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An unusual new fossil shark (Pisces: Chondrichthyes) from the Late Devonian of South Africa

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Abstract – A new stem-group chondrichthyan fish, *Plesioselachus macracanthus* gen. et sp. nov., is described from the Late Devonian Witpoort Formation, representing an estuarine lagoon site, near Grahamstown, South Africa. Based on a single, fairly complete specimen, it is distinctive in its a single dorsal fin braced by a large, stout spine with numerous ribs and posterior denticles, apparently no second dorsal or anal fin, an amphistylic jaw suspension, and a distinctive triangular palatoquadrate. It is suggested that the species may represent a high-latitude, Late Devonian relict taxon.

INTRODUCTION

In 1985 a shale bed was exposed by a road cutting through the Witpoort Formation in the upper Witteberg Group, near Grahamstown, South Africa. It was soon found to be fossiliferous, and the deposits were interpreted as representing a stagnant coastal lagoon sheltered by a barrier island complex in the Famennian stage of the Upper Devonian (Hiller and Taylor 1992; Long *et al.* 1997). The age of the site is based on brachiopods occurring in layers just above the fossiliferous shale beds, and the overall nature of the fish fauna. Fossils of terrestrial and aquatic plants, aquatic invertebrates and fishes have been reported (Taylor and Hiller 1993; Anderson *et al.* 1994; Gess and Hiller 1995a, 1995b; Hiller and Gess 1996; Long *et al.* 1997). We consider that the site represents the earliest, relatively complete, aquatic community so far discovered in Africa.

Among the fishes collected is a 44 cm long chondrichthyan represented on two slabs of shale as asymmetrical counterparts. Skeletal tissue of all of the fishes from the site has been remineralized into kaolinite and mica (Taylor and Hiller 1993; Anderson *et al.* 1994), so specimens are generally poorly preserved as shallow impressions. The disarticulated nature of the specimens also suggests that a considerable degree of decomposition occurred before final burial. This is seen in the present specimen through the fact that the jaws lie under the scapulocoracoid and are separated at the symphysis, the dorsal fin spine and basal have reversed their positions, and the pelvic girdle is rotated about 90° posteriorly. We are unable to place the specimen in any of the chondrichthyan orders as arranged by Nelson (1994) or Janvier (1996), mainly because of uncertainty in the interpretation of many anatomical parts (see below).

The specimen is deposited in the Albany Museum (AM), Grahamstown; and a latex rubber cast of the specimen is held in the Western Australian Museum vertebrate palaeontological collection. All measurements given below are greatest straight-line distances.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Plesioselachus gen. nov.

Diagnosis

Chondrichthyan having a truncated body; jaw suspension amphistylic with upper jaw roughly triangular in lateral view; dorsal fin spine long and robust, in height about 1/3 total body length, bearing about 13–15 ribs near the base, with numerous minute posterior denticles; vertebrae with neural arches only; scapulocoracoid simple with low articular crest; pectoral radials *c.* 10–11; anal and second dorsal fins not known (presumed absent). Dentition and nature of squamation unknown.

Type species

Plesioselachus macracanthus sp. nov.

Etymology

From the Greek 'plesios' (common, used to denote primitive in zoological nomenclature), and 'selachus' a shark, referring to its plesiomorphic anatomy.

Plesioselachus macracanthus sp. nov.

Figures 1–5

Chondrichthyan: Anderson *et al.* 1994: 401.

Chondrichthyan: Gess and Hiller 1995a: 290–293, figures 57, 58.

Material Examined

Holotype

AM 4817, entire fish (Figures 1, 2), slightly damaged, 44 cm in length, asymmetrically preserved as two counterparts.

Referred Material

AM 4866 an isolated dorsal fin spine (Figure 4).

Type Locality and Horizon

N-2 highway bypass shale bed, *c.* 3 km south of central Grahamstown, Eastern Cape Province, South Africa. Collected by R.W. Gess and M. Stonestreet, June 1990. Middle part of the Witpoort Formation, Witteberg Group, Cape Supergroup. Middle Famennian stage of the Late Devonian.

Diagnosis

As for genus.

