The apparatus architecture and function of *Promissum pulchrum* Kovács-Endrödy (Conodonta, Upper Ordovician) and the prioniodontid plan

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SUMMARY

More than 100 complete apparatuses of the conodont *Promissum pulchrum* have been collected as natural assemblages on bedding surfaces of the Soom Shale Member, Cedarberg Formation, South Africa. Recurrent patterns of flattening shown by the assemblages reflect the orientation of the conodont head on the sediment surface prior to decay and collapse of the soft tissues; we have used these patterns to model the three-dimensional architecture of the apparatus of *Promissum*. The apparatus is bilaterally symmetrical and comprises 19 elements: two Pa, two Pb, two Pc, two Pd, two M and nine S elements. The Pa, Pb and Pc elements are horizontally aligned as opposed pairs, with the Pd pair positioned below the Pb elements; the S elements form an oblique array below the P elements and a pair of M elements is at the anterior.

Functional interpretation of the apparatus is difficult but it probably operated as an integrated set of movable mouthparts, the S element array grasping prey to be crushed by the P elements. The *Promissum* animal was probably macrophagous, feeding on soft-bodied members of the Soom Shale fauna.

The apparatus of *Promissum* is more complex than that known or reconstructed for any other conodont taxon. Interpretation of evolutionary pathways in Ordovician conodonts with denticulate elements must await evaluation of other prioniodontid taxa in the light of the *Promissum* template.

1. INTRODUCTION

Conodonts were primarily soft-bodied animals that possessed a mineralized, phosphatic feeding apparatus (Briggs *et al.* 1983; Aldridge *et al.* 1993). The fossil record of the true conodonts (euconodonts) ranges from the Upper Cambrian to the uppermost Triassic and consists almost entirely of their dissociated skeletal elements; these became scattered in the sediment on the death and subsequent decay of the animals. Rare finds of conodont skeletal apparatuses preserved with associated soft tissues (including myotomes, a noto-chord and eye capsules) have led to the interpretation that conodonts were primitive vertebrates (Aldridge *et al.* 1993). This conclusion has been supported by investigation of the histology of the elements which has revealed hard tissues comparable to vertebrate enamel, cellular bone and dentine (Briggs 1992; Sansom *et al.* 1992, 1994).

In conditions where the conodont carcasses were buried and decayed without disturbance from currents, scavengers or burrowing organisms, the elements of the skeletal apparatus may be preserved in association on bedding surfaces, rather than dispersed in the sediment. Natural assemblages of this type are mostly known from Carboniferous shales although a few specimens have been reported from other strata (see review in Aldridge 1987). Partial or complete apparatuses are also found in the form of clusters, where elements lying in juxtaposition have become fused together during diagenesis. Only a few localities worldwide have yielded well-preserved bedding-plane assemblages or clusters and they represent only a small range of conodont taxa.

Despite their rarity, natural assemblages are of paramount importance in conodont palaeontology. Conodonts have no close living relatives; without homologous structures in extant organisms to aid

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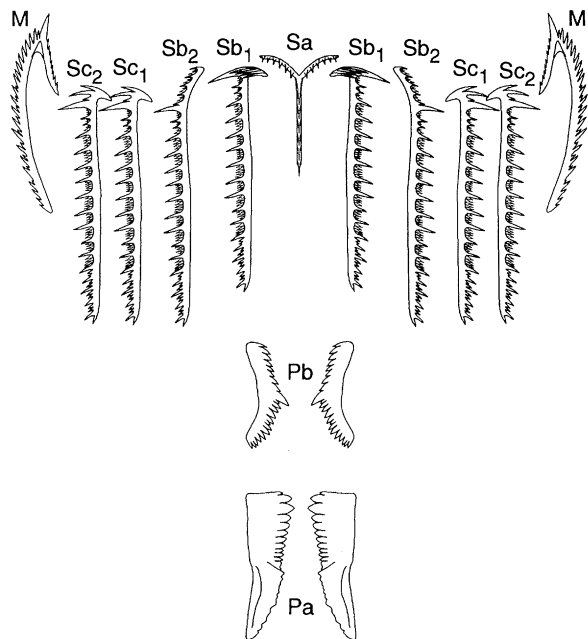
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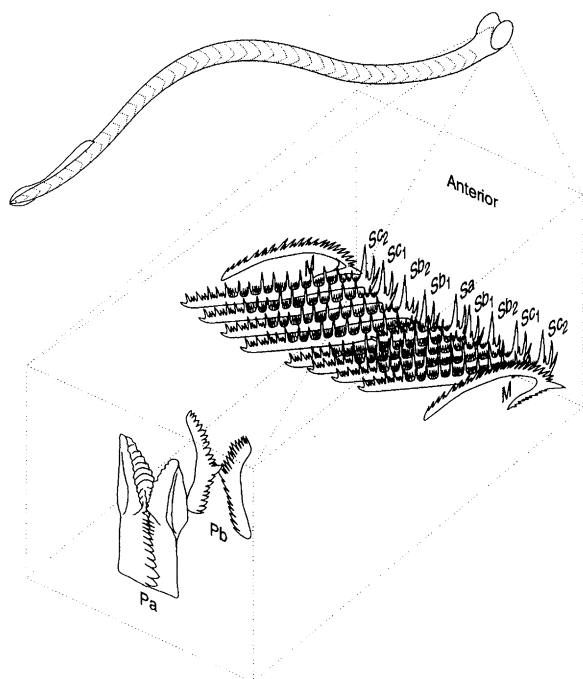Figure 1. Diagrammatic plan of the ozarkodinid conodont apparatus.

Figure 2. The feeding apparatus of *Idiognathodus* illustrating the architecture of the ozarkodinid apparatus and its location in the animal (after Purnell 1994). Apparatus architecture is based on Aldridge *et al.* (1987), S elements are more widely spaced than in nature. Animal morphology is based on Aldridge *et al.* (1993). Scales: elements approximately × 8.5; animal approximately × 1.3.
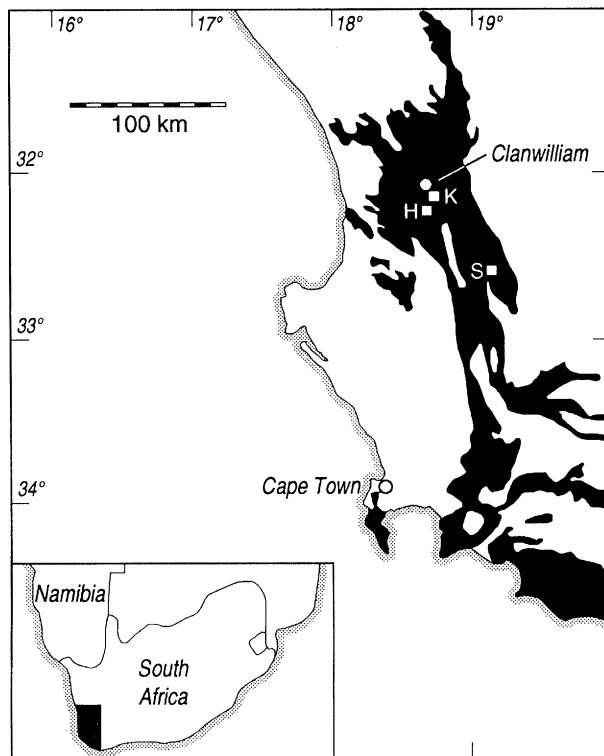

Figure 3. Outline map of the southwestern Cape Province, showing the outcrop of the Table Mountain Group and the *Promissum* localities: K = Keurbos, H = Holfontein, S = Sandfontein.

interpretation, natural assemblages present the only evidence for the original arrangement of the components of the conodont skeleton. They, therefore, provide templates for reconstructing the apparatuses of taxa known only from dissociated remains, serving as references for the development of conodont taxonomy. In palaeobiology they are fundamental in the recognition of homologies between taxa and in the inter-

pretation of evolutionary pathways; they are also prerequisite for the investigation of functional morphology.

Recent classifications of euconodonts recognize up to seven orders, four of which have only morphologically simple elements in their apparatuses (Sweet 1988; Dzik 1991; Aldridge & Smith 1993). The other three orders – the Prioniodontida, Prioniodinida and Ozarkodinida – embrace the majority of genera with more complex apparatuses. These incorporate elements with denticulate processes (ramiform elements), usually together with blade-like or platform-like components (pectiniform elements). Most bedding plane assemblages represent genera of the order Ozarkodinida and historically these have formed the basis of most attempts to reconstruct apparatus architecture (see Aldridge 1987).

Ozarkodinid apparatuses comprise 15 elements (see figure 1). At the anterior are two pick-shaped elements flanking a set of nine elongate elements. Behind these are two pairs of pectiniform elements. Lettering of these elements follows Sweet (1981), after Sweet & Schönlaub (1975) on the basis of their location within the apparatus. However, because particular morphologies are characteristically found in particular positions, this notational scheme also has a morphological connotation. As a result, the reconstruction of the apparatuses of taxa known only from scattered elements normally involves the selection of elements of particular morphologies to fill relevant locations, using the bedding plane assemblages as templates.

The composition of ozarkodinid apparatuses has long been known from the bedding plane assemblages
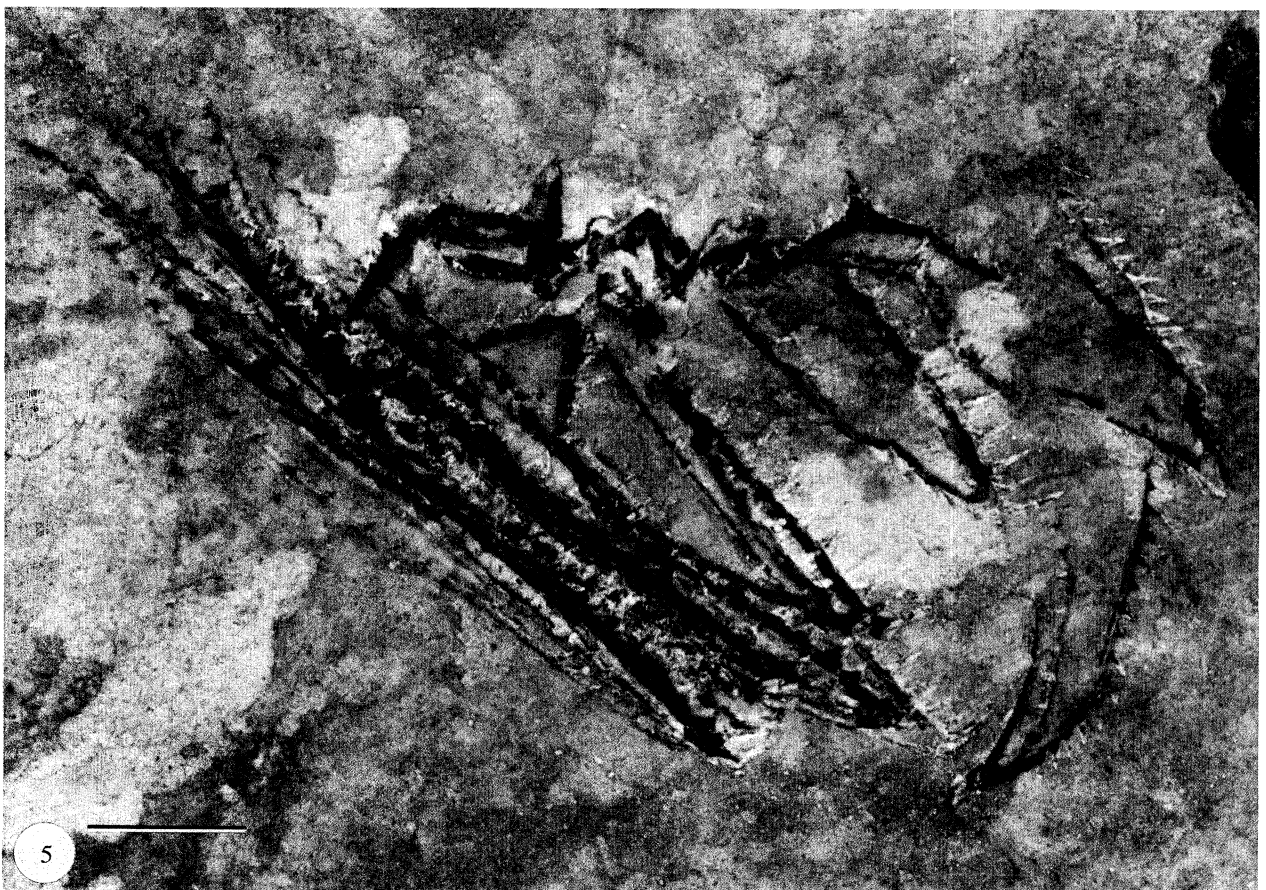
Figure 4. *Promissum pulchrum* specimen C 275. Arrows indicate Pa elements. The spines crossing the specimen belong to the enigmatic organism *Siphonacis parva* (Kovács) (see Chesselet 1992). Scale bar 1 mm.

Figure 5. *Promissum pulchrum* specimen C 351; scale bar 1 mm.

but it is only recently that their three-dimensional architecture has been fully understood. Natural assemblages are found in a variety of patterns, reflecting different attitudes of the conodont carcass relative to the sea bed during decay. A few of these arrangements are symmetrical with the long axes of elements aligned; departures from such linear arrays have been interpreted by some authors as the result of muscle contractions on death or as displacements during decomposition which rotated and translated elements from their life position (e.g. Collinson *et al.* 1972; Walliser 1994). However, Aldridge *et al.* (1987) were able to construct a physical three-dimensional model that could explain all natural assemblage patterns through simple collapse of the skeleton onto a bedding plane during decay of the supporting soft tissue, without invoking muscular or decompositional rotation (see figure 2). This model was based primarily on the apparatus of the first-discovered fossilized conodont animal, dating from the Carboniferous Period, found in Scotland (Briggs *et al.* 1983). The P element pairs are positioned with their long axes transverse to the long axis of the apparatus and the M and S elements at an oblique angle. A subtly but significantly different reconstruction was proposed by Dzik (1991, see page 275), based largely on a natural assemblage figured by Mashkova (1972, figure 2, plate 1). In this restoration, the S elements are oriented with their long axes close to vertical and forming 'a V-shaped structure which gaped anteriorly'. The arrangement of elements in additional conodont animal specimens collected after 1983 (Aldridge *et al.* 1993) conflicts with this interpretation, but is consistent with the model shown in figure 2. It is possible to envisage an integrated functional system for such an apparatus in which the ramiform (M and S) elements grasped prey to be processed by the pectiniform (Pb and Pa) elements (Briggs *et al.* 1983; Aldridge *et al.* 1987). This interpretation has been corroborated by analyses of functional morphology and ontogeny (Purnell & von Bitter 1992; Purnell 1993*a*).

The architecture of apparatuses representing other conodont orders is much more poorly understood. Evidence for the arrangement of elements in prioniodinids comes from just two natural assemblages. The apparatuses of *Oulodus angulatus* (Hinde) and *Kladognathus* were described by Nicoll (1977, 1985) and Purnell (1993*b*) respectively, revealing a skeletal plan closely comparable with that of known ozarkodinids (Purnell, 1993*b*).

