I element configuration anterior-anterior, bases outward; CPC 22472. D—Cluster with single pair of I elements and only a few cone elements; I element configuration anterior-anterior, bases outward; CPC 22473.

Clusters

In this study over 850 clusters have been recovered that contain elements of *Icriodus expansus*. Over 350 of the clusters contain cone elements and at least one I element. The rest consist of only cone elements. These figures may be misleading, because the clusters are relatively easily fragmented and many may have been broken into smaller clusters during physical preparation of the samples (washing, heavy liquid separation).

Of 347 clusters containing at least one I element, roughly 25 per cent contained two I elements and a number of cone elements. In no cluster is there any indication of more than two I elements. Owing to the three-dimensional nature of the clusters and mineral overgrowth in some examples, accurate counts of the total cone elements and numbers of individual cone types are not possible. At least 141 cone elements have been counted in one of the larger and cleaner clusters (Fig. 4A).

The orientation and relationship of elements within the clusters have been examined. There is a general tendency for the clusters to be elongated and for the I elements to be located at or toward one end of the clusters (Figs. 3A,D). Cone element types Ca, Cb, Cc, and Cd, may be randomly distributed, but are frequently associated with the I elements. There is no observable size gradation of the Ce and Cf cone elements from one end of a cluster to another.

The relative configuration of the I elements has been examined (Table 1). Almost half the 83 clusters with

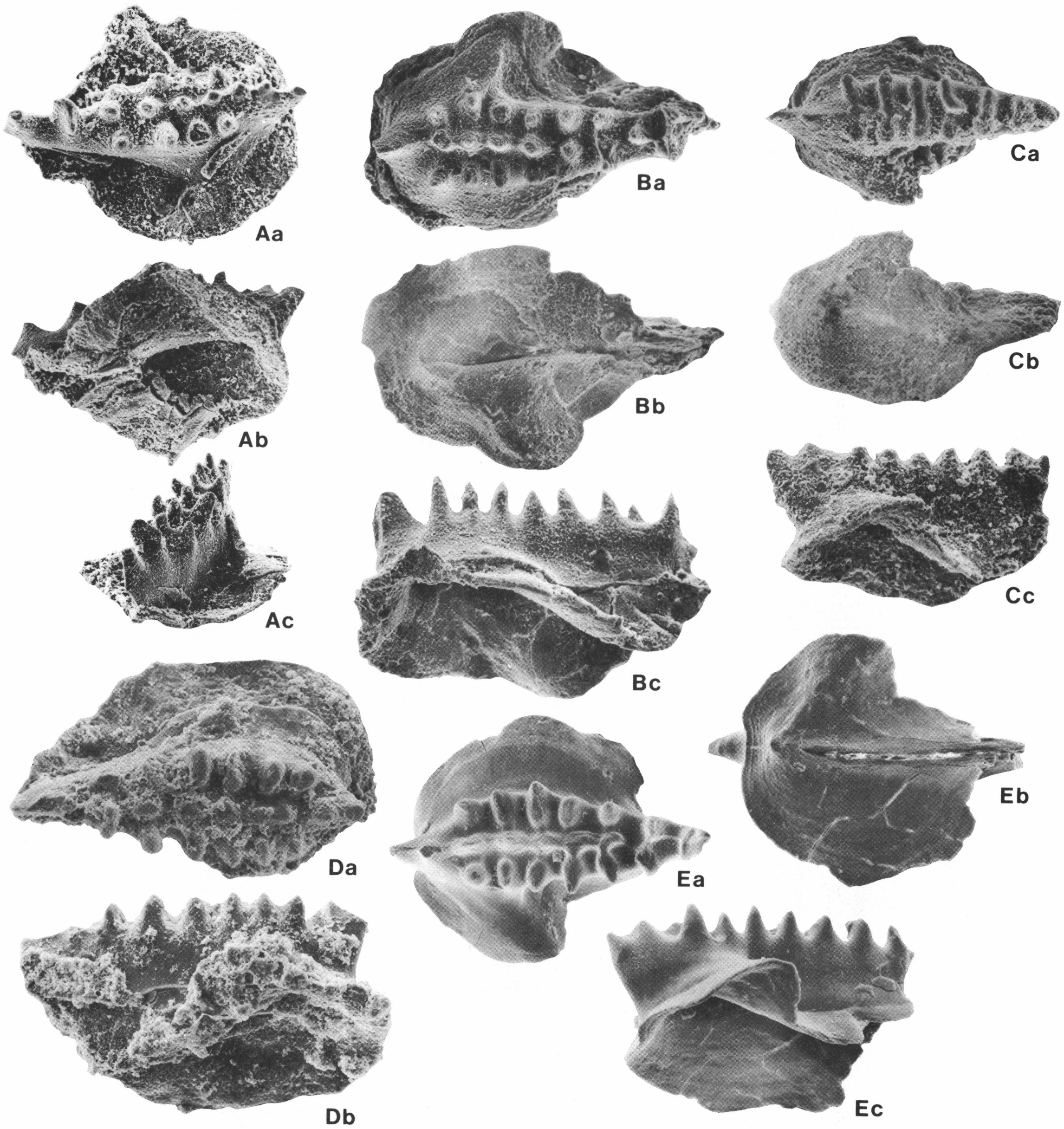


Figure 5. I element basal plate morphology (all specimens 90x).
A—I element: Upper (Aa), basal (Ab), and posterior (Ac) views; CPC 22474. B—I element: Upper (Ba), basal (Bb), and lateral (Ac) views; CPC 22475. C—I element: Upper (Ca), basal (Cb), and lateral (Cc) views; CPC 22476. D—I element: Upper (Da) and lateral (Db) views; CPC 22477. E—I element; Upper (Ea), basal (Eb), and lateral (Ec) views; CPC 22478.

