The first Bothriolepis-associated Devonian fish fauna from Africa

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A black carbonaceous shale, exposed in road cuttings that intersected rocks of the Witpoort Formation (Witteberg Group), Eastern Cape Province, South Africa, has yielded the fragmentary remains of about 50 fishes, in addition to numerous plant fossils. The depositional site is interpreted to have been a stagnant coastal lagoon sheltered by a barrier island. The fish fauna comprises acanthodian spines, a nearly complete probable holocephalan chondrichthyan, various armour plates of the antiarch placoderm Bothriolepis, *portions of head and trunk plates of placoderms of the families Groenlandaspididae and Phyllolepidae, and probably Macropetalichthyidae, the parasphenoid bone of a lungfish, a small crossopterygian (probably a coelacanth) dissociated palaeoniscoid scales and large sarcopterygian scales, which may be from the lungfish. This is the first record of the cosmopolitan Devonian genus* Bothriolepis *from Africa with an associated ichthyofauna. The presence of* Bothriolepis *with groenlandaspidid and phyllolepid placoderms indicates a Late Devonian age.*

Immediately south of Grahamstown, Eastern Cape Province (Fig. 1), construction work in 1985 for a new road exposed sedimentary strata of the Witpoort Formation (Witteberg Group) in a number of cuttings. In one of these, a relatively thick (2–6-m) band of black shale was interbedded with the typical pale grey to white sandstones of the formation. Attention was initially drawn to the shale by the presence of numerous plant fragments, but the discovery of several large fish scales led to a more intensive search for additional remains. This preliminary notice documents the discovery of the initial fish finds at the site, including acanthodians, a chondrichthyan, palaeoniscoids, a dipnoan, a crossopterygian and four placoderm groups, and presents the first record of the cosmopolitan antiarch *Bothriolepis* from the African continent. No formal taxonomic identifications are made at this time, pending further study. The specimens are rather poorly preserved as virtually two-dimensional impressions and internal casts in which skeletal tissues have been remineralized by kaolinite and a 2M (metamorphic) mica. The fragmentary nature of the specimens suggests that the fish were decomposing and that skeletal elements were largely dissociated by currents and/or scavengers prior to burial.

Fish anatomical terminology follows standard use.[1,2,3] All specimens are deposited at the Albany Museum (AM), Grahamstown.

Stratigraphic setting

The Witpoort Formation is a predominantly quartz-rich sandstone unit that makes up the middle part of the Witteberg Group, the youngest division of the tripartite Cape Supergroup. In the Grahamstown area it is underlain by the shales, siltstones and minor sandstones of the Weltevrede Formation, and is overlain by shales of the Lake Mentz Subgroup. Within the Witpoort Formation, black carbonaceous shales of 1 m or more in thickness are interbedded with the more typical pale grey to white quartz arenites, quartz wackes and subarkoses at a number of horizons. That which has yielded the fish fossils occurs in the upper part of the formation.

The new fossil locality is in a road cutting approximately 300 m long and 20 m high, in which the beds dip gently (10°)

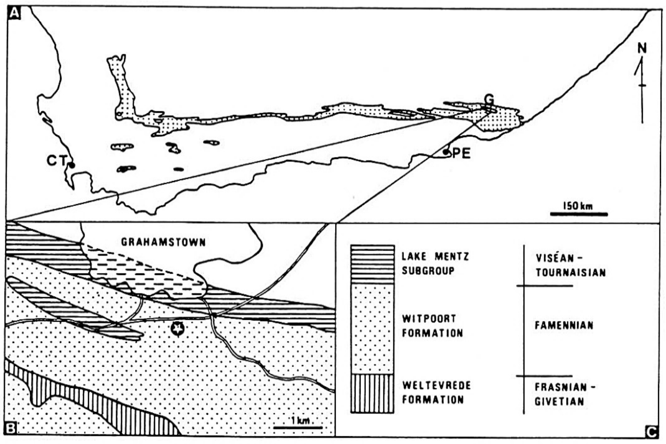

Fig. 1. *A*, Distribution of Witteberg Group rocks in South Africa (CT = Cape Town, G = Grahamstown, PE = Port Elizabeth; *B*, Simplified geological map of the Grahamstown area showing the position (starred) of the fossil fish locality; *C*, Key and stratigraphic column for the Witteberg Group in the eastern Cape Province.