Prioniodontid apparatuses are even less well known. The prioniodontid conodonts arose in the Tremadoc and radiated impressively in the Ordovician, dominating many faunas. They are also important members of early Silurian collections but declined in later Silurian times, becoming extinct by the end of the Devonian Period (for a review see Sweet 1988, pages 59–78). The multi-element composition of many species has been determined through numerical, distributional and morphological analyses of collections of discrete elements; but no architectural model for the prioniodontid apparatus has been proposed. The only documented prioniodontid bedding plane

assemblages are of the exceptionally large species *Promissum pulchrum* Kovács-Endródy from the Upper Ordovician Soom Shale Member in the Cedarberg Formation, Table Mountain Group, South Africa (see figure 3). Elements in these *Promissum* apparatuses reach 14 mm in length (compared with the normal range of 0.5–3 mm). Three complete apparatuses, initially described by Kovács-Endródy (in Theron & Kovács-Endródy 1986), were shown by Theron *et al.* (1990) to be prioniodontid conodonts. Subsequently, additional apparatuses were collected, some of which were associated with preserved soft tissue interpreted as the eye capsules of the *Promissum* animals (Aldridge & Theron 1993).

Intensive collection has now yielded more than 100 complete or near-complete *Promissum* apparatuses (see figures 4 and 5), preserved in a variety of configurations. Most of the specimens are from the original locality at Keurbos (18° 58′ E, 32° 16′ S), near Clanwilliam in the Southwestern Cape Province of South Africa (Theron *et al.* 1990). Two additional Soom Shale localities, at Holfontein (18° 57′ E, 32° 16′ S) and Sandfontein (19° 14′ E, 32° 40′ S), 8 km south and 52 km southeast of Clanwilliam respetively (see figure 3) have also yielded natural assemblages. There is now sufficient material available for us to evaluate the composition of the *Promissum* apparatus, to determine the nature of its component elements and to reconstruct its three-dimensional architecture.

2. THE COMPOSITION OF THE *PROMISSUM* APPARATUS

Reconstruction of the apparatus plan of *Promissum* presented some problems. Preservation is usually in the form of moulds and often it is impossible to determine the relative superposition of elements. The apparatus is more complex than those previously reconstructed: the
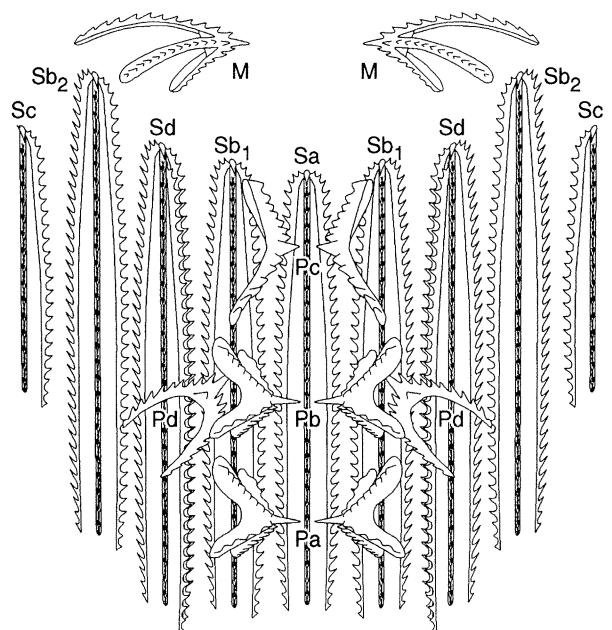

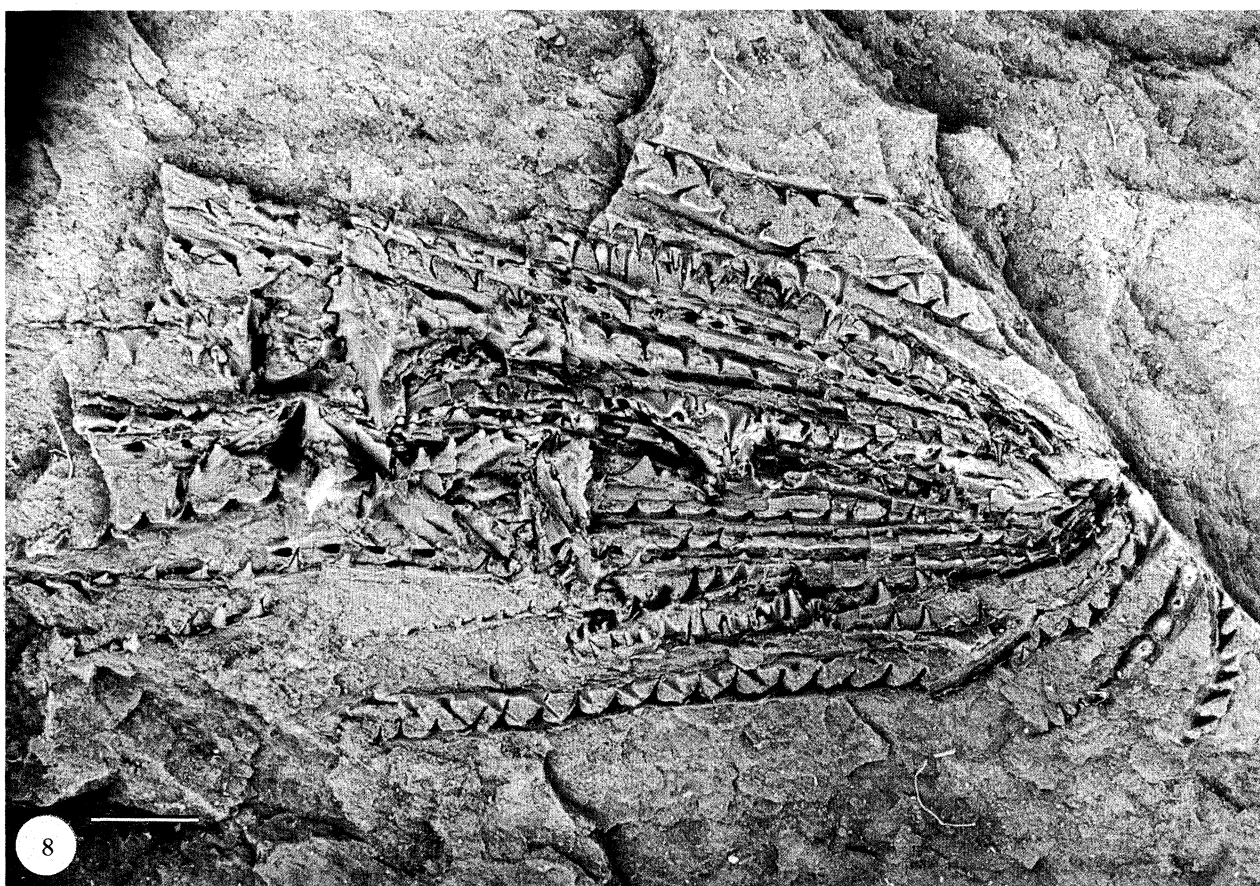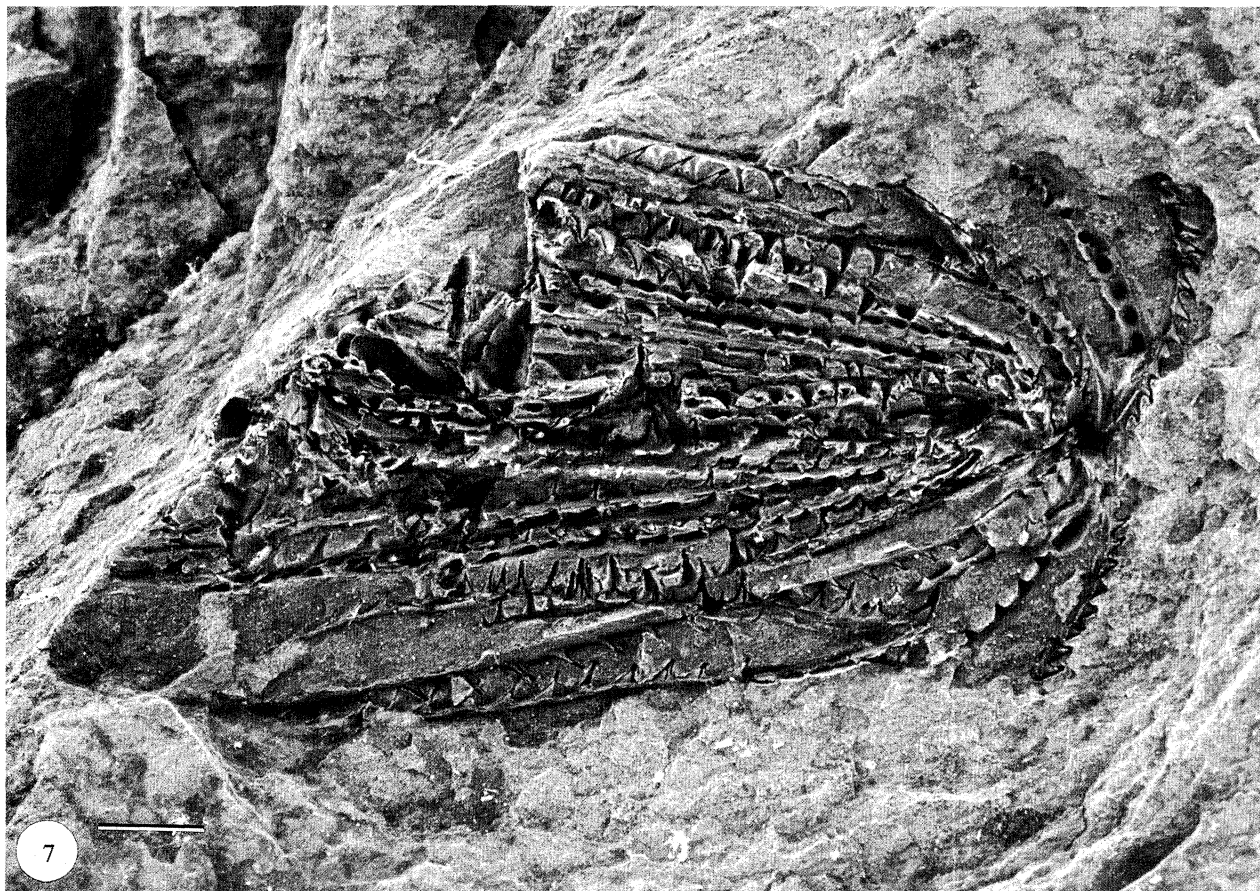Figure 6. Plan of the apparatus of *Promissum pulchrum*.

Figure 7. *Promissum pulchrum* specimen C 279 part; scale bar 1 mm.

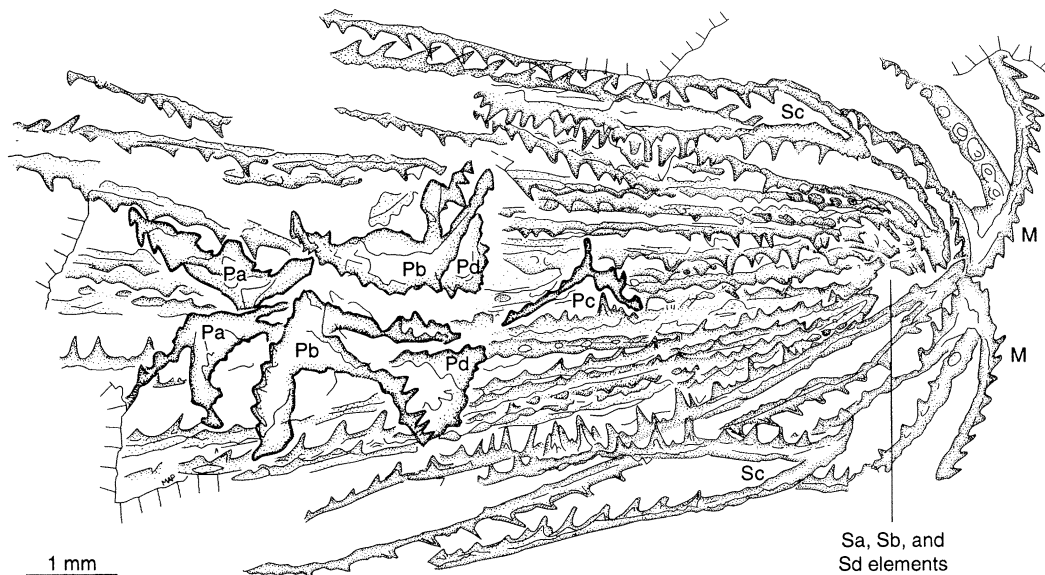Figure 8. *Promissum pulchrum* specimen C 279 counterpart; scale bar 1 mm.

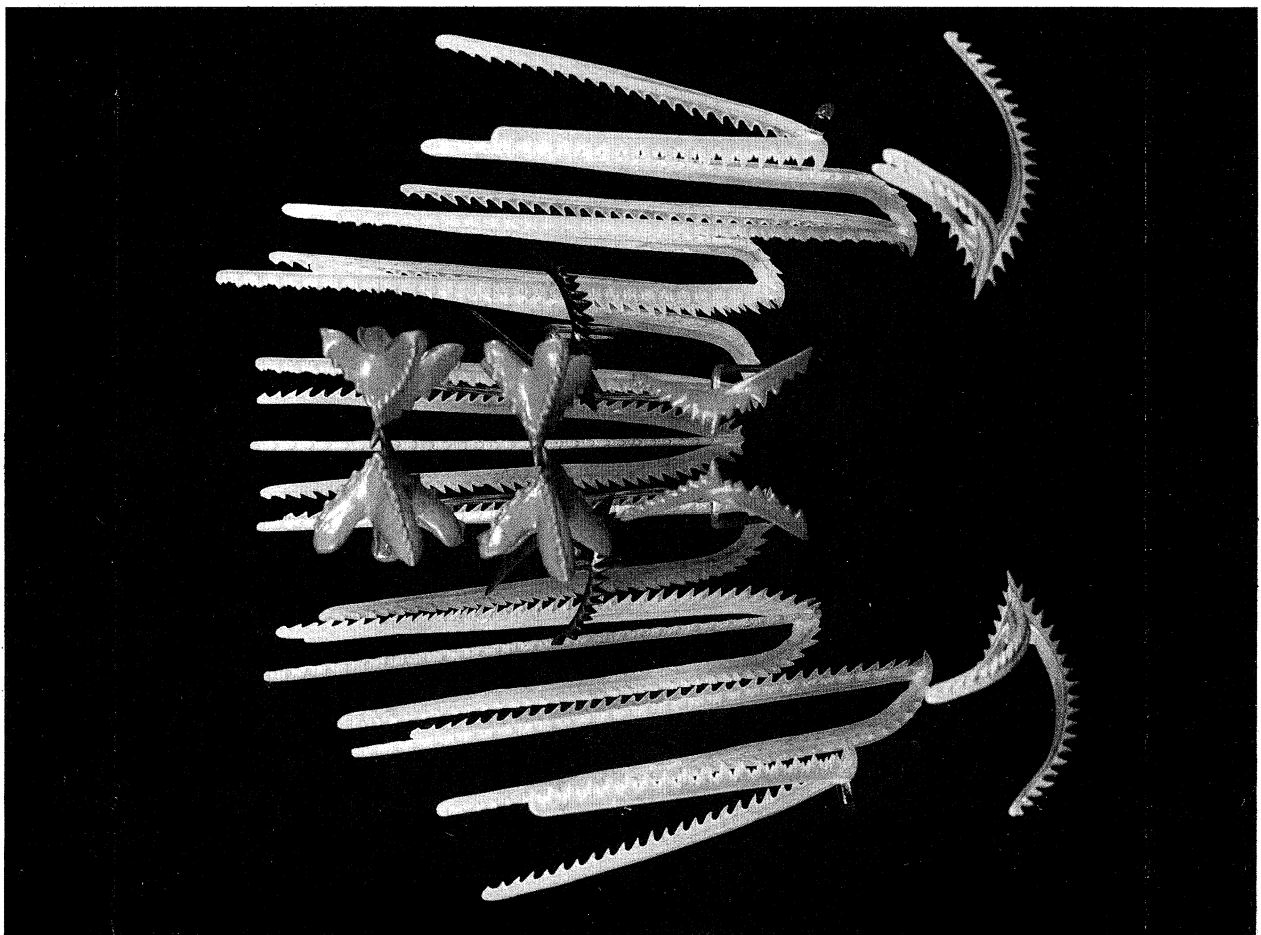Figure 9. *Promissum pulchrum* specimen C 279 composite camera lucida drawing of part and counterpart.

