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Devonian Vertebrates from Australia

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Abstract

A vertebrate microfauna from the Lower Devonian (Emsian) of Australia is described. It is a taxonomically diverse assemblage, including disarticulated dermal skeletal fragments and/or teeth of Thelodonti, Placodermi, Cladodontida, Acanthodii, Onychodontidae, Rhipidistia, and Paleoniscida. Elements of this fauna have been described previously from geographically diverse localities of approximately equivalent age, but this Australian fauna is unique in possessing all of the above taxonomic groups in a single assemblage. This occurrence reinforces previous suggestions that the Lower Devonian fish fauna was widespread and uniform.

Introduction

The vertebrate material discussed below was collected by B. D. E. Chatterton from a series of micrites, biomicrites, and biosparites in the lower 200 feet of the *Receptaculites* Limestone. The *Receptaculites* unit is one of a sequence of limestones of the Taemas Formation (Murrumbidgee Group) that occurs near the locality site (Fig. 1) designated as Locality Γ, Bloomfield Property, Portion 229, Parish of Warroo, near Yass, New South Wales, Australia (personal communication, B. D. E. Chatterton to K. S. Thomson, 1968). The age of the Murrumbidgee Group has been assigned on the basis of its invertebrate and conodont faunas (Philip and Pedder, 1964, 1967; Pedder, 1967; Savage, 1973) as near the Siegenian/Emsian boundary. Chatterton (personal communication, 1978) now places the *Receptaculites* unit itself in the middle Emsian on the basis of conodont occurrences.

The general area surrounding the collection site described here has yielded a large number of vertebrate remains over a considerable period of years. Etheridge (1906) described the dipnoan *Ganorhynchus* (later assigned to *Dipnorhynchus* by Jaeckel, 1927) from this locality, and a series of placoderms were described by Woodward (1941) and White (1952). More recently Schultze (1968) described a microvertebrate fauna that included some, but not all, of the forms described here. Schultze's fauna was also collected from the Taemas Formation, but the majority of it was from the *Spirifer yassensis* limestone, a lithic unit some 800–1200 feet beneath the base of the *Receptaculites* Limestone (Chatterton, 1971). Schultze described scales of the new paleoniscoid *Ligulalepis toombsi* from his fauna, and mentioned the occurrence of fragmentary remains of *Ohiolepis, Ohioaspis,* and *Onychodus* with them.

In addition to the vertebrate material, the *Receptaculites* Limestone contains a diverse invertebrate fauna composed of brachiopods, gastropods, tabulate and rugose corals, trilobites, ostracods, and conodonts. The diversity of this assemblage and

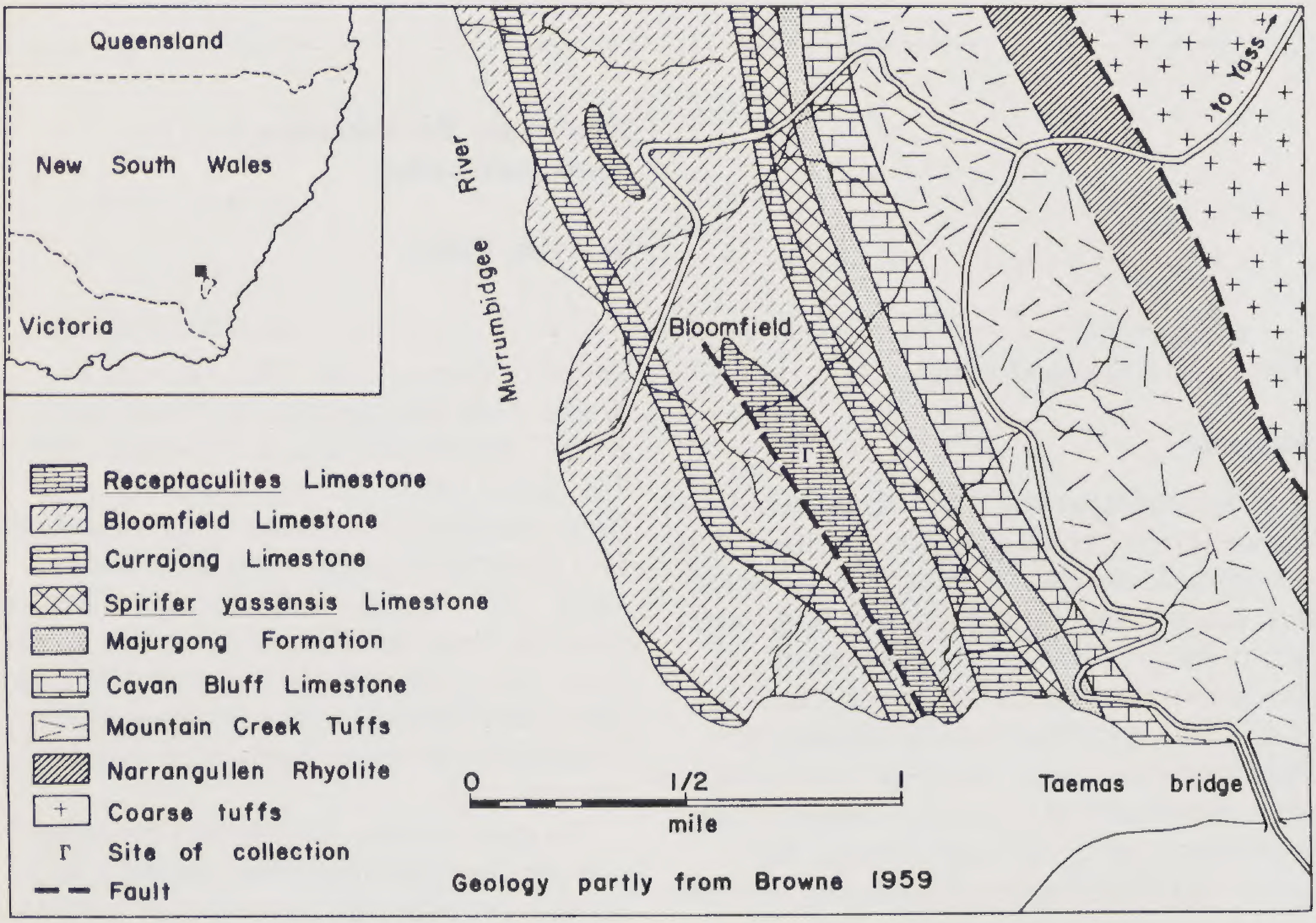

Fig. 1
Collection site of vertebrate fauna, near Yass, New South Wales, Australia. Map prepared by Brian D. E. Chatterton.

the presence of calcareous algae suggest that the environment of deposition was a warm shallow sea of low-to-moderate energy. The regime was apparently strictly marine.

Description of Specimens

The recovery of vertebrate material from the matrix was a byproduct of its preparation for conodonts. This was accomplished by digestion of the rock in 10% monochloracetic acid, sieving, and heavy mineral separation. The resulting vertebrate fossils are extremely fragile and lack all microstructure, although fine surface detail is retained. Unfortunately, damage occurred to some of this very fragile material during the processes required for SEM photography.

The vertebrate fauna, like the invertebrate fauna, is remarkable for its diversity. Although lack of microstructure makes even generic identification difficult, fish remains belonging to a number of the larger taxonomic groups can be recognized. These include Thelodonti, Placodermi, Cladodontida, Acanthodii, Onychodontidae, Rhipidistia, and Paleoniscida, as well as various indeterminate fish fragments.