Etymology

From the Greek 'makros', long, and 'akantha', thorn, in reference to the dorsal fin spine.

Description

The skeletal elements of the head (Figures 1, 2) are preserved slightly dissociated, deeply embedded in the right counterpart. The head, as preserved, measures 41 mm in length, and about 20 mm of the snout is estimated to be missing (giving a total estimated length of at least 61 mm). The orbits are not seen, nor is there any trace of the neurocranium or visceral skeleton, these structures are added to the reconstruction in Figure 3 purely for relative placement of the jaw and shoulder girdle structures.

The palatoquadrates (PAL, Figures 2, 3) are fragmented. One side (possibly the left) is about 3/4 intact, missing only the anterior region of the suborbital lamina. The cleaver-shaped dorsal lamina is highly arched and the ventral surface is gently bowed with a shallow articular notch posteriorly situated. Only the broken posterior end of the other palatoquadrate (presumed to be the

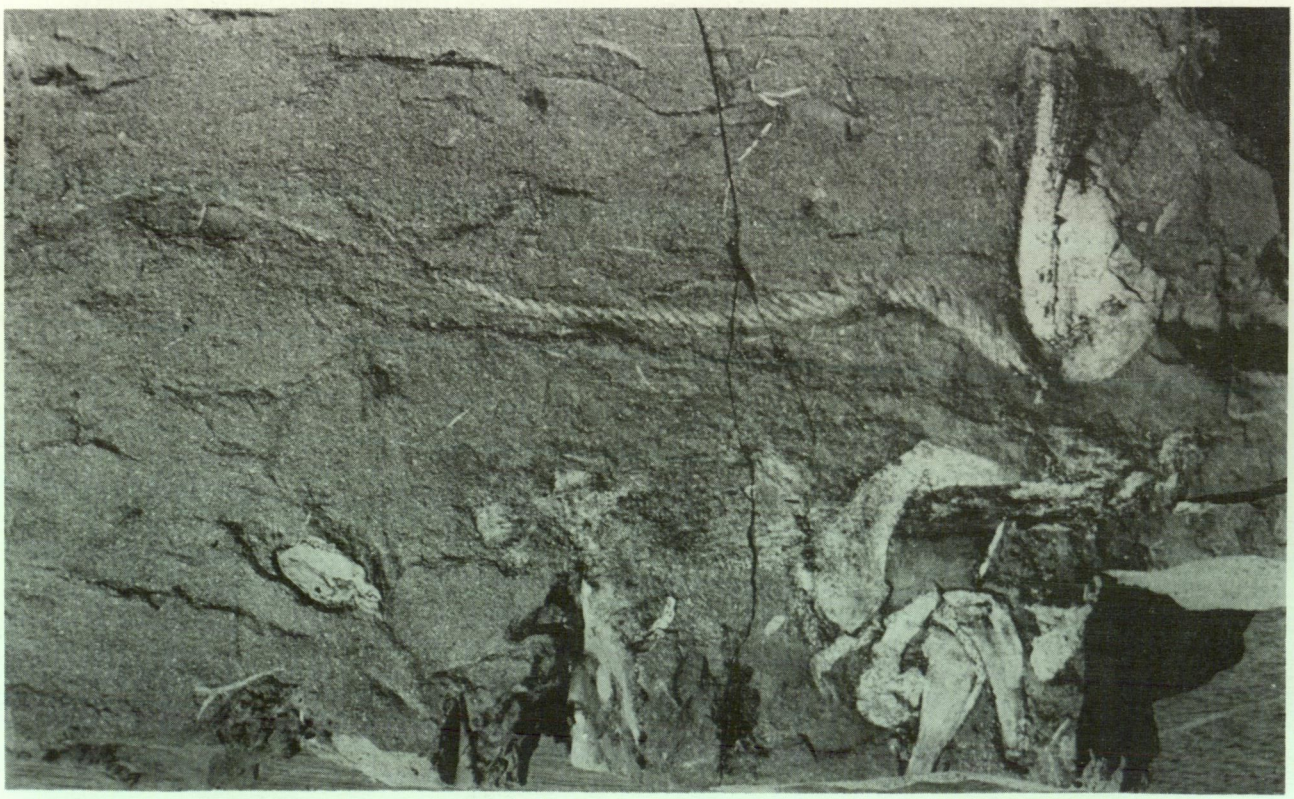

Figure 1 Left counterpart of holotype of *Plesioselachus macracanthus* gen. et. cp. nov., AM 4817.

right side) is preserved. No teeth are evident either near the palatoquadrates or lower jaws, or anywhere in the vicinity of the head (Figure 1).

