# A LATE PERMIAN FRESHWATER SHARK FROM EASTERN AUSTRALIA

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ABSTRACT. A new genus and species of elasmobranch, *Surcaudalus rostratus*, is described from the Late Permian Rangal Coal Measures, Blackwater, central Queensland. *Surcaudalus* is characterized by a palatoquadrate with a well-developed ethmoidal articulation, cladodont (phoebodontiform) dentition, absence of ribs, dorsal fin-spines with an anterior keel and a flat to concave posterior wall whose posterolateral margins bear three rows of barb-like denticles, and a non-lunate caudal fin with a well-developed epicaudal lobe. The phylogenetic significance of fin-spine characteristics, caudal fin morphology, and broad, expanded occipital segments is discussed.

THE Rangal Coal Measures in the Utah Development Company's open-cut coal mine, 20 km south-south-west of Blackwater, central Queensland (text-fig. 1), contain several lacustrine mass-mortality horizons that have yielded a genus of the Bobasatraniformes (Campbell and Duy Phuoc 1983), at least twelve new genera of Palaeonisciformes, and two new genera of Elasmobranchii.
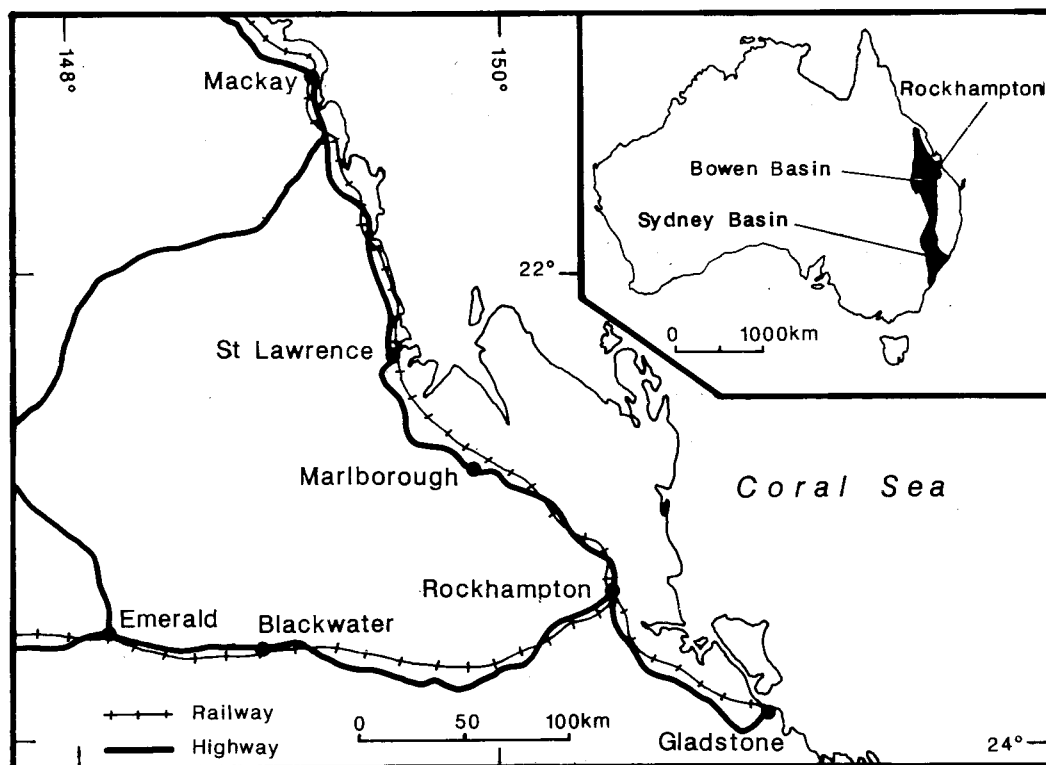
TEXT-FIG. 1. Location of Blackwater (modified after Burgis 1975).

AGE in Ma.	PERIOD	EPOCH	AGE	SUPERZONE	SPORE-POLLEN ZONES West Australia	SPORE-POLLEN ZONES East & South Australia	AGE in Ma
250	TRIAS	EARLY	243 SCYTHIAN 248	SPORITES	T.PLAYFORDII	A.TENUISPINOSUS	250
					P.SAMOILOVICHII	P.SAMOILOVICHII	
					L.PELLUCIDUS	L.PELLUCIDUS	
	PERM	LATE	TATARIAN 253 KAZANIAN	FALCISPORITES	P.MICROCORPUS	P.MICROCORPUS	
					UPPER STAGE 5	UPPER STAGE 5	

TEXT-FIG. 2. Correlation of the Late Permian to Early Triassic palynological zones of west, east, and south Australia (modified after Helby et al. 1987).

The Rangal Coal Measures, the uppermost formation in the Late Permian Blackwater Group, comprises coal, labile sandstone, carbonaceous shale, siltstone, and mudstone, and is between 107 m and 137 m thick near the Utah Development Company's mine (Staines 1972; Burgis 1975). Mortality horizons occur frequently above the Argo Seam; the latter averages 6·1 m in thickness, dips gently eastwards, and occurs towards the base of the Rangal Coal Measures.

Truswell (in Campbell and Duy Phuoc 1983) identified spores and pollens from a mortality horizon 6 m above the Argo Seam. She regarded the assemblage as being high in the Upper Stage 5 of Kemp et al. (1977); this is equivalent to a Late Permian (Late Kazanian) age (text-fig. 2).

Three closely spaced mortality horizons occur at a site known as Clinker Hill. The new elasmobranchs were collected from the middle horizon; it is separated vertically by 300 mm and 400 mm respectively from the horizons immediately above and below. The uppermost mortality horizon is covered by between 100 mm and 500 mm of overburden, enabling extensive lateral excavation. The underlying coal seam has ignited, and the original light-grey shales and mudstones have been oxidized red and baked 'brick' hard, thus faithfully preserving the fossils from the rigours of surface weathering.

PALAEOENVIRONMENTAL INTERPRETATION

Burgis (1975) viewed the Rangal Coal Measures as having accumulated in an environment characterized by laterally migrating river channels and associated floodplain and lacustrine deposits. She envisaged peat accumulating in extensive swamps above point-bar sands and muddy overbank sediments. Differential compaction was thought to have resulted in shallow lakes forming in depressions over former peat swamps. Burgis (1975, p. 56) interpreted the sequence of events in the development of the lake basins as one in which 'compactional growth of mounds . . . disrupted the system of ephemeral channels and small lakes'.

All three horizons have been excavated, each over an area of 8 m × 4 m. The two lower horizons are about 5 mm thick; the uppermost horizon is variable and up to 50 mm in thickness. All contain ontogenetically young fishes (chondrosteans and elasmobranchs); much larger specimens of the same species have been found in drag-line dumps. The fish are densely packed within the mortality horizons. Those in the uppermost horizon were obviously buried rapidly in a turbid mass flow, as evidenced by rip-up clasts and by fish contorted and buried in all orientations; this may have been caused by mass slumping in a lake or by rapid burial in overbank splay deposits.

Abbreviations and symbols used in text and text-figures

Anatomical: AP, articular process; BCDF, basal cartilage of dorsal fin; CB, ceratobranchials; CT, cusps of teeth; DF, dorsal fin; DFS, dorsal fin-spine; EART, ethmoidal articulation; ECL, epicaudal lobe; FECL, fragmentary epicaudal lobe; FS, fleshy snout; FVHL, fragmentary ventral hypochordal lobe; LHL, longitudinal hypochordal lobe; LSL, lateral sensory line; MC, Meckel's cartilage; MSP, mesopterygium; MTP, metapterygium; NCR, neurocranium; NE, neural element; NM, notochordal mass; OCCR, occipital region; OR, orbit; PF, pectoral fin; POP, postorbital process; PQ, palatoquadrate; PRP, propterygium; SC, scapulocoracoid; SCD, sensory canal denticles; STL, subterminal lobe; TBR, tooth bearing ramus; TBRMC, tooth bearing ramus of the Meckel's cartilage; TBRPQ, tooth bearing ramus of the palatoquadrate; VHL, ventral hypochordal lobe; W, white unoxidized region; WCRPQ, weakly calcified region of the palatoquadrate.

Institutional: AMF, Australian Museum Fossil; CMNH, Cleveland Museum of Natural History; QMF, Queensland Museum Fossil.

Other: PDH, plugged drill hole.

Symbols: regular heavy stipple indicates calcified cartilage; diagonal cross hatching indicates damaged cartilage surfaces; lines comprising alternating dashes and dots indicate incomplete outline of body.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley 1880
Subclass ELASMOBRANCHII Bonaparte 1838
Order EUSELACHII Hay 1902
Superfamily *incertae sedis*
Genus SURCAUDALUS n. gen.

Etymology. From the Latin *sur* (above, on) and *cauda* (tail); in reference to the well-developed epicaudal lobe.

Type species. *Surcaudalus rostratus* n. sp.; monotypy.

Diagnosis. Small elasmobranch with a blunt fleshy snout extending beyond the mandibular symphysis; palatoquadrate with a well-developed ethmoidal articulation; Meckel's cartilage relatively deep and robust; dentition cladodont (phoebodontiform); ribs absent; dorsal fin-spines with an anterior keel and a flat to concave posterior wall whose posterolateral margins bear, apically, three pairs of small closely spaced barb-like denticles; lateral surfaces of fin-spines having three major longitudinal costae; caudal fin comprising 26–27% of the total body length and possessing a well-developed epicaudal lobe.