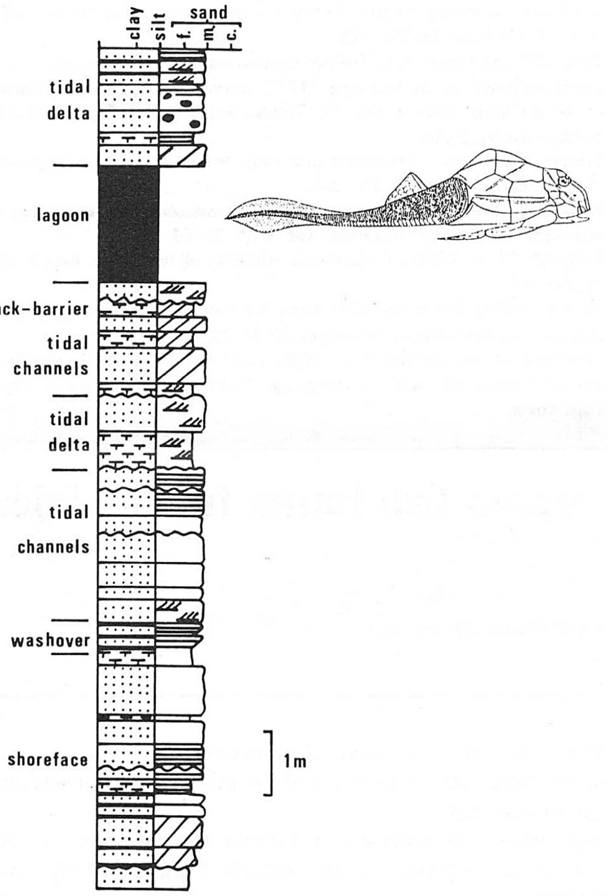

Fig. 2. Summary measured vertical section through the fossil locality indicating interpreted depositional settings.

northwards. A detailed sedimentological log (Fig. 2) was measured through the sequence exposed near the eastern end of the cutting in order to assess the general characteristics of the succession. The lowermost part of the rock sequence consists of alternating beds of brown-grey quartz arenite separated by thin shales. The quartz arenites appear structureless for the most part but some trough cross-bedding and horizontal lamination have been recorded.

Above these sandstone/shale units are 50 m of thickly bedded, pale grey quartz arenites with occasional thin, dark grey shales and quartz wackes. Erosional contacts are common. Primary structures include horizontal lamination, ripple cross-lamination and trough cross-bedding. Paleocurrent data derived from the cross-bedding suggest a general westerly to south-westerly transport direction. Some bioturbation is evident in the quartz wackes.

The middle part of the sequence comprises the laminated black carbonaceous shale, up to 6 m thick, from which the fossils have been taken. This is overlain by creamy-coloured, mica-rich quartz wackes in which several lenses of black shale occur. The top of the sequence consists of white quartz arenites displaying trough cross-bedding, ripple cross-lamination and horizontal lamination. These are overlain by horizontally laminated micaceous quartz wackes.

The sandstones of the Witpoort Formation in the Grahamstown area are thought to show many of the features of a barrier island depositional environment, including tidal inlet sequences, tidal deltas, beach and shoreface deposits and washover fans.[4,5] Within this setting the carbonaceous shales represent a stagnant back-barrier lagoon (Fig. 3), an environment that received both marine and significant freshwater input. Preliminary geochemical work supports this conclusion.

Age of the fauna

Plant remains from a carbonaceous shale low down in the Witpoort Formation were determined to be Lower Devonian in age.[6] However, this is contradicted by the evidence of the marine invertebrates from the Bokkeveld Group, which indicate a Lower-Middle Devonian (Emsian-Eifelian) age.[7,8] The presence of the articulate brachiopod *Tropidoleptus* in the upper part of the Weltevrede Formation was taken as indicative of a Givetian-Frasnian age for those sediments.[9] Cooper[10] used eustatic sea-level changes to effect a correlation with Devonian rocks in Europe and North America. On this basis he was able to suggest that the Witpoort Formation was deposited during Famennian times, with the black shale of the overlying formation corresponding to the early Tournaisian transgression. Therefore, the accumulated evidence seems to indicate an Upper Devonian, probably Famennian, age for the Witpoort Formation. This is borne out by the presence in the fauna of groenlandaspidids, a phyllolepid and the genus *Bothriolepis*.[11] The presence of *Archaeopteris* among the associated plant fossils[12] means that the fauna cannot be older than Frasnian.

The Witpoort fish fauna

Four major groups of Paleozoic fishes are represented in the Witpoort ichthyofauna. Two groups, the acanthodians and placoderms, are extinct; the other two groups are extant: the chondrichthyans (chimaeras plus sharks and allies) and the osteichthyans (bony fishes). No agnathan (jawless) fish material has been taken at the site, but these are very rare in Late Devonian rocks, especially in Gondwana (J.A. Long, pers. commun.).

Acanthodii

The acanthodians (spiny sharks) are the earliest-known jawed fishes (Early Silurian to Permian).[11] Du Toit[13] identified a fish spine as representing the acanthodian genus *Machaeracanthus* from the Bokkeveld Group (Early and Middle Devonian), a genus also known from Euramerica, Antarctica and possibly Brazil.[1,14] No documentation of its identification was given, and Chaloner *et al.*[15] implied du Toit may have used a name of convenience for a reference to a vague 'railroad rail'-like fish spine among Bokkeveld fossils.[16] Other acanthodian remains have been more recently reported from South Africa. Gardiner[17] identified an *Acanthodes* sp. (portions of bodies) and an undetermined fin spine. His specimens were from Witteberg deposits dating from the Early Carboniferous. Chaloner *et al.*[15] reported a pectoral spine of a *Gyracanthides* sp. from the upper Bokkeveld of the Western Cape Province

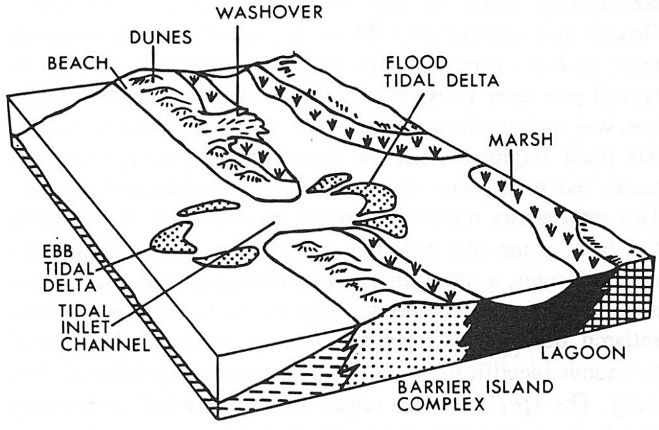

Fig. 3. Conceptual model of the environmental setting of the Witpoort Formation, indicating the major subdivisions of the barrier island depositional complex.

that was indistinguishable from the Antarctic *G. warreni* White, 1968.