The lower jaw (Meckel's cartilage; MECK, Figures 2, 3) is asymmetric on each counterpart, lying beneath the scapulocoracoid. It is deep posteriorly with a small articular notch (interpreted as if the left jaw is in a reversed position). The left lower jaw is 47 mm long, the right lower jaw is 37.5 mm as preserved (both measured on the left counterpart). Labial cartilages (LAB, Figures 2, 3) are seen as roughly triangular elements with their anterior margins slightly bowed.

The anterior half of the vertebral column is represented on both counterparts, consisting only of sharply pointed, basally rounded neural arches ("neurapophyseal rods") which lack centra (NA, Figures 2, 3). Mineralized impressions of 45 vertebrae occur on the counterparts before giving way to low, unsculptured ridges visible only on the left counterpart representing the rest of the vertebral column (Figure 1). Total vertebrate number about 80.

Distal-most regions of the caudal area and flank above the pelvic girdle show patches of diamond-shaped dermal denticles (the longest patch is at the level of the vertebral column 62 mm on the right counterpart). The denticle ornament is not evident owing to the unusual mineralization of the specimen. The shape of the caudal fin is unclear owing to rock damage in the region. There is a small area showing an impression of part of the ventral lobe of the caudal fin.

The dorsal fin basal (BAS, Figures 2, 3) is triangular, somewhat elongated, with a length of 46 mm. The dorsal fin spine base lies on and behind the basal. The dorsal fin spine (SP, Figures 2, 3) has many finely noded ribs present along its entirety, and rows of small denticles along its posterior face. The right counterpart has the anterior portion of the dorsal fin spine missing, but the impression of the posterior portion present to spine tip has a length of 157 mm, with approximately 13–15 spine ribs near its base (where total breadth of spine can be observed, on the left counterpart; Figure 2). There are nine ribs present at the mid-height of the spine on the right counterpart. There are 15 rib tubercles per cm near the spine base and 6–7 posterior denticles per cm near the dorsal extremity. AM 4866, a single, isolated spine which is 88 mm long as preserved (base missing) shows 11 ribs ventrally and 21 spine denticles in the 26 mm segment where an accurate count is possible (Figure 4).