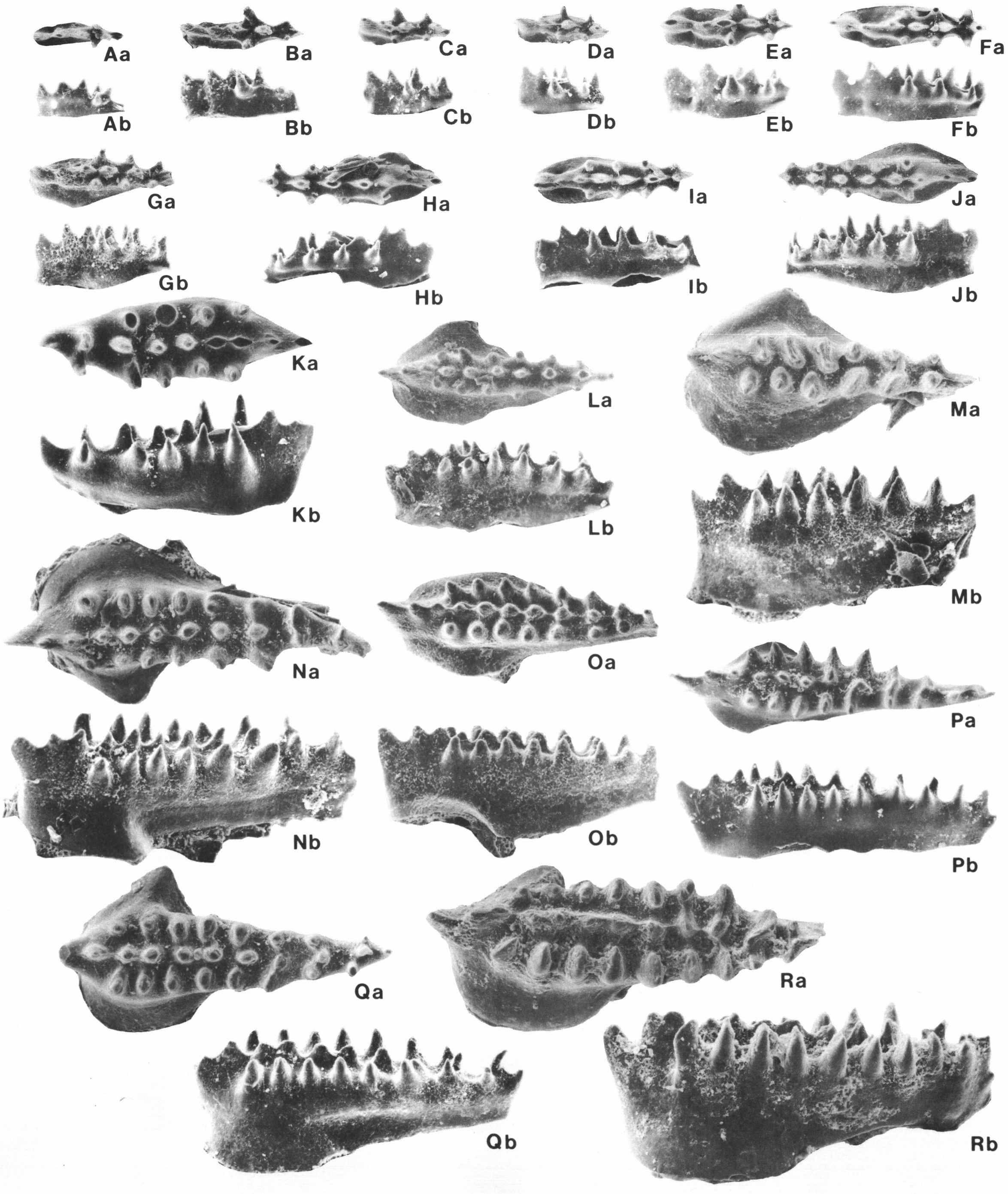


Figure 6. Growth series of I elements of *Icriodus expansus* from the first triad (one pair lateral denticles) stage to the ninth triad (nine pair lateral denticles) stage (all specimens 80x).

A—First triad and developing second triad stage, three blade denticles; CPC 22479. B—First triad and developing second triad stage, three blade denticles; CPC 22480. C—Second triad stage, two blade denticles; CPC 22481. D—Second triad stage, two blade denticles; CPC 22482. E—Second triad stage, three blade denticles; CPC 22483. F—Third triad stage, three blade denticles; CPC 22484. G—Third triad stage, three blade denticles; CPC 22485. H—Fourth triad stage, three blade denticles; CPC 22486. I—Fourth triad stage, three blade denticles; CPC 22487. J—Fifth triad stage, three blade denticles; CPC 22488. K—Fifth triad stage, three blade denticles; CPC 22489. L—Sixth triad stage, three blade denticles; CPC 22490. M—Sixth triad stage, two blade denticles; CPC 22491. N—Seventh triad stage, three blade denticles; CPC 22492. O—Seventh triad stage, three blade denticles; CPC 22493. P—Eighth triad stage, two blade denticles; CPC 22494. Q—Eighth triad stage, two blade denticles; CPC 22495. R—Ninth triad stage, three blade denticles; CPC 22496.

two I elements have those elements oriented with the long axes roughly parallel, the basal cavities facing outward, and the anterior ends pointing in the same direction. The elements are either in a side by side configuration (Fig. 4A, C, D) or with denticles intermeshed (Fig. 4B). Other configurations occur with less frequency.

In all examples where two I elements are observed together in a cluster, both elements are at the same stage of development. The elements are of about the same size and have the same number of lateral denticles. There is no indication of loss and replacement of one of the I elements in any of these clusters.

From the data, it seems clear that the configuration of the I elements in the living conodont animal must have been with the denticulate surfaces close together on either side of a groove. This differs from the orientation suggested by Schmidt (1950), in which the Pa elements are side by side with the upper surfaces not opposed.

Systematic palaeontology.

GENUS *ICRIODUS* BRANSON & MEHL, 1938

Type species. *Icriodus expansus* Branson & Mehl, 1938

Icriodus expansus Branson & Mehl, 1938

(Figures 3–12)

1938 *Icriodus expansus* Branson & Mehl, p. 160, Pl. 26, Fig. 19.

1975 *Icriodus expansus* Branson & Mehl; Klapper & Ziegler in Ziegler ed. p. 109, Pl. Icriodus 1, Figs. 1, 2 (with synonymy).

Diagnosis. Multielement taxa with seven element types —I, Ca, Cb, Cc, Cd, Ce, and Cf. I element is incriodontan, C elements are cone type.

Description of elements

I Element. (Figs. 5–8); material studied—more than 1000 discrete elements.

The crown of the I element has from three to twelve central row denticles and one to nine pairs of lateral row denticles. In juvenile specimens all denticles are discrete with the central row denticles laterally compressed and the lateral row denticles rounded. Mature specimens with five or more pairs of lateral row denticles may show fusion of the central row denticles with one or the other of the lateral row denticles of the denticle triad. However, most specimens show little or no denticle fusion.