Figure 10. Model of the apparatus of *Promissum pulchrum* photographed from above to simulate dorso-ventral collapse, as shown by specimen C 279.

number of elements is large and most of them have complicated three-dimensional morphologies. However, we have determined that the *Promissum* apparatus comprises a total of 19 elements (see figure 6). The arrangement of these elements in the apparatus is different from that of ozarkodinids (see figures 1 and 2) but there is sufficient similarity for homologies to be recognized (see Appendix). We have, therefore, been able to apply an extension of the standard P, M and S notation (Sweet & Schönlaub 1975; Sweet 1981) to the elements. Element descriptions and notations are given in the Appendix.
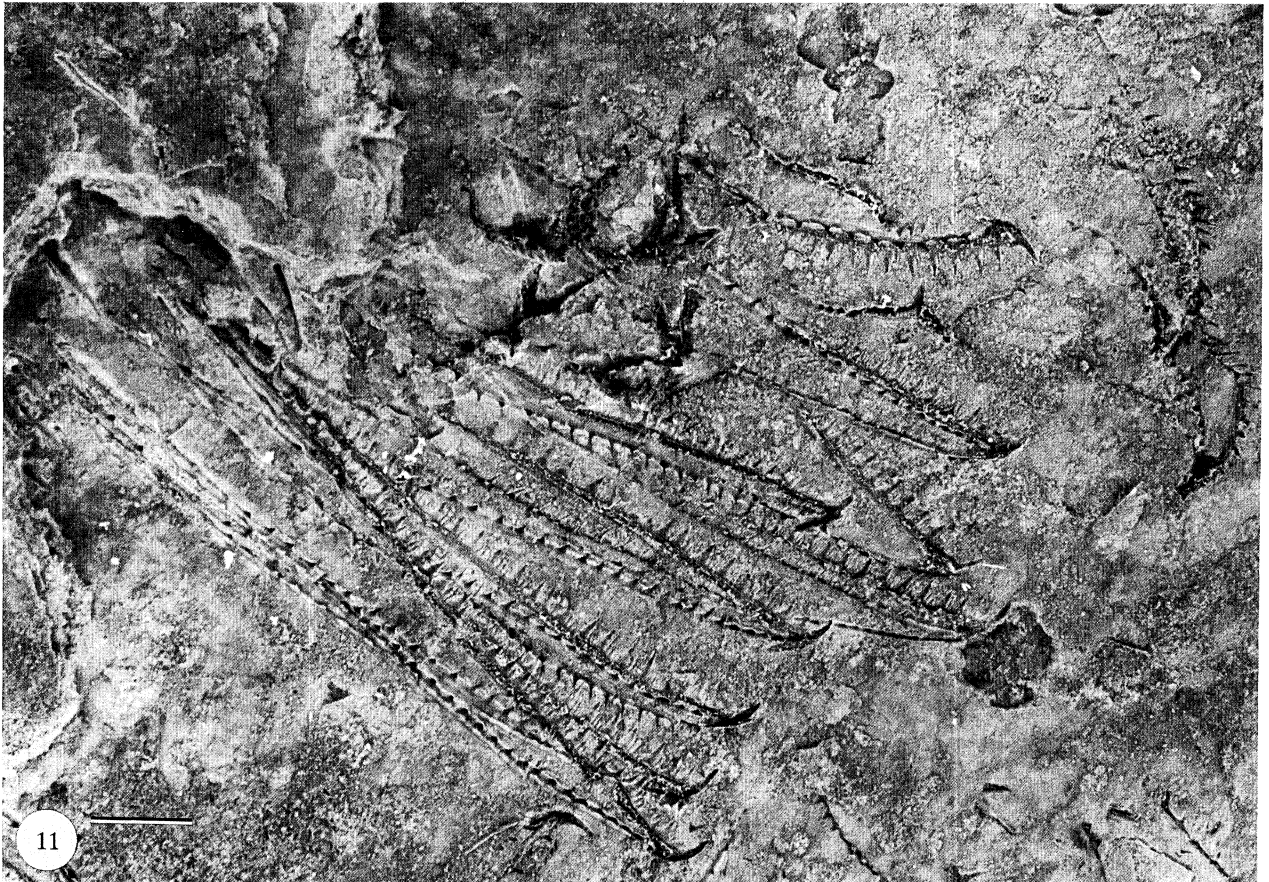
Figure 11. *Promissum pulchrum* specimen C 616 counterpart; scale bar 1 mm.

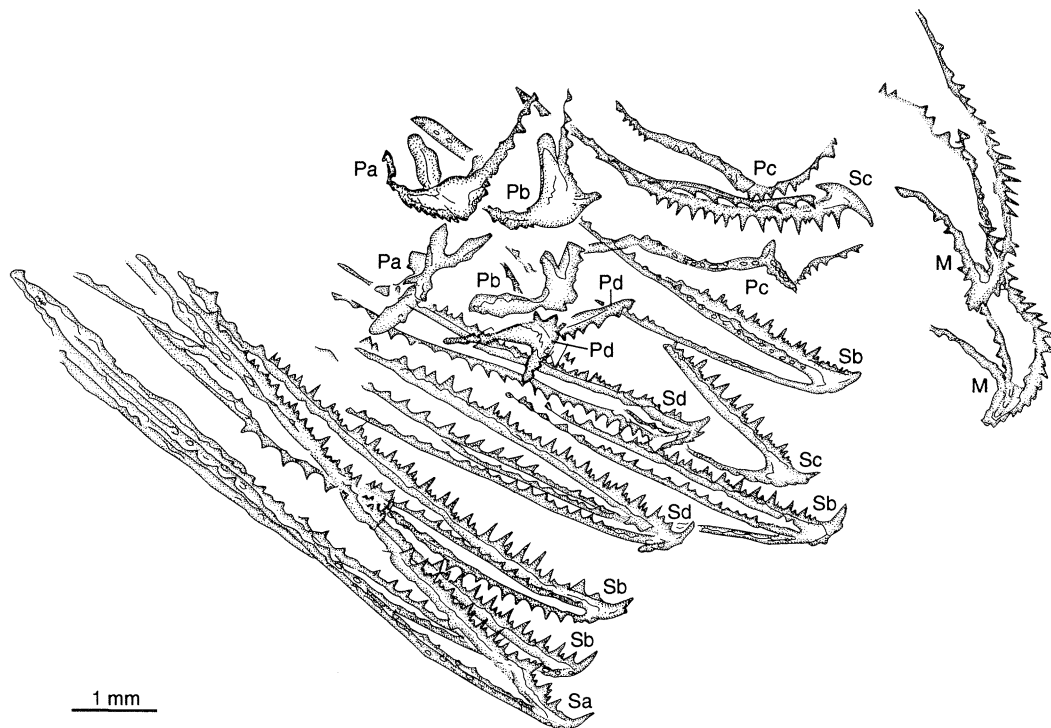Figure 12. *Promissum pulchrum* specimen C 616 part; scale bar 1 mm.

Figure 13. *Promissum pulchrum* specimen C 616 composite camera lucida drawing of counterpart and part.

3. THE ARCHITECTURE OF THE *PROMISSUM* APPARATUS

Of the complete *Promissum* assemblages recovered, some are disrupted and may be faecal, and a few others have become spread apart (presumably during decay of the animal). Most, however, conform to a small number of recurrent patterns which represent vertical collapse of the apparatus onto the bedding plane as the supporting soft tissue decayed. The different arrangements of the elements reflect the various orientations of the conodont head relative to the sediment surface prior to this collapse.

Fourteen specimens display a bilaterally symmetrical or near symmetrical array of elements (see figures 7 and 8). Conodont animals were elongate (Briggs *et al.* 1983, Aldridge *et al.* 1993) and on death usually came to rest with their long axis parallel to the sediment surface. Symmetrical assemblages, therefore, record dorso-ventral or near dorso-ventral collapse. It is not always possible to distinguish individual elements in these specimens, as the P and S sets are superimposed. However, the bilateral symmetry of the opposing S arrays is clear, as is the inward opposition of the cusps of the M elements at the anterior (see figures 7 to 9). Specimens showing somewhat oblique dorso-ventral flattening have previously been illustrated by Theron *et al.* (1990, see plate 1, figure 1; plate 3, figure 1) and by Aldridge & Theron (1993, see figure 2, plate 1, figure 3).

Some 20 specimens are preserved in lateral aspect with opposing elements superimposed. In these assemblages (e.g. figures 4 and 5; also, Aldridge & Theron 1993, plate 1, figure 1), the Pa, Pb and Pc elements are aligned, with the Pc elements at the anterior. In the Pa and Pb pairs the oral surfaces are opposed so that the denticulated surfaces of elements on the far side of the apparatus face the observer, whereas the nearside elements show their basal cavities. Both Pc elements have their cusps directed dorsally. The Pd element on each side is positioned below the Pb element, with the cusp directed away from the S elements and inclined anteriorly. The Sa, Sb_1, Sd, Sb_2 and Sc elements are piled upon each other in lateral assemblages. They form an array with their posterior processes generally oriented at an angle to the line of P elements; those of the Sc elements are at about 30°, increasing to 50° for the Sa elements. The cusps of the S elements are below the Pc elements and the distal ends of their processes terminate behind the Pa elements. The cusps of the Sb_2 elements are commonly a little to the anterior of the remainder, which are otherwise arranged in a line at about 30° from the vertical so that the Sa cusp is posteriormost. The M elements are positioned clearly to the anterior, with their ventrally directed cusps below the line of the P elements and facing the cusps of the S elements; their processes curve upwards and a little backwards towards the Pc elements.

Following the approach adopted for ozarkodinid apparatuses by Aldridge *et al.* (1987), we have used the dorso-ventral and lateral assemblages of *Promissum* as templates for the construction of a three-dimensional model. Figure 10 shows the model from above, corresponding to dorso-ventrally collapsed assemblages (see figures 7 to 9), although we have spaced the elements more widely than in nature so that their relative positions are clearly visible. The ability of this model to explain a variety of other natural assemblage patterns provides a critical test of its accuracy. To this end, photographs of the model were taken from various angles, simulating the results of collapse and flattening in different orientations (cf. Briggs & Williams 1981).
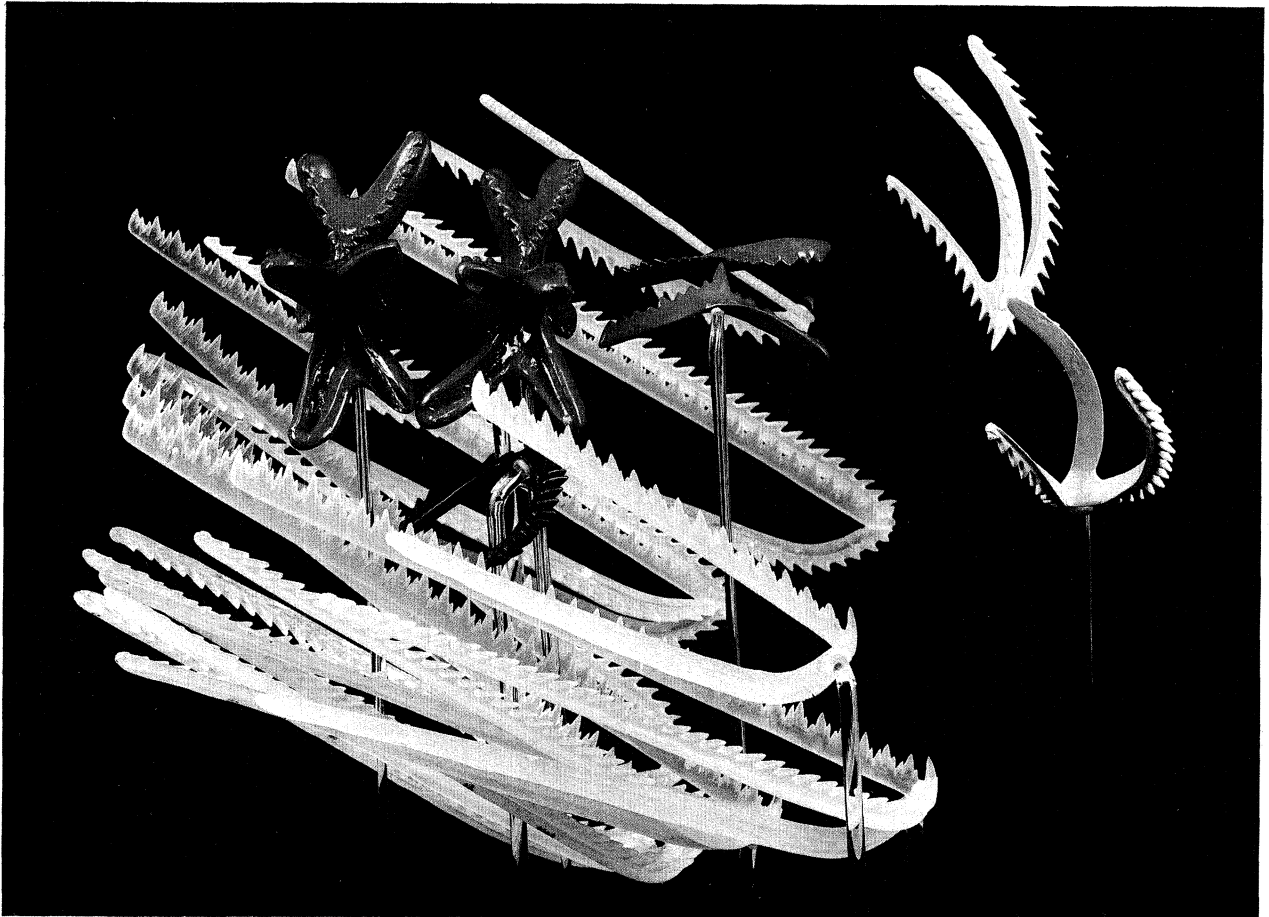
Figure 14. Model of the apparatus of *Promissum pulchrum* photographed from the side and slightly above to simulate near lateral collapse, as shown by specimen C 616.

The morphology of most well-preserved assemblages corresponds well to photographs of our model. For example, in specimen C616 (see figures 11–13), the farside P and M elements are positioned above those on the nearside, with the cusp of the nearside Pc directed dorsally and that of the farside Pc perpendicular to bedding. The S elements are more widely separated than in laterally flattened assemblages and the far Sc element has become flipped over so that the denticles of the posterior process point downwards; a similar inversion is shown by the far Pd element. A photograph of the model taken from the side and slightly above replicates these features (see figure 14) and shows the same ordering of S elements. A similar arrangement is shown by specimen C530 (see figure 15) but in this case the nearside P and M elements are positioned above those of the farside. This is replicated by a view of the model from the side and slightly below.

Specimen 632 (see figures 16 and 17) has a similar pattern to the laterally flattened configurations, except that the nearside row of M and P elements is set a little behind and below the far row and the far Sc is positioned well above the remainder of the S elements. This arrangement can be reproduced by photographing the model from a little above and in front of the direct lateral aspect (see figure 18).

A photograph of the model from the anterior (see figure 19) shows details of the architecture of the apparatus that are not clear from other views but are

necessary to explain all the bedding plane assemblages. In this view, the S elements are arranged in an arc. The cusp of the axial Sa element is vertical; away from the axis, those of the other S elements become increasingly inclined inwards so that the Sc element cusps are at about 45°. The lateral processes of each M element lie in a single plane, which is also inclined at about 45°. The Pa and Pb elements are vertical but the cusps of the Pc and Pd elements are inclined inwards at about 30° and 20° respectively to the horizontal.

