



A REVISION
OF THE REDFIELDIIFORM
AND PERLEIDIIFORM FISHES
FROM THE TRIASSIC OF
BEKKER'S KRAAL (SOUTH AFRICA)
AND BROOKVALE
(NEW SOUTH WALES)

BY

PETER HUTCHINSON

Drayton, Berks., England

xref

Pp. 233-354; 54 Text-figures

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 22 No. 3

LONDON : 1973

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY) *instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 a separate supplementary series of longer papers was instituted, numbered serially for each Department.

This paper is Vol. 22 No. 3 of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.

*World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).*

© Trustees of the British Museum (Natural History), 1973

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 22 February, 1973

Price £4.30

A REVISION OF
THE REDFIELDIIFORM
AND PERLEIDIFORM FISHES
FROM THE TRIASSIC OF
BEKKER'S KRAAL (SOUTH AFRICA)
AND BROOKVALE
(NEW SOUTH WALES)

By PETER HUTCHINSON

CONTENTS

	<i>Page</i>
I. INTRODUCTION	236
II. SYSTEMATIC DESCRIPTIONS	238
Order REDFIELDIIFORMES	238
Family Brookvaliidae	239
Genus <i>Ischnolepis</i> Haughton	239
<i>I. bancrofti</i> Haughton	240
Genus <i>Atopocephala</i> Brough	249
<i>A. watsoni</i> Brough	250
Genus <i>Brookvalia</i> Wade	251
<i>B. gracilis</i> Wade	252
<i>B. parvisquamata</i> Wade	259
<i>B. propennis</i> Wade	259
<i>B. latipennis</i> (Wade) comb. nov.	262
<i>B. spinosa</i> (Wade) comb. nov.	264
Genus <i>Phlyctaenichthys</i> Wade	267
<i>P. pectinatus</i> Wade	269
Family Redfieldiidae	271
Genus <i>Daedalichthys</i> Brough	271
<i>D. higginsii</i> Brough	273
Genus <i>Helichthys</i> Broom	274
<i>H. elegans</i> Brough	275
Genus <i>Geitonichthys</i> Wade	277
<i>G. ornatus</i> Wade	277
Genus <i>Molybdichthys</i> Wade	280
<i>M. junior</i> Wade	281
Family Schizurichthyidae nov.	285
Genus <i>Schizurichthys</i> Wade	285
<i>S. pulcher</i> Wade	285
Genera provisionally ascribed to Redfieldiiformes	289
Order PERLEIDIFORMES	292
Family Colobodontidae	292
Genus <i>Meidiichthys</i> Brough	292
<i>M. browni</i> (Broom)	293
Genus <i>Procheirichthys</i> Wade	295
<i>P. ferox</i> Wade	295

Genus <i>Manlietta</i> Wade	297
<i>M. crassa</i> Wade	298
Family Cleithrolepididae	302
Genus <i>Cleithrolepidina</i> Berg.	302
<i>C. minor</i> (Broom)	303
<i>C. extoni</i> (Woodward) comb. nov.	305
Genus <i>Cleithrolepis</i> Egerton	311
<i>C. granulata</i> Egerton	212
Family Hydropessidae nov.	316
Genus <i>Hydropessum</i> Broom.	316
<i>H. kannemeyeria</i> Broom	316
Genera provisionally ascribed to Perleidiformes	321
III. DISCUSSION	321
(a) Classification of the Redfieldiiformes	321
(i) Brookvaliidae and Redfieldiidae	321
(ii) Schizurichthyidae	323
(iii) Redfieldiiformes—discussion	324
(b) A functional analysis of the redfieldiiform skull	325
(i) Gill ventilation	326
(ii) Feeding	326
(c) Growth of the tail in <i>Brookvalia</i> , and some notes on palaeonis-	
coid body lobe squamation	328
(d) Classification of the Perleidiformes	333
(i) Colobodontidae	333
(ii) Cleithrolepididae and Hydropessidae	335
(e) Evolution of the Perleidiformes	338
(i) Cleithrolepididae	338
(ii) Hydropessidae	342
(f) Origin of Redfieldiiformes and Perleidiformes	343
IV. SUMMARY	347
V. ACKNOWLEDGEMENTS	349
VI. ABBREVIATIONS	349
VII. REFERENCES	350

SYNOPSIS

All the genera included in the Redfieldiiformes and Perleidiformes (Chondrostei) from the Triassic localities at Bekker's Kraal (South Africa) and Brookvale (New South Wales) are redescribed. In addition, *Ischnolepis*, an early redfieldiiform from Zambia is redescribed. The order Redfieldiiformes is divided into three families; the Brookvaliidae, the Redfieldiidae and the Schizurichthyidae nov. The order Perleidiformes is divided into four families; the Aetheodontidae, the Colobodontidae, the Cleithrolepididae and the Hydropessidae, a new family erected for the inclusion of *Hydropessum*, a genus previously thought to be a cleithrolepid. A functional analysis is made of the redfieldiiform skull and it is concluded that the Redfieldiidae possessed a unique suctorial feeding mechanism. Growth and development of the tail in *Brookvalia gracilis* is described, and the palaeonisoid body lobe squamation is discussed. It is concluded that reversal of body lobe scale rows does not occur in palaeonisoids.