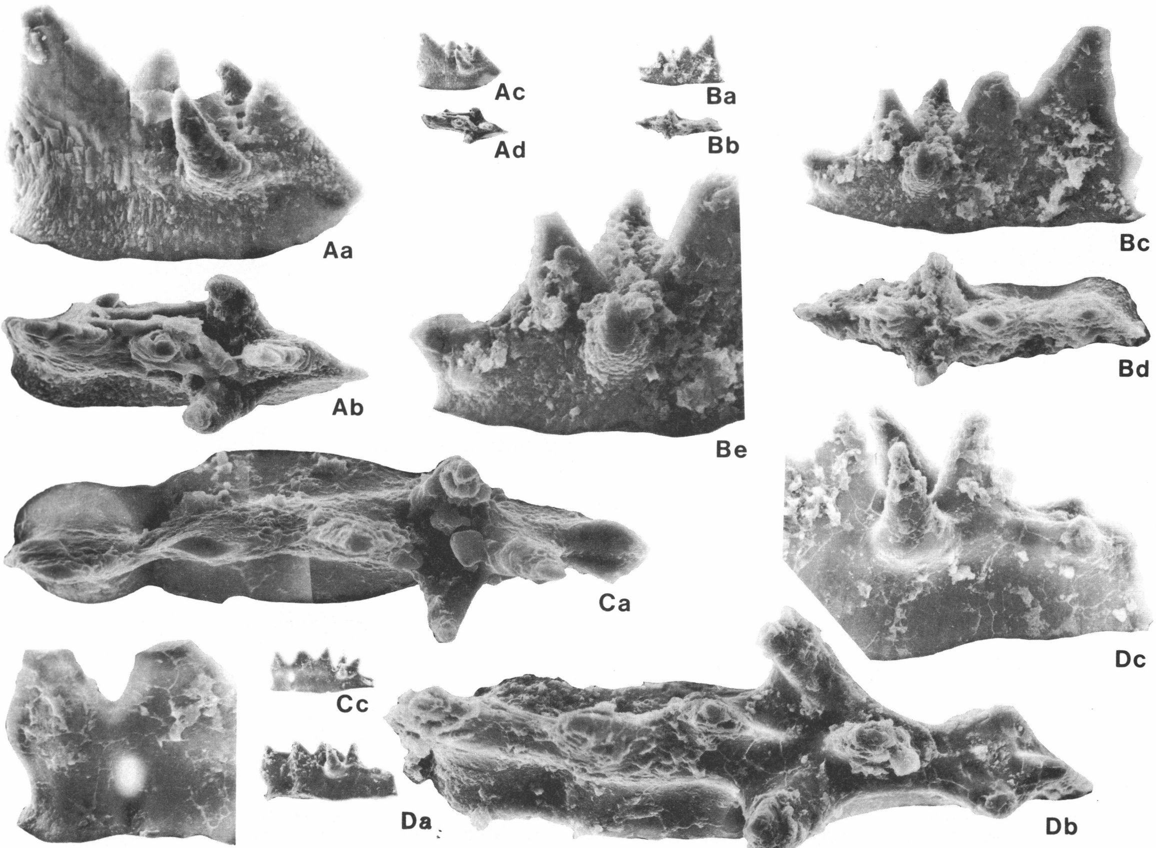


Figure 7. Juvenile I elements—first triad stage (small views 80x, enlargements 420x except as noted). A—I element with two blade denticles; earliest growth stage recovered with first triad of denticles and no indication of second denticle triad; CPC 22497; lateral views Aa, Ac; upper views Ab, Ad. B—I element with two blade denticles; early growth stage with first denticle triad and buds of second denticle triad at initial growth stage; CPC 22498; lateral views Ba, Bc, Be (650x); upper views Bb, Bd. C.—I element with three blade denticles and first triad of denticles developed; growth of second denticle triad showing at posterior tip; same specimen as Fig. 6A; CPC 22479; Ca—enlarged upper view; Cb—enlarged view of anterior blade denticles with thin spot between denticles; Cc—lateral view. D—I element with three blade denticles; first triad of denticles well developed and second triad at an early growth stage; same specimen as Fig. 6B; CPC 22480; Da—lateral view; Db—enlarged upper view; Dc—enlarged lateral view of posterior showing early growth stage of denticles.

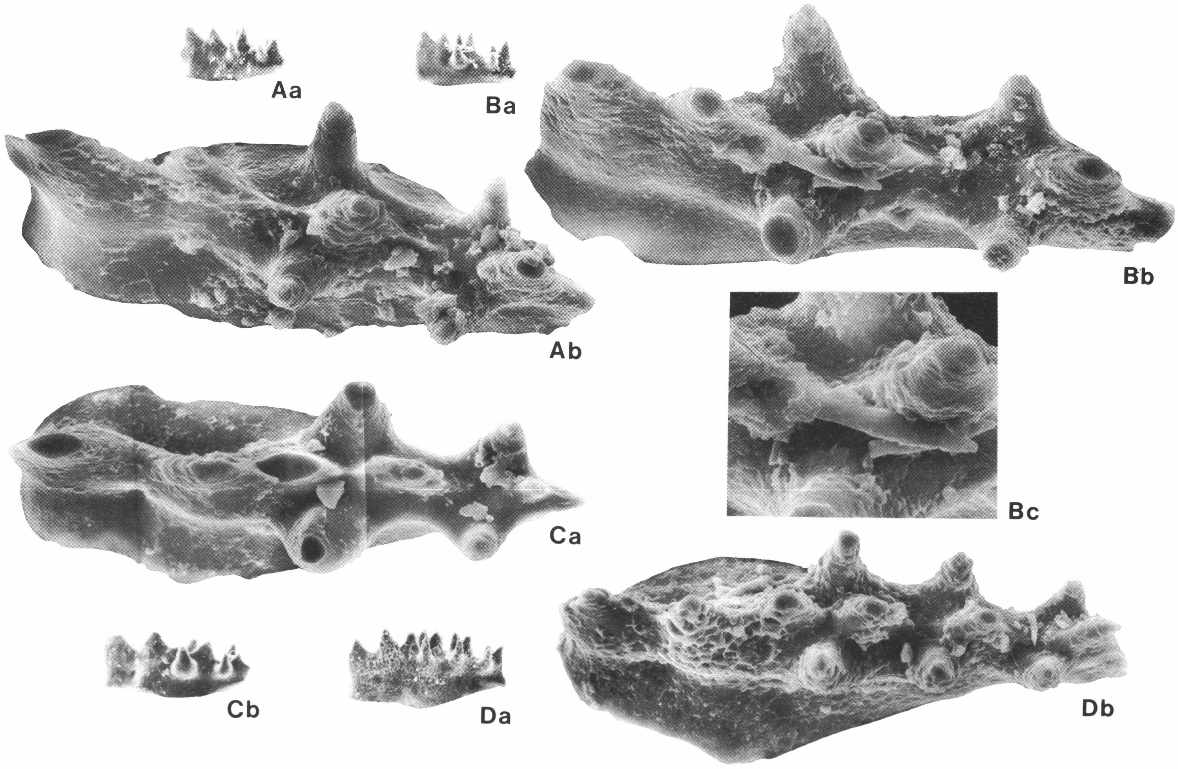


Figure 8. Juvenile I elements—second and third triad growth stage (small views 80x, enlargements 420x except as noted).
A—I element with two blade denticles, second triad growth stage; same specimen as Fig. 6C; CPC 22481; Aa—lateral view; Ab—enlarged upper view. B—I element with two blade denticles, second triad growth stage; same specimen as Fig. 6D; CPC 22482; Ba—lateral view; Bb—enlarged upper view; Bc—enlargement of two very small denticles fused to upper surface (700x). C—I element with three blade denticles, second triad growth stage; same specimen as Fig. 6E; CPC 22483; Ca—enlarged upper view; note that flange at base of crown has not filled out to smooth margin between anterior two denticles; Cb—lateral view. D—I element with three blade denticles, third triad growth stage; same specimen as Fig. 6G; CPC 22485; Da—lateral view; Db—enlarged upper view; note that flange at base of crown has almost filled out to smooth margin.

A short anterior blade is formed by the first two or three anterior-denticles before the first triad of central and lateral row denticles. The basal cavity is deeply excavated with two basal cavity tips. The outline of the cavity is slightly asymmetrical in juvenile specimens, but mature specimens may have a pronounced, slightly posteriorly directed, inner lateral spur. The outer margin is smoothly rounded.

Many specimens (Fig. 5) have a well-preserved basal plate, that extends outward beyond the crown for a width equal to about one third the height of the crown. Around the anterior margin the flange of the basal plate is directed outward, but as the basal cavity narrows posteriorly the flange is directed downward so that the cavity width of the basal plate is no more than that of the crown.