4. THE FUNCTION OF THE *PROMISSUM* APPARATUS

Although we are confident of our geometrical reconstruction of the *Promissum* apparatus, interpretation of its function is more difficult. However, our reconstrutions of element morphology and apparatus architecture do impose a number of constraints and, for the first time, we can consider the function of prioniodontid elements as components of an integrated feeding apparatus.

Evidence for the location of the conodont apparatus in the body comes from specimens with soft part preservation from the Carboniferous Period in Scotland (Briggs *et al.* 1983, Aldridge *et al.* 1993). No specimens preserve any trace of the body around the apparatus but its position, ventral and immediately posterior of the eyes (Aldridge *et al.* 1993), indicates that it lay in
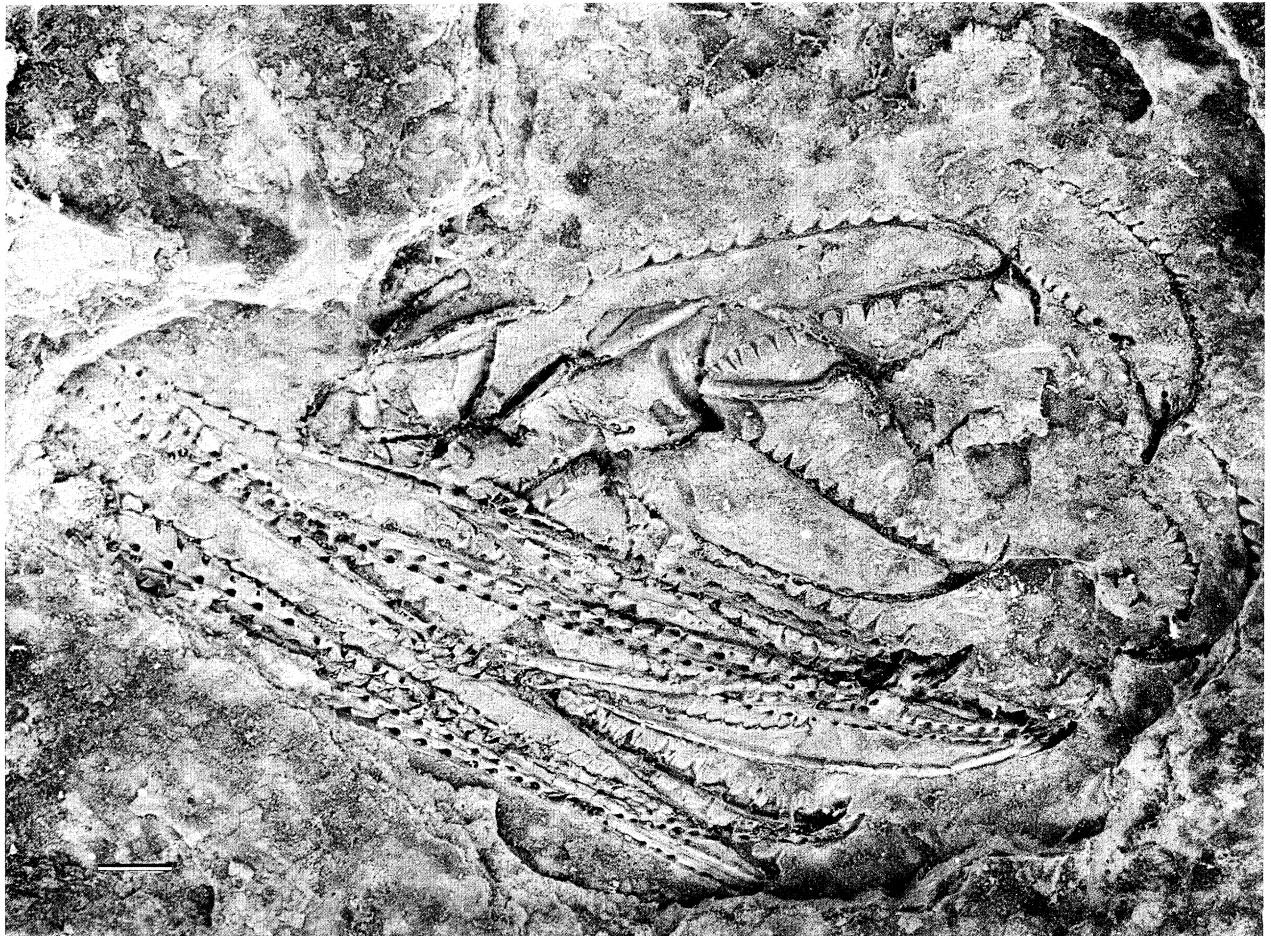
Figure 15. *Promissum pulchrum* specimen C 530; scale bar 1 mm.

the oral cavity with the opening to the pharynx probably behind the Pa elements. Recognition of homologies between the apparatuses of *Promissum* and ozarkodinids and the location of the apparatus relative to the eyes (Aldridge & Theron 1993) indicate that the *Promissum* apparatus occupied a similar position. However, the apparatus of *Promissum* is more complex than that of ozarkodinid conodonts and differs in several important respects.

One of the key features of the ozarkodinid apparatus is its spatial differentiation into an anterior array of M and S elements and a more posterior set of P elements (see figure 2). This reflects a functional division of the apparatus, with these anterior and posterior sets of elements responsible for food acquisition and processing, respectively. The anterior M and S elements have been interpreted as a suspension-feeding system (Nicoll 1985, 1987) or a set of grasping teeth (e.g. Briggs *et al.* 1983; Aldridge *et al.* 1987; Purnell 1993*a*); but recent ontogenetic analyses of ozarkodinids indicates that they could not have been suspension-feeders (Purnell 1993*a*, 1994). Food processing by the Pa and Pb element may have been by gentle bruising and mashing (Nicoll 1985, 1987), but if the S and M elements grasped food, shearing and grinding (Briggs *et al.* 1983; Aldridge *et al.* 1987; Purnell & von Bitter 1992; Purnell 1993*a*, 1994) is more likely.

The anterior–posterior differentiation shown by ozarkodinids does not occur in the *Promissum* ap-

paratus. The P elements are positioned above, not behind, the S elements and the apparatus could not have operated in precisely the same way. *Promissum* does, however, possess two sets of elements that are morphologically comparable with the two sets in ozarkodinids. The S and M elements are elongate and bear numerous denticles, whereas the P elements are shorter and generally more robust. With such differences in morphology these two groups of elements must have performed different functions.

The morphology and arrangement of the S and M elements of *Promissum* suggest two alternative interpretations of function, similar to those suggested for ozarkodinids. They may have been a fixed filtering array, analogous to the gill arches and rakers of living suspension-feeding vertebrates, or they may have formed a movable grasping apparatus. Preservation of the *Promissum* apparatuses is too poor for element growth rates to be determined, so the suspension-feeding hypothesis cannot be directly tested by ontogenetic analysis (cf. Purnell 1993*a*, 1994). It is probable, however, that the S array was not fixed but could move forwards and this forward mobility of elements lends some support to the grasping hypothesis. The evidence for this movement comes from the angular relation between the posterior processes of the S elements and a line drawn through the Pa, Pb and Pc elements. In most laterally collapsed apparatuses these intersect at an angle of approximately 30°–50° (e.g.
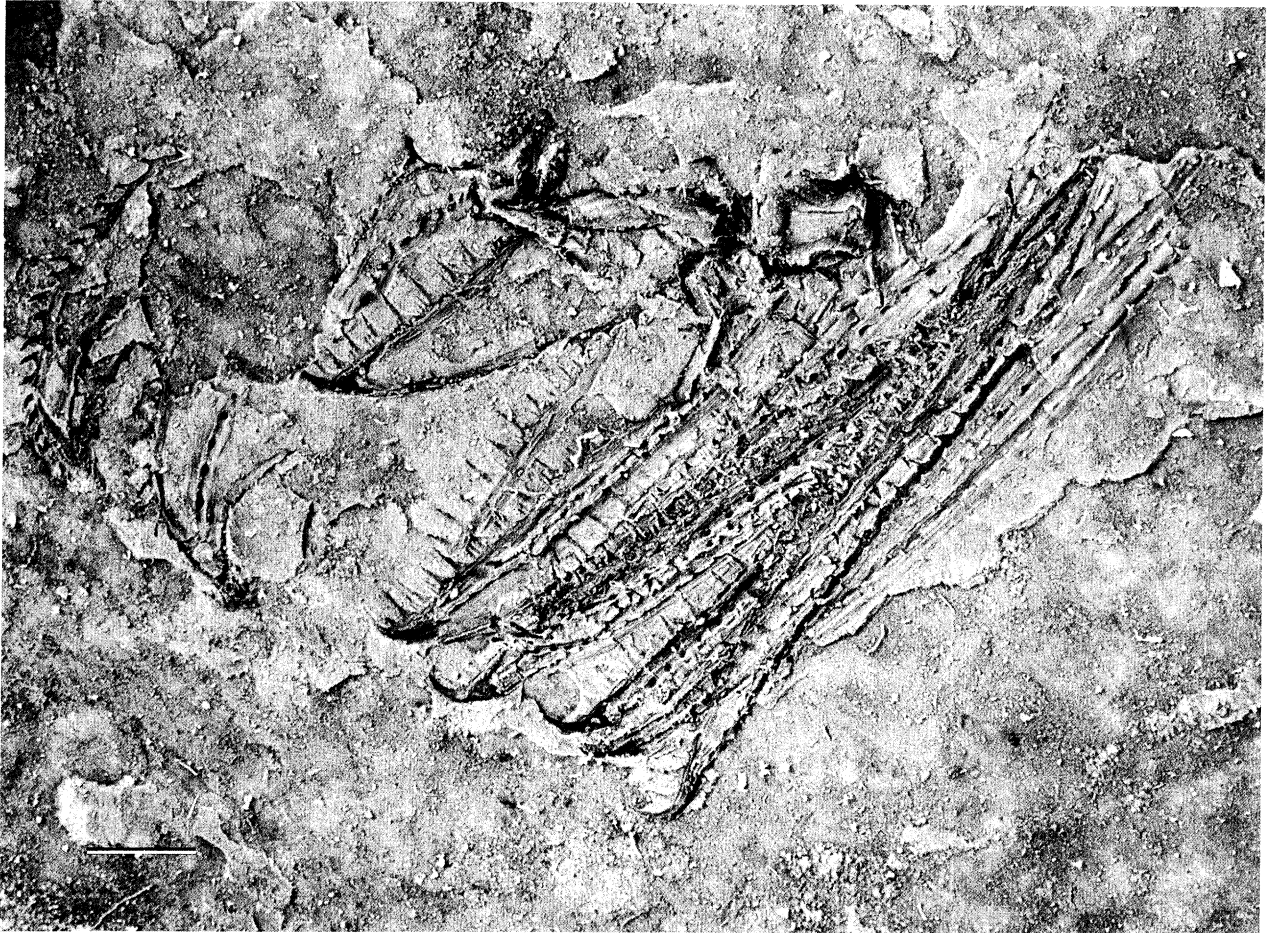
Figure 16. *Promissum pulchrum* specimen C 632; scale bar 1 mm.

figures 5, 16 and 17), but in a few specimens (e.g. figure 4) the S element posterior processes lie almost parallel to the Pa–Pc line. This difference in angle cannot be accounted for by differences in collapse orientation of the apparatus; it must reflect real variability in the original relative inclination of the S elements. Figure 4 also shows the S element cusps to be further forward than in the 'standard' arrangement, indicating that the whole S array has rotated forward about an axis located close to the Pb elements.

The only plausible interpretation of the function of the P elements is that they were involved in processing food collected by the S and M elements. The Pa, Pb and Pc elements were opposed across the axis of the animal and the close complementary symmetry of the Pa and Pb pairs indicates that they worked against one another to masticate food. Their surfaces were probably brought into contact by vertical rocking or rotation similar to that proposed for ozarkodinid Pa elements (Purnell & von Bitter 1992). However, the pyramidal shape of *Promissum* Pa and Pb elements would not have allowed close occlusion of their working surfaces. Without close occlusion they could not have processed microscopic food and it therefore seems most unlikely that the S elements were a suspension-feeding system. The Pa and Pb elements would, however, have worked as effective crushing teeth on the larger food items captured by a grasping array. Unfortunately, preservation of elements is too poor to enable testing of

this hypothesis by observation of crushing related defects in the surface of the Pa and Pb elements (cf. Weddige 1990).

Consideration of the whole apparatus suggests that *Promissum* was a macrophagous organism with a complex set of movable mouthparts functioning as grasping and food processing teeth. Understanding the details of the movement of these teeth is probably not possible, but the feeding process must have involved a sequence of events – with food acquisition preceding trituration. The first stage of feeding probably involved forward rotation of the S elements into a position where the P elements were no longer between them. In this position they could grasp food by simple bilateral closure of the two sides of the array, with the shortness of the Sc elements ensuring that the P elements did not interfere with closure. Next, the M elements rotated down and back, their curved denticulate processes tearing off pieces of ensnared food and moving it towards the Pc elements. The Pd elements and the anteriorly inclined denticles of the lateral processes of the S elements would have prevented the food from being pushed below and behind the Pc elements.