I. INTRODUCTION

TRIASSIC fish from Bekker's Kraal were first described by Broom (1909) and subsequently by Brough (1931, 1934) while those from Brookvale, N.S.W. were described by Wade (1935). It is clear from more recent publications on Triassic fish that

comparative studies have been limited by the incomplete nature of these earlier descriptions (see, for example, Schaeffer 1955 : text-figs 7 and 8; 1967 : text-figs 17 and 18), and a redescription of the Redfieldiiformes and Perleidiformes from Brookvale and Bekker's Kraal has been attempted to remedy this. In addition it was clear that a redescription of *Ischnolepis* from Zambia (Haughton 1934) would help in an attempt to understand the early redfieldiids.

With the exception of *Ischnolepis*, the specimens described here required no preparation. The Brookvale specimens are impressions and natural casts of fish which have been crushed to a thickness of at most a few millimetres. The Bekker's Kraal fossils are, in the main, impressions, although replacement minerals are sometimes present.

Of the material studied here, only *Ischnolepis* was preserved in a relatively uncrushed state. Specimens of this genus were preserved in a matrix of acid resistant, fine grained mudstone, and I have been able to remove this matrix with an ultrasonic probe, revealing many new features. The ages of the three localities will now be discussed briefly:

Zambia. The locality of the type material of *Ischnolepis bancrofti* is the Lunsempfwa valley, Zambia (lower part), and is described as 'probably Upper Beaufort or Lower Stormberg' (Haughton 1934 : 97). However, specimens of *I. bancrofti* in the British Museum (Natural History) are registered as coming from the Madumabisa shales, 82 miles from Kabwe (Broken Hill), and north of the junction between Tutenge and Lunsempfwa rivers, at latitude 14°43' south, and longitude 29°38' east. The Madumabisa mudstones and shales are generally thought to extend from Ecca formation times to the Cistecephalus zone, therefore not extending beyond the uppermost Permian (Gair, 1960 : 9; Drysdall & Kitching, 1963 : 34). It has been suggested, however, that plant remains from the uppermost parts of the Madumabisa mudstone in Rhodesia indicate that these beds in fact extend to the top of the Beaufort Series, and that they include a condensed succession which is equivalent to the Lystrosaurus and Cynognathus zones (Bond 1965). This extension of the possible upper limits of the Madumabisa mudstones to include the Lower Triassic epoch means that, unless the locality of *I. bancrofti* is more exactly identified, its probable age can only be defined as uppermost Permian or Scythian.

Bekker's Kraal. The Bekker's Kraal fish are found in a sandstone layer 20 mm thick which occurs in a 10 metre thick bed of sandstone which, in turn, forms part of the lower Cynognathus zone succession in Orange Free State (Watson 1931). They are therefore Scythian in age—Upper Scythian according to Romer (1947) or Lower Scythian according to Cosgriff (1969).

Gosford, Brookvale and St. Peters. These three Australian localities occur in the Sydney basin where the Triassic is divided into three groups: Narrabeen, Hawkesbury and Wianamatta. These are subdivided as follows (youngest at top):

WIANAMATTA	{ Camden Subgroup Liverpool Subgroup (including the Ashfield shale)	ST. PETERS FAUNA
HAWKESBURY		Hawkesbury sandstone

NARRABEEN	{	Gosford formation	GOSFORD FAUNA
		Collaroy claystone	
		Tuggerah formation	
		Munmorah conglomerate	

(Banks *et al.* 1969)

The Munmorah conglomerate overlies the Newcastle Coal Measures, the uppermost coal seam of which traditionally marks the upper limit of the Permian. However, the validity of this boundary has been questioned by several authors because various coal seams appear to have been regarded as being the uppermost in various localities. The Permo-Triassic contact may in fact be 'an undulating surface with marked relief' (Balme 1969 : 108). Moreover, the lower part of the Munmorah conglomerate contains a Permian flora including *Glossopteris*, *Schizoneura*, *Phyllothea* and *Cladophlebis*, while the upper part contains the first record of the spore *Aratrisporites*, which is characteristic of Lower Triassic strata in many parts of the world (Helby 1966). The true Permo-Triassic contact probably therefore lies within the Munmorah conglomerate.

Above the Munmorah conglomerate there are about 2000 feet of shales and sandstone (Wade 1941b) which, if the age of the Permo-Triassic boundary given above is correct, may be regarded as representing the Scythian. Obviously, with no further information, it is not possible to say whether these sediments represent part or all of the Scythian, or even whether they extend into the Anisian. The Gosford fish fauna, which is found in the uppermost of these beds, is therefore very tentatively placed at the Scythian/Anisian boundary.