By far the greatest bulk of the residue consists of acanthodian scales and onychodontid teeth. All of the remaining taxa are represented by only a few specimens. All of the material is now part of the Australian National University collections, numbers 35606 and 35607.

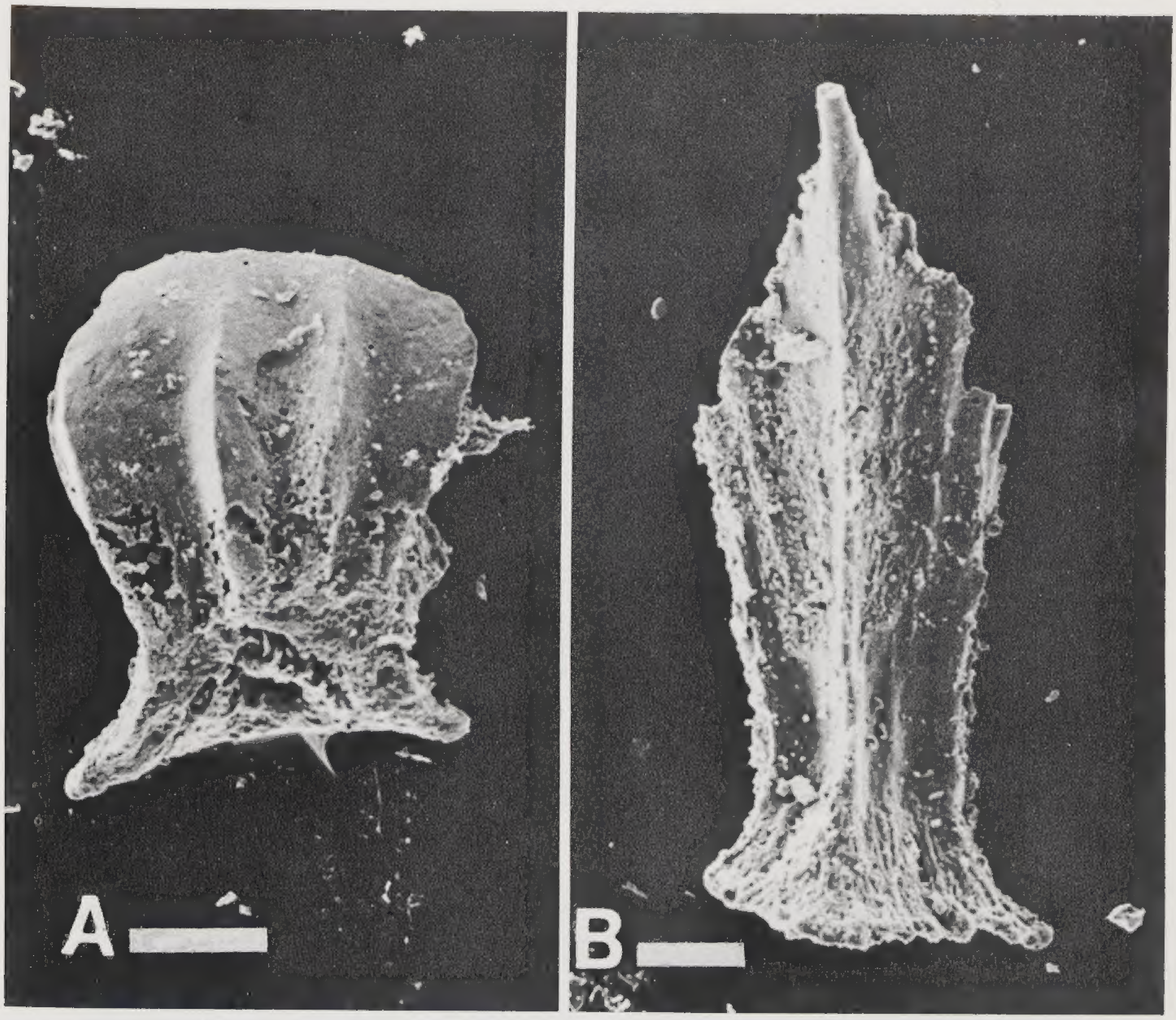

Fig. 2A, B
Skamolepis fragilis, thelodont agnathan scales from the *Receptaculites* Limestone. Scale = 0.1 mm.

Thelodonti

A very small number of scales presumed to be those of the thelodont agnathans were found in the *Receptaculites* Limestone residue. Although at first glance the two specimens figured (Fig. 2A,B) appear to be quite different, they may be considered end forms of the same morphological pattern. This pattern includes a wide open, central pulp cavity and a nearly flat basal plate. The neck is constricted and short. The crown bears a series of linear ornaments and shows suggestions of tripartite structure.

The central pulp cavities of these scales demand their placement in the Thelodonti. Despite lack of histological information, they can be placed in the species *Skamolepis fragilis* because of their remarkable external similarities to this species, which was recently described by Karatajute-Talimaa (1978). *S. fragilis* has been reported previously only from the late Emsian of Latvia and from the Grey Hoek (?Eifelian) of Spitsbergen.

Thelodonts have been reported previously in assemblages similar in age to that found in the *Receptaculites* Limestone. Orvig (1957,