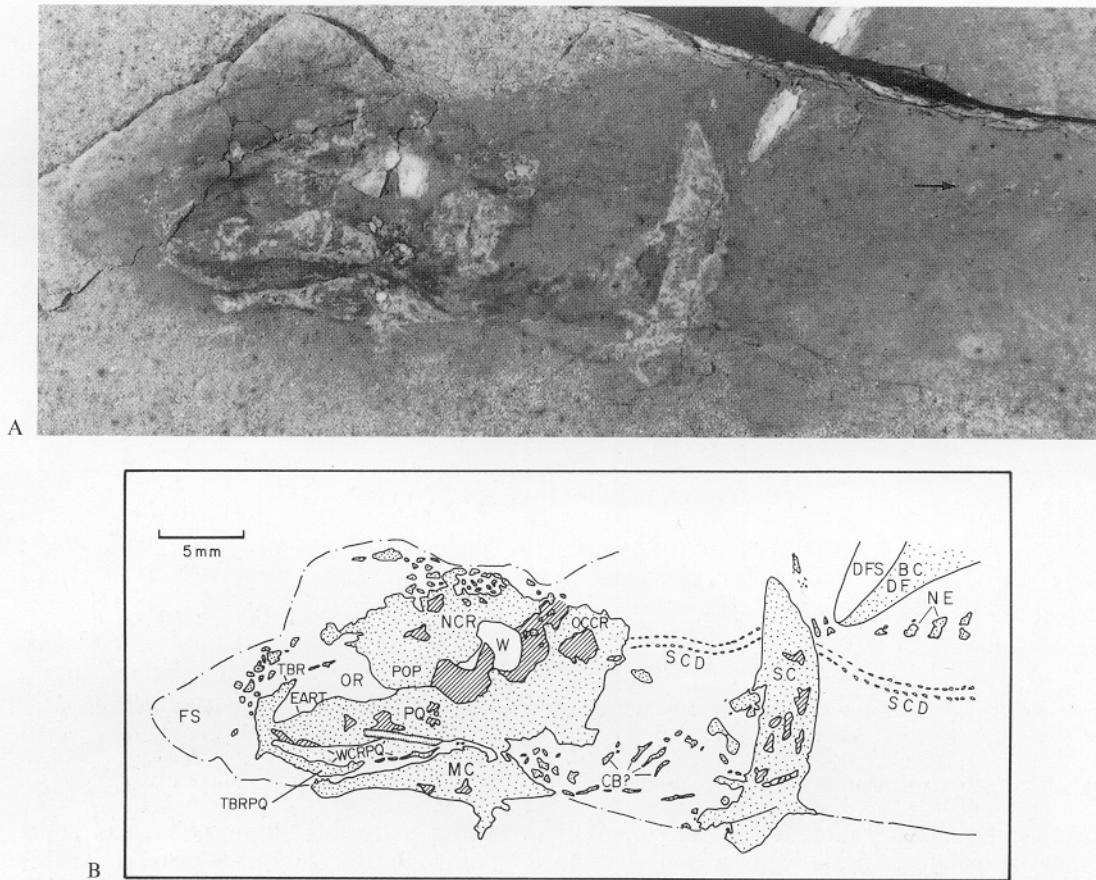*Surcaudalus rostratus* n. sp.

Plates 33 and 34; text-figs. 3–11

Diagnosis. As for genus.

Etymology. From the Latin *rostratus* (rostrum), referring to the elongate fleshy snout extending beyond the mandibular symphysis.

Holotype. QMF14470A and QMF14470B, part and counterpart respectively, of an articulated skeleton of a shark, minus the posterior portion of the caudal fin; exposed in lateral view.

Paratypes. AMF72559A and AMF72559B, part and counterpart respectively, of an articulated skeleton of a shark exposed in lateral view. QMF14471A and QMF14471B, part and counterpart respectively, of an articulated skeleton of a shark, minus the head region, exposed in lateral view.

Horizon and locality. Rangal Coal Measures of the Blackwater Group (Late Permian [Late Kazanian], high in the Upper Stage 5 of Kemp *et al.* 1977), Blackwater, central Queensland, Australia.

TEXT-FIG. 3. *Surcaudalus rostratus* n. gen. n. sp. paratype (AMF72559A). A, head and pectoral girdle in lateral view, × 2·3. B, drawing of the same specimen.

DESCRIPTION

Body form. All specimens of *Surcaudalus rostratus* n. sp. are ontogenetically young individuals with slender fusiform bodies. AMF72559 is 193 mm long and 19 mm deep at its widest point along the trunk. It has a subterminal mouth and a caudal fin which comprises 26–27% of the total body length. It has a tapering, blunt, fleshy snout whose length is at least 24–26% that of the neurocranium.

Neurocranium The neurocrania of both QMF14470 (text-figs. 5 and 6) and AMF72559 (text-figs. 3 and 4) are preserved in lateral view; both are extensively crushed and distorted. The rostrum does not extend beyond the anterior margin of the palatoquadrates. The postorbital process is very prominent and long (anteroposterior), with a gently concave anterior margin. The posterior margin of the orbit is situated at 57–67% of the length of the neurocranium (measured from the posterior). The otico-occipital region is moderately long and is tentatively estimated to comprise 38–43% of the total length of the neurocranium.

EXPLANATION OF PLATE 33

Figs. 1–3. *Surcaudalus rostratus* n. gen. n. sp. 1, an almost complete specimen of the new genus (AMF72559A) in lateral view, × 1. The circular feature is a plugged drill hole. 2 and 3, part and counterpart of the holotype (QMF14470A and QMF14470B, respectively) in lateral view, × 1·5.

PLATE 33
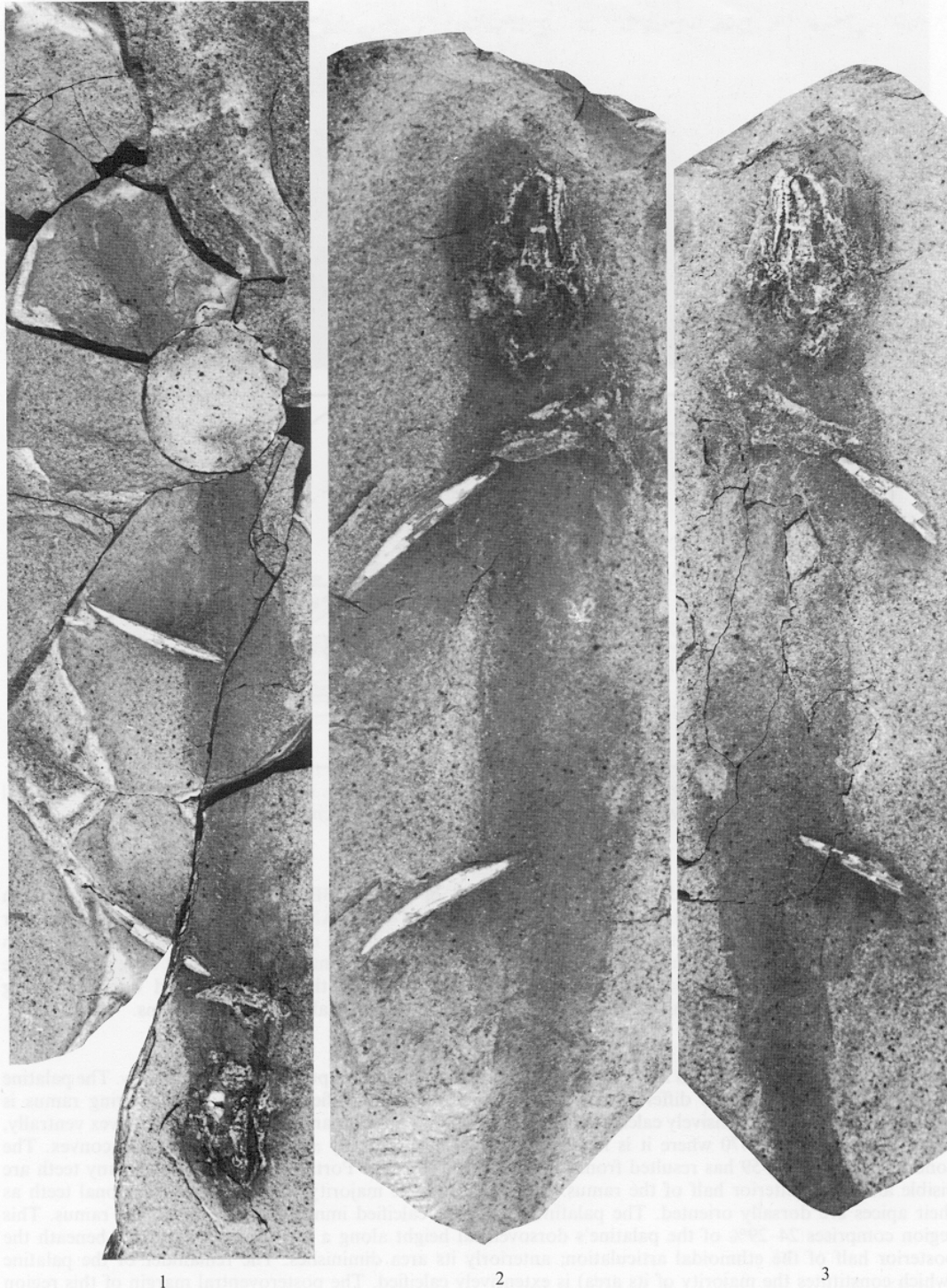
LEU, Australian late Permian freshwater shark
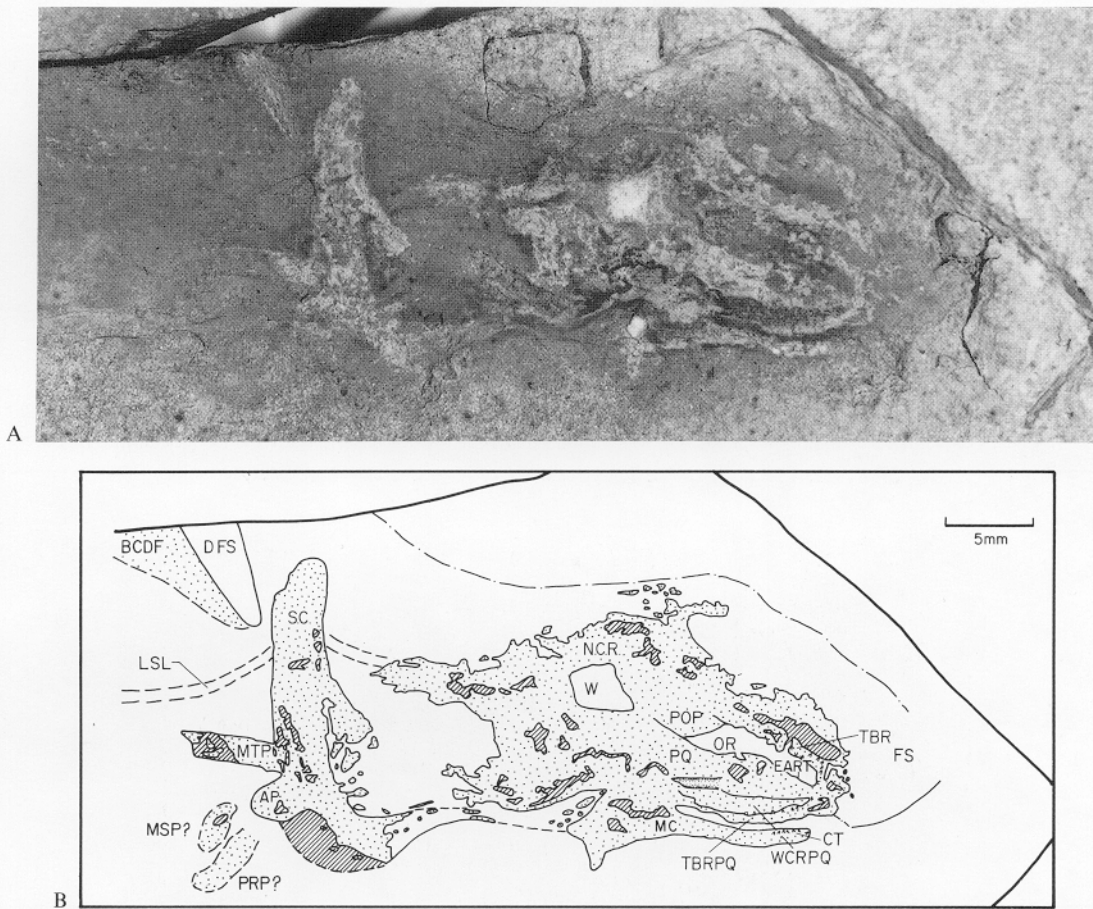
TEXT-FIG. 4. *Surcaudalus rostratus* n. gen. n. sp. paratype (AMF72559B). A, head and pectoral girdle in lateral view, × 2·3. B, drawing of the same specimen.