Twelve spines have been collected at the Grahamstown site and are tentatively identified as belonging to the Gyracanthidae. They represent prepectoral and isolated dorsal and ventral spines. A number of spines found in close proximity to one another (AM 4892) may all have come from the same individual. Most are fragmentary, but diagrammatic renditions of three complete spines are given in Fig. 4. Rib tubercles, now flattened, are observed in a few places. These spines do not appear to be from a specimen of *Machaeracanthus* or *Gyracanthides* that we have seen, and may represent a new form.

Placodermi

The armoured fishes were first reported from South Africa by Chaloner *et al.*[15] from the same collection that yielded the *Gyracanthides* spine above. They reported four arthrodires: two phlyctaenioids and two considered problematical. The remains of at least 35 more individual placoderms were taken at the Grahamstown site, including the first occurrence of the cosmopolitan genus *Bothriolepis* from Africa, a phyllolepid, and two kinds of arthrodires.

The first Grahamstown placoderm was discovered at the site in December 1989 (AM 4818). It consists of two counter pieces of portions of the dorsal aspect of the head and trunk armour, nearly perfectly bisected, of an undetermined phyllolepid (Fig. 5). Plate boundaries are somewhat obscured by the mineralization, but identifiable on the head shield are the preorbital, postnasal, postorbital, marginal, paranuchal and part of the nuchal. Sensory canals visible are the V-shaped infraorbital in the postnasal plate, the central canal of the nuchal plate, and main lateral line canal in the paranuchal, marginal and postorbital plates. The posterior pit line in the nuchal plate is not evident. Identifiable trunk plates are the anterior lateral, one-half of the median dorsal and the spinal plate. The anterior dorsolateral plate is obscured. Based on Long's[2] reconstruction of *Austrophyllolepis*, AM 4818 is estimated to have been about 27 cm in length when alive. Three genera are recognized in this family, *Phyllolepis* Agassiz, 1844, *Austrophyllolepis* Long, 1984 and *Placolepis* Ritchie, 1984. We are uncertain of our specimen's generic placement, as the shape of the pectoral fenestra, the paranuchal, postnasal and postorbital plates are quite different from figured specimens we have seen.[2] The presence of a subrectangular marginal plate, as opposed to the sliver-like marginal in *Phyllolepis*, would suggest that our specimen is closer to *Austrophyllolepis* or *Placolepis*. The nuchal does not appear pentagonal, as in *Placolepis*, but more akin to that of *Austrophyllolepis*.

In April 1991 part of the right side of the head and trunk armour and the proximal segment of the right pectoral appendage of a specimen of *Bothriolepis* (AM 4816) was uncovered at the Grahamstown site (Fig. 6). The specimen was taken at the edge of an outcropping and was severely fragmented when fully uncovered. The following trunk armour plates are preserved: mixilateral, posterior ventrolateral, anterior ventrolateral and posterior median dorsal. The following head armour plates are preserved: lateral (incomplete), postmarginal, paranuchal, nuchal (part) and postpineal. The orbital fenestra is bean-shaped, much as in *B. portalensis* and other Antarctic congeners.[3,18] The orbital fenestra was destroyed upon excavation, except for its rough approximation in a counter piece, but colour photographs showing its complete outline at the excavation are archived at the Albany Museum, Grahamstown. The shape of the articular boundaries between the ventral plates of the pectoral appendage are generally obscure, but the following plates are identified: ventral central 1 and 2, lateral marginal 2 and mesial marginal 2. No external articular area of the second ventral central is preserved. It is estimated the total length of the living fish was about 1 m.

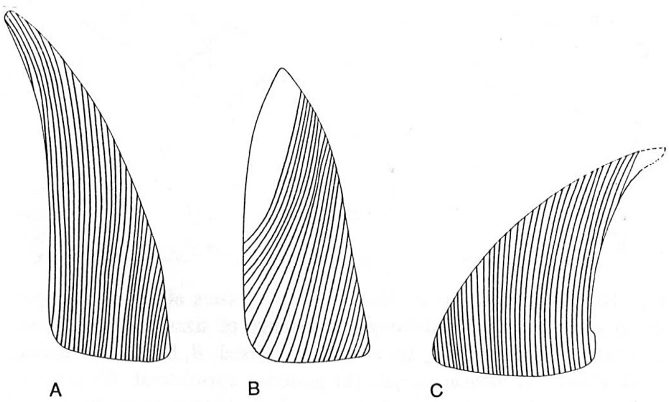

Fig. 4. Reconstructions of three acanthodian spines. *A*, AM 4892, 127 mm in length; *B*, AM 4892, 105 mm; *C*, AM 4880, 94 mm.