The second stage of feeding, the trituration of food, was performed by the Pa–Pc elements. The Pc elements probably operated by rocking against one another; occlusion proceeding from posterior to anterior. These elements were inclined inwards and twisted such that, in addition to possible slicing of food, rocking would
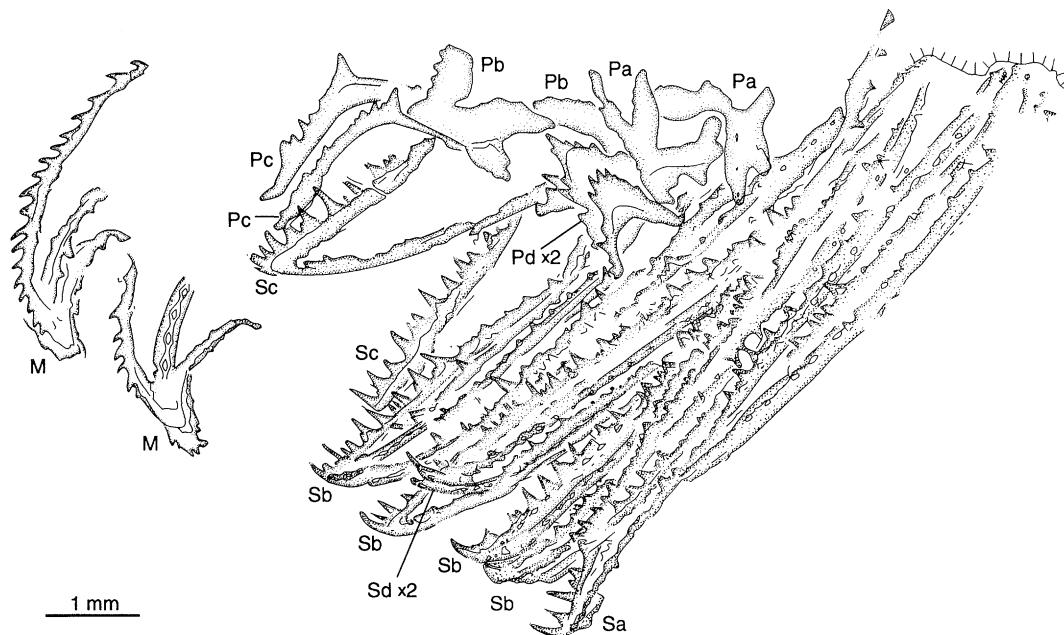
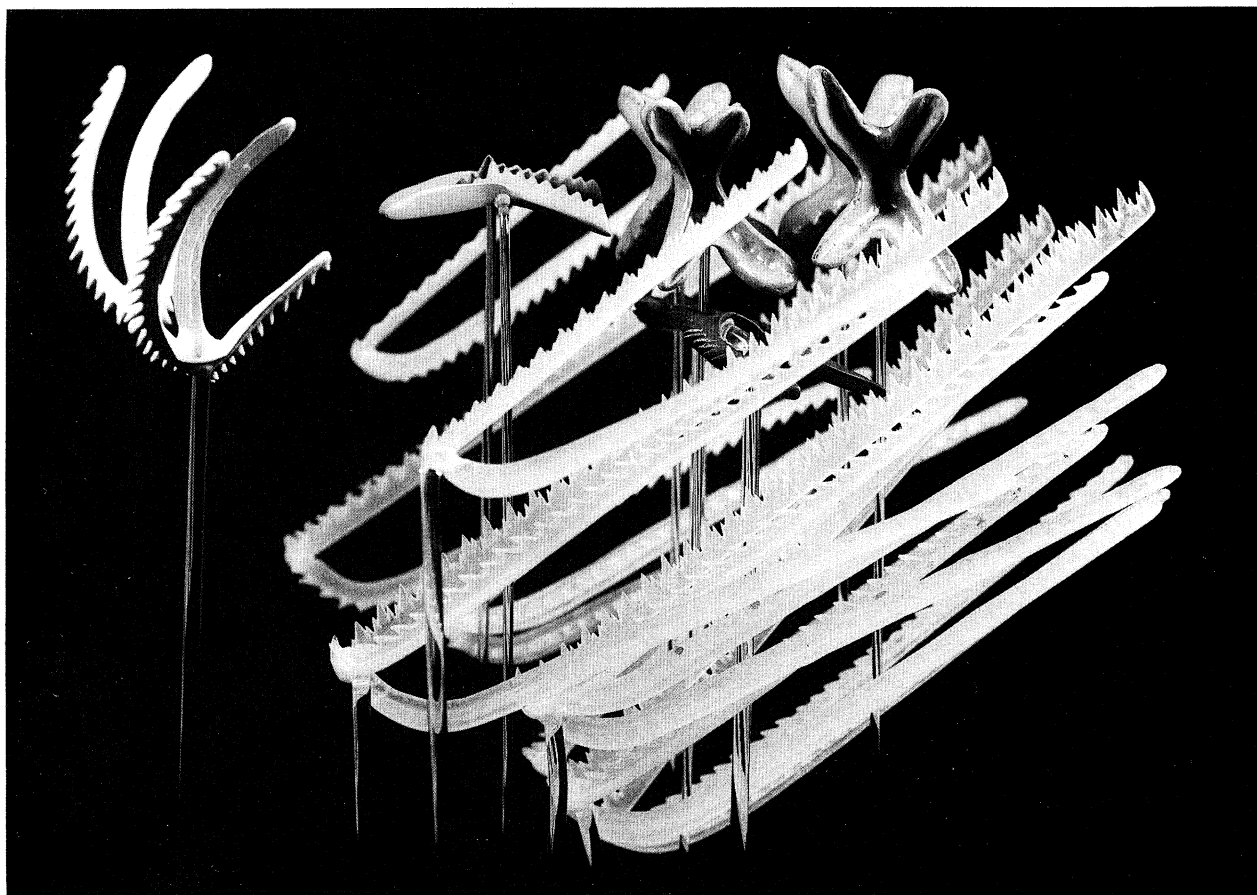Figure 17. *Promissum pulchrum* specimen C 632; camera lucida drawing.

Figure 18. Model of the apparatus of *Promissum pulchrum* photographed from slightly forward and a little above to simulate near lateral collapse, as shown by specimen C 632.

have propelled food posteriorly and upwards, towards the Pb elements. The function of the Pb and Pa elements was to crush the food between their occluding surfaces, prior to its entry into the pharynx.

The question of what *Promissum* ate is difficult to answer. A scavenging mode of life is possible but *Promissum* was also capable of predation; the curvature of the S element cusps and the slight backward inclination of their posterior process denticles, together with the shape and location of the M elements, would have ensured that once in the mouth, food could not have escaped forwards. Direct evidence for trophic interactions in the Soom Shale is lacking but our hypothesis of feeding in *Promissum* does constrain
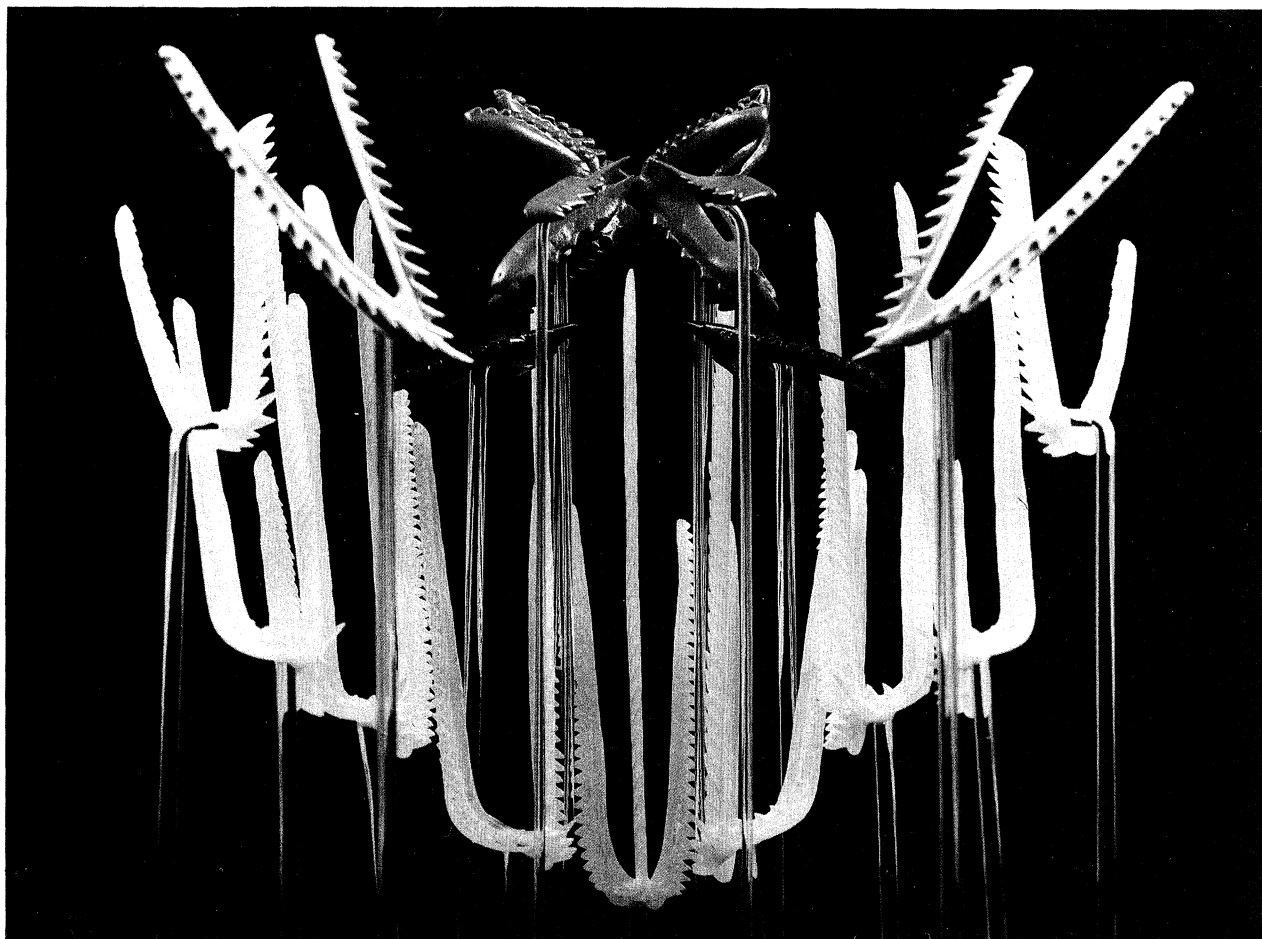
Figure 19. Model of the apparatus of *Promissum pulchrum* photographed from the front to show details of the architecture not apparent in other views.

speculation over what it may have eaten. Potential food items in the Soom Shale fauna include: orbiculoid brachiopods, orthocone nautiloids, eurypterids, naraoiids, polychaete worms, soft bodied problematica and the enigmatic *Siphonacis* (Chesselet 1992). Of these, orbiculoid brachiopods are common and occur as faecal masses of fragmentary material. They were, however, a little large to have been eaten by *Promissum* and it is unlikely that the apparatus was able to crush their heavily mineralized shells. The orthocones, eurypterids and naraoiids were too large to have been prey for *Promissum*, but the remainder of the fauna may have been eaten. Also, disarticulated masses of broken *Promissum* elements have been found in association with articulated *Promissum* apparatuses; *Promissum* may also have indulged in cannibalism.

5. THE PRIONIODONTID PLAN

The prioniodontids are characterized by the presence of Pa elements with three primary processes, or their derivatives (Dzik 1976). From distributional and morphological analyses of collections of disjunct elements, Sweet (1988) regarded the complete apparatus of a typical prioniodontid to be fundamentally seximembrate or septimembrate, comprising two pairs of P elements, a pair of M elements, and a set of S elements of three or four different types. In the absence of any

prioniodontid natural assemblages to provide a template, this reconstruction was based, at least partly, on an understanding of conodont apparatuses derived from natural assemblages of ozarkodinid taxa.

The discovery and interpretation of natural assemblages of *Promissum* allows reconsideration of the prioniodontid plan. The *Promissum* apparatus departs from Sweet's (1988) interpretation, primarily in the possession of four pairs of P elements; we now need to assess the extent to which the *Promissum* architecture may provide a standard for other prioniodontids.

The only direct evidence for the composition of other prioniodontid genera comes from two reports of clusters from Lower Ordovician samples. Stouge & Bagnoli (1988, see plate 8, figures 17A, B) figured a cluster of *Paracordylodus* Lindström from Western Newfoundland, and two clusters of *Oepikodus* Lindström from Greenland were described by Smith (1991). However, all three clusters are incomplete and the elements within them are piled upon one another. This makes them difficult to interpret and limits their their value in determining the closeness of any match with the *Promissum* architecture.

Morphologically, the elements of *Promissum* compare well with those of other taxa from the same family, the Balognathidae (see Sweet 1988, page 63), and it is probable that these close relatives were architecturally similar. However, no other Ordovician prioniodontid

genus has, to date, been reconstructed as having more than two pairs of P elements, although in some cases additional P elements may have been recognized but misinterpreted. For example, the apparatus of the Upper Ordovician *Gamachignathus* McCracken *et al.* (1980) was originally reconstructed as having eight pairs of elements of which two were assigned to e (= M) locations. It is more likely that one of these, possibly the e − 2 (see McCracken *et al.* 1980, plate 10.1, figures 8 and 12) is a Pc or Pd element.

In contrast to the Ordovician, three pairs of P elements have been recognized in a number of Silurian prioniodontid genera: *Pterospathodus* Walliser, *Pranognathus* Männik & Aldridge (Männik & Aldridge 1989) and *Coryssognathus* Link & Druce (Miller & Aldridge 1993). In *Astropentagnathus* Mostler, Armstrong (1990, see pages 59–61) described three pairs of P elements, one pair of M elements (closely similar in style of those of *Promissum*) and a symmetry transition of Sa–Sc elements. However, the complete range of elements found in *Promissum* has not been demonstrated for any other prioniodontid. A four-processed Sd element has not been recognized in any Silurian genus, nor has an element with a morphology corresponding to the *Promissum* Pd. A homologue for the Pd is also difficult to determine in any other Ordovician taxon.

Promissum may have had an unusually complex apparatus, with other prioniodontids possessing a reduced version. This has been suggested, for example, for the Silurian genus *Pterospathodus* Walliser (Theron *et al.* 1990), in which the S array is represented by only Sa/Sb elements. Alternatively, the apparent absence of some elements in other taxa may reflect the fact that until now an adequate template on which to base the reconstruction of prioniodontid apparatuses has been lacking. A rigorous re-examination of well-preserved collections of prioniodontids is now required to test the applicability of the *Promissum* blueprint.

Although the apparatuses of all prioniodontids may not have been as complex as *Promissum*, their element arrangement was probably similar. This has important implications for the assessment of the relationship between the three orders of complex conodonts: the prioniodontids, ozarkodinids and prioniodinids. According to Sweet (1988), the earliest prioniodinid was *Erraticodon* Dzik, from the late Early Ordovician, whereas the first ozarkodinid evolved from the prioniodontid *Plectodina* Stauffer in the late Middle Ordovician. However, known ozarkodinid and prioniodinid apparatuses have similar numbers and arrangements of elements, different from the prioniodontid structure documented here. This suggests that the ozarkodinids have a closer relationship with the prioniodinids than with the prioniodontids. If the times of origin indicated by Sweet (1988) are correct, then the prioniodinids were probably ancestral to the ozarkodinids.

A different scenario was proposed by Dzik (1991); he did not recognize the prioniodinids as a separate order but subsumed them in the Ozarkodinida. He suggested that the evolutionary development of the ozarkodinids from coniform ancestors was through an early Ordovician *Utahconus* Miller-*Histiodella* Harris lineage, whereas the prioniodontids had separate roots

in the coniform genus *Acodus* Pander. The similar S element arrays of prioniodontid and ozarkodinid apparatuses perhaps attest to a rather closer relationship, as it seems unlikely that they had independent origins.

Clearly there are unresolved problems in the early evolution of complex conodont shocks which need to be addressed through careful collection of information and cladistic analysis. Knowledge of element arrangement and apparatus structure will provide fundamental characters for this investigation. Our recognition of a prioniodontid plan is, therefore, an essential step forward in the interpretation of conodont evolutionary patterns and pathways.

APPENDIX. HOMOLOGIES, NOTATION OF ELEMENTS, TAXONOMY AND DESCRIPTIONS

Homologies with ozarkodinid elements

The nine elongate, denticulate elements of *Promissum* are homologous with the nine S elements of the ozarkodinid apparatus (see figures 1 and 6). In both, a symmetrical axial Sa element is flanked on either side by opposing pairs of ramiform elements. In Carboniferous ozarkodinids each of these elements has two processes, with the outer two elements on each side differing slightly from the inner two. They are labelled Sb_1, Sb_2, Sc_1, Sc_2 away from the axis (see figure 2). In *Promissum*, the equivalent positions are occupied by more complex elements with two, three or four processes. Using conventional, morphologically based labelling these would be termed Sb, Sd, Sb and Sc elements away from the axis. A purely locational notation would be preferable but this would result in considerable terminological confusion; for example, four-processed elements very widely termed Sd in the literature would have to be called Sb_2. We have, therefore, continued to use the conventional designations, separating the two pairs of three-processed elements as Sb_1 and Sb_2.

At the front of the *Promissum* apparatus, slightly above the S elements, lies a pair of elements with three denticulate processes. These were tentatively termed Sb elements by Aldridge & Theron (1993) on morphological grounds but do not occur within the S array. From their location we consider them to be the homologues of the ozarkodinid M element.

The four pairs of P elements in *Promissum* form a coherent set to the posterior of the S element cusps, but they are above, rather than behind, the denticulated processes of the S elements. Homologies with the ozarkodinid apparatus are difficult to determine, but

the vertical orientation of the two pairs of platform elements in *Promissum* (e.g. figures 4 and 5) suggests that they are homologous with the ozarkodinid Pa and Pb elements. The other two pairs of P elements in *Promissum* have no homologues in the ozarkodinid apparatus. The blade elements to the anterior of the platforms have been termed Pc elements (Theron *et al.* 1990) and the arched elements below the Pb elements are herein allocated a Pd position. The latter were suggested on morphological criteria to be M elements by Theron *et al.* (1990) and Aldridge & Theron (1993) but their location precludes a homology with the ozarkodinid M.