A robust, extensively calcified band of cartilage (TBR of text-figs. 3B–6B) extends posterodorsally from the anterior extremity of the palatoquadrates of both QMF14470 and AMF72559. This cartilage passes over the ethmoidal articulation and through the dorsolateral portion of the orbit. It exhibits numerous cusps in all orientations, particularly along its anterior half. Its interpretation remains enigmatic; it may represent the tooth-bearing ramus of the palatine portion of a palatoquadrate that was displaced dorsally during compression, ultimately breaking through the weakly calcified ethmoidal and orbital regions.

Visceral skeleton

Palatoquadrate. QMF14470 and AMF72559 have their palatoquadrates preserved in lateral view. The palatine portion has a distinct zonal differentiation in the degree of chondrification. The tooth-bearing ramus is narrow, elongate, and extensively calcified. In AMF 72559 the ventral margin of the ramus is convex ventrally, as opposed to QMF14470 where it is inclined gently posteroventrally and is weakly dorsally convex. The condition in AMF72559 has resulted from post-mortem distortion. Portions of the cusps of many teeth are visible along the anterior half of the ramus. In AMF72559 the majority belong to non-functional teeth as their apices are dorsally oriented. The palatine is sparsely calcified immediately dorsal to the ramus. This region comprises 24–29% of the palatine's dorsoventral height along a line oriented vertically beneath the posterior half of the ethmoidal articulation; anteriorly its area diminishes. The remainder of the palatine (which constitutes the majority of its area) is extensively calcified. The posteroventral margin of this region
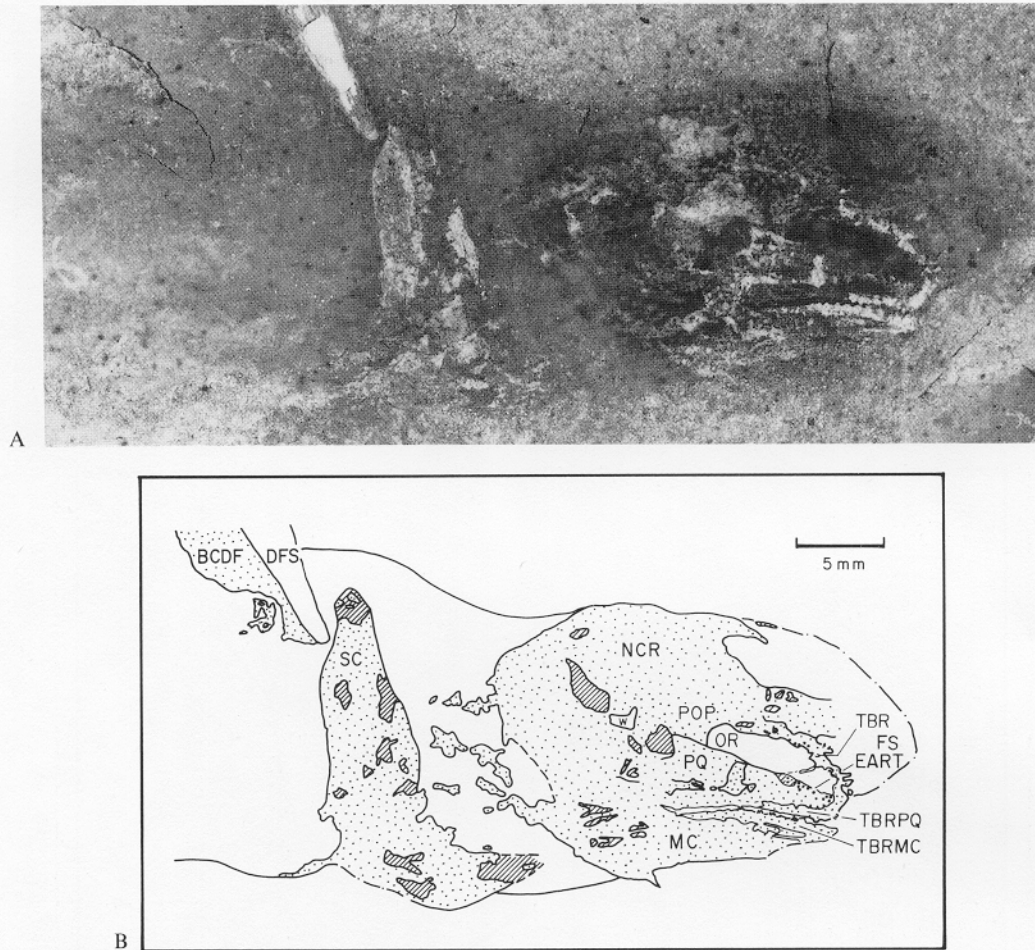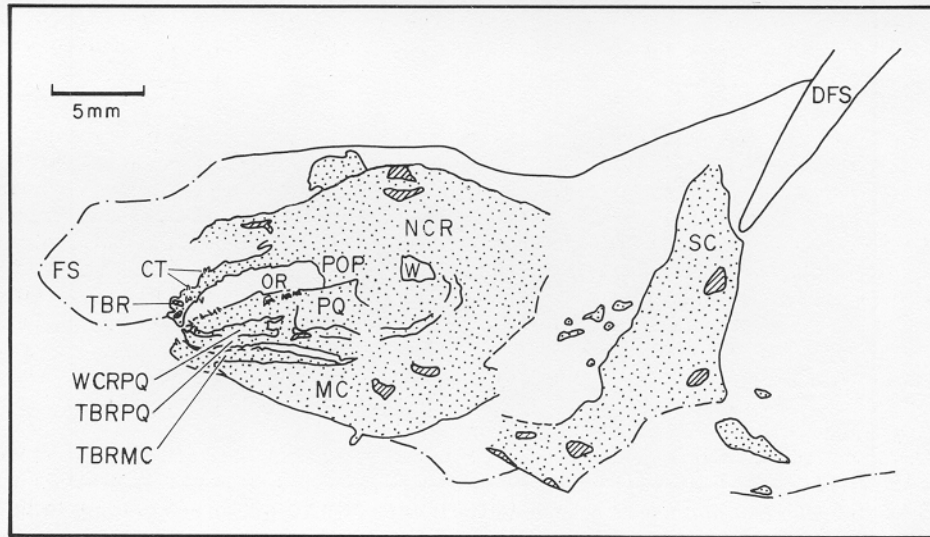
TEXT-FIG. 5. *Surcaudalus rostratus* n. gen. n. sp. holotype (QMF14470A). A, head and pectoral girdle in lateral view, ×2·5. B, drawing of the same specimen.

slopes posteroventrally towards the mandibular articulation. This margin is a robust, narrow, gently convex ridge (best preserved in AMF72559B) and appears to be a raised portion of the palatoquadrate rather than a labial cartilage (text-figs. 3 and 4).