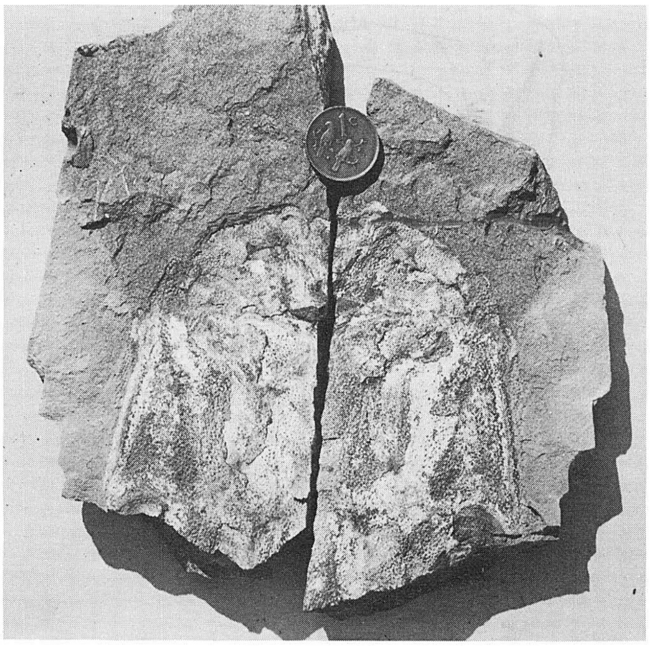

Fig. 5. Phyllolepidae, AM 4818, counter pieces of left half of head and trunk plates, 10 cm in length. Coin is 19 mm in diameter. Specimen almost perfectly bisected, right half not recovered.

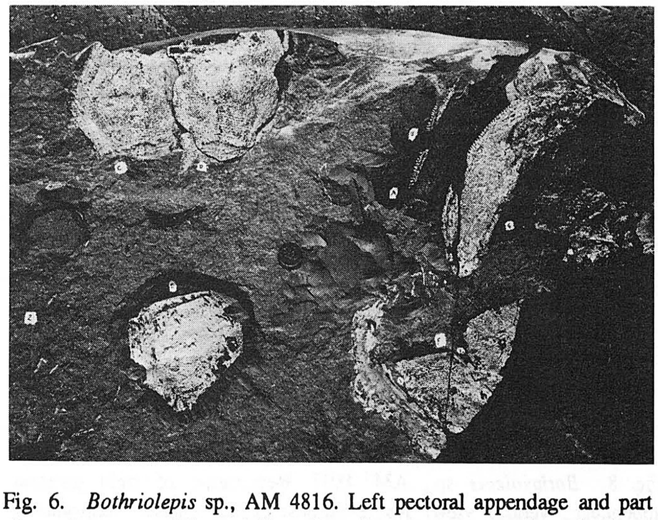

Fig. 6. *Bothriolepis* sp., AM 4816. Left pectoral appendage and part of trunk, upper right; mixilateral and posterior ventrolateral plates, upper left; posterior median dorsal plate, lower left; part of head shield, with incomplete lateral, paranuchal and complete postmarginal plates, lower right. Coin 19 mm in diameter.

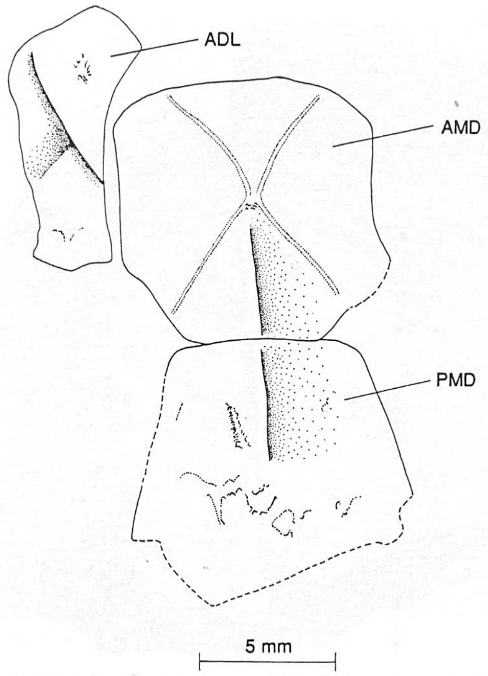

Fig. 7. *Bothriolepis* sp., AM 4881. Restoration of three trunk plates. Abbreviations: ADL, anterior dorsolateral; AMD, anterior median dorsal; PMD, posterior median dorsal. ADL shown anterior to position *in situ*. Portion of broken mixilateral (?) plate not shown.

Seven other *Bothriolepis* were discovered between 1991 and 1993, including large and very small specimens, which may be juveniles of the same species. Preservation is variable but sufficient details can be seen on some of the specimens to allow partial restorations. For example, AM 4881 shows four dorsal trunk plates, mostly as good impressions with poor remineralization, comprising an entire anterior median dorsal, a nearly complete posterior median dorsal and anterior dorsolateral (Fig. 7). Part of another damaged plate, presumably a separated mixilateral, is also present. AM 4897 displays part of an anterior ventrolateral plate with an entire pectoral appendage in ventral position (Fig. 8). Unfortunately, both proximal and distal portions are remineralized so as to obscure most plate margins. AM 4891 is two large (109-, 126-mm) trunk plates, possibly anterior and posterior ventrolateral plates of another *Bothriolepis* (Fig. 9).