The scapulocoracoid (SCAP, Figures 2, 3) and

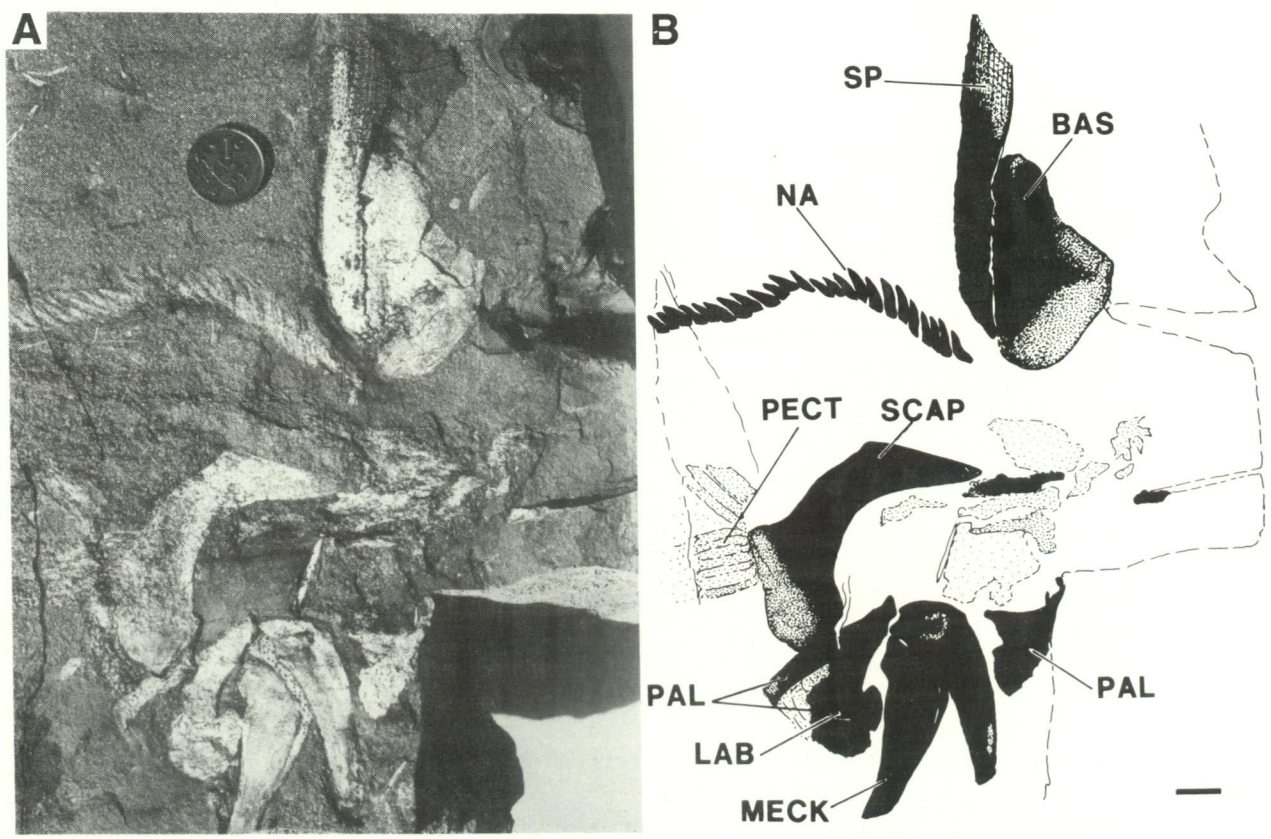

Figure 2 Anterior region of left counterpart of holotype of *Plesioselachus macracanthus* gen. et sp. nov., AM 4817. A, photograph; coin diameter = 19 mm. B, sketch; abbreviations: BAS: dorsal fin basal; LAB: labial cartilage; MECK: Meckel's cartilage (lower jaw); NA: neural arches of vertebral column; PAL: palatoquadrate (upper jaw); PECT: pectoral fin radials; SCAP: scapulocoracoid; SP: dorsal fin spine; scale bar = 10 mm.