Along the anterodorsal margin of the palatoquadrate a well-developed ethmoidal articulation rises (from the anterior edge of the palatoquadrate and extending to what appears to be the anteroventral edge of the orbit) at 23–25° to the notochordal axis. In QMF14470 the ethmoidal articulation is reinforced by extensive chondrification. Heading backwards from the ethmoidal articulation the dorsal surface of the palatoquadrate rises into the floor of the orbit. Its slope steepens as it passes along the anteroventral portion of the postorbital process. Unfortunately, the dimensions of the otic portion of the quadrate region and the presence or absence of a postorbital articulation cannot be accurately determined. Traces of cartilage in this region are irregular; there is uncertainty in differentiating neurocranial from palatoquadrate cartilage. In AMF72559A a lateral expansion of the ventral quadrate region is present but no trace of the otic portion is preserved. In AMF72559B extensive calcified cartilage is present but its origin is uncertain. In QMF14470 the dorsal portion of the quadrate region terminates abruptly and is posteriorly concave. In QMF14470B a roughly arcuate, posteriorly convex band of cartilage extends dorsally from the posteroventral half of the quadrate region.
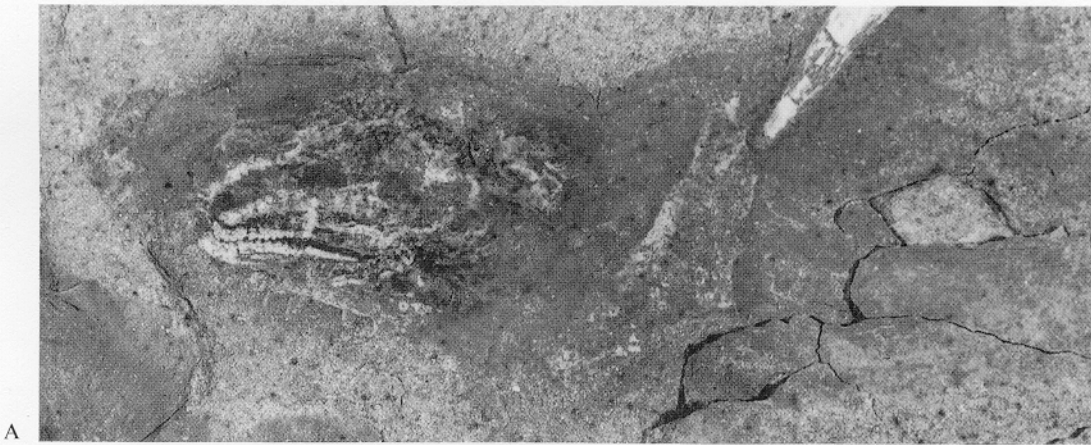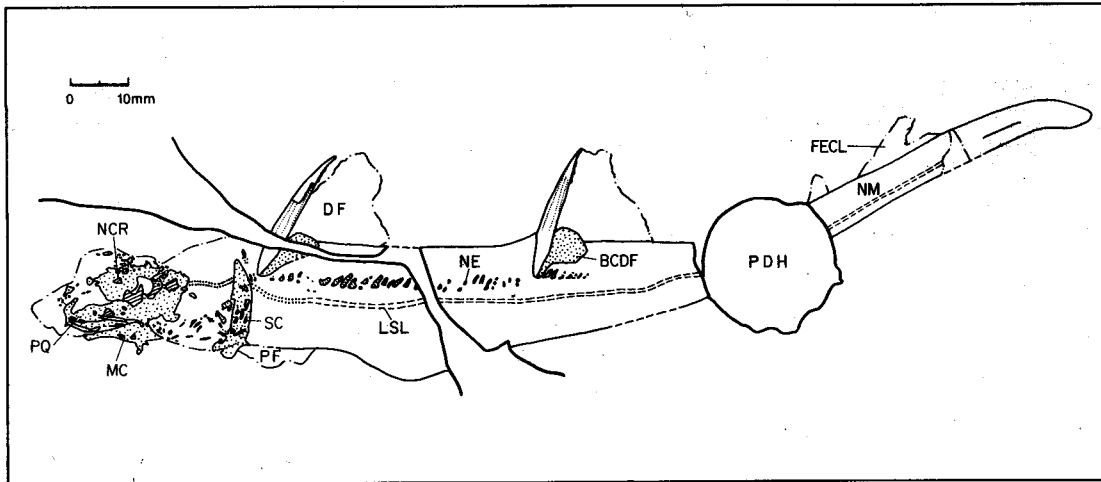
TEXT-FIG. 6. *Surcaudalus rostratus* n. gen. n. sp. holotype (QMF14470B). A, head and pectoral girdle in lateral view, ×2·5. B, drawing of the same specimen.

Meckel's cartilage. The lower jaw of QMF14470 deepens rapidly posteriorly and is 84% of the height of the palatoquadrate directly beneath the anterior edge of the postorbital process. Meckel's cartilage is laterally convex beneath the tooth-bearing ramus. The ventral margin (heading posteriorly) is inclined posteroventrally; it turns sharply posterodorsally beneath the poorly preserved articular region. The tooth-bearing ramus is extensively calcified and robust relative to the majority of Meckel's cartilage. It is weakly convex dorsally and tapers posteriorly. It exhibits numerous central cusps of teeth of disparate preservation, particularly along its anterior half. Meckel's cartilage of AMF72559 is relatively distorted with the tooth-bearing ramus poorly preserved along its anterior half. Its posteroventral border is crushed and attenuated.

Axial skeleton

Notochord. The notochord is unconstricted, persistent, and uncalcified. QMF14470 and AMF72559 contain calcified neural cartilages of disparate preservation (Pl. 33, figs. 1–3; Pl. 34, fig. 7; text-figs. 3A (arrowed), B and 7). In the cervical region of AMF72559, sparse traces of cartilage dorsal to the notochord indicate the presence of weakly calcified neural elements of uncertain form. In its thoracic region, extending backwards

TEXT-FIG. 7. *Surcaudalus rostratus* n. gen. n. sp. paratype (AMF72559A); articulated specimen in lateral view.

from the ventral tip of the anterior fin-spine to the posterior margin of the basal plate of the second fin-spine, there is a series of between thirty-four and thirty-seven neural cartilages whose apices extend dorsally beyond the most ventral point of the fin-spines. The first six (approximately) neural cartilages occur ventral to the anterior basal plate and are preserved as irregular patches of calcified cartilage of indeterminable morphology. Immediately posterior to these, the series is better preserved and the vertebral cartilages consist of calcified, wide-based neural arches bearing tapering neural spines. They are 3 mm long, closely spaced, presumably paired and unfused, and are inclined at 50–55° to the notochordal axis. The anteroventral corners of the neural arches are anteriorly elongated. There are six neural cartilages beneath the posterior basal plate; they are shorter and less robust than those anterior to them. Posteriorly only minor traces of neural calcifications are visible, though presumably they extended to the tip of the dorsal lobe of the caudal fin but were not, or only weakly, calcified. In QMF14470 a series of approximately thirty-two neural cartilages is present between the inserted portions of the fin-spines.

No haemal calcifications are present in the cervical and thoracic regions. In QMF14471A there are at least twelve slender, tapering rods extending backwards for a short distance from the anterior margin of the anal fin. These haemal cartilages are 3·5 mm long and are inclined posteroventrally at 40° to the notochordal axis.

Dorsal fins. The anterior and posterior dorsal fins (Pl. 33, figs. 1–3; text-fig. 7) are situated above, and extend posteriorly beyond, the posterior half of the pectoral and pelvic fins, respectively. Both fins extend dorsally above the apices of the fin-spines, with the anterior fin being the largest of the two. The anterior dorsal fin of AMF72559 (text-fig. 7) is detached from the posterior edge of the anterior fin-spine at a point just ventral to the origin of the most ventral barb-like denticle. Both fins are mildly folded and contorted indicating they were relatively flexible during life.

Most of each fin is preserved, enabling accurate estimation of their dimensions; nevertheless the precise lateral outline of the fins is unknown because their dorsal tips and posterior borders are not preserved.

Both fins are supported by a 'triangular' cartilaginous basal plate (Pl. 34, fig. 7; text-fig. 10), whose anterior portion is inserted in the posteroventrally situated basal notch of the fin-spine. Each basal plate consists of an expanded dorsal portion and a tapering, anteroventrally directed process extending to near the dorsal margin of the notochord. The expanded dorsal portion of the anterior basal plate occupies a smaller area than that of the posterior basal plate. Conversely, its anteroventrally directed process is wider and approximately one and a half times longer than the latter.

Radial cartilages, if present, were not calcified.

Anal fin. The anterodorsal portion of the anal fin is preserved on QMF14471; its origin is indicated by a slight widening of the body in this region. The most anterior point of the fin is located immediately ventral to the ventral tip of the most anterior haemal element. The dimensions and configuration of the anal fin are unknown.

TEXT-FIG. 8. *Surcaudalus rostratus* n. gen. n. sp. para-
type (AMF72559B); notochordal mass and portions
of appended fin lobes.
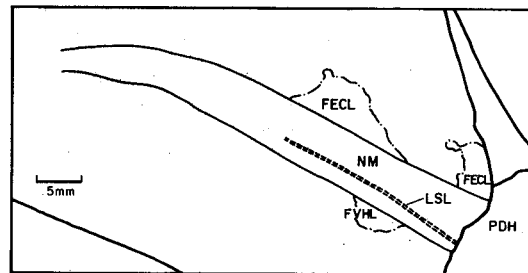
Caudal fin. In AMF72559 and QMF14471 the entire notochordal mass and portions of the appended fin lobes are present (Pl. 33, fig. 1; Pl. 34, fig. 4; text-figs. 7 and 8).

The following description is based on characters (text-fig. 12) defined by Thomson (1976, p. 19). It should be noted that many authors when referring to the epicaudal lobe are in fact describing the notochordal mass, rather than a distinct dorsally appended fin lobe.

The caudal fin length of *Surcaudalus* is estimated to comprise 26-27% of the total body length. The notochordal mass is inclined at 17-25° (heterocercal angle) to the main anterior body axis. The tip of the caudal fin is characterized by a subterminal lobe (Pl. 34, fig. 4). Portions of the epicaudal lobe are preserved in AMF72559 (Pl. 34, fig. 4; text-figs. 7 and 8). It extends to the posterior perimeter of the plugged drill hole; its height (as preserved) is equivalent to that of the notochordal mass, indicating that *Surcaudalus* had an elongate, well-developed epicaudal lobe.

The preserved portions of the ventral hypochordal lobe are insufficient to enable an accurate reconstruction of its shape and dimensions. However, the functional analyses of Thomson and Simanek (1977) suggest that *Surcaudalus* possessed at least a moderately well-developed (in terms of the ventral hypochordal lobe development in squaloids) ventral hypochordal lobe (text-fig. 11). They determined that the presence of an epicaudal lobe requires a larger angle of rotation for stability and that it significantly reduces the magnitude of the upward force components in the tail. They concluded that sharks (e.g. *Surcaudalus*) which possess low to moderate dorsal thrust angles and a well-developed epicaudal lobe are characterized by a moderately well-developed ventral hypochordal lobe, because it is essential in order to maintain a balanced thrust that passes through the centre of balance. Such sharks are usually characterized by a small longitudinal hypochordal lobe and a large subterminal lobe. Thomson and Simanek (1977, p. 347) also established that a subterminal lobe is crucial in sharks with a low dorsal thrust angle because it 'acts somewhat like a kite, passively helping the fish maintain the correct angle of rotation along the whole of the caudal fin and protecting the tip from fluttering'.

Appendicular skeleton

Pectoral girdle. This consists of a pair of dorsoventrally elongate scapulocoracoid cartilages (Pl. 33, figs. 1-3; text-figs. 3-6) that were presumably not fused along the ventral mid-line and which extend dorsally to just beyond the most ventral point of the anterior dorsal fin-spine. The long scapular portion is inclined posterodorsally at an angle of 9-10° to the notochordal axis. It tapers moderately dorsally until 70-73% of its length, whence the posterior margin curves sharply anterodorsally and the scapular narrows rapidly to a rounded, blunt apex. Its anterior and posterior margins are weakly concave and convex, respectively. In AMF72559 the anteroventral flank of the scapular process was shattered during compression. This region is crushed and attenuated in QMF14470. Traces of the cartilage of the articular process and the coracoid portion are best preserved in AMF72559B (text-fig. 4), preservation is poor and the following reconstruction must be regarded as tenuous.