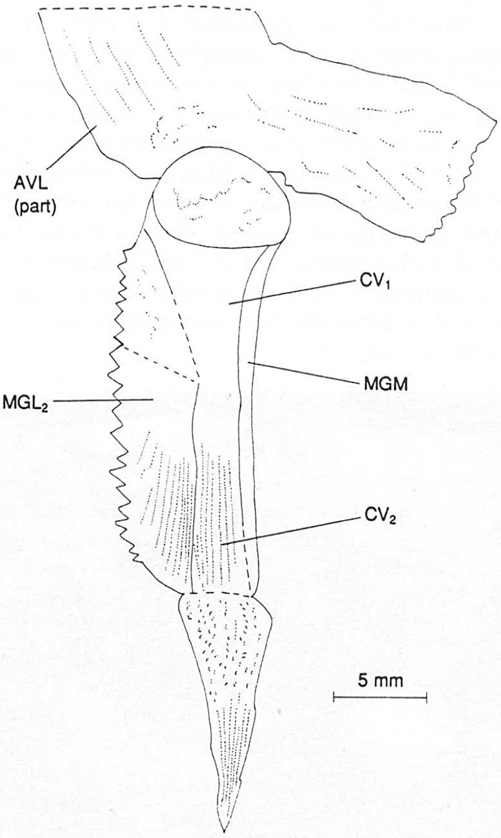

Fig. 8. *Bothriolepis* sp., AM 4897. Restoration of right pectoral appendage, ventral view. Abbreviations: AVL, anterior ventrolateral plate; CV, first and second ventral central plates (margin not evident); MGL, second lateral marginal plate; MGM, first and second mesial marginal plates (margin not evident).

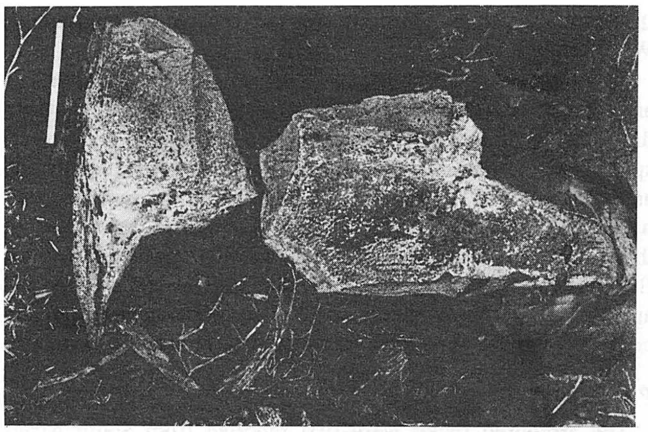

Fig. 9. *Bothriolepis*, AM 4891. Left anterior and posterior ventrolateral trunk plates. Scale bar = 4 cm.

Following the initial discovery of a phlyctaenioid arthrodire at the Grahamstown site in December 1991, a considerable amount of additional material has come to light. Most of the specimens comprise partially or wholly disarticulated plates of the trunk armour, sometimes with associated head shield plates. We now have sufficient material to identify the genus *Groenlandaspis* Heintz, 1932 in the fauna.[19] These specimens possess a crested median dorsal plate and a relatively short spinal plate that extends beyond the anterior lateral by about one-quarter to one-third of its length (Fig. 10).

Several very small specimens but a single, large, isolated spinal plate (AM 4867) found among numerous sarcopterygian scales and plant material (Fig. 11) are thought to belong in the Macropetalichthyidae. All the specimens show the spinal plate to be relatively long and slender, projecting posteriorly by about one-half of its length (Fig. 12).

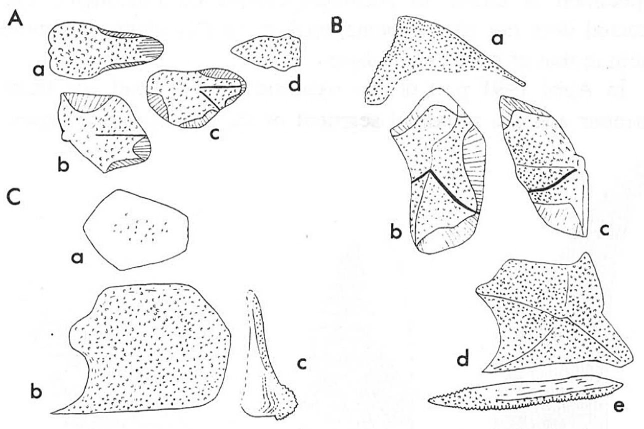

Fig. 10. Reconstruction of head and trunk plates of *Groenlandaspis* sp. to scale, based on individuals of a range of sizes. *A*, head plates; (a) nuchal; (b) paranuchal; (c) central; (d) pineal. *B*, Dorsal and lateral trunk plates: (a) median dorsal; (b) posterior dorsolateral; (c) anterior dorsolateral; (d) anterior lateral; (e) spinal. *C*, Ventral trunk plates: (a) posterior median ventral; (b) anterior ventrolateral; (c) interolateral.