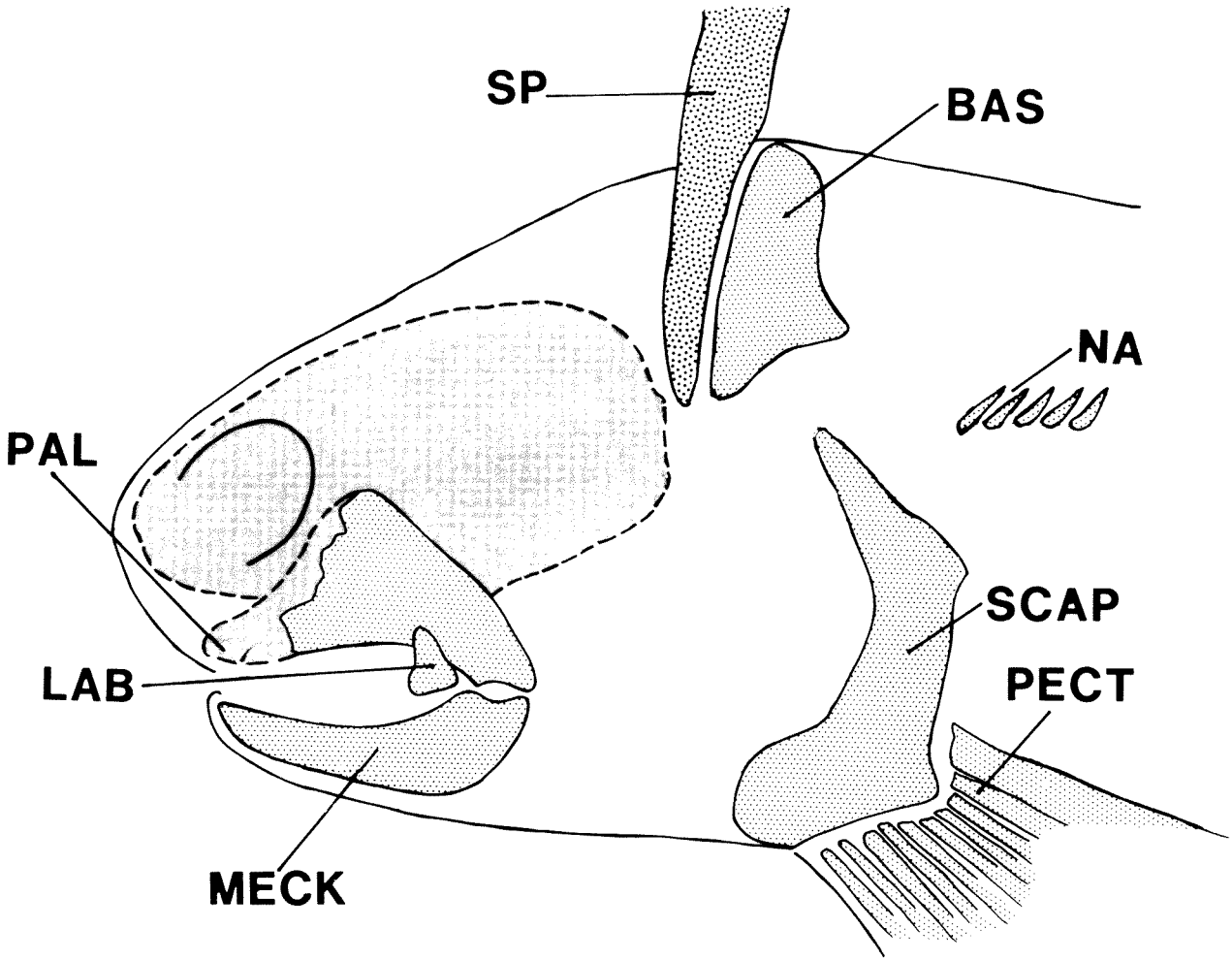

Figure 3 Reconstruction of anterior portion of *Plesioselachus macracanthus* gen. et sp. nov. Abbreviations: BAS: dorsal fin basal; LAB: labial cartilage; MECK: Meckel's cartilage (lower jaw); NA: neural arches of vertebral column; PAL: palatoquadrate (upper jaw); PECT: pectoral fin radials; SCAP: scapulocoracoid; SP: dorsal fin spine. Grey area: imaginative reconstruction of chondrocranium. Light stipple: preserved cartilage impressions. Heavy stipple: bone/osteodentine of fin spine.

proximal pectoral radials (PECT, Figures 2, 3) are well preserved. The bases of the radials indicate 10 or 11 elements are present in the pectoral fin. The posterior margin of the pectoral fin is only faintly visible as an impression in the matrix, indicating that the radials extend about half way to the margin. The pectoral fin length from the posterior margin of the scapulocoracoid to the margin of the fin impression is 98 mm.

The scapulocoracoid measures 61 mm, and is dorsally triangular with an acute tip. It has a stout, broadly rounded base with a low, triangular articular crest posteriorly. The pectoral metapterygium is not evident.

The biramal pelvic basipterygia lie ventral to the end of the visible extent of the vertebrae (Figure 1). These are best observed on the left counterpart. The maximum measured lengths of these are 33 mm (left counterpart) and 29 mm (right counterpart). The main body of each ramus is unsculptured, with an elongate to ovoid shape. There are one (dorsal) or two (ventral) separate, bulbous bodies which we here interpret as axial elements. As the shale matrix is slightly irregularly layered in this region, causing some distortion in these structures, we have reconstructed them in a straightened state (Figure 5). No pelvic radials, clasper, anal fin, or even impressions of these are seen on the specimen.