The dorsal edge of the articular process extends posteroventrally; its posterior margin is bluntly rounded and projects only slightly beyond the posterior margin of the coracoid; its ventral edge is distinguished from the latter by a distinct change in slope.

The coracoid portion is widest (antero-posterior) immediately ventral to the articular process, is inclined and narrows moderately anteroventrally before extending and tapering anterodorsally. Its dorsal and ventral margins are concave and convex, respectively. The posteroventral section of the coracoid is extremely poorly calcified relative to the portion immediately dorsal to it (text-fig. 4). The ventral portion of the coracoid

extends beyond the ventral margin of the body and indicates that, in life, this region was inclined towards the mid-line.

Pectoral fins. A pectoral fin lobe is present in QMF14470 and AMF72559 (text-fig. 7). In both specimens it is distorted with the dorsal half preserved against the ventral portion of the flank, its precise shape and dimensions are indiscernible.

Weakly calcified cartilages of the basipterygial region (text-fig. 4) are present in AMF72559B. The metapterygium has been dislocated dorsally and lies immediately above the articular process with its proximal margin against the posterior border of the scapular. It is 5·4 mm long and 1·6 mm wide; approximately rectangular in outline with a concave, anteroventrally inclined posterior border. Two irregular patches of cartilage, which may be traces of the mesopterygium and the propterygium (text-fig. 4), are located just posterior to the articular process.

Pelvic girdle and fins. In QMF14470 a calcified pelvic cartilage of indeterminable morphology is located at the ventral margin of the body, immediately anterior to the most ventral point of insertion of the posterior fin-spine. Portions of the right fin lobe are present in QMF14471 (Pl. 34, figs. 5 and 10) but they are insufficient to enable an accurate reconstruction of its outline and dimensions.

Dermal skeleton

Denticles. The head, trunk, and notochordal mass exhibit a shagreen of stellate (*Petrodus*-like) denticles (Pl. 34, figs. 5, 8, 10) whose crowns consist of smooth, rounded ridges radiating out from a central pointed axis. The radial ridges vary in number from eight to twelve, are generally unevenly spaced, rarely bifurcate, and distally taper. The perimeter of the denticles is usually circular to rhombic in outline; the denticles, along the trunk, are 0·42 mm–0·76 mm in diameter. Occasionally two denticles appear to have fused or coalesced. All denticles are preserved as external moulds in crown view and consequently the morphology of their bases is unknown.

The lateral flanks of the trunk are densely covered in denticles which ventrally tend to diminish somewhat in diameter. Posterior to the posterior dorsal fin they gradually diminish in size and become very sparse along the terminal portion of the notochordal mass. The denticles are sparse in the ventral half of the lateral flank adjacent to the anal fin; a dense covering is maintained in the dorsal portion. The dorsal half of the branchial area and head are densely covered in denticles; they appear to be absent along the ventral portion of the branchial region and are scattered along the rostrum, although this may be an artifact of preservation.

Minute denticles of indeterminable morphology (inferior preservation) are present on all fin webs. The dorsal fins are extensively covered in denticles that appear rectangular in outline and are aligned in posteroventrally inclined rows. The pelvic fins exhibit a sparse covering of denticles anteriorly; posteriorly they become fewer and finally absent. All other fin lobes have denticles but their density and distribution is uncertain. The notochordal mass exhibits closely packed stellate denticles for most of its length; they become very sparse towards the origin of the subterminal lobe.

Lateral line. The lateral sensory line is indicated by dual, parallel rows of closely spaced denticles. They are well preserved along the trunk (text-figs. 3 and 7) where the denticles of the dorsal row tend to be elongated anteroposteriorly and are approximately horizontally aligned. Those of the ventral row are triangular in outline and 0·37 mm–0·45 mm in length from their apices to the mid-line of their bases. The vertical spacing between the apices of the ventral denticles and the ventral edge of the dorsal denticles is 0·45 mm–0·52 mm along the trunk; this gap decreases (tapers) posteriorwards.

The lateral line (text-fig. 3), extending posteriorly from the posterior margin of the neurocranium, arches gently dorsally across the scapulocoracoid adjacent to the region where the scapular portion begins to rapidly narrow dorsally, beyond which it levels out and continues posteriorly, immediately ventral and more or less parallel to the notochordal axis. It appears to terminate close to the ventral margin of the posterior half of the notochordal mass of the caudal fin.

Teeth. Both QMF14470 and AMF72559 contain numerous teeth that are, with few exceptions, very poorly preserved. QMF14470B exhibits three disarticulated teeth (Pl. 34, fig. 1) along the dorsal margin of the palatine portion of the palatoquadrate. These teeth are phoebodontiform; the crown is tricuspid, comprising a central cusp and two lateral cusps that diverge at 18·5–27·5° from the central cusp. The central cusp appears to be approximately the same length as the lateral cusps, although the apices of most cusps are damaged. The teeth are preserved in labial view; their bases are 0·35 mm wide, extremely narrow and gently arched apically. The teeth are 0·15 mm—0·18 mm long from the ventral margin of the base to the dorsal tip of the
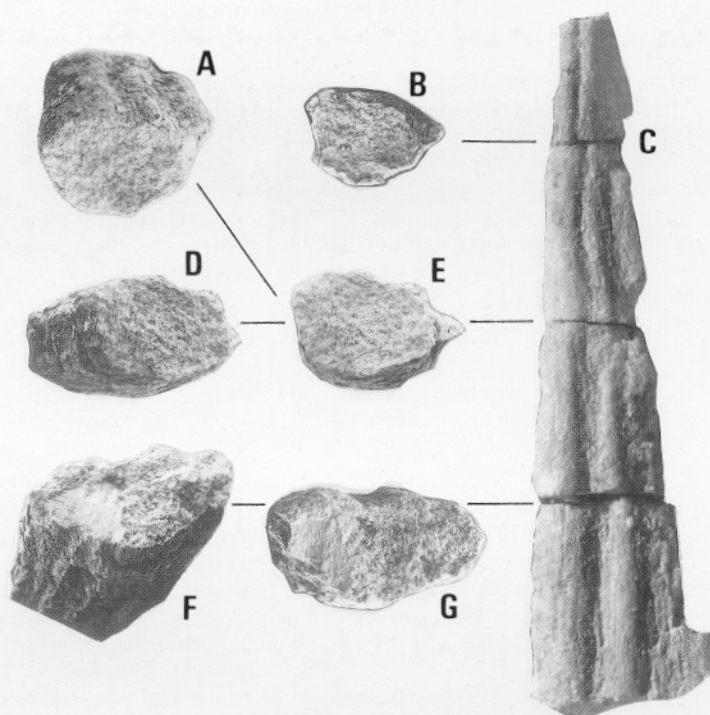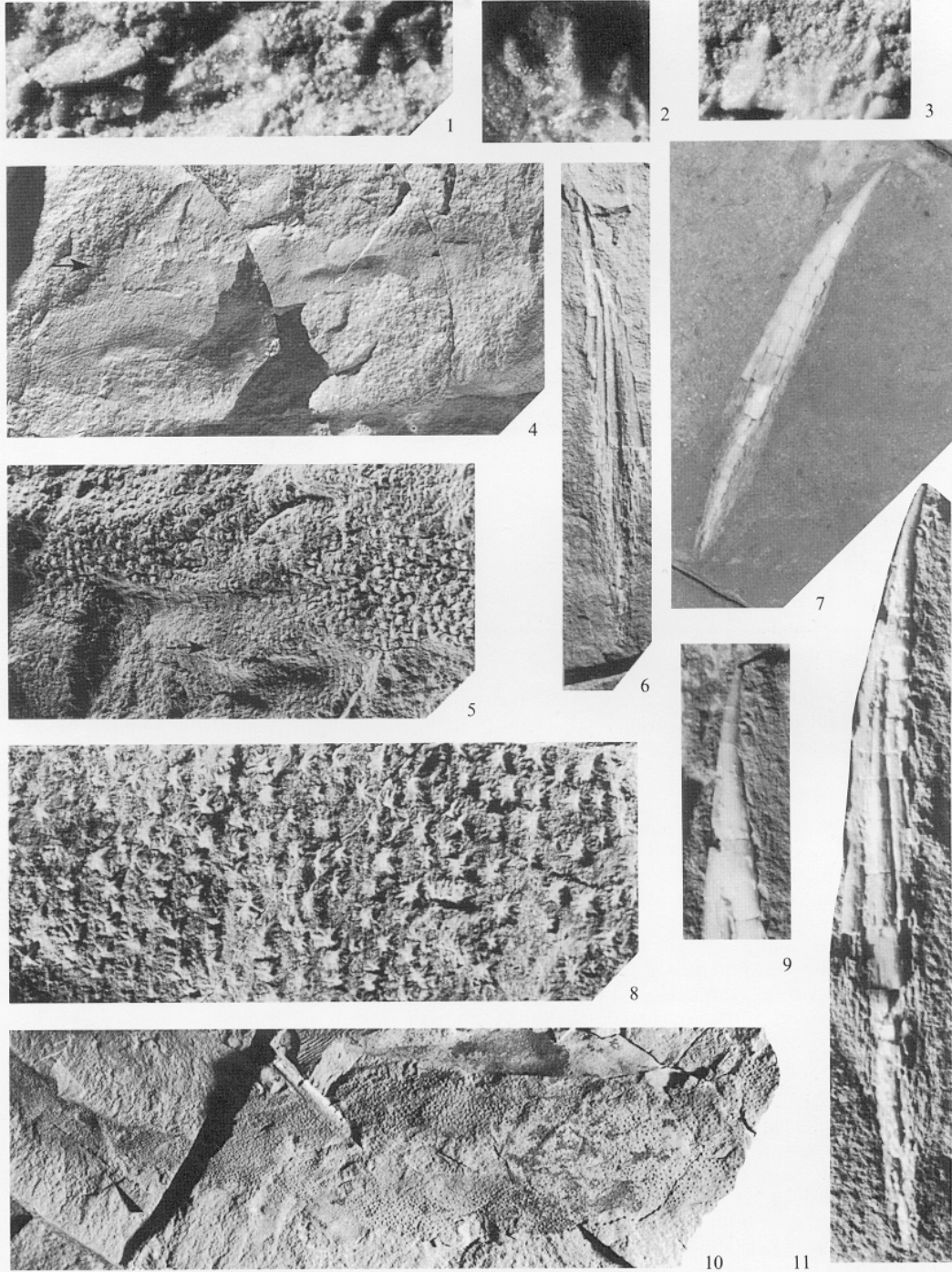
TEXT-FIG. 9. *Surcaudalus rostratus* n. gen. n. sp. paratype (QMF14471B). C, dorsal half of the anterior dorsal fin-spine in lateral view; note most of the anterior keel (right-hand side) is missing, apart from vestigial remnants, × 12. B, E, G, transverse sections through the same fin-spine, all figures × 20. The specimen in text-fig. 9G has been distorted by lateral compression, so that the posterior border is obliquely aligned to the sagittal axis of the fin-spine. A, D, lateral and posterior views, respectively, of the specimen shown in text-fig. 9E, both figures × 20. F, posterior view of the specimen shown in text-fig. 9H, × 20. Note costae along the posterior surface.

central cusp. QMF14470A has a tooth (Pl. 34, fig. 2) preserved in labial view on the Meckel's cartilage, close to the mandibular symphysis; it is 0·42 mm wide and 0·35 mm long. The lateral cusps diverge at 19–21° from the central cusp.