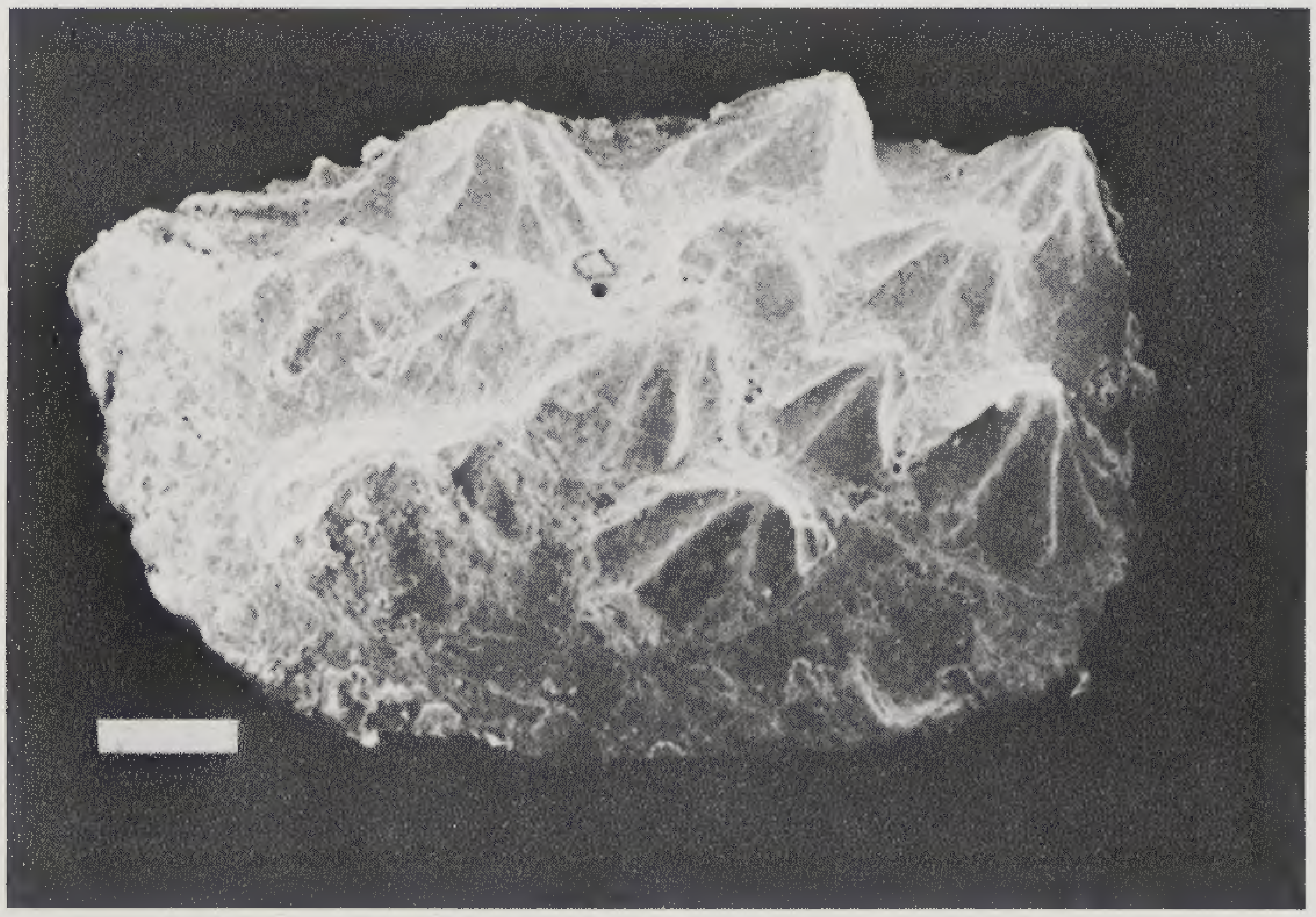

Fig. 3
Ohioaspis tumulosa, placoderm tessera from the *Receptaculites* Limestone. Scale = 0.1 mm.

1969a, 1969b) described the thelodont *Amaltheolepis winsnesi* from the Grey Hoek of Spitsbergen, part of a fauna that also includes fragments of a petalichthyid, *Arctolepis*, a struniiform, and acanthodians. Orvig particularly noted (1969b) that this fauna is unlike the characteristic Emsian/Eifelian fauna that contains ptyctodonts, *Ohioaspis*, *Ohiolepis*, and undetermined Struniiformes from a variety of localities. Schultze (1968) noted the presence of "horn-like thelodontid scales" from this same unit in association with the paleoniscoid *Orvikuina* and *Porolepis*-like scales.

Placodermi

The placoderm material of the *Receptaculites* Limestone consists of dermal tesserae of varying size and generally polygonal shape (Fig. 3). A base and sculptured crown surface can be differentiated, but there is no discrete neck. The base is usually flat or slightly convex, and is often penetrated by several vascular canals. The sculpture consists of star-shaped tubercles which vary in micro-ornament, shape, and number. The tesserae range from 0.5 to 1.2 mm in greatest diameter.

These tesserae closely resemble those placed in the genus *Ohioaspis* by Wells (1944) from the Middle Devonian bonebeds of Ohio, Indiana, and Kentucky. Although Wells recognized three species of *Ohioaspis*, one with four "forms," Gross (1973) has grouped them all into the species *O. tumulosa*. Gross also suggested that *Ohioaspis* and the rhenanid placoderm genus *Asterosteus* are identical, but retained the genus *Ohioaspis* until confirmation of the identity.

In addition to Wells' localities, specimens of *Ohioaspis* have been reported previously from the Murrumbidgee area of Australia by Schultze (1968) and from New York State (Onondaga) and Spitsbergen (Lower/Middle Devonian) by Orvig (1969b).

Cladodontida

Among the vertebrate remains of the *Recep-*

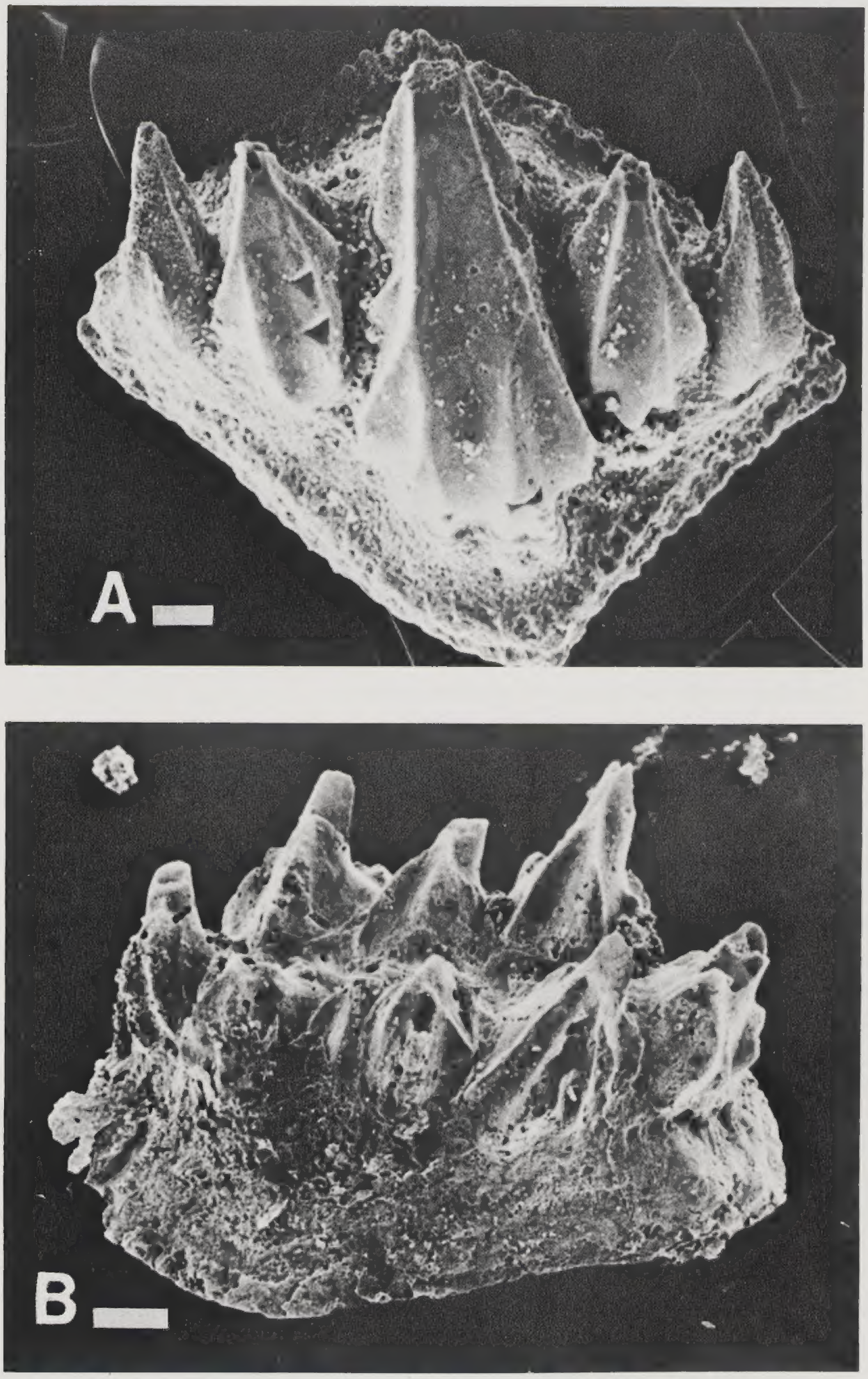

Fig. 4A, B
Ohiolepis sp., cladodont chondrichthyan scales from the *Receptaculites* Limestone. Scale = 0.1 mm.