Taxonomy

Class Conodonta Pander, 1856
Order Prioniodontida Dzik, 1976
Family Balognathidae Hass, 1959
Genus *Promissum* Kovács-Endrödy (in Theron & Kovás-Endrödy) 1986

(i) *Revised Diagnosis*

Apparatus of 19 elements: one pair each of pastiniscaphate Pa and Pb elements, pyramidal with four processes; pair of twisted, angulate Pc elements; pair of bipennate Pd elements, subsymmetrically arched; pair of tertiopedate M elements with curved processes; one alate Sa element; two pairs of tertiopedate Sb elements, one pair more asymmetrical than other; pair of bipennate Sc elements; pair of asymmetrical quadriramate Sd elements. Processes on S elements all very long.

(ii) *Repository of specimens*

Geological Survey of South Africa, Silverton, Pretoria.

Element descriptions

Apparatuses are mostly preserved as leached alumino-silicate replacements (Theron *et al.* 1990) with the elements piled upon each other. Element details are, therefore, not always clear, and single three dimensional elements cannot be isolated by disaggregation of sediment. For these reasons descriptions of element morphology are conflated from a large number of well-preserved apparatuses and a few single elements preserved on bedding planes. Inevitably, understanding of some elements is better than that of others. For example, the Pa element is represented clearly in some assemblages and we are confident of our reconstruction: on the other hand, the Pb element is commonly poorly preserved or disrupted by adjacent elements and our reconstruction is more equivocal; and Pd and Sa elements are obscured by sediment or other elements in most assemblages.

In the descriptions of the *Promissum* elements terms for orientation follow convention (pages W5–16, Sweet 1981) not orientation within the animal. Although this may be biologically confusing, to change orientation terminology now would necessite redefinition of basic morphological terms – rendering all existing descriptions of conodont elements incomprehensible. In

addition, it would become impossible to describe most isolated conodont elements, the apparatus architectures of which are unknown. Hence, we continue to designate the side towards which the cusp apex is curved or inclined as the posterior and a process continuous with the posterior margin of the cusp is termed a posterior process. The denticulate margin of any process is regarded as its oral margin. Full definitions of the terms used in the diagnosis and the morphological descriptions were given by Sweet (1981).

The element sizes given in the descriptions are based on specimens in which process terminations are clearly observable; these do not necessarily include the smallest and largest specimens. It is clear from a number of assemblages, however, that except for the Sc (which is always shorter), the S elements of an individual apparatus are all of approximately the same length.

(i) *Pa element*

One pair, pastiniscaphate (three primary processes, with capacious basal cavity); pyramidal, length greater than height, length 1.3–3.7 mm. Cusp relatively small, gently recurved, triangular in lateral aspect with sharp anterior and posterior edges and an outer lateral costa. Four processes directed away from cusp and strongly downwards, expanded into narrow, thin-walled platforms. Primary posterior process gently curved inwards; proximally with short, sharp ridge confluent with posterior margin of cusp, beyond ridge oral surface bears about nine discrete nodose medial denticles. Secondary lateral process arises from posterior process at distal termination of ridge, directed at about 45° to posterior process, with about five medial nodes. Anterior process confluent with anterior margin of cusp, bearing low, erect, sharp denticles that decrease a little in size distally. Primary, outer lateral process confluent with costa on cusp that diverges from anterior edge proximally; bears about five, low discrete nodes. Basal cavity wide and deep beneath all processes.

(ii) *Pb element*

One pair, pastiniscaphate, pyramidal, very similar in size and morphology to Pa element. Processes may be a little twisted with asymmetrical development of platforms about medial axis of process, especially distally on posterior process. Secondary lateral process may be shorter than on Pa.

(iii) *Pc element*

One pair, angulate pectiniform (arched blade with anterior and posterior processes), length 1.7–4.2 mm. Cusp central, erect, triangular in lateral aspect. Anterior and posterior processes bear discrete, low, rounded denticles; anterior process laterally expanded into narrow platform. Processes commonly flexed in opposite directions giving element a digyrate appearance. Basal cavity not clearly seen on any specimen.

(iv) *Pd element*

One pair, bipennate (ramiform with anterior and posterior processes), symmetrically or subsymmetrically arched; normally incompletely exposed, height at

least 1.6 mm. Cusp prominent, erect. Anterior and posterior processes gently curved, bearing discrete, erect, robust denticles that decrease a little in size distally; proximal denticle on anterior process may be conspicuously larger than remainder. Basal cavity conical with flared lip on one side.

(v) *M element*

One pair, tertiopedate (asymmetrical ramiform with three processes), 2.5–4.6 mm long. Cusp small, reclined, gently recurved. Posterior process curved inwards and a little downwards; outer lateral process a little longer, curved downwards; inner lateral process shorter than others, curved towards the posterior process and twisted outwards a little. Processes bear discrete, proclined triangular denticles of subequal size, directed away from element axis. Basal cavity flanked by small areas of webbing between processes.

(vi) *Sa element*

Single alate (symmetrical ramiform with three processes), axial element, up to 9.3 mm long. Posterior process very long and straight, bearing regular stout, erect, primary denticles with smaller, slender secondary denticles irregularly developed between. Lateral processes probably symmetrically disposed, arising from antero-lateral margins of cusp; processes directed downwards from cusp but curved strongly proximally to become subparallel to posterior process; denticles widely spaced, conical, of subequal size, proclined proximally, increasingly erect distally, and directed away from element axis. Basal cavity small and conical, with small lips.

(vii) *Sb elements*

Two pairs, tertiopedate, 5.3–14.0 mm in length, Sb_2 more asymmetrical than Sb_1. Cusp small, erect or slightly reclined, very gently recurved. Posterior process straight and very long, bearing regular stout, erect, triangular primary denticles with smaller, slender, erect secondary denticles irregularly developed between them and often partially fused to their anterior margins; up to four primary denticles per mm in smaller specimens, 1.5 per mm in the largest. Inner lateral process arises close to anterior margin of cusp, outer lateral process arises medially on cusp; outer process lies closer to posterior process. Both processes long, laterally expanded into narrow ledges, and directed downwards from cusp but curved proximally to become sub-parallel to posterior process; bear conical denticles of subequal size, more closely spaced and proclined proximally, widely spaced distally, directed away from element axis. Basal cavity small and conical beneath cusp.

(viii) *Sc element*

One pair, bipennate, up to 4.8 mm long. Cusp small, upright, gently recurved. Posterior process shorter than those of other S elements (2.3–3.4 mm) but with similar denticulation; four to five large denticles

present per mm. Inner antero-lateral process also relatively short, laterally expanded into narrow ledges, directed downwards from cusp and curved proximally to become slightly divergent from posterior process; denticulation inwardly directed, developed as on lateral processes of other S elements. Basal cavity small and conical.

(ix) *Sd element*

One pair, quadriramate (ramiform with four primary processes), asymmetrical, up to 14.0 mm long in preserved apparatuses, one isolated specimen 18.8 mm long. Cusp small, upright, gently recurved. Posterior and outer lateral processes as in Sb element. Inner face of cusp gives rise to inner lateral and inner antero-lateral processes, both very long, directed downwards from cusp and curved proximally to become subparallel to posterior process; bearing inwardly directed conical denticles of similar style to outer process. Basal cavity small and conical.

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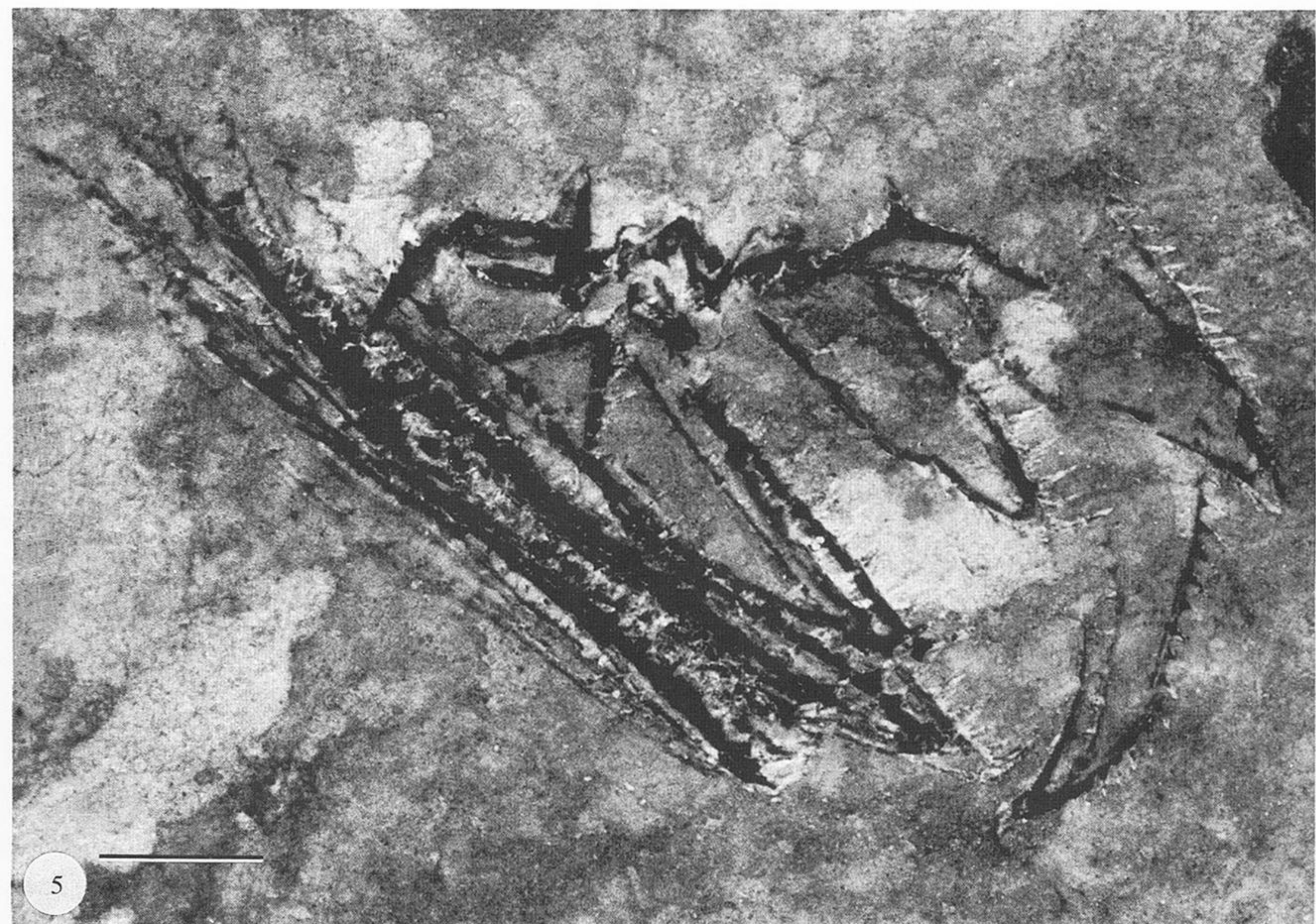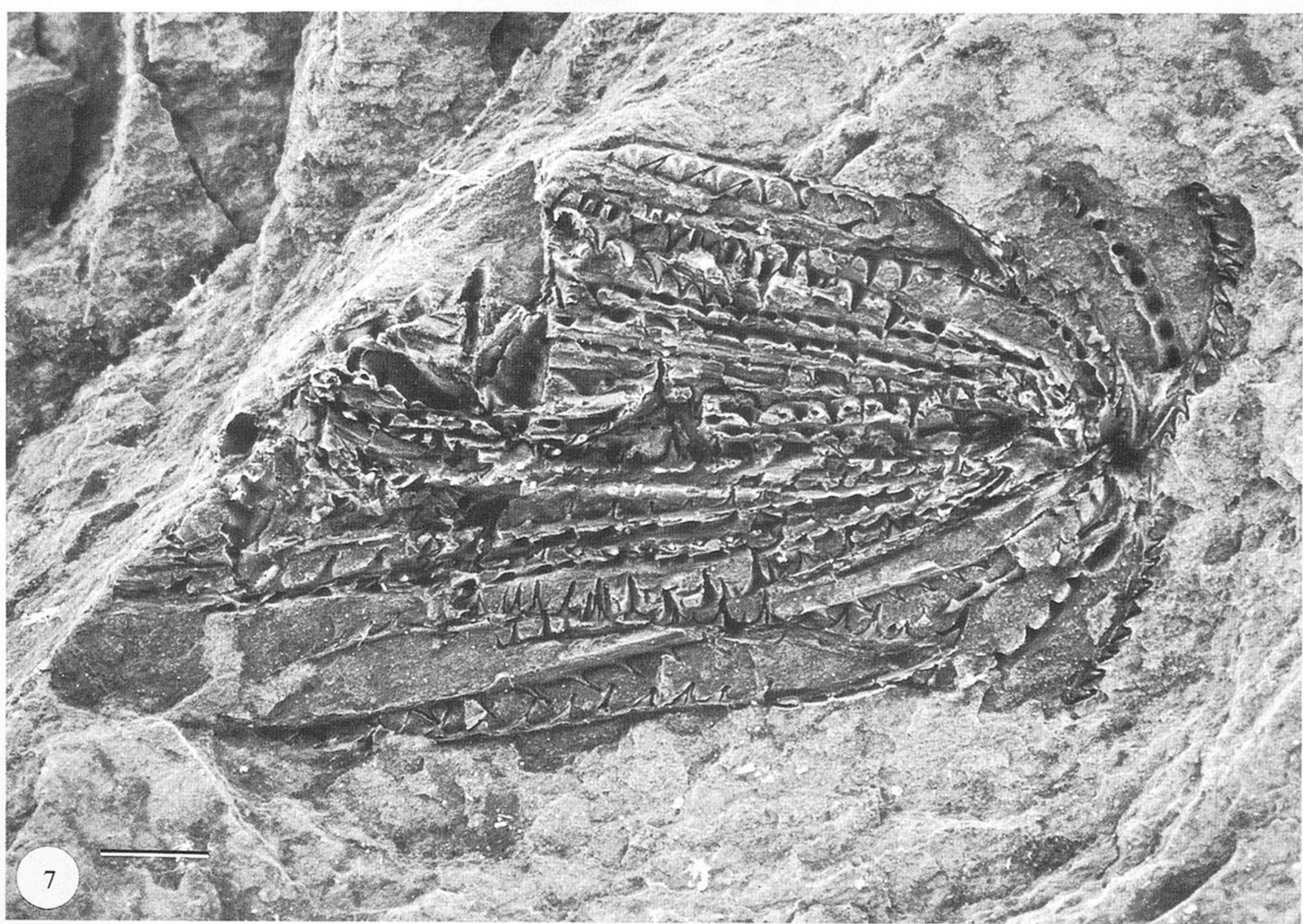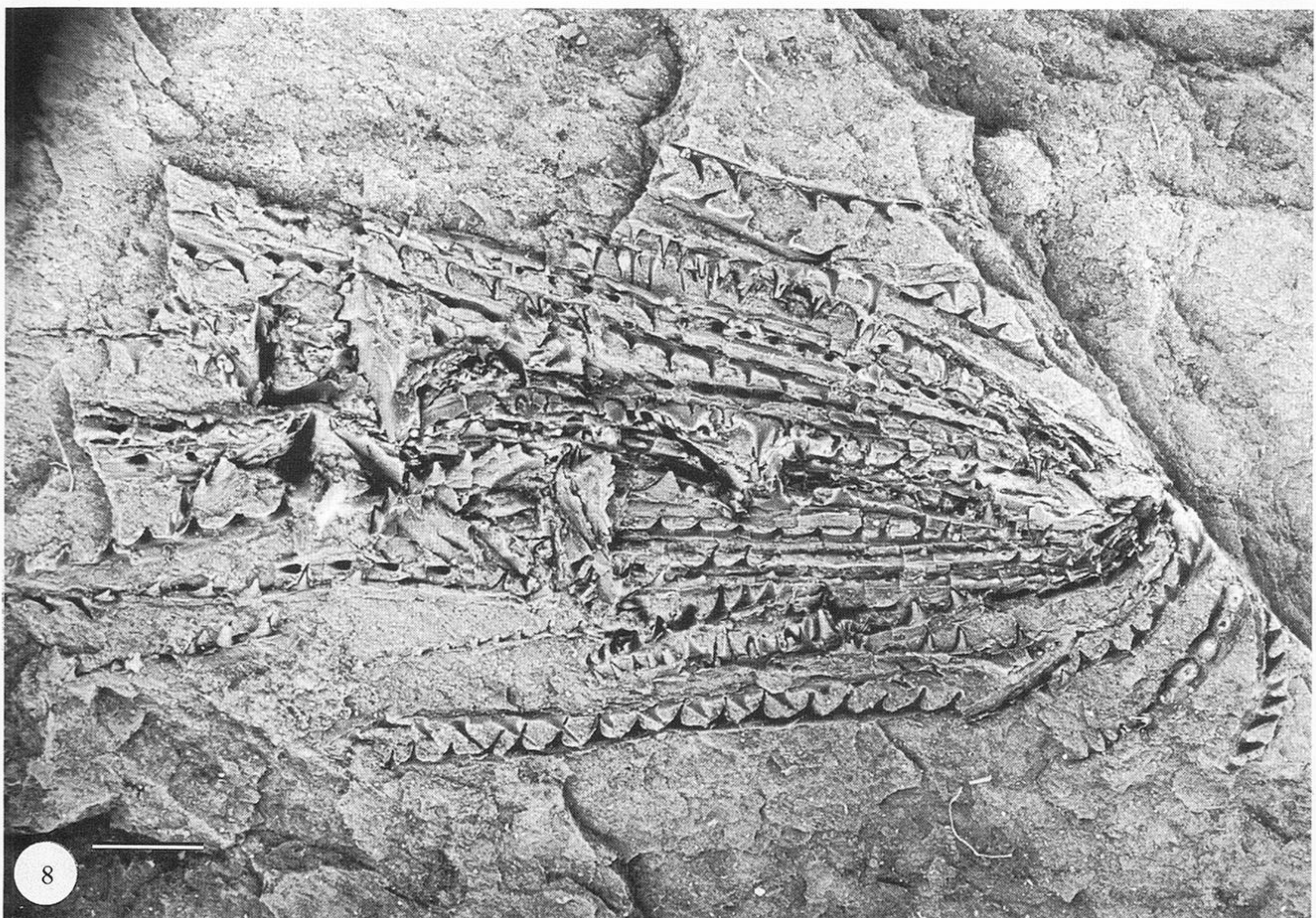Weddige, K. 1990 Pathological conodonts. *Cour. Forsch. Inst. Senckenberg* **118**, 563–589.