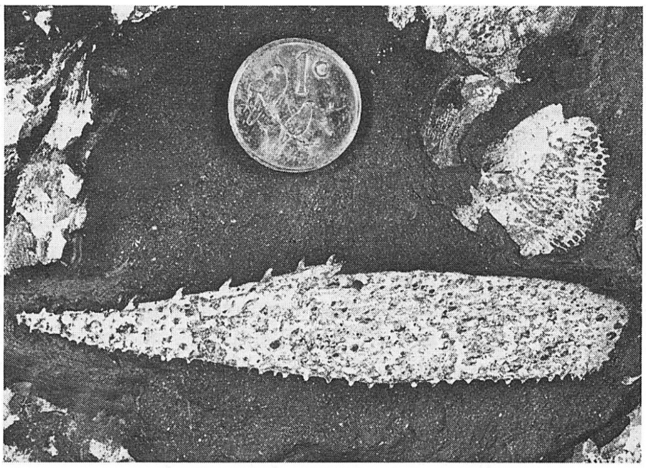

Fig. 11. Petalichthyformes, Macropetalichthyidae, AM 4867. Spinal plate with sarcopterygian scales. Coin measures 19 mm in diameter.

There are also a number of specimens that cannot be assigned unequivocally to any of the above placoderms and may represent further types.

Chondrichthyes

Oelofsen[20] reviewed the fossil record of chondrichthyans in southern Africa. He discussed three finds in the Cape Province that are relevant to the Witpoort fauna: (1) impressions of pleuracanth-type shark teeth from the Tra-Tra Formation, Bokkeveld Group (Middle Devonian); (2) placoid scales, a spine and impressions of calcified cartilage of a shark from the upper Witteberg shales; (3) a shark chondrocranium recovered from a siliceous nodule in the lower Ecca Group (Lower Permian) that he later described as *Dwykaselachus oosthuizeni* and of uncertain affinity.[21] In addition, a freshwater shark, *Lissodus africanus* (Broom), is known from about 20 specimens from the upper Beaufort Series (Lower Triassic) of the Orange Free State, but Oelofsen[20] had not seen a paper redescribing this form.[22]

A chondrichthyan was discovered at the Grahamstown site in June 1990 (AM 4817; Fig. 13). Much of the anterior portion of the fish is represented on two counter pieces, and the greatest length *in situ* is 44 cm. The head region is distorted and deeply imbedded in one slab only. A toothless, slender element under the head is interpreted as the palatoquadrate, and its anterior end is missing. Two toothless lower jaws are identifed and asymmetrically represented on both slabs. The vertebral column consists entirely of the neurapophysial rods, basally rounded and sharply pointed dorsally. They are evident for just less than half the length of the impression of the vertebral

Fig. 12. Petalichthyiformes, AM 4908. Dorsal view of head and trunk of almost complete specimen. Scale in mm.

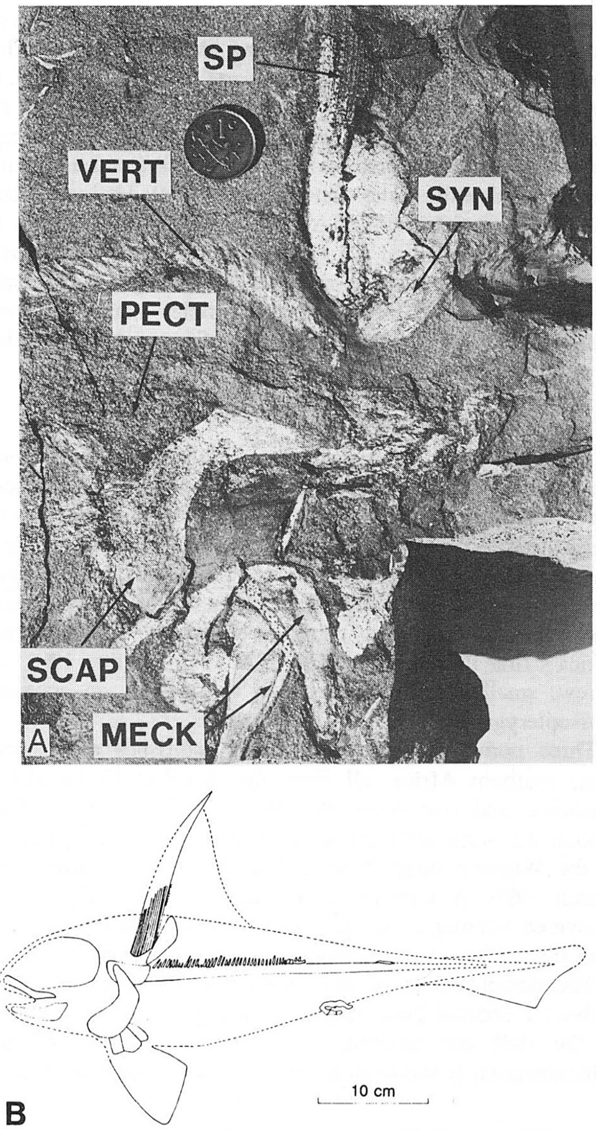

Fig. 13. Chondrichthyan, AM 4817. *A*, Photograph of portion of one counter piece showing anterior region of body. Meck: lower jaw (Meckel's cartilage); Pect: pectoral fin (impressions of ceratotrichia; Scap; scapulococoroid; Sp; dorsal spine; Syn: suynarcuum; Vert: vertebral column. Coin is 19 mm in diameter. *B*, Restoration based on entire specimen, caudal region largely conjectural.

column. At the head of the vertebral column and angled upward is a large ovoid element that is interpreted as a synarcuum. A short, stout scapulocoracoid and poorly mineralized impressions of three simple pectoral basals are present. The pectoral fin's cartilaginous radials extend to an impression of the fin's margin and number 21 or 22. A single, enormous first dorsal spine is present, the entirety of which (preserved mostly as a fine impression) is present on one slab. The spine measures 170 mm in length and has 13 ribs at its base, nine at its mid-height, 15 rib tubercles per cm near the base and six to seven posterior denticles per cm near the base (Fig. 13). No trace of a second dorsal, anal or pelvic fin or radials are evident. An odd, elongate and twisted structure with bulbous tips is present in the region of the pelvic girdle and is interpreted as parts of the puboischiadic bar and basipterygium. Integumentary dermal denticles are visible only in the tail region and are diamond-shaped and featureless because of distortion.