Fig. 5
Cheiracanthoides comptus, acanthodian scale from the *Receptaculites* Limestone. Scale = 0.1 mm.

taculites Limestone, scales of the cladodont chondrichthyan genus *Ohiolepis* are readily identified by their crown sculpture (Fig. 4A, B). This ornamentation consists of numerous short, posteriorly directed thorn-shaped projections. Although arrangement and size of the projections are variable, they are generally symmetrical in distribution. This pattern and the low, flat profile of the crown are reflections of the scale's growth pattern. Cladodont scales grow by the addition of successive, overlapping, and marginal increments rather than by complete encircling layers as in acanthodians. The ontogenetically oldest part of the scale crown is central in position (Gross, 1973).

The basal outline of the *Ohiolepis* scale is round to rhombic, and forms the largest part of the scale. On some specimens it bears one or more vascular canal openings. The base extends further anteriorly than the crown but is overlapped by crown ornament posteriorly. There is no discrete neck.

Other reported occurrences of *Ohiolepis* include the Middle Devonian of Ohio, Indiana, and Kentucky (Wells, 1944), the Heisdorf beds of Germany (Schmidt, 1961; Orvig, 1969b), the Murrumbidgee Group of Australia (Schultze, 1968), and the Onodaga of New York State (Orvig, 1969b).

Acanthodii

Acanthodian scales are a large component of the vertebrate residue of the *Receptaculites* Limestone. All acanthodian scales present are variants of a single morphological pattern (Fig. 5). The scale base is spherical, and like all acanthodian scales lacks a pulp cavity opening. It is typically broader than the scale crown, and extends further forward than the anterior end of the crown. The neck is low and bears the opening of the vascular system that supplied the crown. The

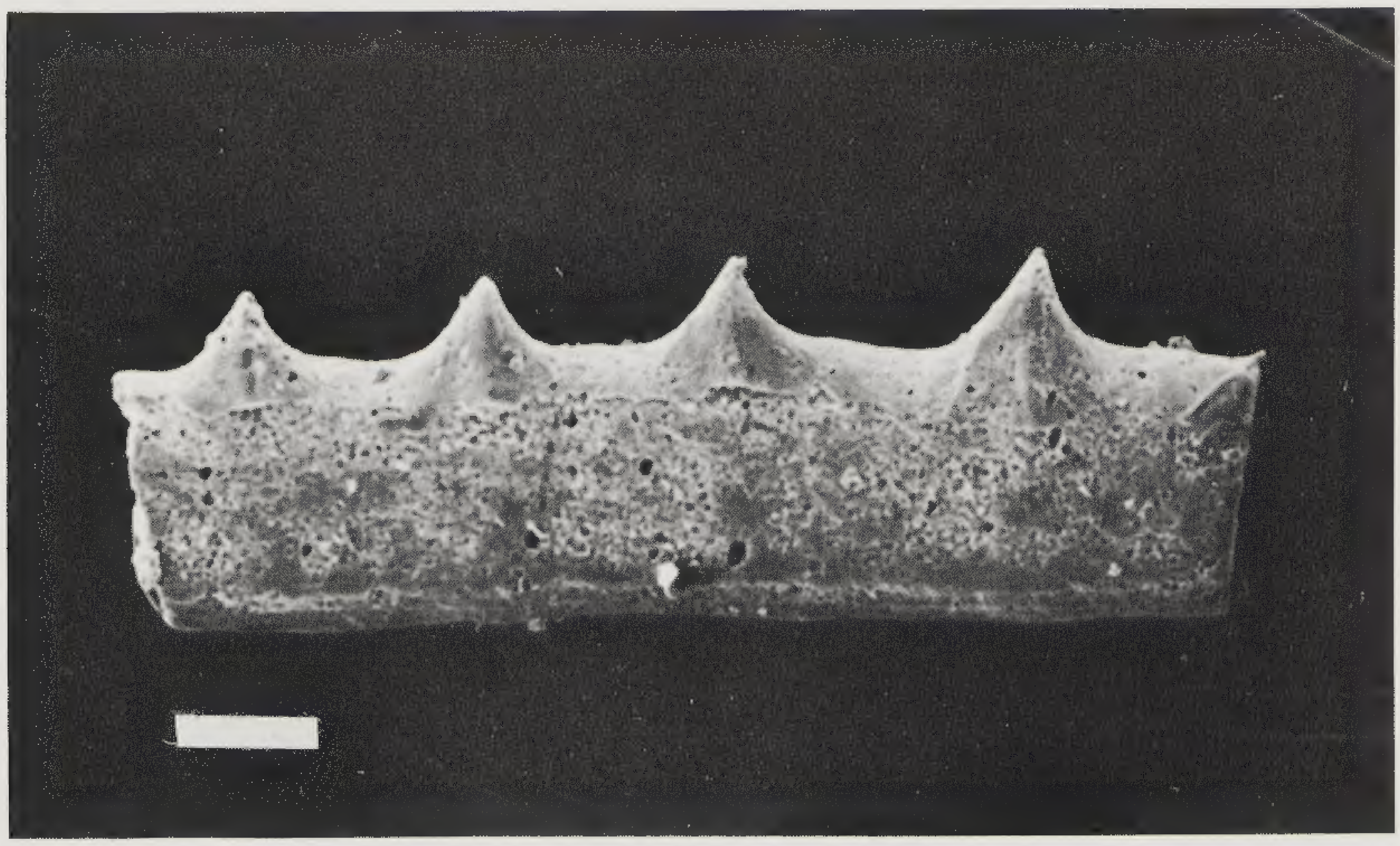

Fig. 6
Indet. acanthodian spine from the *Receptaculites* Limestone. Scale = 0.1 mm.

crown is nearly flat, rhombic in shape, and possesses a pointed posterior tip. The characteristic crown sculpture consists of more or less radial ribs that are broadest at the anterior end of the crown. The ribs narrow and often disappear near the center of the scale. Although microstructure is not preserved in this material, this structural pattern is consistent with acanthodian scale genus *Cheiracanthoides comptus*. *Cheiracanthoides* is known to possess a *Nostolepis*-type histology. Scales range from 0.3 to 0.8 mm in length.

Wells (1944) first described the genus *Cheiracanthoides* from the Middle Devonian bonebeds of Ohio, Indiana, and Kentucky. He recognized a total of two genera and six species on the basis of slight differences in crown sculpture and relative size of base and crown. Gross (1973) grouped all of these variants into the single species *C. comptus*. He reported the genus from various localities near the Ostsee in Germany.

A single specimen of an acanthodian spine was found in the fish residue (Fig 6). This short (0.8 mm) fragment is flattened and very slightly tapered. Its surface is smooth except for a series of four conical projections in a single row. These projections rise perpendicular to the spine shaft without curving.

Acanthodian spine fragments were reported by Wells (1944) from the Middle Devonian bonebeds noted above. He assigned them provisionally to the organ genus *Gyracanthus* because of their similarity to *G. primaevus*, described by Eastman (1908) from the Marcellus of New York State.

The specimen described here differs from *G. primaevus* in the straightness of its conical projections, which are more typical of those of *G. sherwoodi* as illustrated by Newberry (1889). However, the specimen is much smaller than either of these species, and cannot be certainly assigned to either.