Figure 4. *Promissum pulchrum* specimen C 275. Arrows indicate Pa elements. The spines crossing the specimen belong to the enigmatic organism *Siphonacis parva* (Kovács) (see Chesselet 1992). Scale bar 1 mm.

Figure 5. *Promissum pulchrum* specimen C 351; scale bar 1 mm.

Figure 7. *Promissum pulchrum* specimen C 279 part; scale bar 1 mm.

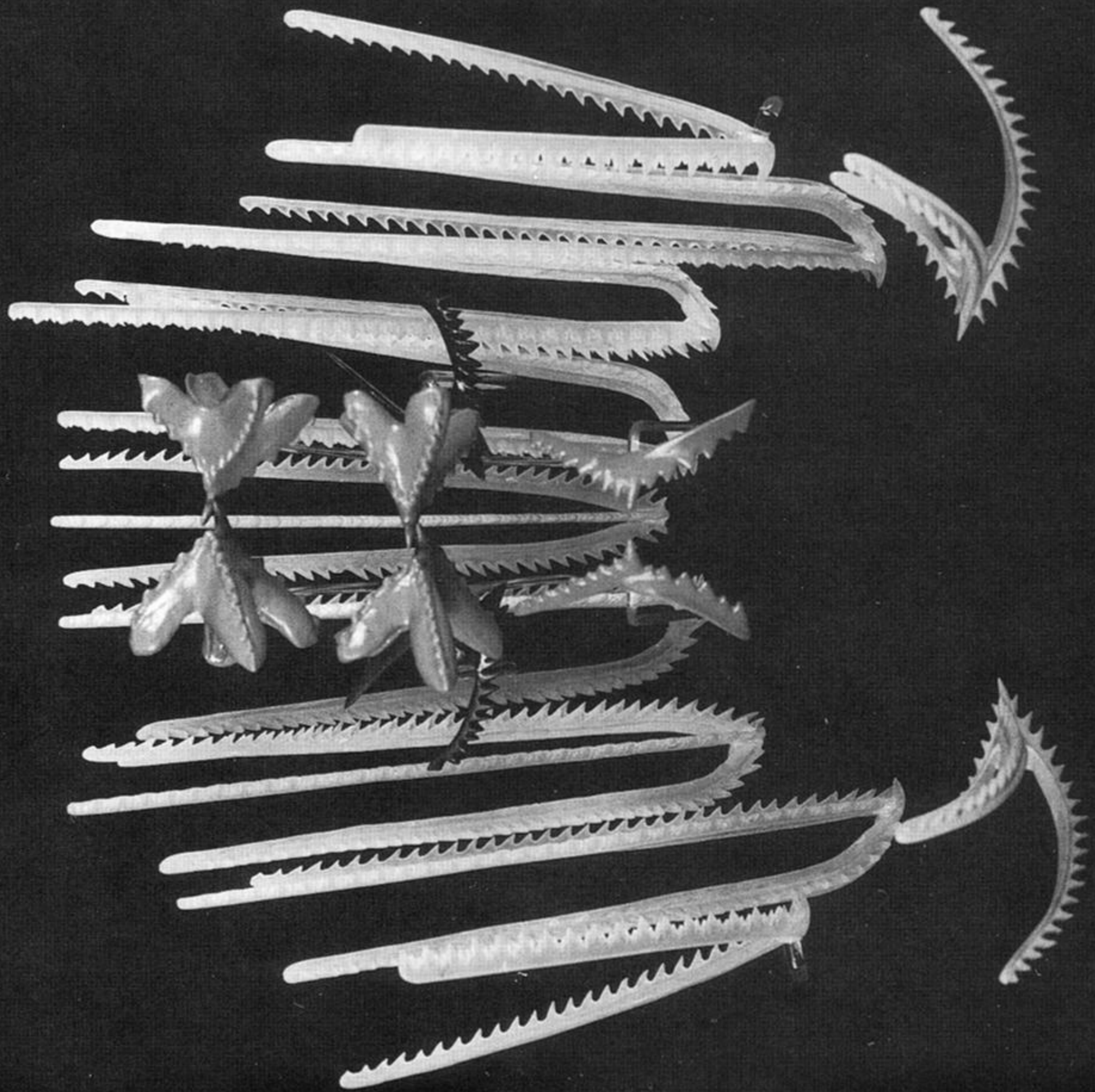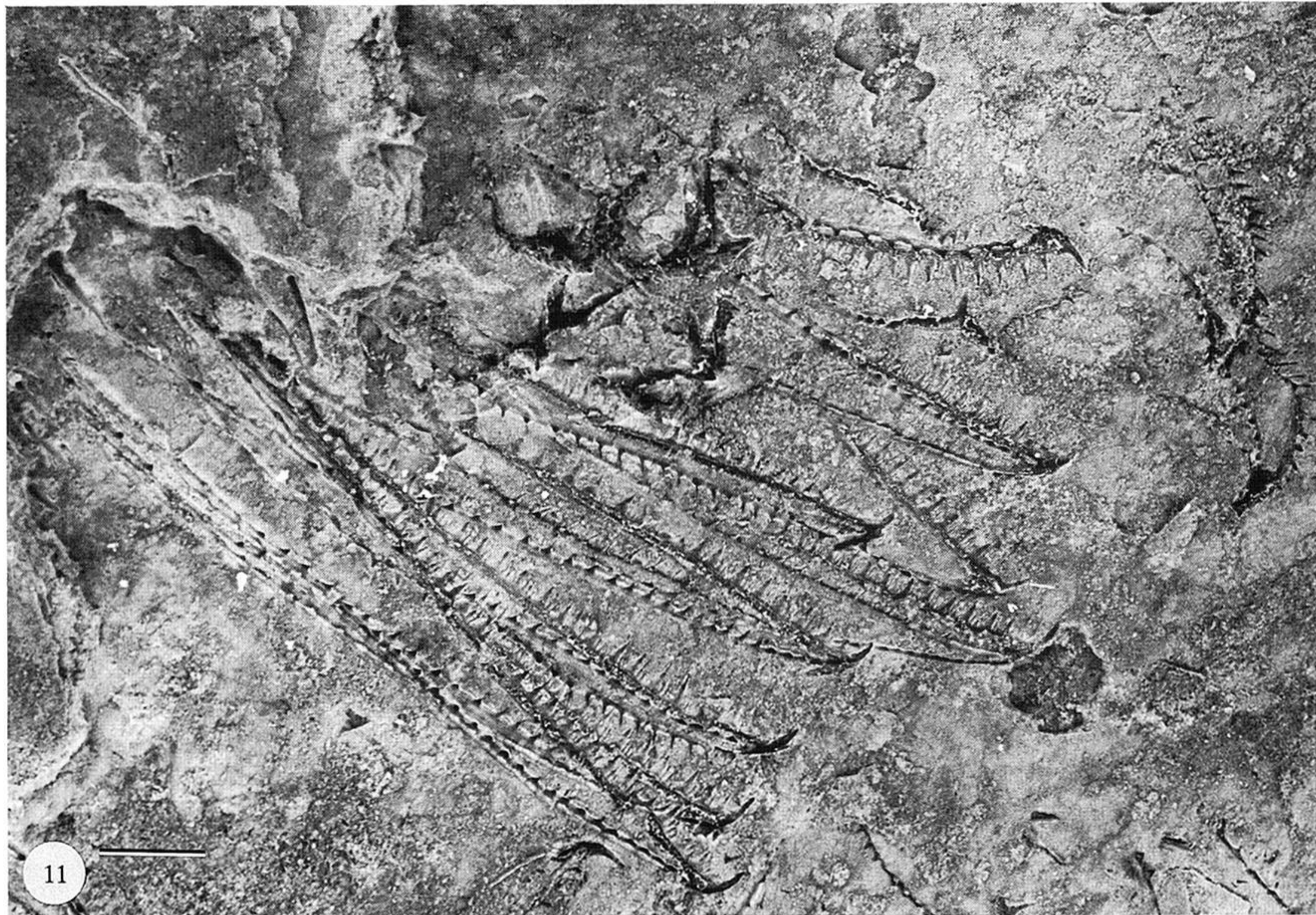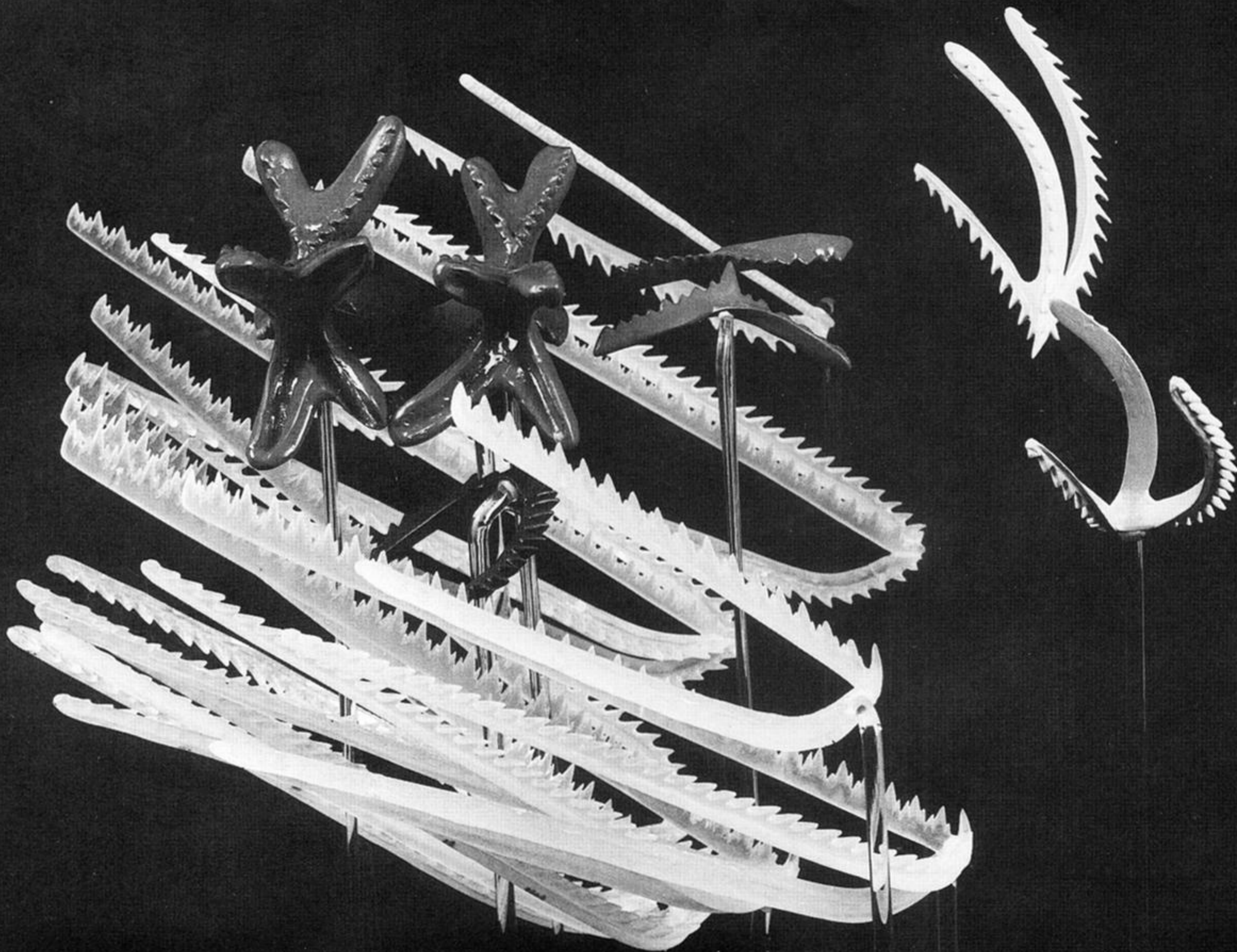Figure 8. *Promissum pulchrum* specimen C 279 counterpart; scale bar 1 mm.

Figure 10. Model of the apparatus of *Promissum pulchrum* photographed from above to simulate dorso-ventral collapse, as shown by specimen C 279.

Figure 11. *Promissum pulchrum* specimen C 616 counterpart; scale bar 1 mm.

Figure 12. *Promissum pulchrum* specimen C 616 part; scale bar 1 mm.