A growth series of the I element is shown in Figure 6. The smallest juvenile form (Fig. 7A) consists of only a single pair of lateral denticles and three central row denticles, two of which form the blade. Growth takes place in a posterior direction with the addition of successive denticle triads composed of one central row denticle and a pair of lateral row denticles. It appears that denticle growth of each triad may be initiated from a central point. Denticles of each triad appear to grow to moderate size before the next denticle triad appears.

No specimens have been observed at a stage prior to the first denticle triad. However, the pre-triad growth stage must have consisted of only two or three laterally compressed denticles.

An interesting morphologic pattern in early growth stages may explain the origin of the dual tip of the basal cavity of *Icriodus*, as well as the related genera of *Pelekysgnathus* and *Pedavis*. Some I elements (Figs. 7, 9) show the anterior blade denticle partly separated from the adjacent blade denticle. In one or two examples there appears to be a very thin spot or cavity at mid-denticle height between the two denticles (Fig. 7C). This is also reflected in a corresponding "coke bottle"-like constriction or waist in the margin of the crown. It appears that the blade of *Icriodus* may have originated with the fusion of two cone denticles.

Cone elements

In this study six cone element types are recognised in the apparatus structure of *Icriodus expansus*. All cone elements have in common the development of striations on the upper part of the element and a shoulder effect that interrupts the smooth taper of the anterior and posterior edges of these laterally compressed elements.

Four of the cone types (Ca, Cb, Cc, and Cd) appear to be represented by only a single pair of elements in the apparatus and are analogous to the S_2 elements of other authors. The rest of the cone elements, in excess of 130 elements, are divided between Ce and Cf type cones and are analogous to the M_2 element. Owing to the partial preservation and three dimensional

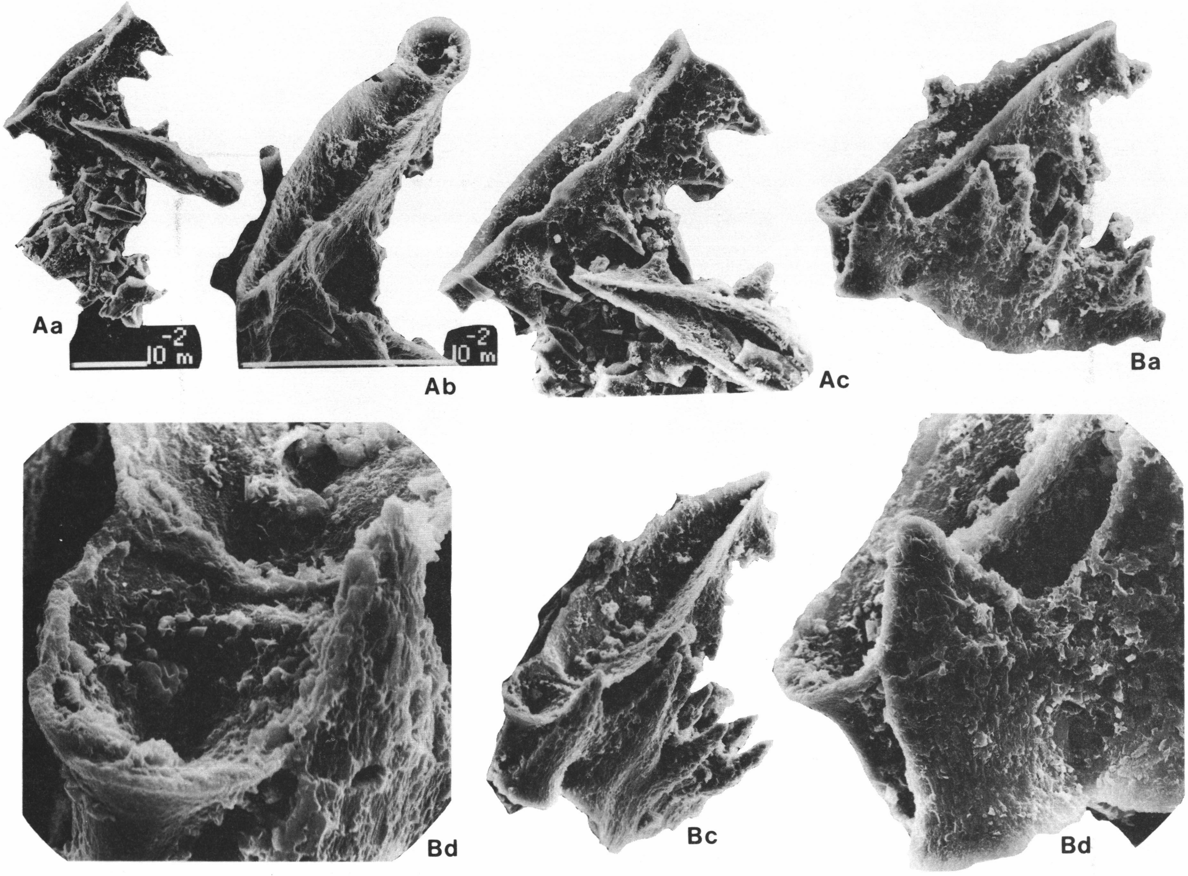


Figure 9. Juvenile I element clusters.
A—Cluster of single pair I elements, at second triad growth stage, and 55 cone elements; I elements are slightly skewed, but with posterior ends together; CPC 22499; Aa—view of cluster (100x); Ab—basal view of one I element showing dual basal cavity (290x); Ac—lateral view of same I element showing what appears to be lack of complete fusion of anterior blade denticles (290x). B—Cluster of single pair I elements, at second triad growth stage, and a few cone elements; I element configuration anterior-anterior, bases outward; the blade consists of three denticles, the anterior one showing a separate basal cavity and not at this stage surrounded by the same width of the lower flange of the crown found on the posterior part of blade; note the depression separating the two denticles at mid denticle height; CPC 22500; Ba—lateral view of element pair (300x); Bb—enlarged view of dual tip basal cavity (900x); Bc—oblique view showing base of one element and anterior view of second I element (300x); Bd—enlarged lateral view of anterior blade denticles (850x).

nature of the clusters, it is impossible to make an accurate count of the number of elements in larger, and thus presumably more complete, clusters. Two of the larger clusters contained 120 and 141 cone elements, mostly of types Ce and Cf.

Ca Element (Fig. 10N–R); material studied: 90 discrete elements.

Erect, bilaterally asymmetrical, laterally compressed cone element with bowed outer lateral margin and a slightly posteriorly directed outer lateral spur. In lateral view the element expands slightly, in the plane of the anterior-posterior axis, above the base and then narrows abruptly to form the shoulder on the anterior and posterior margins. Above the shoulder the element tapers gradually to the tip. The anterior and posterior margins have sharp keels. The cross-sectional shape of the base is similar to that of a large I element with a prominent spur that is directed slightly posteriorly. Fine striations are present on the lateral surfaces of the element above the shoulder. Some specimens (Fig. 10N) have a prominent costa associated with the lateral spur.

Cb element. (Fig. 10J–M); material studied—16 discrete elements.