Onychodontidae

The onychodont material present in the *Receptaculites* residue consists of both dermal

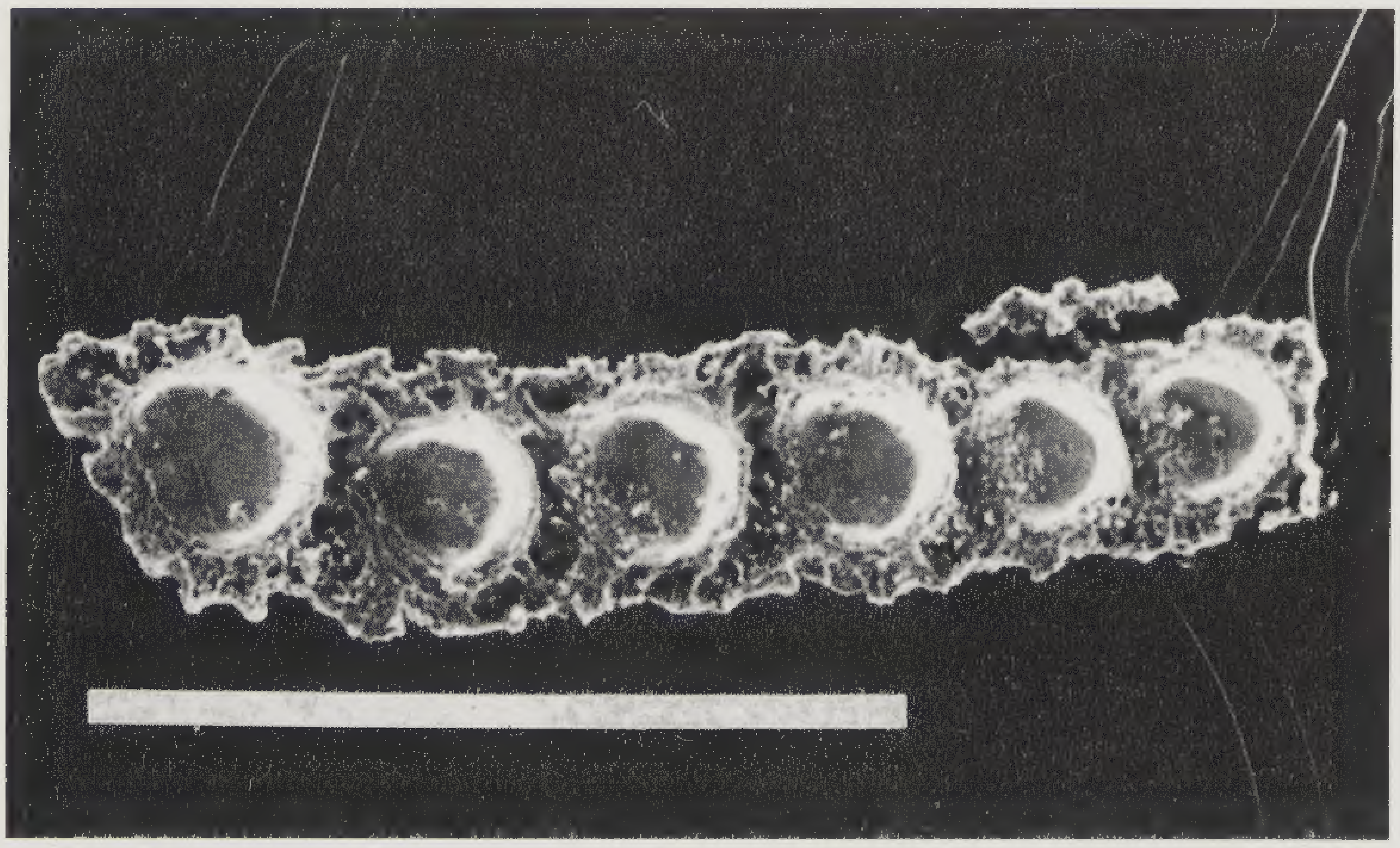

Fig. 7
Dermal ornament, possibly of *Onychodus sigmoides,* from the *Receptaculites* Limestone. Scale = 1.0 mm.

ornament and teeth. The fragments of dermal ornament are small and rare, but the teeth form the most common element in the residue.

The dermal ornament (Fig. 7) is recognized by its peculiar pattern of raised, horseshoe-shaped tubercles, which occur in neatly ordered rows. The tubercles are about 0.2 mm in diameter, and the dermal fragments range up to 1.5 mm in greatest dimension. They are most probably the "first generation" tubercles on the dorsal surface of early crossopterygian scales. In these forms, radiating rows of first generation tubercles ornament an area between the unornamented and overlapped anterior portion and the ridged and exposed posterior portion of the scales. In detail they most closely resemble those described as *Onychodus sigmoides* by Newberry (1873), Wells (1944), and Orvig (1957). However they are similar in general form to those identified as *Litoptychus* (Denison, 1951) and *Glyptolepis* (Gross, 1930; Orvig 1957). The small amount of the material and the variability of dermal ornament within all of these genera makes definitive identification difficult.

The teeth (Fig. 8) are narrow, pointed, and hollow, without any identifiable ornamentation. The shaft tapers and is distinctly curved. The base is typically constricted, and bears a flange. They average about 1.1 mm in length.

Wells (1944) identified very similar teeth as *Onychodus* interlaniaries. However, Gross (1969) described teeth of almost identical morphology among *Lophosteus* material from the *Beyrichia* Limestone of northern Germany. His study included a histological examination of these teeth and comparable material of known actinopterygian and crossopterygian origin. It revealed no histological characteristics suitable for distinguishing between isolated teeth of these groups. This tooth type is possessed by the earliest known representatives of the Osteichthyes, *Andreolepis* and *Lophosteus*, and is presumably primitive to the group as a whole.