DISCUSSION

We regard the current classifications of Palaeozoic chondrichthyans as being unsatisfactory mainly owing to the incomplete interpretations of anatomical features and their cladogenesis in the known material, coupled with the existence of many undescribed forms (L.J.V. Compagno, R. Lund, pers. comm.). Thus, we defer placing *Plesioselachus* in a phylogenetic structure until more of it is known. Details of its chondrocranium, teeth, fin architecture, hyoid, branchials, and dermal denticles are obscure, or unknown, in the present specimen so any phylogenetic placement would be unsatisfactory.

During the Devonian Period, elasmobranchs

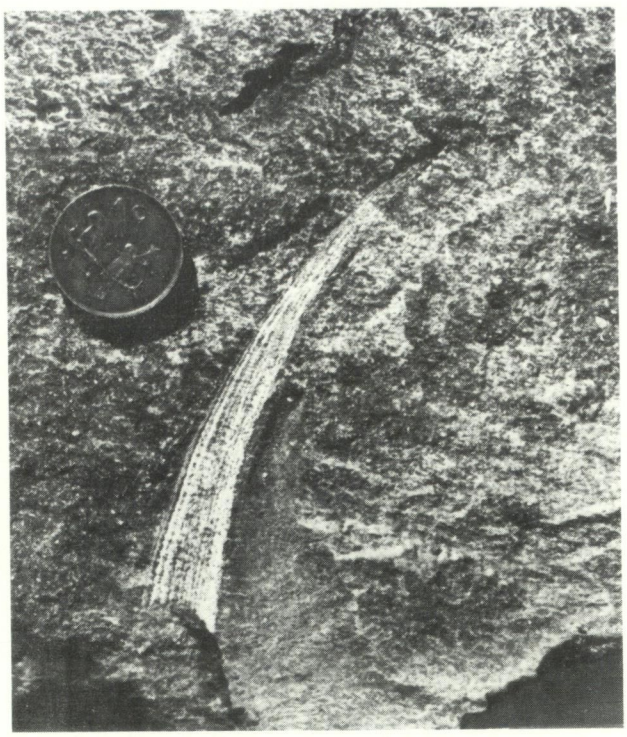

Figure 4 *Plesioselachus macracanthus* gen. et sp. nov. Referred isolated dorsal fin spine, AM 4866. Traces of the base of the spine reach to the edge of the photograph. Coin diameter = 19 mm.

radiated into many groups from basic stethacanthid-type cladodonts (e.g. *Cladoselache*), to stem group xenacanths (*Antarctilamna, Portalodus, Aztecodus*; Long and Young 1995), protacrodids, 'phoebodontids' (Ginter 1990; Ginter and Ivanov 1992; Long and Young 1995) and coronodontids (*Diademodus* Harris 1951 and *Siamodus* Long 1990), amongst others. However, despite their good record from teeth and isolated spines, the overall structure of the jaws and chondrocrania of these early sharks is based on very few taxa, mostly the well-preserved Late Devonian Cleveland Shale sharks (e.g. *Cladoselache*), a Tennessee cladodont (Maisey 1989), the isolated chondrocranium of *Cladodus wildungensis* (Gross 1937), and the braincase and partial skeleton of *Antarctilamna* (Young 1982). Thus, the South African *Plesioselachus* shows that this Late Devonian chondrichthyan, while differing from other elasmobranchs principally in overall body and fin architecture, retained an essentially basal chondrichthyan-like set of characters, particularly its lack of second dorsal and anal fins, short body and simple pectoral girdle.

One explanation for such a primitive elasmobranch appearing so late in the Devonian of western Gondwana may be the high-latitude relict hypothesis of Anderson *et al.* (this volume). The long dorsal fin spine and fin architecture suggest *Plesioselachus* may be some pre-xenacanthiform relict (*sensu* Long and Young 1995), but without teeth further speculation on its relationships is premature. The absence of dentition may be due either to its possession of few rows of viliform teeth which were not preserved since a good part of the head is missing, or alternatively due to it having very few large teeth (as in petalodonts), or compound tooth-plates (as in holocephalomorphs),