Erect, bilaterally asymmetrical element with a triangular basal outline. The anterior side is broad and the element tapers posteriorly. There is a shoulder on the posterior margin and there may be a slight anterior shoulder. The striation pattern is similar to that of the Ca element.

Cc element. (Fig. 10E–I); material studied—53 discrete elements.

Bilaterally asymmetrical, laterally recurved element with straight outer lateral margin and an expanded inner basal flange. The anterior margin of the base is broadly rounded and expands slightly to mid-length before tapering toward the posterior margin. The thickness of the element is reduced along the anterior and posterior margins just above the base of the element, so that the margins are both sharp, as in the Ca element. There are prominent shoulders on both anterior and posterior margins.

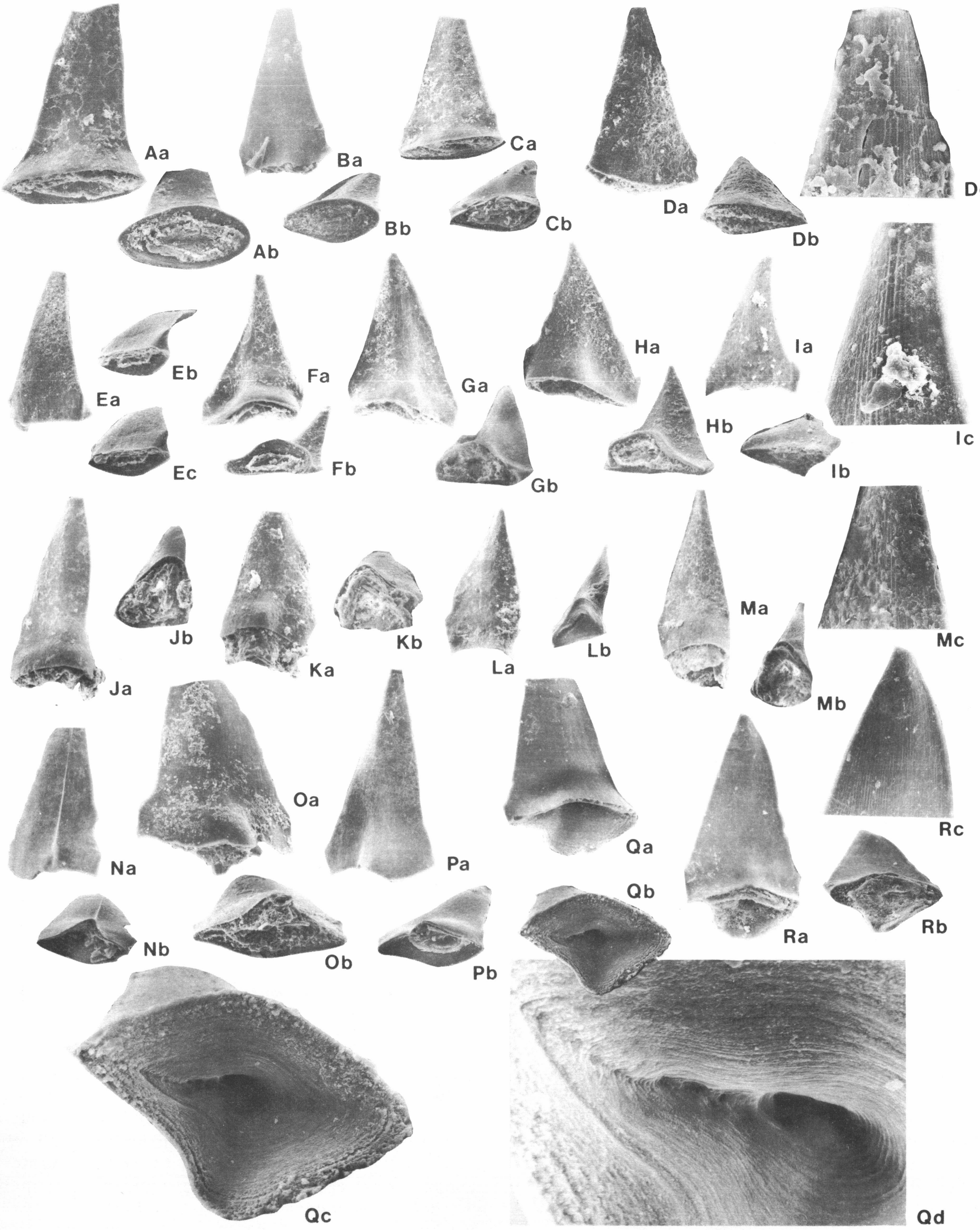


Figure 10. Cone elements Ca, Cb, Cc and Cd (All specimens 110x, except as noted).
A-D—Cone element Cd. A—CPC 22501, inner lateral (Aa) and basal (Ab) views; B—CPC 22502, outer lateral (Ba) and basal (Bb) views; C—CPC 22503, inner lateral (Ca) and basal (Cb) views; D—CPC 22504, outer lateral (Da), basal (Db) views, and enlargement (Dc) showing striation (385x). E-I—Cone element Cc. E—CPC 22505, outer lateral (Ea), oblique (Eb) and basal (Ec) views; F—CPC 22506, inner lateral (Fa) and basal (Fb) views. G—CPC 22507, inner lateral (Ga) and basal (Gb) views. H—CPC 22508, inner lateral (Ha) and basal (Hb) views. I—CPC 22509, outer lateral (Ia), basal (Ib) views, and enlargement (Ic) showing striations (385x). J-M—Cone element Cb. J—CPC 22510, lateral (Ja) and basal (Jb) views; K—CPC 22511, lateral (Ka) and basal (Kb) views; L—CPC 22512, lateral (La) and basal (Lb) views; M—CPC 22513, lateral (Ma), basal (Mb) views, and enlargement (Mc) showing striations (270x). N-R—Cone element Ca. N—CPC 22514, outer lateral (Na) and basal (Nb) views; O—CPC 22515, outer lateral (Oa) and basal (Ob) views; P—CPC 22516, outer lateral (Pa) and basal (Pb) views; Q—CPC 22517, inner lateral (Qa), basal (Qb), and enlarged basal interior views Qc (250x), Qd (800x) showing attachment grooves on inner basal surface of crown. R—CPC 22518, inner lateral (Ra), basal (Rb) views, and enlargement (Rc) showing striations (200x).