Figure 14. Model of the apparatus of *Promissum pulchrum* photographed from the side and slightly above to simulate near lateral collapse, as shown by specimen C 616.
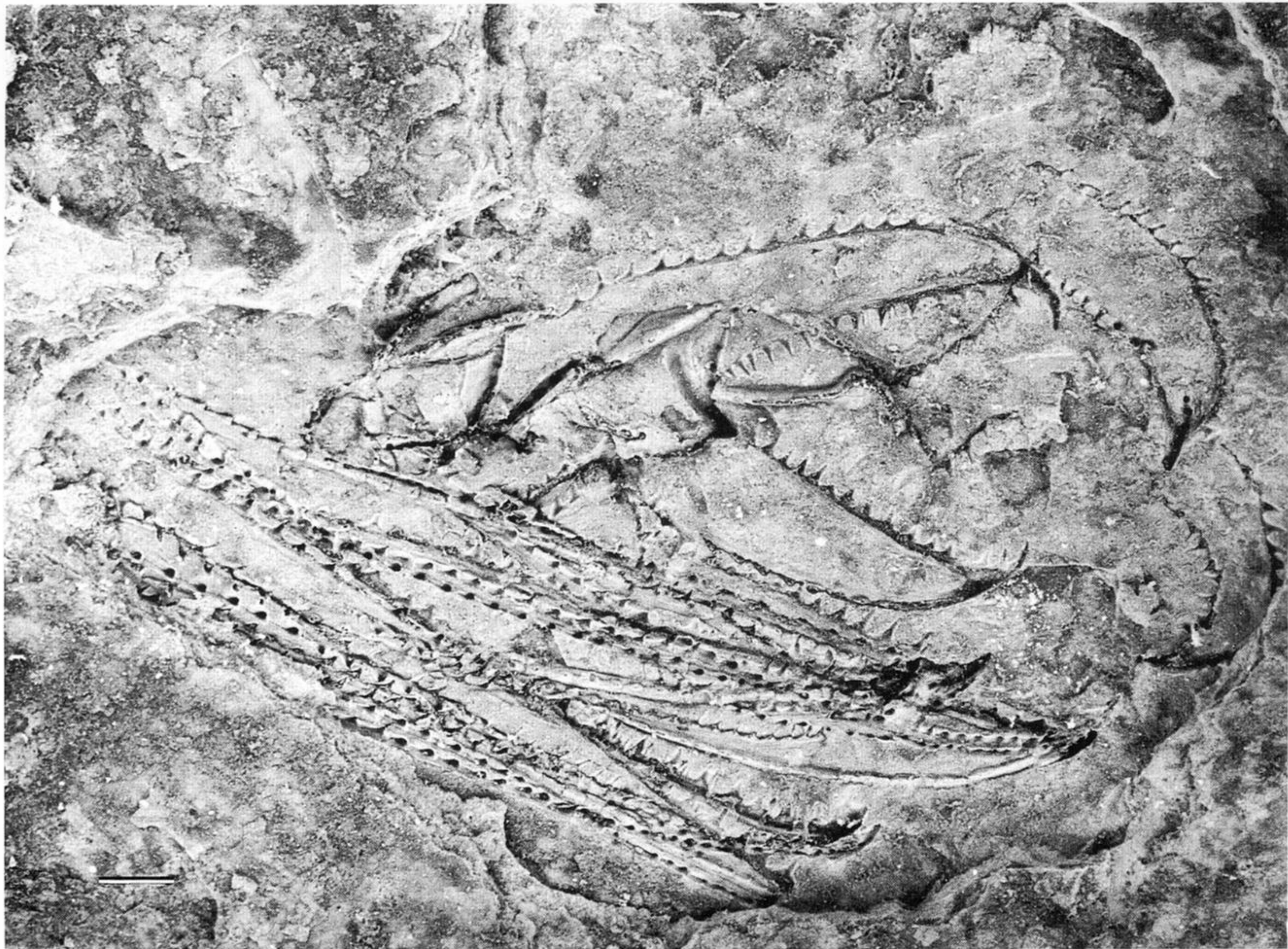
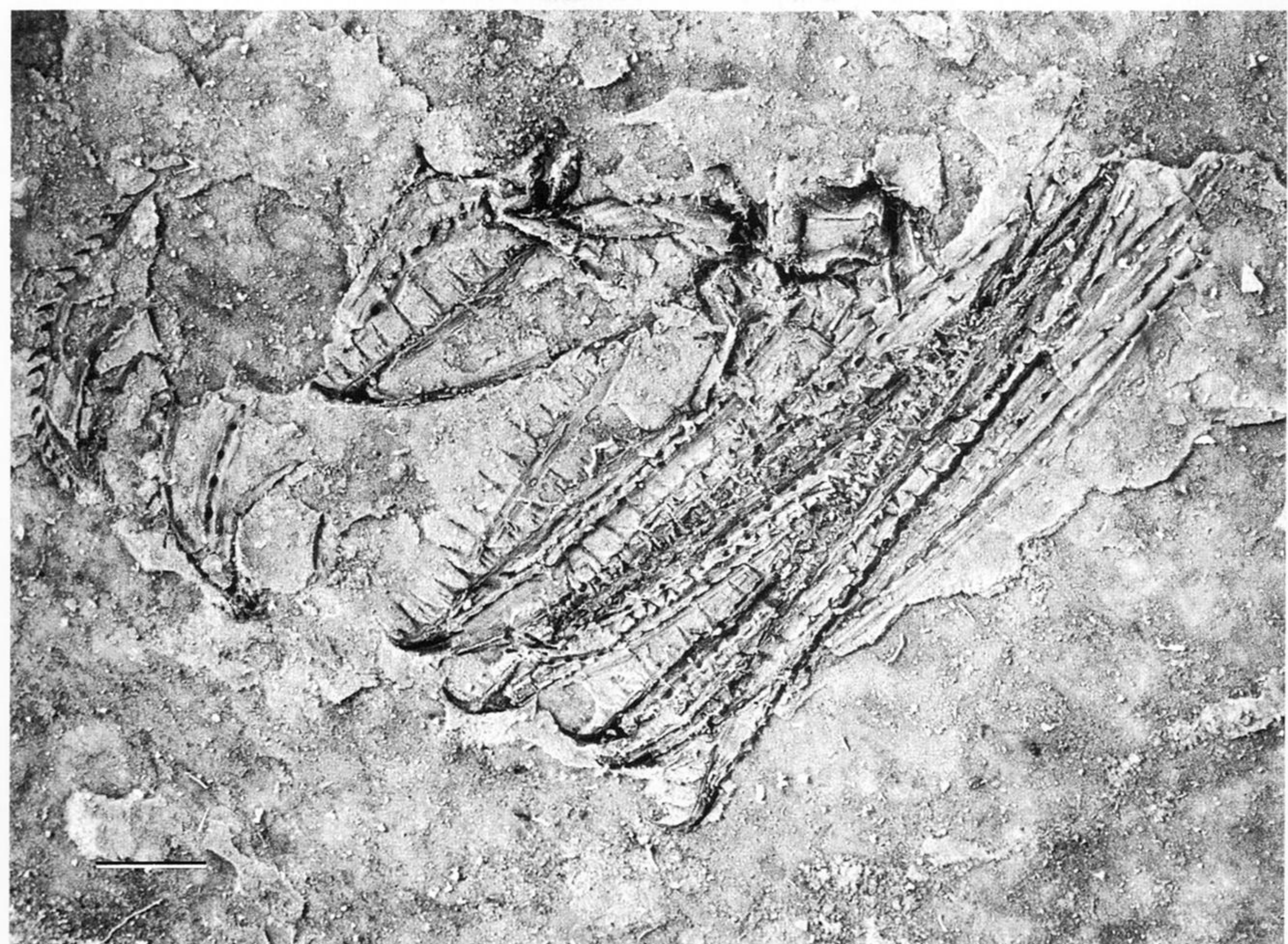Figure 15. *Promissum pulchrum* specimen C 530; scale bar 1 mm.

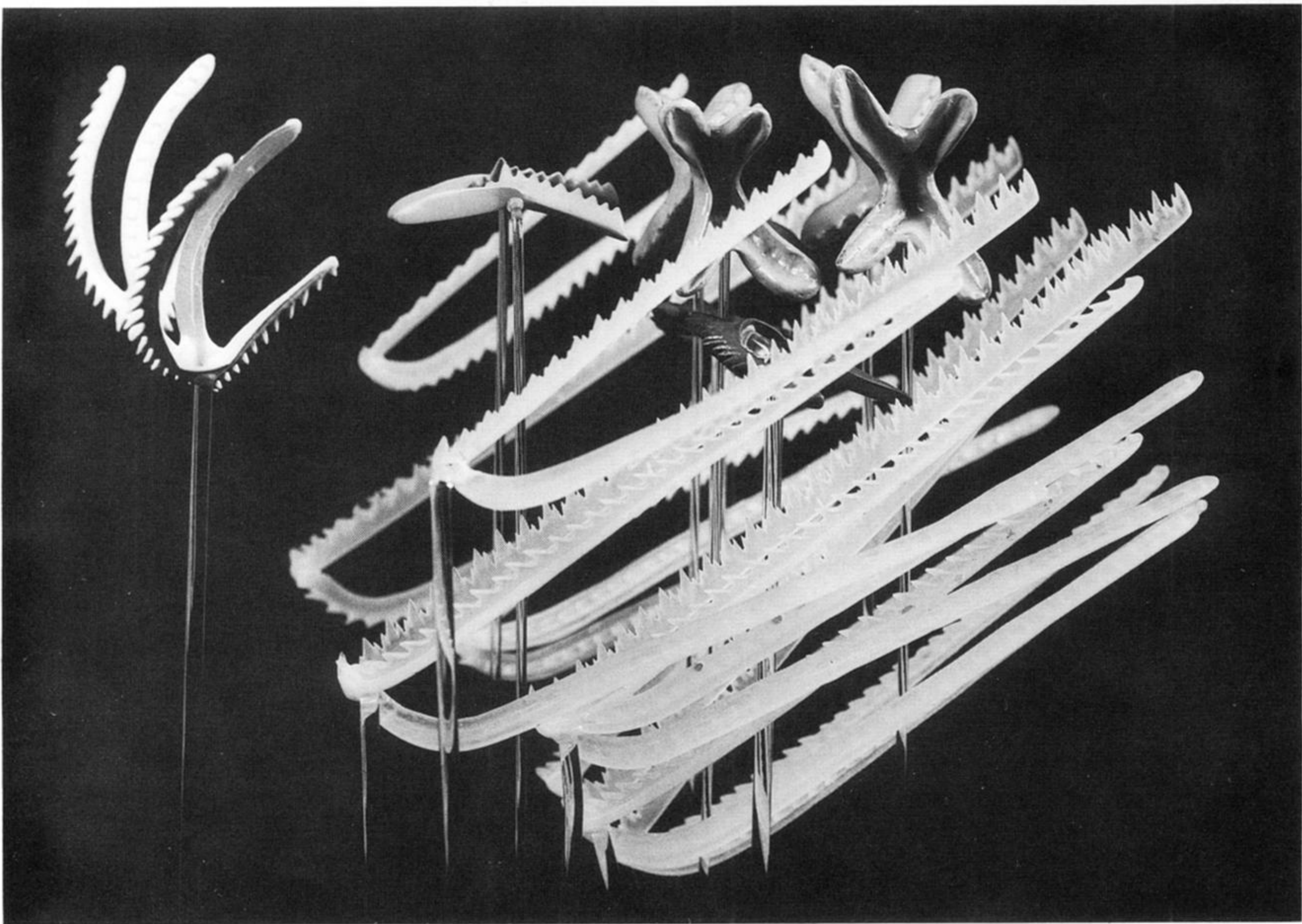Figure 16. *Promissum pulchrum* specimen C 632; scale bar 1 mm.

Figure 18. Model of the apparatus of *Promissum pulchrum* photographed from slightly forward and a little above to simulate near lateral collapse, as shown by specimen C 632.
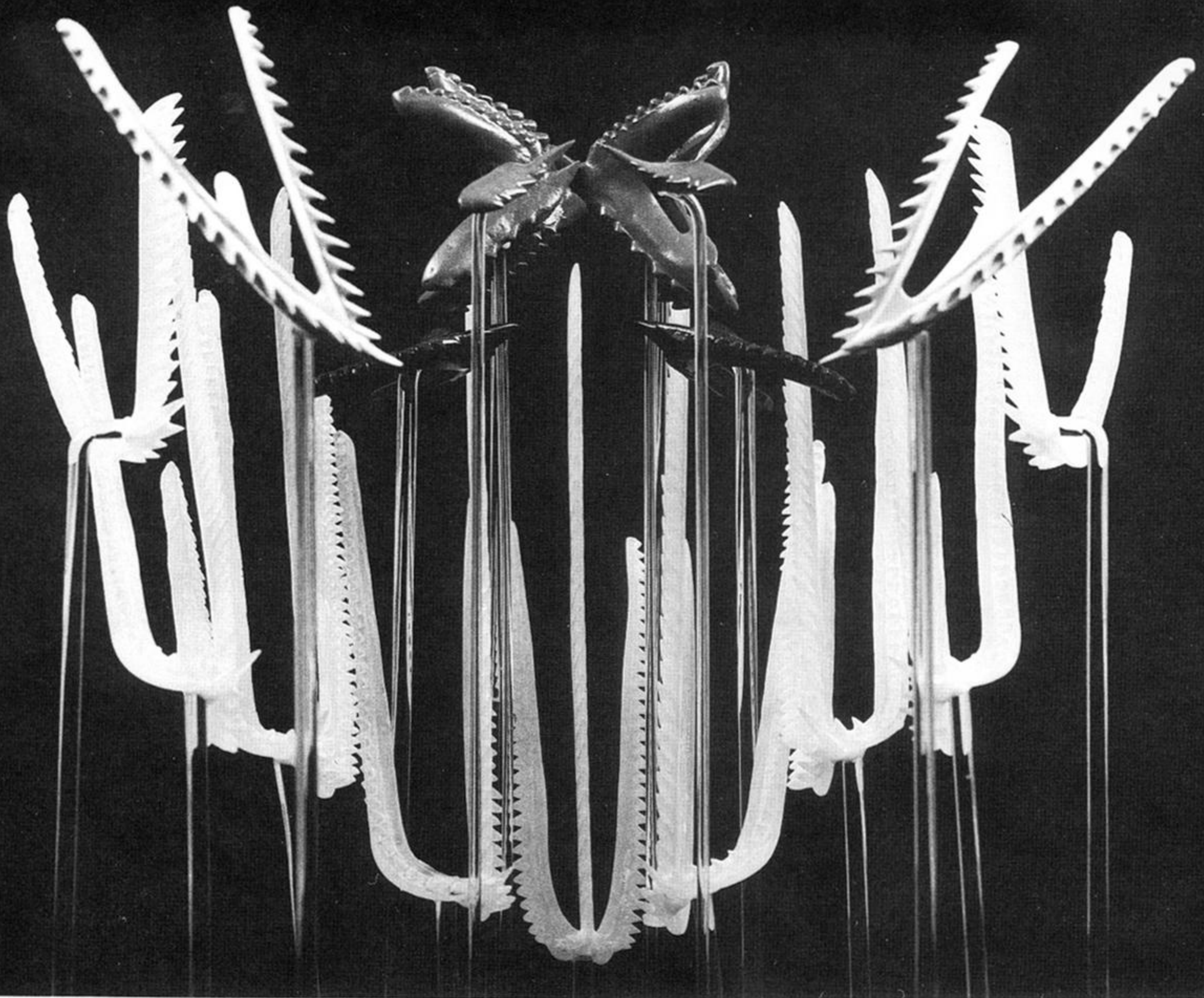
Figure 19. Model of the apparatus of *Promissum pulchrum* photographed from the front to show details of the architecture not apparent in other views.