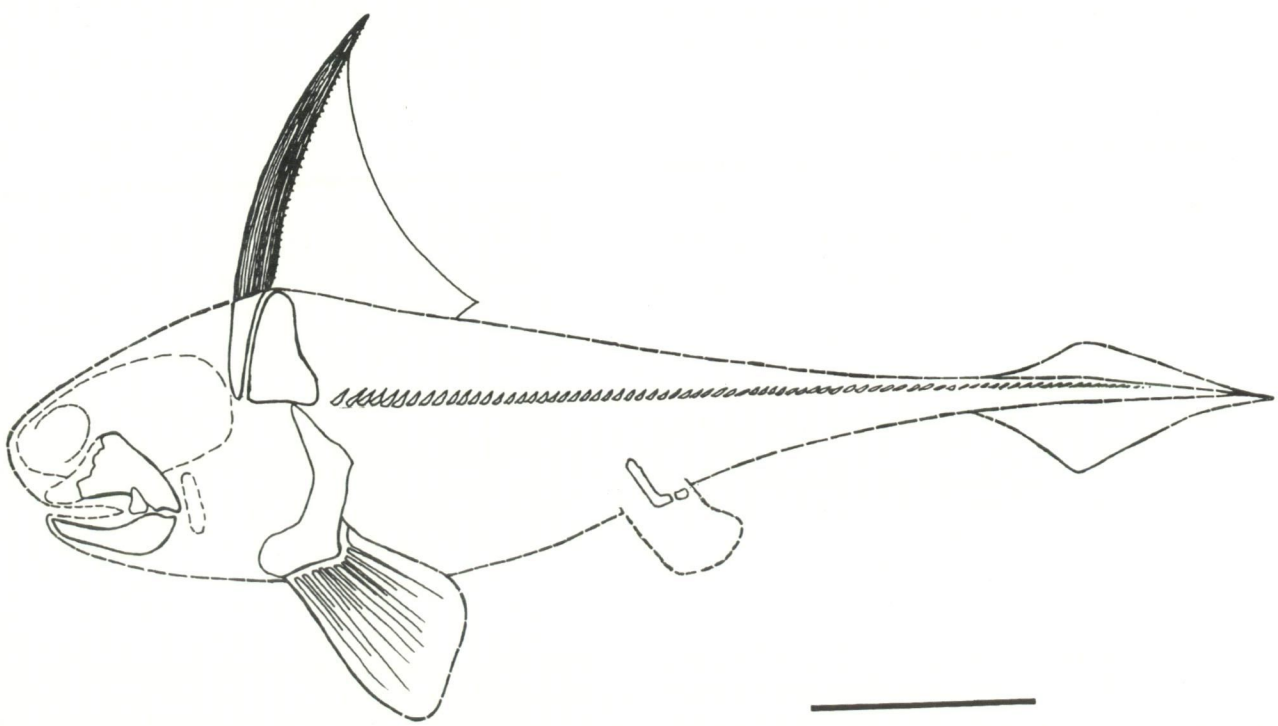

Figure 5 Reconstruction of entire specimen of *Plesioselachus macracanthus* gen. et sp. nov. Pelvic fin and most of caudal area largely conjectural. Scale bar = 10 cm.

which, following post-mortem disruption, may be dissociated from the jaw cartilages and therefore not be seen on the specimen. The latter scenario would also account for the absence of small, isolated teeth in the vicinity of the head, a feature expected in specimens of cladodont-level sharks which have articulated or only partially disarticulated preservation (Williams 1985).

The short body shape, long whip-like tail and high dorsal fin spine are reminscent of early holocephalomorphs like *Echinochimaera* (Lund 1977). Without dentition preserved it is unsatisfactory to refer this specimen to the Holocephalomorpha, although on body characteristsics alone we would suggest that *Plesioselachus* is most likely related to this group. Lund and Grogan (1997) have presented a cladogram of 'cochliodontomorph' relationships, which places the Chimaeriformes as a monophyletic group sharing unique tooth plate mineralogy, lack of enlarged dorsal cranial spines, lack of mandibular spines or plates, specialized mid-dorsal sensory-line, a pectoral fin with low midflank articulation, pelvic girdle with prepelvic tentaculum, and endoskeleton mineralized by continuous calcified cartilage. Unfortunately none of these characters can be verified on *Plesioselachus*.

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