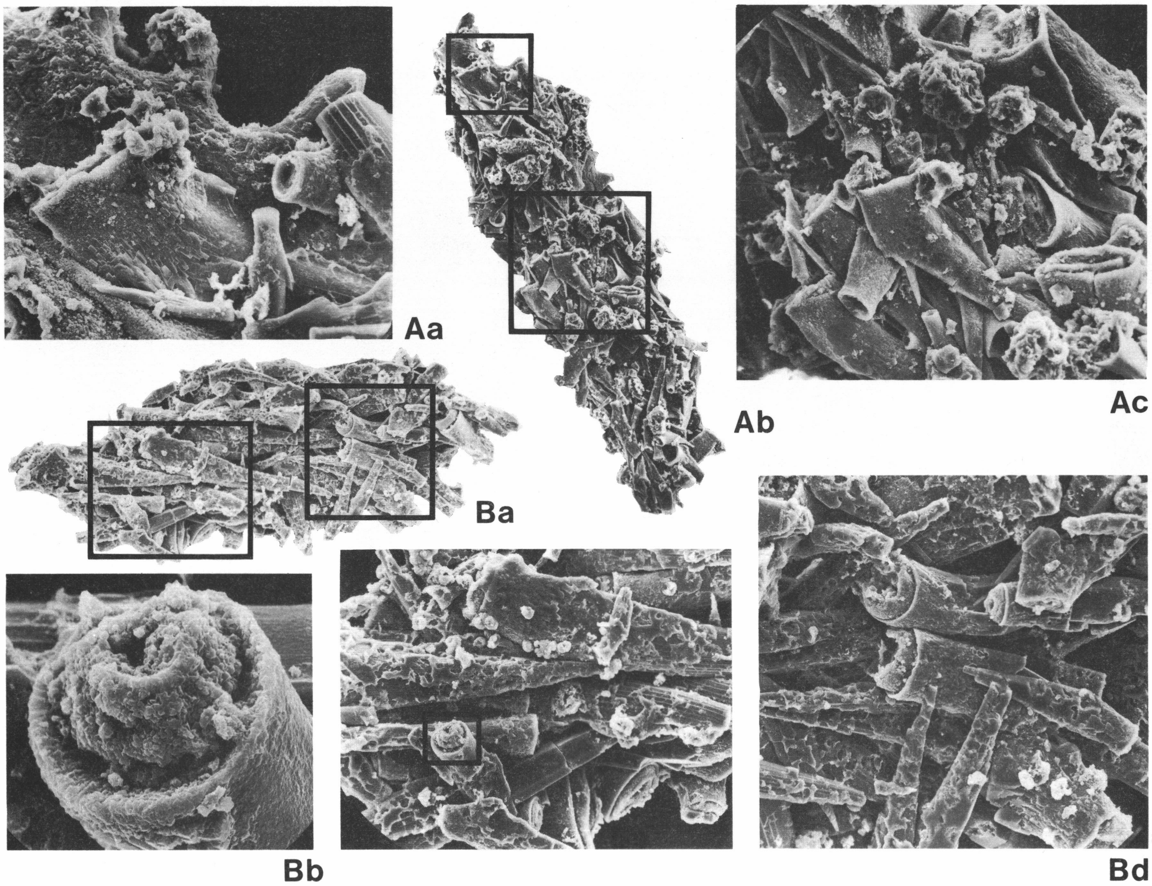


Figure 11. Cone elements Ce and Cf.
A—Cluster with single I element and 130 cone elements, many showing the slightly ovate basal cross-section typical of the Ce element; same specimen as Fig. 3D; CPC 22468; Aa—enlargement showing very small Ce element with well-developed shoulder spurs (550x); Ab—view of cluster, I element toward top of plate (115x); Ac—enlargement showing several Ce elements as well as a Ca element near top right corner (325x). B—Cone cluster (Ba) with more than 80 elements, mostly Cf elements and some Ce elements (120x) CPC 22519. Bb—enlargement of area outlined in view Bc, showing basal plate of Cf element (1800x); Bc—enlargement showing striation on elements and basal plates (285x); Bd enlargement showing basal plates of Cf elements (350x).

Cd element. (Fig. 10A–D); material studied—20 discrete elements.

Erect, bilaterally symmetrical to slightly asymmetrical element with oval base. Element tapers from base to tip with only very minor shoulders on anterior and posterior margins. The striation pattern is similar to that of the Ca element.

Ce element. (Fig. 11); material studied—more than 1000 specimens in clusters.

Cf element. (Fig. 11); material studied—more than 1000 specimens in clusters.

Erect to slightly recurved elements with fewer but coarser, more prominent, striations than those found on the Ca-Cd elements. The shoulders are also generally more prominent than those of the Ca-Cd elements, and are developed relatively higher above the base of the element. These are less robust elements than those described above, and taper to a finer point.

The elements are morphologically similar in all respects except for the cross-section outline of the base. The Ce element has an oval base and the Cf element has a circular base. There does not appear to be any significant intergradation of these two element types.

Apparatus element numbers

The number of discrete elements in the apparatus structure of *Icriodus expansus*, here estimated to be more than 140, seems excessive when compared with an element abundance of 15 in genera such as *Ozarkodina* or *Polygnathus*. However, a direct comparison of apparatus element numbers between *Icriodus* and other genera is misleading, and it may be more accurate to compare total apparatus denticle numbers. The multielement *Oulodus angulatus*, described by Nicoll (1979), can be taken as a simple example. That almost complete multielement apparatus with its simple morphology of large discrete denticles, which make a count easy, had a total of 189 denticles when allowance is made for missing fragments of elements by doubling the denticle count of the comparable complete element. The total number of denticles of some individual hindeodelliform Sc element is in excess of 50. Thus, by comparison, the 140+ denticles of the *I. expansus* apparatus is well within what might be expected for denticle numbers of a Devonian platform type conodont species.