Problems of interpretation in the identification of this fish include the complete lack of teeth, anal and pelvic fins. However, the jumbled nature of the specimen and unjoined

Meckel's cartilage indicate a taphonomy of considerable decomposition in moderately flowing water prior to fossilization that may include loss of some parts before final burial. On the basis of evident features, such as the synarcuum, long first dorsal-fin spine, lack of a second dorsal fin and spine, simple scapulocoracoid and three simple pectoral basals, the specimen is interpreted as the earliest known whole-bodied holocephalan.

A single, isolated spine (AM 4866), resembling that of the holocephalan described above, may be all that remains of a second individual. The 88-mm preserved length of the spine shows 11 shallow ribs and small denticles along the curved posterior margin, numbering 21 in the 26-mm segment where an accurate count was possible.

Osteichthyes

Three groups of bony fish are represented in the Witpoort fauna: the Actinopterygii (ray-fins), the Dipnoi (lungfishes) and Crossopterygii (fringe-fins). The actinopterygian remains are a few isolated palaeoniscoid scales, some occurring in small patches. These scales are rhomboidal and usually preserved without showing any horizontal ridge ornamentation. The other osteichthyan material collected so far includes Africa's first Paleozoic lungfish (J.A. Long, in litt., 1991) and a few, small external impressions of possibly an actinistian crossopterygian.

Three nominal species of ancient lungfishes are recorded from southern Africa, all from the Beaufort Group (Lower Triassic), and one from the Molteno Formation of South Africa. All were assigned to the genus *Ceratodus*.[23] Remains of the Witpoort lungfish were discovered at Grahamstown in March 1990. A slab of shale measuring 16 x 24 cm was recovered bearing a nearly intact dipnoan parasphenoid bone with about 17 large sarcopterygian scales (AM 4821).

The dorsal aspect of the parasphenoid is exposed and is without a counter piece (Fig. 14). The posterior-most few cm of the stalk are missing; what remains measures 67 mm. Mineralization is incomplete. The corpus is squarish, with the edge of the posterior section evenly sloping; the anterior edge bears an irregular, raised ridge for articulation with the pterygoids. The buccohypophysial foramen is not apparent. The stalk is somewhat elongate but is interrupted by the edge of the slab, its sides parallel. The median groove is poorly defined owing to the specimen's flattening and mineralization.

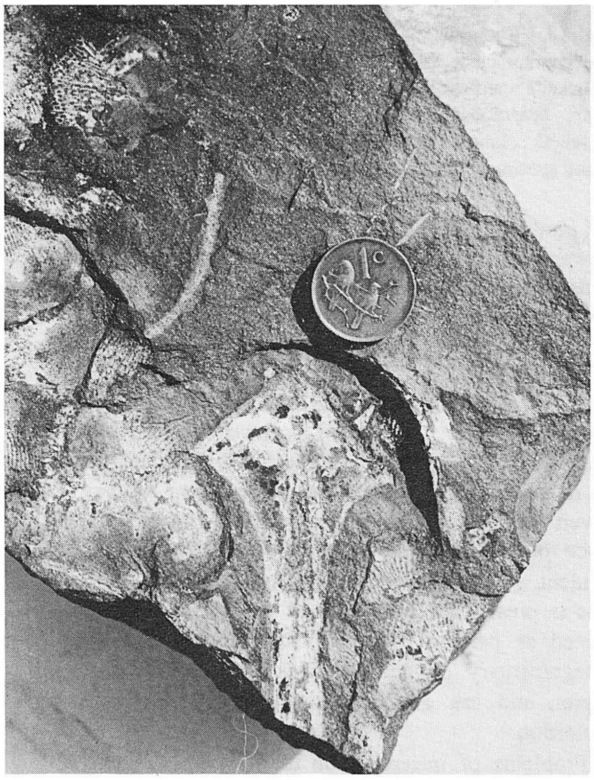

Fig. 14. Dipnoi, AM 4821. Parasphenoid bone with sarcopterygian scales. Coin measures 19 mm in diameter.

Several large slabs and a number of smaller ones have been recovered from the site, bearing in total hundreds of rounded or ovoid sarcopterygian scales (Figs 11, 14), fragments of the bony skeleton, and the impression of a large fin. The best preserved scales show detailed concentric rings on the rear subsurface portion and fine parallel ridges on the exposed surface. Fine impressions of some scales reveal no trace of an inner boss.