Several poorly exposed teeth, the majority of which have only the central cusp visible, are present on

EXPLANATION OF PLATE 34

Figs. 1–11. *Surcaudalus rostratus* n. gen. n. sp. 1, disarticulated teeth of QMF14470B, × 42. 2, tooth of Meckel's cartilage of QMF14470A, in labial view, × 73. 3, teeth of the anterior portion of Meckel's cartilage of AMF72559A, in labial view. Note only the central cusps are exposed, × 45. 4, caudal fin of AMF72559A showing notochordal mass, lateral line, fragmentary traces of the epicaudal lobe (arrowed), and the subterminal lobe, × 1·7. 5, portion of the pelvic fin of QMF14471A (arrowed), note sparser density of denticles relative to the ventral flank of the trunk, × 3·5. 6, external mould of the posterior dorsal fin-spine of AMF72559B, × 3. 7, posterior dorsal fin-spine, basal plate, and neural elements of AMF72559A, × 2·5. 8, details of the dermal denticles of the anteroventral flank of QMF14471A, × 7. 9, apical view of the posterior dorsal fin-spine of AMF72559A, note the posterolaterally placed denticles, × 7. 10, QMF14471A showing dense shagreen of dermal denticles and the basal portion of the posterior dorsal fin-spine, × 1. The dorsal margin of the trunk is overlain by a *Glossopteris* sp. 11, posterior dorsal fin-spine of AMF72559A, note anterior keel, × 4·7.

PLATE 34

LEU, Australian late Permian freshwater shark
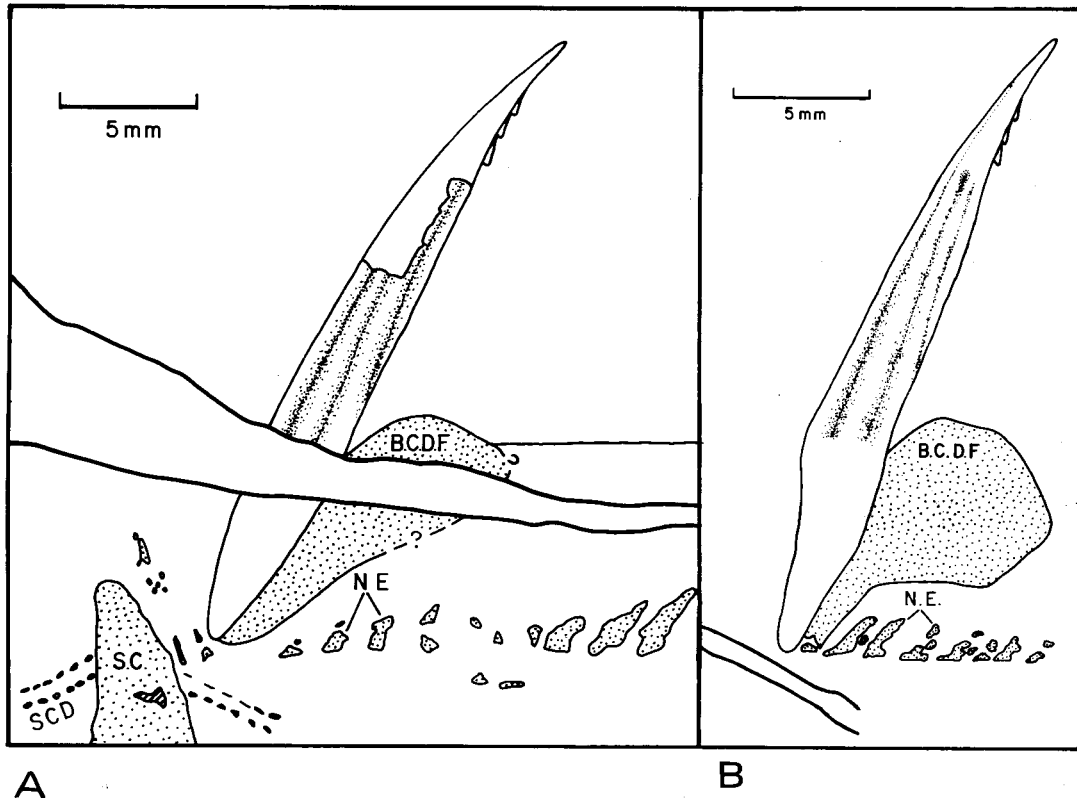
TEXT-FIG. 10. *Surcaudalus rostratus* n. gen. n. sp. paratype (AMF72559A). A, anterior dorsal fin-spine, basal cartilage of dorsal fin, neural elements and dorsal portion of scapular region of the scapulocoracoid. B, posterior dorsal fin-spine, basal cartilage of the dorsal fin and neural elements.

Meckel's cartilage and the palatoquadrate of AMF72559. A single tooth (Pl. 34, fig. 3) on Meckel's cartilage of AMF72559A (located beneath the anterior end of the orbit) has the medial portion of the labial side uncovered. The tooth is 0·29 mm long from the dorsal tip of the central cusp to the ventral margin of the base and, at least (distance exposed) 0·25 mm wide along the base. The central cusp is gently inclined posterodorsally, its maximum basal width being 0·075 mm. The flanks lateral to the principal cusp are obscured by matrix and too fragile to be prepared, thus the number of lateral cusps is uncertain. A small inflexion, inclined posterodorsally at 74° to the ventral margin of the base, occurs approximately midway along the base. Laterally, the flanks on either side of this ridge are gently directed lingually. The spacing between the mid-points of the principal cusps of the teeth in this region is 0·38 mm; this would also represent the maximum basal width of a single tooth. A broken tooth (situated two teeth posteriorly from the tooth described above) exposing the inner surface of the lingual side demonstrates that the base is lingually expanded. No trace of ornament is preserved on any tooth.

Fin-spines. A fin-spine is present along the anterior margin of both dorsal fins (Pl. 33, figs. 1–3). In AMF72559 the anterior and posterior fin-spines are both 2·6 cm in length and are inclined to the notochordal axis at 56–58° and 69–71°, respectively; they curve gently posteriorly towards their apices. In QMF14470 the anterior and posterior fin-spines are inclined, respectively, at 53° and 64° to the notochordal axis.

The lateral surfaces of both fin-spines bear three major longitudinal costae (Pl. 34, figs. 6 and 11; text-figs. 9 and 10). The costae fade approximately adjacent to the dorsal limit of the triangular basal plate. Dorsally they tend to merge and become indistinct adjacent to the barb-like denticles. Fine longitudinal striations cover the entire surface of the fin-spine; they are more or less parallel but do coalesce in places. The anterior and posterior costae bear five and four striae, respectively; the middle costa has four striae increasing to five
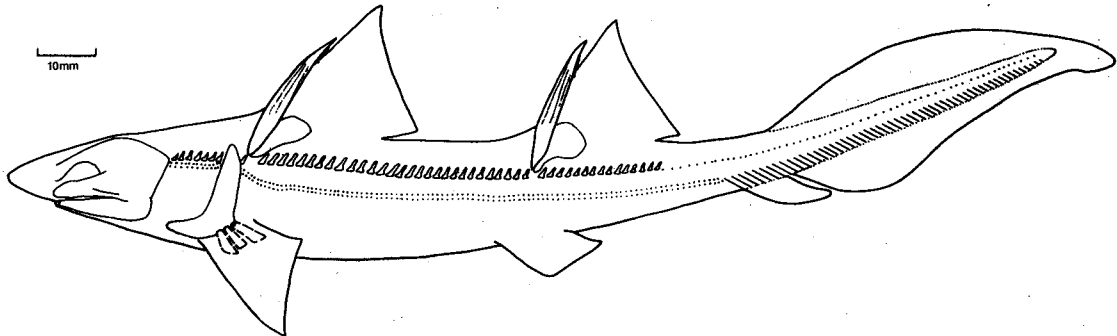
TEXT-FIG. 11. A reconstruction of *Surcaudalus rostratus* n. gen. n. sp. The outline of all fins is hypothetical, although the dimensions (see text) of the dorsal and caudal fins are regarded as accurate.

ventrally. The posterior surface of the fin-spines is flat to shallowly concave (text-fig. 9B, F, H) and possesses at least three longitudinal costae (text-fig. 9E, G). It bears along its posterolateral margins three pairs of closely spaced, small, barb-like, posteriorly directed denticles that increase in size ventrally (Pl. 34, fig. 9; text-fig. 10A, B). The ventral and dorsal limits of the denticle series occur at, respectively, 76% and 88% of the distance from the most ventral point of the fin-spine to the apex. Their posterior and ventral margins are inclined, respectively, at 17° and 45° to the posterolateral surface of the spine. A large median costa, resembling a carina, is present on the anterior surface of the fin-spine. It narrows dorsally and becomes indistinct close to the apex; it tapers anteriorly in transverse section. The most posterior striae on the anterior costal ridge are irregularly disjunct in places but remain more or less aligned with the longitudinal axis of the fin-spine. The most anterior series (comprising at least three rows of striations) are often obliquely inclined anteroventrally and disjunct.