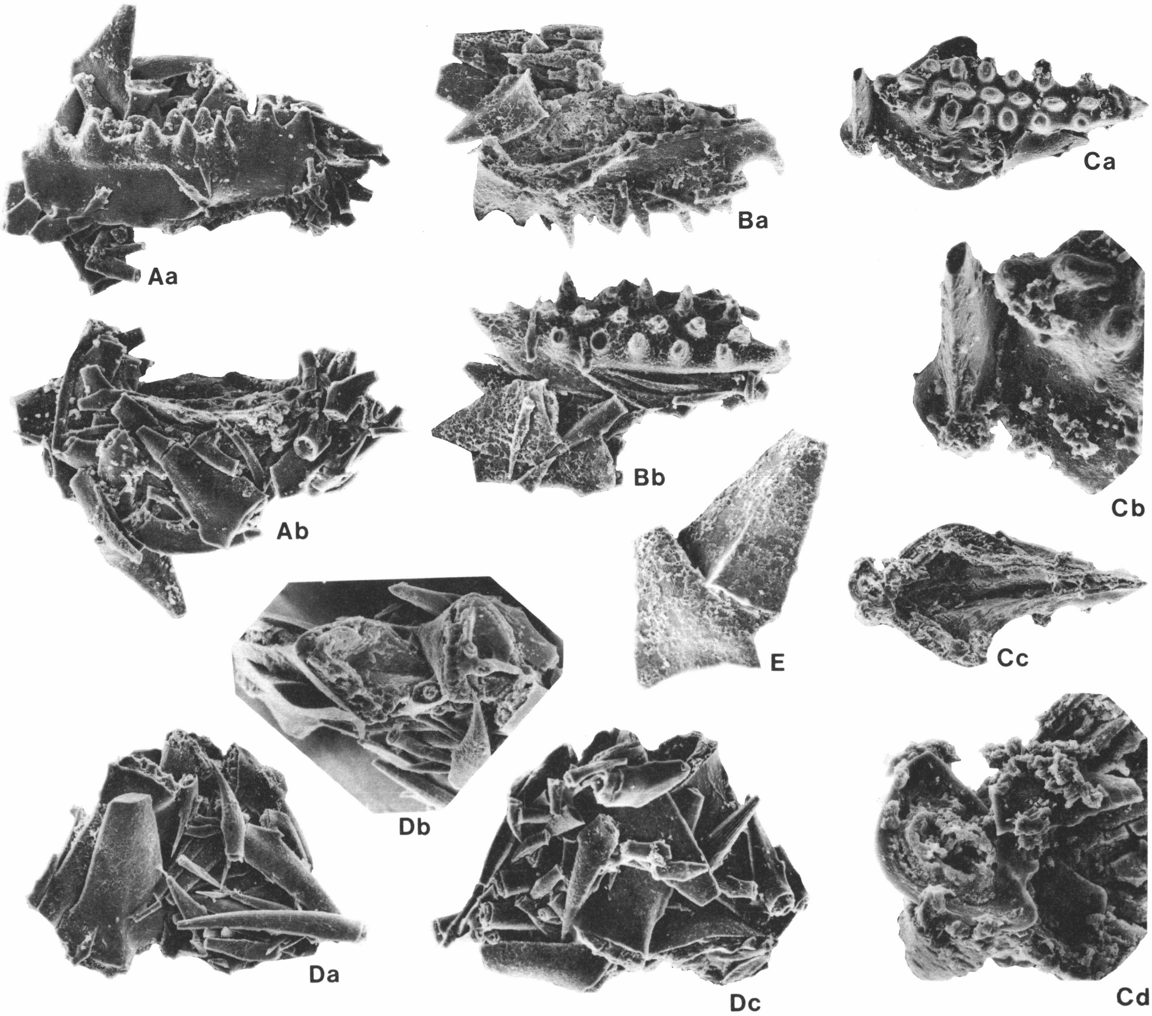


Figure 12. Cone element types in clusters.
A—Two views of cluster containing a single I element and at least 55 cone elements; two of the cones are Cc type elements and one may be a type Cd element; most of the elements are cone types Ce and Cf; CPC 22520 (100x). B—Two views of cluster containing a single I element and at least 30 cone elements; cone element types Cc, Ce, and Cf are recognised; CPC 22521 (105x). C—four views of cluster containing a single I element and at least five cone elements; cone element attached to anterior of I element is type Ca and large element on side is a Cd element; CPC 22522; Ca—upper view (75x); Cb—upper view, enlargement of anterior margin (180x); Cc—basal view (75x); Cd—basal view, enlargement of Ca element showing basal plate (260x). D—Three views of cone cluster containing at least 60 elements; cluster contains two Ca elements and two Cb elements as well as Ce and Cf elements; CPC 22523; Da and Dc—lateral views; Db—view showing distinctive outline of Ca and Cb elements (85x). E—Cluster of two cone elements, one Ca and one Cc element. CPC 22524 (120x).

Phyletic composition and origin of the Family Icriodontidae

Several authors (Klapper & Philip, 1972; Klapper & Murphy, 1975; Cooper, 1977) have recently discussed the composition of the Family Icriodontidae, with general agreement. Genera usually included in the family are *Icriodus*, *Pelekysgnathus*, *Pedavis*, *Steptotaxis*, *Sannemannia*, and *Icriodella*. However, in light of our present knowledge of the apparatus structure of these taxa, it is probable that *Icriodella* should be excluded from the Icriodontidae.

The oldest recognised species of the Icriodontidae, excluding *Icriodella* species, is *Pelekysgnathus dubius* Jeppsson (1972) from the Yass Basin sequence of eastern Australia, and is dated as early Ludlovian. The Australian material, originally described as *Coryssognathus dentatus* by Link & Druce (1972), has been considered to be conspecific with *Pelekysgnathus dubius* Jeppsson (1972) by both Jeppsson (1974) and Klapper & Murphy (1975). Klapper & Murphy, on morphologic grounds, did not believe that *P. dubius* should be assigned to *Pelekysgnathus*. However, examination of additional samples from the Euralie Limestone Member of the Laidlaw Formation of the Yass Basin has produced cone elements associated with *P. dubius* (= *C. dentatus*) that are nearly identical with the cone elements of *P. index* Klapper & Murphy from the Pridoli of the Roberts Mountains of Nevada and of *P. australis* Nicoll & Druce from the Famennian of the Canning Basin of Western Australia. For this reason, I suggest that Jeppsson was correct in this original assignment of the species to *Pelekysgnathus*. The importance of this discussion is that the oldest recognised elements of a species assigned to the Icriodontidae, *P. dubius*, are simple in character, and the cone elements lack secondary denticulation.

The next oldest taxon assigned to the Icriodontidae is *Pedavis latialata* (Walliser), which differs significantly from the *Pelekysgnathus* group by the development of triad denticulation on processes of the I element and the presence of denticulation on the S_1 (sagittodontan) cone element. In this morphology, both the I and S_1 elements of *Pedavis* are more similar to *Icriodella* than to *Pelekysgnathus*. The other recognised cone element of *Pedavis*, the M_2, is more similar to the cone element of *Pelekysgnathus* than to the denticulate elements of *Icriodella*.

The relationship of *Pelekysgnathus*, *Pedavis*, *Steptotaxis*, and *Icriodus* is not well defined, and there are some significant gaps in the geologic record as well as a lack of species that show morphologic intergradation between species or genera. Cone element types of the above genera are generally similar, but it is probable that only in the present case has the full nature of the range and number of element types in the apparatus structure been recognised. *Pelekysgnathus* generally lacks the development of denticle triads in the I element. *Icriodus*, *Pelekysgnathus*, and *Steptotaxis* all have cone elements of acodinan (Ca, S_2) morphology, and these are generally similar to the sagittodontan (S_1) element of *Pedavis*, except for the minor denticle development of the latter. The other cone elements, M_{2a} and M_{2b}, recognised for *Pel. australis* by Nicoll & Druce (1979) and also found with *Pel. index* (Klapper, pers. comm.), are generally similar to the M_2 element of *Pedavis pesavis pesavis* (Bischoff & Sannemann) and the Ce and Cf elements here recognised for *I. expansus*. I think that using the present study of *I. expansus* as a model will mean that other workers may more closely examine the cone elements associated with Icriodontidae I elements and differentiate more elements in the apparatuses of *Pelekysgnathus*, *Pedavis*, and *Steptotaxis*.

The possible relationship of *Icriodella*, if any, to the Icriodontidae is not known. Most elements in the *Icriodella* apparatus, except for the saggittodontiform element, are denticulate. If *Icriodella* is ancestral to the Icriodontidae, this would mean that, between its last occurrence in the Llandovery and the first occurrence of *Pelekysgnathus* in the early Ludlow, all the elements lost their secondary denticulation and there were other gross morphologic changes. Because the icriodontid type of process denticulation has been repeated in several taxa, from *Icriodella* in the Ordovician to *Eotaphrus* in the Carboniferous, the presence of a triad style denticulation may be the result of an adaptation to a feeding mode rather than an indication of a close phyletic relationship.

It is possible that ancestral forms to *Pelekysgnathus* and *Pedavis* should be looked for in cone elements of the late Ordovician or the Silurian.