The teeth found in the *Receptaculites*

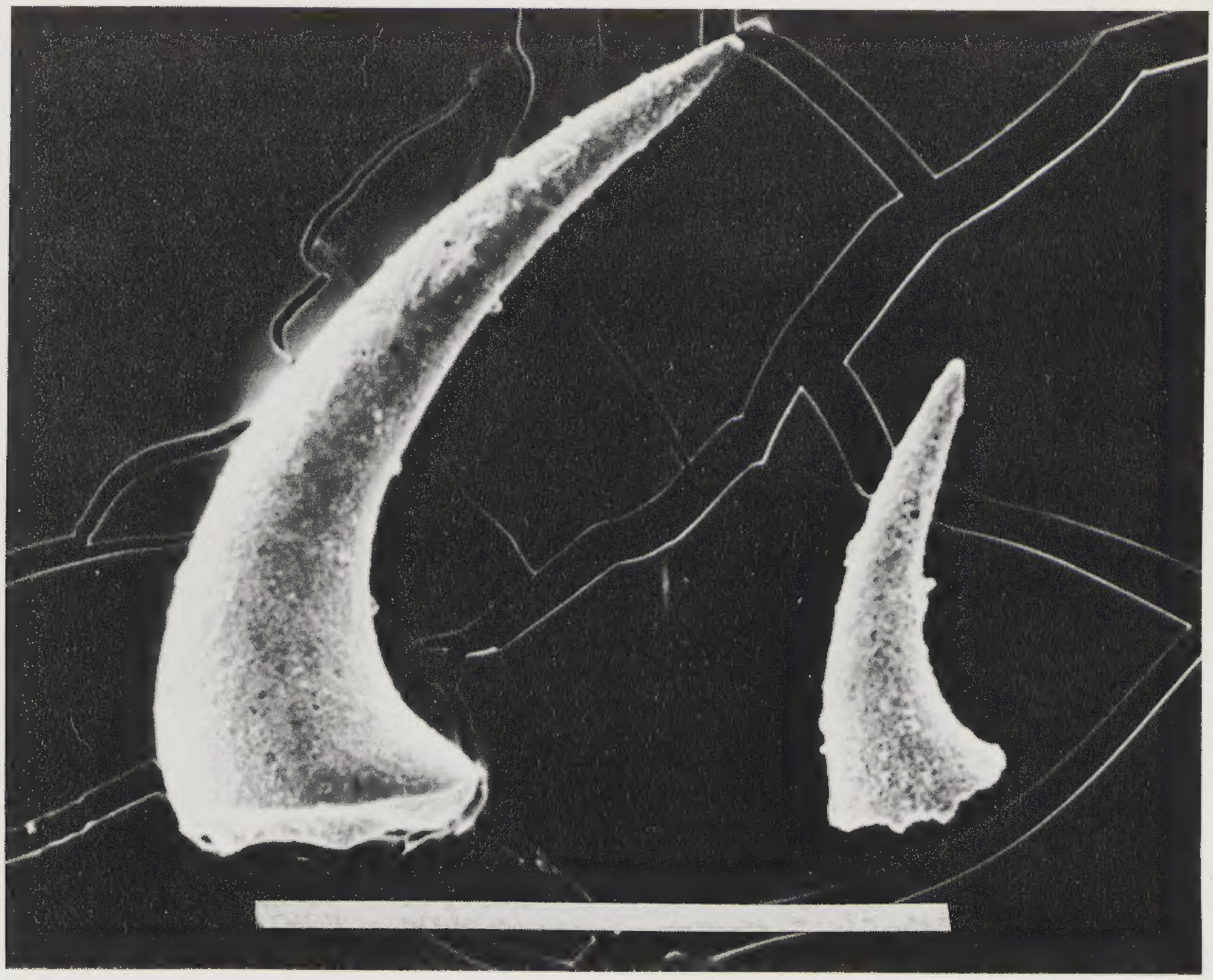

Fig. 8
?*Onychodus* sp. teeth from the *Receptaculites* Limestone. Scale = 1.0 mm.

fauna are tentatively identified as *Onychodus* because other *Onychodus* remains are presumed present in the residue. However, no structural characteristic was found that would prohibit their assignment to Lophosteiformes or to several other Devonian taxa.

Rhipidistia

The *Receptaculites* fauna contains a single isolated cosmoid scale (Fig. 9) and various cosmine-covered dermal fragments. The scale is distinguished by a continuous enamel (cosmine) layer that covers the crown and a series of pores that puncture this layer. The enamel surface of the crown is slightly grooved near the pores, but is otherwise completely smooth. The crown is irregularly polygonal in outline and nearly flat, with its margins turned slightly downward. There is no evidence of a crown area that was overlapped by neighboring scales, nor of the groove that commonly separates overlapped and exposed areas.

The neck of the scale is essentially indistinguishable from the high, straight-walled base. Pores can be seen to open on its surface. On the inner surface of the base two ridges parallel the long axis of the scale, with a broad groove between them. There is a distinct peg and socket for articulation with neighboring scales.

The complete cosmine covering of this scale suggests that it be classified as rhipidistian. Further, the thick base and polygonal shape are reminiscent of scales of early members of this group, either Osteolepidae or Porolepidae. With some exceptions (Jarvik, 1950), these two groups may be distinguished by the absence (osteolepid) or presence (porolepid) of scale ornament (Jarvik, 1950; Orvig, 1951).

Despite similarities to osteolepid and porolepid scales, the *Receptaculites* cos-

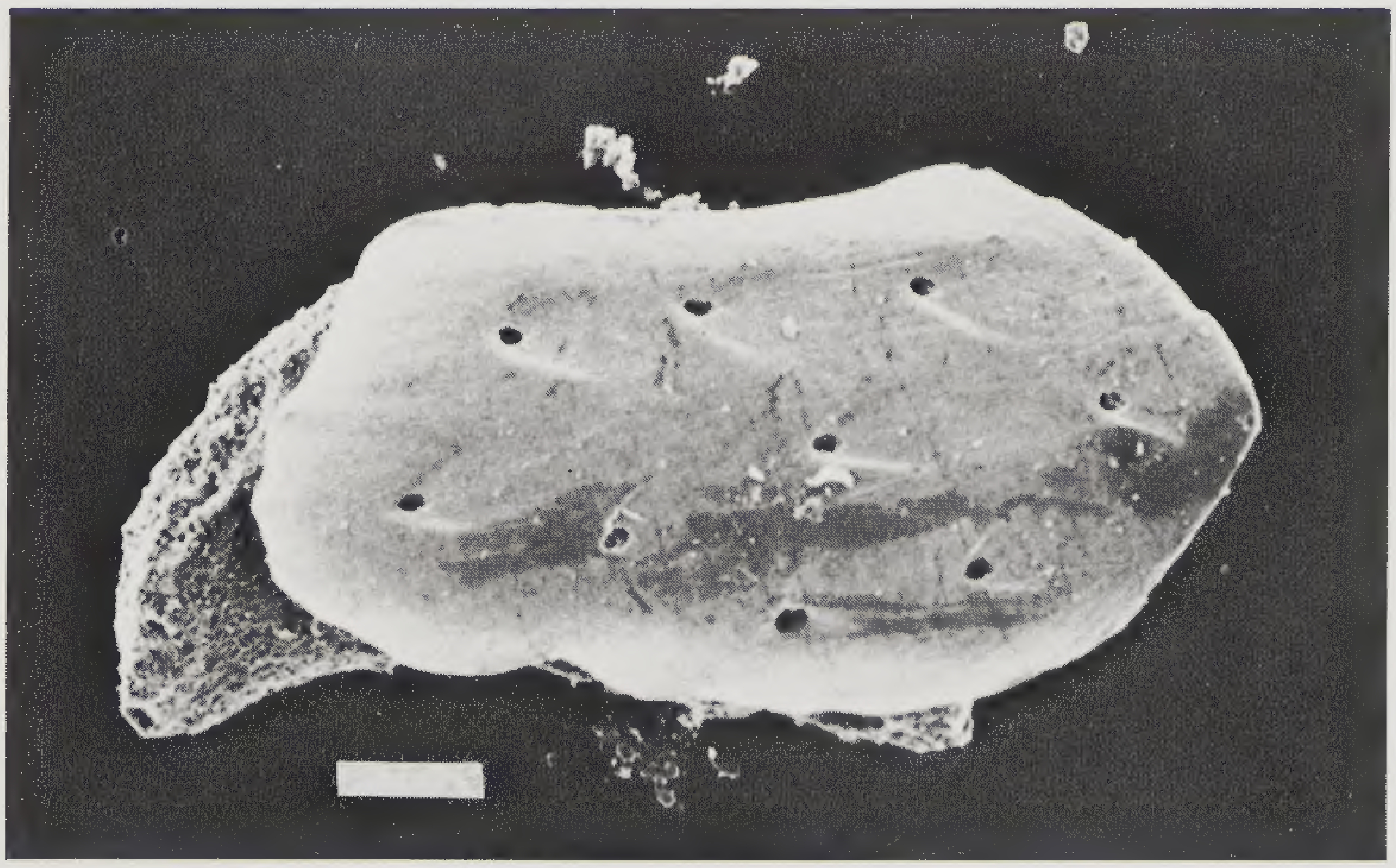

Fig. 9
Cosmine scale from the *Receptaculites* Limestone.
Scale = 0.1 mm.

moid scale differs from previously described specimens in two major respects. The first is size. Jarvik (1948) lists osteolepid scales in the 2 × 4 mm to 4 × 6 mm range, and porolepid scales are of generally equivalent size or even larger (Bystrow, 1960). The Australian specimen is much smaller, about 0.9 mm in length. Secondly, the scale has no overlap area. Previous reports of cosmoid scales with no overlap area are unknown to me.