A basal opening for the triangular supportive cartilage is present along the posterior margin of both fin-spines. It extends dorsally to a point of closure located 34% of the way towards the apex.

The widest (antero-posterior) point of the fin-spines is proportional to 12% of their length and is located adjacent to the dorsal closure of the basal notch. Dorsally their widths decrease evenly until about the position of the most ventral barb-like denticle, after which it decreases rapidly towards their pointed apices. It rapidly decreases ventrally from the point of insertion.

FUNCTIONAL MORPHOLOGY

The following interpretation is based on studies (Thomson 1976; Thomson and Simanek 1977) of the body form and locomotion in sharks, specifically the mechanical action of the heterocercal tail.

Thomson and Simanek demonstrated that for a shark to cruise efficiently, the line of net thrust from the caudal fin must pass through its centre of balance. To attack prey or evade predation, a shark can turn suddenly in any direction by altering the balance of forces acting in the tail, thus causing powerful turning moments about the centre of balance. The head will revolve dorsally and ventrally, respectively, if the principal forward thrust is directed either posterior or anterior to the centre of balance. It can then employ its pectoral fins to manoeuvre swiftly at any angle.

The caudal fin of *Surcaudalus* is characterized by a heterocercal angle of between 17° (estimated, QMF14470) and 25° (AMF72559), a dorsal thrust angle (Thomson and Simanek 1977, p. 346) estimated to be between 7·5-10°, a large epicaudal lobe, a subterminal lobe, and a ventral hypochordal lobe.

The moderate heterocercal angle of *Surcaudalus* indicates that it would have been capable of producing relatively strong turning moments around the centre of balance, enabling it to rapidly and efficiently change direction.

Thomson (1976) determined that the epicaudal lobe produces a thrust that is antagonistic to the
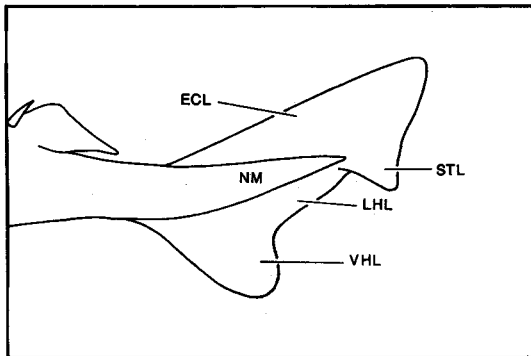
TEXT-FIG. 12. Characteristics of the heterocercal tail, after Thomson (1976), showing the notochordal mass and various appended fin lobes. Based on the caudal fin of *Centrophorus molluccensis* Bleeker, 1860.

hypobatic effect of the notochordal mass and the longitudinal hypochordal lobe, resulting in a lowering of the centre of effort and restricting the dimensions of the heterocercal and dorsal thrust angles. He concluded that sharks (specifically squaloids) possessing a well-developed epicaudal lobe and low to intermediate dorsal thrust angles (intermediate angles range from 10° to 25°) are characterized by slow cruising speeds. At high speeds, such sharks would not be capable of maintaining in balance the various thrusts developed by the respective fin lobes. The net thrust would no longer be directed through the centre of balance and the shark would be unable to maintain an even keel in a horizontal plane.

In summary, *Surcaudalus*, when active, would have been capable of high manœuverability, slow cruising speeds, and incapable of sustaining high speeds.

In many Recent sharks, particularly the pelagic species, the posterior dorsal fin is typically small compared to the anterior dorsal fin. This highly adaptive condition results in thrust enhancement (Lighthill 1975; Webb and Keyes 1982) through hydrodynamic interactions between the first dorsal fin and the caudal fin. This interaction improves cruising efficiency but limits transient swimming (fast starts and powered turns) performance because of the reduced body area (Webb and Keyes 1982). The large second dorsal fin of many Palaeozoic sharks (*Ctenacanthus costellatus*, *Goodrichthys eskdalensis*, *Tristychius arcuatus*, *Dabasacanthus inaskasi*, and *Surcaudalus rostratus*) suggests a greater reliance on transient swimming relative to most Recent sharks. The major variable affecting thrust in fast-start kinematics (Webb and Keyes 1982) is the distribution of body depth (to maximize the mass of water accelerated), especially in the caudal area. Webb and Keyes (1982) noted that large increments in fast-start performance are developed with relatively small increases in fin and body depth. They recognized that among actinopterygians, at each successive adaptive level, a recurring morphology is the fusiform carnivore with a design favouring transient swimming. They concluded this could be because of the importance of fast starts and powered turns in critical activities (particularly for juveniles) such as catching prey and avoiding predators. The more generalized morphology of those Palaeozoic sharks with enhanced transient swimming capabilities would be at the expense of steady swimming (cruising), because the large posterior dorsal fin would increase frictional drag (the fins of sharks are not collapsible) and significantly impair thrust enhancement between the median fins.

DISCUSSION

Several fin-spine characteristics of euselachians—concave posterior wall, posterolaterally situated denticles, and posteriorly placed central cavity—are widely shared among groups (Rieppel 1982) such as xenacanths, ctenacanths, hybodonts, and neoselachians (Table 1). I concur with Dick (1978, p. 107) that the similarities between ctenacanth and neoselachian fin-spines are symplesio-morphies, and with Young (1982, p. 838) that the same applies to the fin-spines of *Antarctilamna*. If

TABLE 1. Some fin-spine characteristics of euselachians.

FINSPINE CHARACTERISTICS	Antarctilamna	Ctenacanthus	Goodrichthys	Surcaudalus	Wodnika	Sphenacanthus	Acronemus
Posterior Wall	Slightly concave with elevated lateral rims and a low median ridge.	Posterior face with a pronounced median ridge or convexity, that is separated from the posterolateral margins by a flat or slightly concave area.	Concave	Flat, becoming shallowly concave towards the apex.	Concave	Strongly concave and lacking a pronounced median ridge or convexity.	Concave
Posterolaterally Situated Denticles	Absent	Posterolateral margins ornamented apically by a row of low, posteriorly directed denticles.	Absent	The posterolateral margins bear apically, three pairs of small, closely spaced barb-like denticles.	Absent	Posterolateral margins ornamented by a row of low, posteriorly directed denticles.	A longitudinal row of rounded, unmodified tubercles runs along the posterolateral edges of the crown.
Posteriorly Placed Central Cavity	Present	Present	Present	Presumably present	Present	Present	Present
Anterior Keel	Absent	Absent	Absent	Present	Anterior ribbing present	Absent	Present

FINSPINE CHARACTERISTICS	Tristychius	Amelacanthus	Eunemacanthus	Nemacanthus	Palaeospinax	Heterodontus	Squaloids
Posterior Wall	Slightly concave	Concave or flat, rarely with a low rise medially.	Concave	Concave	Concave or flat	Gently concave or flat	Normally concave, posterior wall infolded at the margins.
Posterolaterally Situated Denticles	A series of sharp, posteriorly directed denticles are present along each lateral margin.	Posterolateral margins armed apically by small, usually down curved and rounded or pointed denticles.	Marginal denticles occur apically.	Rows of small but pointed denticles run along the posterolateral edges of the crown.	Absent	Absent	Absent
Posteriorly Placed Central Cavity	Present	Present	Present	Present	Present	The trunk is effectively an elongated hollow cone.	The trunk is effectively an elongated hollow cone.
Anterior Keel	Single median costa on the anterior margin of the spine.	Absent	Present	Present	Absent	The leading edge of the cap is usually swollen into a carina.	Absent

so, this would require that the common ancestor of the xenacanths, ctenacanths, and neoselachians had already differentiated by Middle Devonian time. Young (1982, p. 840) believes that, if the similar fin-spines of ctenacanths and neoselachians are symplesiomorphous, then the aplesodic fin evolved independently in the common ancestor of the neoselachians, and in the common ancestor of *Hybodus* and *Tristychius*. Maisey (1984, p. 366) disputes the supposition that the plesodic condition is primitive and points out that plesodic pectoral fins occur in Recent euselachians and are associated with specific modes of life. It is conceivable that a similar distribution occurred in both ctenacanths and hybodonts and their respective common ancestors. This is clearly the case among the few 'hybodonts' where the pectoral fin is known in detail; *Onychoselache* is plesodic (Dick and Maisey 1980), whereas *Tristychius* and *Hybodus* are aplesodic. Locomotory adaptations could be the selective pressure that governs the length of pectoral fin radials and this character could frequently be derived by convergence in several lineages.

Schaeffer (1981, fig. 26) regards the xenacanths as representing a sister-group to the Cleveland '*Ctenacanthus*' (CMNH6219) on the basis that they both possess multilayered prismatic calcite and pronounced lateral otic processes. Maisey (1984, fig. 1) noted that both these characters are shared with other taxa and considers xenacanths to be a specialized group of ctenacanthiform sharks on the basis of the following synapomorphies (characters 18 and 19, p. 365): dorsal fin-spines with a pectinate ornament (implies that the ctenacanths and xenacanths [*Antarctilamna*] had already separated during or prior to the Middle Devonian); and a broad, expanded occipital segment (the Cleveland '*Ctenacanthus*').

Pectinate ornament (Maisey 1984, character 18) of the ctenacanthiform variety may be a plesiomorphic euselachian character or convergently derived. The fin-spines of '*Ctenacanthus*' *vetustus* have a pectinate ornament, be it only on the anterior ribs, which Maisey (1981, p. 15) notes are coarser and more irregular than the pectinations of *C. major*. Maisey (1981, p. 20) regards the fin-spines of '*C.*' *vetustus* as 'notably like those of Mesozoic hybodonts'. Maisey (1982a, p. 2) notes that Recent squaloid and heterodontid fin-spine morphology and ornamentation does not vary above generic level, and that the same apparently applies to hybodont fin-spines. The fin-spines of *Antarctilamna* differ from those of *C. major* in being relatively short and broad with little curvature. They lack posterolaterally placed denticles and typically have a very narrow zone of insertion, although in two specimens (Young 1982, p. 828) the inserted portion was much more extensive. The fin-spines of some acanthodians possess pectinate ornament, e.g. *Nodacosta* Gross, 1940. Lund (1985, p. 16) regards the superficially inserted small and thorn-like fin-spines of *Antarctilamna* and *Heteropetalus* as representing the primitive condition of the dorsal spine. He also considers the deep, sagittally inserted fin-spines of the ctenacanths, hybodonts, and many neoselachians to be an apomorphic state. Maisey (pers. comm.) disputes this and regards the spines of *Cladoselache* and stethacanthids as deeply inserted.