Interpretation of the structure of *Icriodus expansus*

The linear sequence of elements in the conodont organism, suggested by myself (Nicoll, 1977) and many others, would seem to be confirmed by the linear pattern of elements in some of the better-preserved *Icriodus* clusters recovered in this study. The general sequence of ramiform anterior elements to platform or platform-like posterior elements, well developed in *Polygnathus* and *Ozarkodina* clusters, appears to be analogous to the cone to platform sequence in *Icriodus*.

The general pattern of element and denticle distribution in the condont organism is that of numerous anterior denticles and a few posterior denticles with the posterior elements frequently having broad, flat surfaces, which may contain trough structures or complex patterns of ribs or nodes. There thus appears to be some fundamental functional differentiation between the anterior and posterior elements of this sequence. I have suggested earlier (Nicoll, 1977, p. 277) that the conodont elements were structures located along a food groove, the function being to filter, pass, and direct food particles into the gut opening and that the Pa elements had a special function, which may have been the final manoeuvring of the food particles into the gut opening.

In the *Icriodus* apparatus, there is less differentiation of the cone element types than usually found for the ramiform elements of other genera. However, the triad denticle pattern of the posterior part of the I element is clearly analogous to the platform of other genera. The central denticle row is equivalent to the carina of the *Polygnathus* Pa element and the lateral rows to the nodose or upturned inner and outer platform margins of the Pa element.

In this study it is apparent that the configuration of the I elements is of opposition rather than the side by side configuration suggested in some conodont reconstructions. This configuration is also suggested by the *Polygnathus xylus xylus* Pa elements recovered in this study, many of which are fused with upper surfaces together.

Conclusions

- The apparatus structure of *Icriodus expansus* consisted of seven element types: one pair of I elements, probably one pair each of the cone element types Ca, Cb, Cc, and Cd, and numerous cone elements of types Ce and Cf.
- The apparatus contained in excess of 150 discrete elements.
- The orientation of the I elements is laterally opposed with upper surfaces together or in close proximity when the conodont organism was alive.
- Despite its apparent morphologic differences, the apparatus structure *Icriodus* was probably functionally very similar to the apparatus structures of other genera, such as *Polygnathus* or *Ozarkodina*.
- The lack of recognition of the apparatus structure components of *Icriodus* in discrete element collections is probably a function of sorting. Part of this sorting probably occurred at the time of deposition, when the small and thus lighter cones were separated from the I element by current action. In support of this, one should remember that there have been very few examples of early growth stages of the I element described or illustrated in the literature. The second part of the sorting has probably occurred in the laboratory, where the small Ce and Cf cone elements would be washed through most sieves.

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References

BARNES, C. R., KENNEDY, D. J., McCRACKEN, A. D., NOWLAN, G. S. & TARRANT, G. A., 1979—The structure and evolution of Ordovician conodont apparatuses. *Lethaia*, 12, 125-51.

BARRICK, J. E., 1977—Multielement simple-cone conodonts from the Clarita Formation (Silurian), Arbuckle Mountains, Oklahoma. *Geologica et Palaeontologica*, 11, 47-68.

BISCHOFF, G. & ZIEGLER, W., 1957—Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. *Abhandlungen des Hessischen Landesametes fur Bodenforchung*, 22, 1-136.

BRANSON, E. B., & MEHL, M. G., 1934—Conodonts from the Grassy Creek Shale of Missouri. *University of Missouri Studies*, 8, 171-259.

BULTYNCK, P., 1972—Middle Devonian *Icriodus* assemblages (Conodonta). *Geologica et Palaeontologica*, 6, 71-86.

COOPER, B. J., 1977—Toward a familial classification of Silurian conodonts. *Journal of Palaeontology*, 51, 1057-71.

JEPPSSON, L., 1972—Some Silurian conodont apparatuses and possible conodont dimorphism. *Geologica et Palaeontologica*, 6, 51-69.

JEPPSSON, L., 1974—Aspects of Late Silurian conodonts. *Fossils and Strata*, 6, 1-54.

JOHNSON, D. B. & KLAPPER, G., 1981—New Early Devonian conodont species of central Nevada. *Journal of Paleontology*, 55, 1237-50.

KLAPPER, G., 1969—Lower Devonian conodont sequence, Royal Creek, Yukon Territory, and Devon Island, Canada. *Journal of Paleontology*, 43, 1-27.

KLAPPER, G. & MURPHY, M. A., 1975—Silurian-Lower Devonian conodont sequence in the Roberts Mountains Formation of Central Nevada. *University of California Publications in Geological Sciences*, 111.

KLAPPER, G., & PHILIP, G. M., 1971—Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia*, 4, 429-52.

KLAPPER, G., & PHILIP, G. M., 1972—Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica*, SB1, 97-114.

KLAPPER, G. & ZIEGLER, W. 1975—*Icriodus. In* ZIEGLER, W. (editor), Catalogue of conodonts. *E. Schweizerbart'sche Verlagsbuchhandlung*, 2, 67-8.

KLAPPER, G. & ZIEGLER, W. 1979—Devonian conodont biostratigraphy. *In* HOUSE, M. R., SCRUTTON, C. T., & BASSET, M. G. (editors). The Devonian System, *Special Papers in Palaeontology*, 23, 199-224.

LANGE, F. G., 1968—Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. *Geologica et Palaeontologica*, 2, 37-57.

LINDSTROM, M., 1964—Conodonts. *Elsevier, Amsterdam.*

LINK, A. G. & DRUCE, E. C., 1972—Ludlovian and Gedinnian conodont stratigraphy of the Yass Basin, New South Wales. *Bureau of Mineral Resources, Australia, Bulletin* 134.

NICOLL, R. S., 1977—Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics*, 2, 217-28.

NICOLL, R. S., 1981—Conodont colour alteration adjacent to a volcanic plug, Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics*, 6, 265-7.

NICOLL, R. S. & DRUCE, E. C., 1979—Conodonts from the Fairfield Group, Canning Basin, Western Australia. *Bureau of Mineral Resources, Australia, Bulletin* 190.

NORRIS, A. W. & UYENO, T. T., 1981—Stratigraphy and paleontology of the lowermost Upper Devonian Slave Point Formation on Lake Claire and the lower Upper Devonian Waterways Formation on Birch River, northeastern Alberta. *Geological Survey of Canada, Bulletin* 334.

SEDDON, G., 1970—Frasnian conodonts from the Sadler Ridge—Bugle Gap area, Canning Basin, Western Australia. *Journal of the Geological Society of Australia*, 16, 723-53.

SCHMIDT, H., 1950—Nachtrage zur Deutung der Conodonten. *Decheniana*, 104, 11-19.

SWEET, W. C. & SCHONLAUB, H. P., 1975—Conodonts of the genus *Oulodus* Branson and Mehl, 1933. *Geologica et Paleontologica*, 9, 41-59.

UYENO, T. T. & KLAPPER, G., 1980—Summary of conodont biostratigraphy of the Blue Fiord and Bird Fiord Formations (Lower-Middle Devonian at the type and adjacent areas, southwestern Ellesmere Island, Canadian Arctic Archipelago. *In* Current Research, Part C, *Geological Survey of Canada, Paper* 80-1C, 81-93.

VAN DEN BOOGAARD, M. & KUHRY, B., 1979—Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric, and specific level. *Scripta Geologica*, 49, 1-57.