These two characters preclude assignment of this isolated scale to previously established genera. It is most similar to rhipidistian scales, and possesses the primitive rhipidistian characters of thickness, rhombic shape, and complete cosmine layer. These are characters shared by early members of both osteolepid and porolepid rhipidistians.

Osteolepid remains are unknown beneath the Middle Devonian. Porolepid scales are rare in the Lower Devonian. Kulczycki (1960) reports them from the Polish Lower Devonian, while Jarvik (1950), Orvig (1957) and Schultze (1968) all report them from the Grey Hoek of Spitsbergen, which is near the Lower/Middle Devonian boundary.

Paleoniscida

Only a few scales of known paleoniscoid origin were preserved whole in the *Receptaculites* Limestone residue. They are of two general types, one of which can be identified as *Ligulalepis toombsi* (Fig. 10). This genus was originally described by Schultze (1968) from the Taemas Formation of the Murrumbidgee area, with the majority of the material from the *Spirifer yassensis* limestone. Schultze lists one whole scale and several fragments from the overlying *Receptaculites* Limestone. *L. toombsi* is not known from other sites.

The scales of *Ligulalepis toombsi* are flat, with a rhombic outline. Their length is greatly exceeded by their height. The sculptured crown consists of variously joined, obliquely running, ganoin-covered riblets. A very marked, spoon-shaped process is set off from the anterior edge at a sharp angle. The inner side of the scale possesses two parallel keels, between which is a broad groove. The peg and socket are both strongly expressed.

The second group of paleoniscoid scales is very different. These scales (Fig. 11) are typically rhombic, but with very elongate

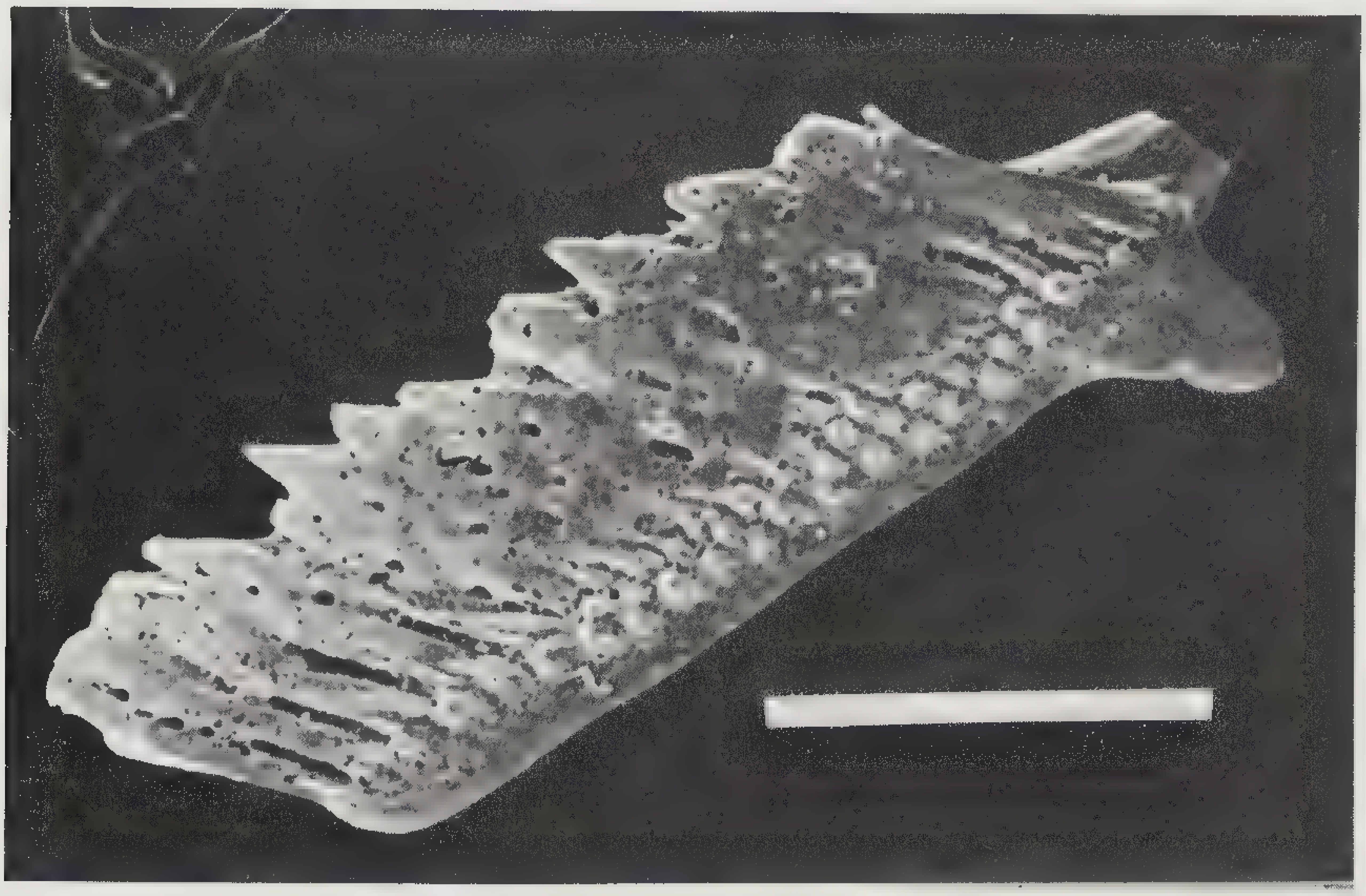

Fig. 10
Ligulalepis toombsi, a paleoniscoid scale from the *Receptaculites* Limestone. Scale = 1.0 mm.

shape. The height of these scales is 3 to 6 times that of their rostral-caudal dimension (=length). The scales have a peg and socket imbrication system that seems to involve not only the base, as is usual in paleoniscoids, but the crown as well. This results in an outline that resembles an elongate, skewed parallelogram.

The crown of these scales is set off from the base by a groove, but there is no discrete neck. The enamel layer covering the crown is discontinuous, consisting of elongate ribs that run parallel to the long dimension of the scale. The edges of the ribs are themselves sculptured with a fluted ornamentation. The grooves between the enamel ribs are pierced by numerous openings, presumably of the pore canal system.

The base of the scale is very distinctive, possessing two equal keels, one running along each of the two elongate scale edges. The double keel is reminiscent of that found on *Ligulalepis* scales (Schultze, 1968) but differs in encompassing the entire scale base rather than only the medial portion of the base. A deep, perforated groove runs between the two keels.

The morphology of these scales is distinct and differs from that of paleoniscoid scales previously described from the Lower Devonian (Schultze, 1968) and Middle Devonian (Schultze, 1968; Gross, 1953). Their early occurrence makes them especially interesting, but paucity of material prevents their formal description.