In most respects, the lungfish material resembles most closely that of the genus *Andreyevichthys*, recently described from Russia,[24] *Barwickia* from Australia,[25] or *Oervigia* from Greenland.[26] Details of the bone illustrated for *Andreyevichthys* were not sufficient for comparison, but the outline shape is remarkably similar to AM 4821. The parasphenoid of AM4821 differs from that of *Barwickia* in the shape of the posterior edge of the corpus, the lack of a buccohypophysial foramen and having a stalk with parallel edges. If the hundreds of scales found are of the lungfish and not another sarcopterygian, they are less finely ornamented than in *Barwickia*. The AM 4821 parasphenoid is similar to that of *Oervigia* in its squarish corpus and more parallel stalk edges.[26]

Ten specimens of a small (45–60-mm) crossopterygian (Fig. 15) are so placed because they possess a symmetrical caudal fin, lobed pectoral, pelvic and anal fins, impression of a lobe of the second dorsal in one specimen (with disattached rays in another), a large, rounded operculum (plus part of the preopercle?) and impressions of a pectoral girdle and gular plate. In addition, and although poorly remineralized, the orbit, portions of the skull, and an isolated urohyal can be discerned. On the basis of the fin shapes and their positions, number of rays, the distinctive urohyal and the head structures, the specimens are probably referrable to the Coelacanthiformes (Actinistia).

Discussion

Young[14] analysed a Devonian vertebrate taxonomic data base and discussed distributional patterns. Placoderms were

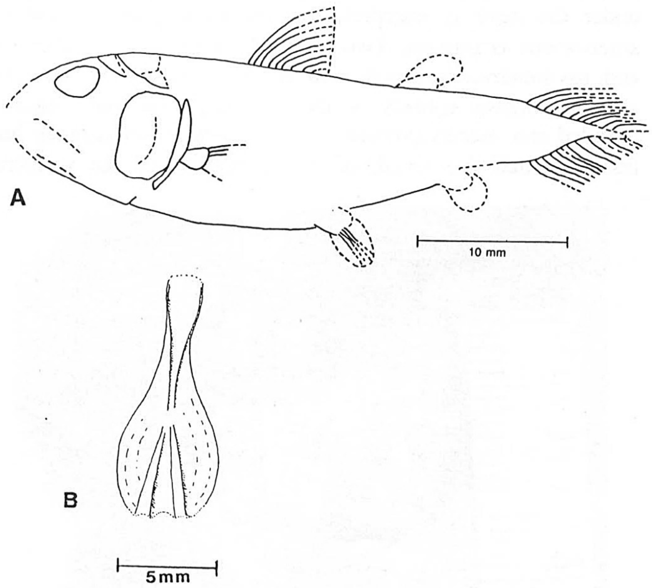

Fig. 15. Crossopterygian, AM 4912. Reconstruction using parts of three specimens. *A*, Entire fish; mostly after one specimen 44.2 mm in length. Scale impressions not shown. Second dorsal lobe not evident. *B*, Isolated urohyal.

shown to be the most abundant and diverse vertebrate group then and some were used as age- or regional-indicator taxa. The work was significant, especially in view of the fact that about $^2/_3$ again as many placoderm genera had been described or were known in collections since a previous authoritative review had been published.[18] Throughout the Devonian, evidence from fish and invertebrate distributions has indicated that there was a breakdown of regional provincialism to produce cosmopolitan patterns by Frasnian times.[14,27,28] Endemic fish taxa shared by eastern Australia and Antarctica indicated that an East Gondwana faunal province persisted until late Middle Devonian times.[14] The association of groenlandaspids, phyllolepids and *Bothriolepis* was considered to be typical of the latest Devonian (Famennian).[11] All three of these taxa were present in Euramerica and East Gondwana by at least the Frasnian–Famennian boundary,[14] and all three are present in the Witpoort ichthyofauna as well, suggesting at least an extension forward in time for a persistence of East Gondwana elements in southern Africa.

Copper[27] stated 'no shelly or coral marine faunas are known from the cool Malvinokaffric region from Givetian through Famennian time.' However, the brachiopod genus *Tropidoleptus* was reported in South Africa and this evidence was used to indicate that Late Devonian provincialism already had been breaking down by Givetian times.[9,29] This was corroborated with the fishes[11,14] which showed a relationship between presumed Malvinokaffric elements and part of the East Gondwana ichthyofauna (the shark *Antarctilamna*, the agnathan *Turinia* and possibly the acanthodian *Machaeracanthus*).

A number of paleogeographic reconstructions of the Devonian world based on palaeomagnetic data, such as that of Scotese *et al.*,[30] were criticized for not corroborating the fossil evidence.[14,29] Young[11] presented two alternative paleogeographic reconstructions of the Late Devonian world which placed East Gondwana at about 60–70°S paleolatitude or at 25–30°S. In these reconstructions, and the modified one of Scotese and Barrett,[31] southernmost Africa remains at very high latitudes (70–80°S). The Grahamstown assemblage indicates that if cold-water conditions existed at high latitudes in Famennian times,[10] then the Witpoort ichthyofauna may represent cold-adapted forms of the otherwise cosmopolitan 'tropical' taxa. However, Scotese and Barrett[31] concluded that western Gondwana had a generally warm climate at the end of the Devonian. The question that now remains is: are the high-latitude Witpoort fishes an endemic holdover of an earlier Malvinokaffric subprovince, having only affinites with East Gondwana, or are they more representative of the Middle Devonian radiation that produced the more cosmopolitan distributions? Only more refined taxonomic resolution of the specimens will help elucidate this.

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