Schaeffer (1981, p. 60) regards 'the strong projection of the occipital segment behind the auditory capsules in *Xenacanthus* and *Tamiobatis* . . . as a derived condition that relates these taxa'. He also stated that 'the considerable projection of the occipital segment behind the capsules in *Xenacanthus*, *Tamiobatis* and *Tristychius* (Dick 1978) is correlated with several pairs of well spaced occipitospinal nerve foramina'. Maisey (1984, p. 365) considers the broad, expanded occipital segments of *Xenacanthus*, *Tamiobatis*, and the Cleveland '*Ctenacanthus*' to be synapomorphic. The terms 'broad and expanded' and 'strong or considerable' projection are subjective and need to be quantified to enable more precise comparisons. Various dimensional relationships of the occipital segments of shark neurocrania are presented in Table 2. Expressed as percentages, the length of the occipital segment extending behind the otic capsules vs. both the length of the occipital segment and the total length of the neurocranium for *Tamiobatis*, *Hybodus basanus*, and *Squalus* are 76 : 71 : 33 and 16 : 20 : 5, respectively. The maximum and minimum widths of the occipital segment behind the otic processes vs. the postorbital width for *Xenacanthus*, *Tamiobatis*, and *Hybodus* are 45 : 44 : 57 and 45 : 30 : 24, respectively. The minimum width of the occipital segment behind the otic capsules (width of occipital cotylus) vs. the maximum width for the latter three genera and '*Cladodus*', *Cladoselache*, and *Squalus* are 100 : 68 : 42 : 44–51 : 76 : 57, respectively. The

TABLE 2. Dimensions of the occipital segments of shark neurocrania, expressed as percentages.

	Tamiobatus (Schaeffer 1981, figs. 19 & 21)	Xenacanthus (Schaeffer 1981, fig.6)	'Cladodus' (Schaeffer 1981, fig.25)	Hybodus (Maisey 1982, fig.2)	Cladoselache (Maisey 1983, fig.15D)	Cobelodus (Maisey 1983, fig.15F)	Squalus (Maisey 1983, fig.15A)
LENGTH OF OCCIPITAL SEGMENT / TOTAL LENGTH OF NEUROCRANIUM	19	29		29	17	16	16
LENGTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / TOTAL LENGTH OF NEUROCRANIUM	16			20	8	8	5
LENGTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / LENGTH OF OCCIPITAL SEGMENT	76			71	49	50	33
MAXIMUM WIDTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / WIDTH ACROSS POSTORBITAL PROCESSES	44	45	43–48	57	24	28	54
MINIMUM WIDTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / WIDTH ACROSS POSTORBITAL PROCESSES	30	45	20–22	24	20		30
MINIMUM WIDTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / MAXIMUM WIDTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES	68	100	44–51	42	76	43	57
MAXIMUM WIDTH OF OCCIPITAL SEGMENT BEHIND OTIC CAPSULES / WIDTH ACROSS LATERAL OTIC PROCESSES	57	43		66	51	50	54

only significant dimensional discrepancy between the occipital segments of *Hybodus* and *Xenacanthus* (regardless of the differences in the relative positions of their postorbital processes) is the degree to which the lateral flanks of the occipital segment taper posteriorly behind the otic capsules. The range of variability of this character within the xenacanths and amongst distantly related sharks, e.g. *Cladoselache* and *Squalus*, clearly demonstrates that it is not phylogenetically significant.

It is apparent from the above that the dimensions of the occipital segment of *Hybodus* resemble closely the xenacanth/Cleveland '*Ctenacanthus*' condition, and differ significantly from most neoselachians. In fact, Maisey (1983, pp. 30–31) considers that the otico-occipital region of *Hybodus*, although foreshortened, resembles the condition of *Xenacanthus* and *Tamiobatis* more than the neoselachian condition, and he states (1982*b*, p. 7) that 'the otico-occipital region [of *Hybodus*] is short, although the deeply concave articular cotylus of the occiput forms a prominent posterior extension bounded laterally by triangular extensions'. He (1983, p. 58) also notes that there are no 'appreciable differences in the extent to which the occipital arch extends between the otic capsules in *Hybodus* and *Xenacanthus*'. Some extant sharks, such as the hexanchoids (*sensu* Compagno 1977), *Chlamydoselachus*, *Hexanchus*, and particularly *Notorynchus*, have occipital segments that extend much farther posteriorly beyond the otic capsules relative to the majority of Recent sharks. It is more parsimonious to regard a broad expanded occipital segment as a primitive character shared by xenacanths, ctenacanths, and hybodonts. In the absence of other shared characters, it is too tenuous to demonstrate confidently that xenacanths are a specialized group of ctenacanthiform sharks. I intuitively agree, from a phenetic viewpoint, with Schaeffer's (1981, p. 61) conclusion that the Cleveland '*Ctenacanthus*' represents a sister-group to *Xenacanthus*, *Tamiobatis*, and '*Cladodus*'. Maisey (1985, p. 15) notes that the different configurations of the

shortened posterior portion of the braincases of *Hybodus* and neoselachians could readily be derived from a primitive morphotype in which the parachordals were much longer.

Comparisons with the placoderms and acanthodians suggest that a broad expanded occipital region may be a primitive gnathostome character. Amongst the arthrodires the phyctaeniniids (*Kujdanowiaspis*) and the brachythoracids (*Pholidosteus* and *Tapineosteus*) possess extremely long and broad occipital segments. The petalichthyids (*Epipetalichthys*, *Macropetalichthys*, and *Ellopetalichthys*) have elongate narrow occipital segments that extend considerable distances beyond the otic region. The occipital region of the rhenanid *Jagorina* extends beyond the otic section, albeit to a much lesser extent (16% of the total length of the neurocranium) in comparison to the above arthrodires. *Acanthodes* has a broad, expanded occipital segment that extends beyond the otic region for 20·5% of the total length of the neurocranium.

During the ontogeny of Recent sharks, the occipital region becomes much shortened (Holmgren 1940). Holmgren (1942) and Jarvik (1980), influenced by their belief in a placoderm ancestry for sharks, both interpreted this as phyletic recapitulation.

Surcaudalus possesses the following 'ctenacanthiform' characteristics: absence of calcified ribs, 'cladodont' dentition, fin-spines which have a concave posterior wall, and apically situated posterolateral denticles. These characters (apart from the posterolaterally placed denticles) are shared equally with the neoselachian *Palaeospinax* and, additionally, they both have a non-lunate caudal fin. The well-developed epicaudal lobe of the caudal fin of *Surcaudalus* is a character which, according to Thomson (1976, p. 20), is present only in squalomorph selachians.

Surcaudalus differs from *Ctenacanthus* and *Goodrichthys* in possessing an elongate fleshy snout, a non-lunate caudal fin, basal plates with a well-developed anteroventrally directed process, and fin-spines which bear lateral longitudinal costae covered by fine longitudinal striations and have an anterior keel. *Tristychius* and *Surcaudalus* both share the latter three characters. *Surcaudalus* and *Wodnika* both lack calcified ribs and have fin-spines with fairly smooth, broad ribs and a concave posterior wall. *Wodnika* differs, however, in possessing a more weakly calcified skeleton, fin-spines of unequal size, and teeth that are low rounded and tumid; although the dentition may be a function of dietary specialisation.

The non-lunate caudal fin of *Surcaudalus* is a character that Compagno (1977) and Young (1982, character 10) regard as a synapomorphy uniting *Tristychius*, *Onychoselache*, *Hybodus*, *Palaeospinax*, and Recent euselachians. Using multivariate analyses, Thomson and Simanek (1977) distinguished four distinct patterns of shark body shape, each intrinsically related to one of four discrete types of caudal fin ranging from nearly symmetrical to straight. Thomson (1976, fig. 14) also plotted various dimensional relationships of elasmobranch tails for both living and fossil genera. He demonstrated that all fossil genera plot within the same dimensional limits as the Recent forms.

Thomson and Simanek (1977) noted that the morphology of neoselachian caudal fins (whether lunate or non-lunate) do not equate with current shark systematics (*sensu* Compagno 1977). They concluded (1977, p. 352) that the various tail patterns have been 'convergently developed in sharks of different major groups' and that 'the four morphological groupings accord better with differences in mode of life'.

Only three ctenacanthiform sharks with well-preserved caudal fins have been described to date. Of these, *Ctenacanthus* and *Goodrichthys* have lunate caudal fins, whereas *Bandringa* is non-lunate. In view of the small sample size, and considering the distribution of caudal fin morphology within the various neoselachian groups, it is probable that ctenacanthiform sharks possessed a variety of caudal fin architecture in response to adaptations for specific life habits. This diversity would have been maintained at successive adaptive levels. Because of possible convergence, the non-lunate caudal fin of ctenacanths (*Bandringa*), hybodonts, and neoselachians cannot be safely assumed to be synapomorphic, regardless of whether the morphotypic condition was deeply forked and almost equilobate. Maisey's amendment of this character (Maisey 1984, character 35, hypaxial endoskeleton of tail reduced) is consistent with the record. Bearing in mind the case developed for convergent derivation of plesodic pectoral fins connected with specialized modes of life, further comparative anatomy of the caudal endoskeleton of Recent sharks is required to ascertain if discrete caudal fin

shapes are congruent with classifications based on other characters. 'Advanced' ctenacanths may have independently achieved this condition.

It is apparent that, in the absence of well-preserved neurocranial and pectoral fin cartilages, it would be extremely subjective to differentiate between a ctenacanth and a hybodont. *Surcaudalus* has many 'ctenacanthiform' characters that are present in other groups, such as fin-spines with a concave posterior wall, and the absence of calcified ribs, shared with *Wodnika, Sphenacanthus, Palaeospinax*, and some Recent euselachians. The scales of *Surcaudalus* are preserved as external moulds of the crowns, whilst the fin-spines and teeth have been replaced by a clay mineral from the illite group during thermal metamorphism of the fish-bearing shales by combustion of the underlying coal seam. Therefore, it is not possible to determine if *Surcaudalus* had non-growing placoid scales, a feature which Maisey (1984, character 34) believes unites *Hybodus, Acronemus, Tristychius, Onychoselache, Palaeospinax*, and Recent euselachians.

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