Distribution and Paleogeography

As early as the Late Silurian it is possible to distinguish ecological preferences among various groups of vertebrates. Denison (1956) has identified two Late Silurian assemblages. Osteostraci and Anaspida (with eurypterids) comprise a brackish-to-freshwater group, while Heterostraci, Thelodonti, and Acanthodii comprise a marine group. The *Receptaculites* Limestone, both in lithology and invertebrate fauna, strongly indicates a marine origin. Its vertebrate microfauna is both younger and more

Fig. 11
Unnamed paleoniscoid scales from the *Receptaculites* Limestone. Scale = 1.0 mm.

diverse than those discussed by Denison, but resembles the marine assemblage in the presence of Acanthodii and Thelodonti.

The early vertebrate record in Australia is sparse. There is no pre-Devonian record. Hills (1958) listed a limited fauna from Australia's Lower Devonian (originally considered to be Middle Devonian), much of which was collected at localities near the material described here. It included several arthrodires, petalichthyids, and the dipnoan *Dipnorhynchus*. This genus is also known from the Lower Devonian of Germany (Lehmann and Westoll, 1952).

Since Hills' work, several new discoveries have added to the fauna known from the Lower Devonian of Australia. In 1968 Schultze reported a microvertebrate fauna containing elements very similar to those reported here. It included *Onychodus*, *Ohiolepis*, and *Ohioaspis* in addition to the new paleoniscoid *Ligulalepis*, which was described in detail. Gross (1971) described the thelodont *Turinia australiensis* and undetermined acanthodians from the Lower Devonian of western Australia. Turner (1973) noted an as yet unpublished report of *Turinia* sp. from the Lower Devonian of the Toko Syncline of Australia.

The *Receptaculites* Limestone fauna is notable among known Emsian/Eifelian assemblages for its remarkable taxonomic diversity. It includes components of faunal assemblages found at other, widely distributed Lower Devonian localities, all within a single assemblage. *Skamolepis fragilis* is previously known only from the Grey Hoek of Spitsbergen and Latvia (Karatajute-Talimaa, 1978). *Cheiracanthoides* has been found at its original localities in North America (Wells, 1944) and a variety of localities near the Ostsee in Germany (Gross, 1973). The rhipidistian scale is unique.

The subassemblage of *Onychodus*, *Ohioaspis*, and *Ohiolepis*, which is often associated with ptyctodontid tooth plates, has a wider distribution. The original association was described by Wells (1944) from Ohio,

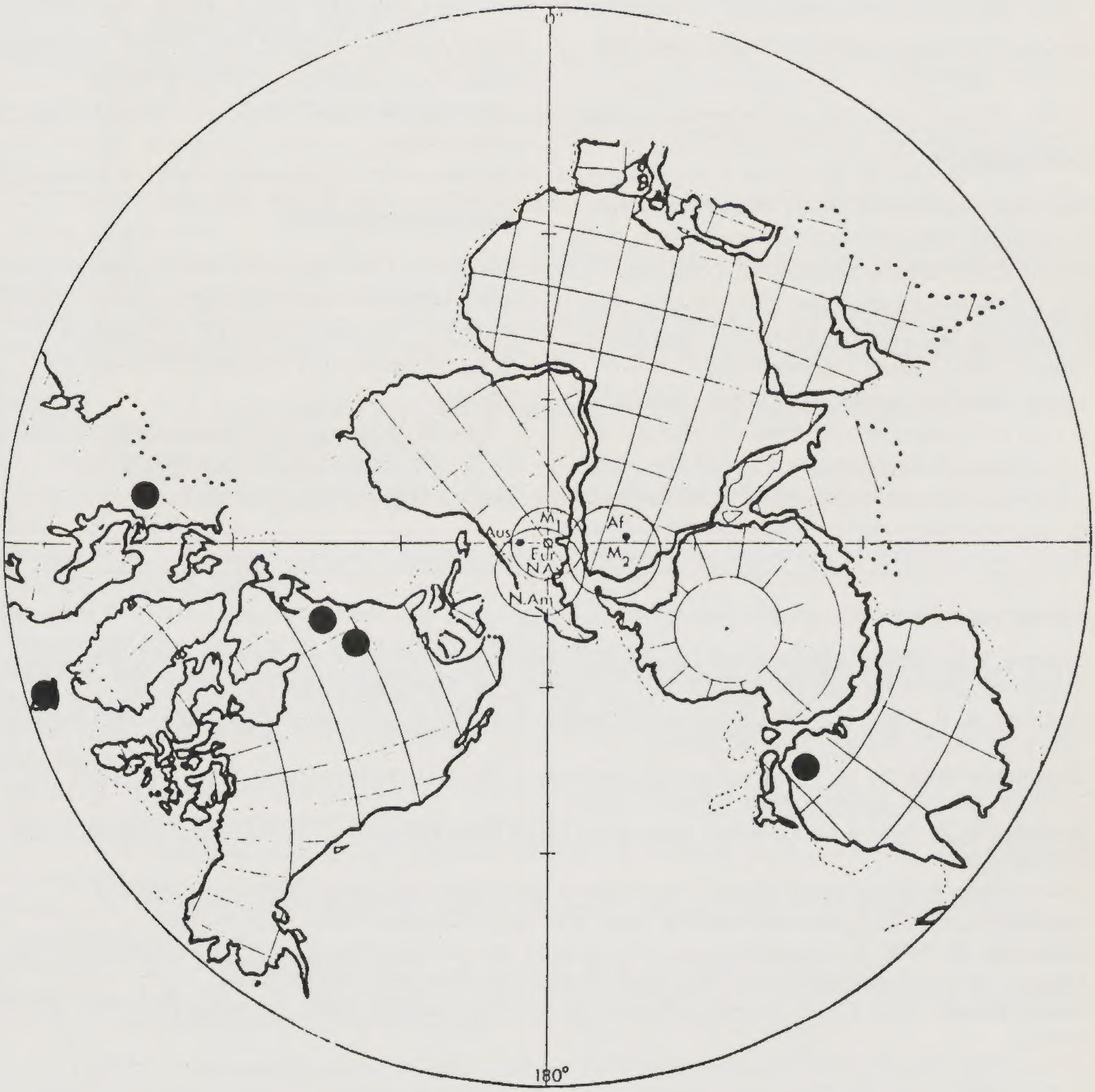

Fig. 12
Known distribution of Lower Devonian vertebrate assemblages with composition similar to that of the *Receptaculites* Limestone. Base map of southern hemisphere in Lower Devonian from Smith, Briden, and Drewry, 1973.

Indiana, and Kentucky. It was subsequently reported by Orvig (1969b, p. 317) from the Onondaga of New York State and by Schultze (1968) from the Murrumbidgee area of Australia. Schmidt (1961) and Orvig (1969b) reported *Ohiolepis* scales from the Heisdorf beds of Germany.

Conclusions

The diverse fauna from the *Receptaculites* Limestone includes species found in a variety of other, widely separated locations. This occurrence suggests two conclusions. First, it confirms that Australia was not faunally isolated in the Lower Devonian and that the fauna itself had wide geographic distribution. A plot of known occurrences of the fauna on a paleogeographic map of the Lower Devonian (Fig. 12) suggests that the localities occurred in shallow epicontinental marine seas of the southern hemisphere and that latitude was not a limiting factor of distribution. Secondly, the occurrence of diverse members of the known Lower Devonian vertebrate fauna in a single locality suggests that the fauna forms a uniform whole that cannot be separated into subgroups with different environmental, stratigraphic, or geographic implications.

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