There are 550 feet of sandstones (the lower part of the Hawkesbury sandstone) between the Gosford and Brookvale horizons (Wade 1935), but within these sediments there are signs of an erosional hiatus, and incomplete palynological data indicate that this may represent a substantial time break (Helby, pers. comm). The Brookvale fauna may therefore be considerably younger than that of Gosford, and is here tentatively regarded as being Ladinian in age.

II. SYSTEMATIC DESCRIPTIONS

Order REDFIELDIIFORMES

DIAGNOSIS. Small to moderately large fusiform chondrosteian fishes. Skull bones usually ornamented with ridges or tubercles. Skull roof composed of extrascapulars, parietals, dermosphenotic, frontals and dermopterotic. Extrascapulars and parietals sometimes divided. Dermopterotic deep, dermosphenotic either rectangular or crescent-shaped. A postrostral may or may not be present. Snout composed of nasals, antorbital and rostral, and sometimes adnasals and premaxillae. A single nostril present. Nasals small, bordering dorsal edge of nostril. Antorbital bordering anterior edge of orbit and ventral edge of nostril and, in forms which lack premaxillae, the ventral edge of the snout. Opercular series oblique to vertical, composed of opercular, subopercular and one, or rarely two, plate-like branchioste-

gals. Preopercular high and 'r'-shaped. Maxilla expanded posteriorly and attached to cheek. Teeth conical and pointed. Braincase of palaeoniscoid type.

Scales rhombic to leaf-shaped or, in the Schizurichthyidae, rectangular to sub-circular with peg and socket articulation; dentine layer absent. Dorsal and anal fin-rays more numerous than endoskeletal supports, jointed and bifurcated; leading rays usually bearing fringing fulcra. Jointing and fringing fulcra often reduced in paired fin-rays. Caudal fin with abbreviated body lobe.

Family **BROOKVALIIDAE** Berg 1940

DIAGNOSIS. Orbit large. Two pairs of parietals (except in *Atopocephala*). Dermopterotic deeper than dermosphenotic. Posterior extension of supraorbital sensory canal, if present, on dermopterotic. Dermosphenotic narrow and crescent-shaped, tapering to a point anteriorly. Frontal curved, and running close to, or actually touching, orbital edge. Snout composed of rostral, and paired antorbitals, nasals and premaxillae. Postrostral present in some genera, probably lost in *Atopocephala*. Antorbital a narrow curved element, bordering the anterior edge of the orbit, with a narrow anterior extension bordering the ventral edge of the nostril. Antorbital separated from the ventral edge of snout by premaxilla. Adnasal absent, or, if present, small and diamond-shaped, having no contact or point contact with dermosphenotic. A single dermohyal present. An antopercular present. Infraorbital elements either separating maxilla from orbital edge or reduced so that maxilla actually borders orbital edge for a short distance. Gular plate present. Lower jaw slender, long and curved dorsally towards the symphysis. Elements of pectoral girdle generally narrow. Fulcra on dorsal and anal fins small or absent. Scales rhomboidal to leaf-shaped. Hinge line at base of body lobe not usually marked by abrupt change in orientation of scales.

Genus **ISCHNOLEPIS** Haughton 1934

1934 *Ischnolepis* Haughton: 97.

DIAGNOSIS (emended). Head bullet-shaped with an extremely large orbit anteriorly placed. Skull bones ornamented with small tubercles. Two pairs of parietals, posterior element triangular, though smaller than in *Brookvalia*. Dermopterotic rectangular. No extension of the supraorbital sensory canal on dermopterotic. Frontal extending anteriorly just beyond the level of the midpoint of the orbit. Opercular series longer than in *Brookvalia*, and moderately oblique. Preopercular with an antero-ventral extension running for a short distance above the antero-dorsal edge of the maxilla. Infraorbital elements very narrow. Teeth slightly recurved.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped, each ornamented with a row of tubercles. Jointing regular on all fin-rays except on those of the pectoral fin. Anal fin opposite the dorsal fin, with an extended base and long anterior rays. Caudal fin hemiheterocercal.

TYPE (and only) SPECIES. *Ischnolepis bancrofti* Haughton.

REMARKS. *Ischnolepis* is probably the earliest known redfieldiiform genus. This new description was made possible only after preparation of specimens in the British Museum (Natural History) using an ultrasonic probe—a remarkably sensitive tool in certain circumstances (Macadie 1967).

Ischnolepis is similar to members of many palaeonisciform families, but it already displays characters which are diagnostic of the family Brookvaliidae, such as a narrow crescent-shaped dermosphenotic and an opercular series which includes a single branchiostegal ray.

Ischnolepis bancrofti Haughton
(Figs 1–6)

1934 *Ischnolepis bancrofti* Haughton: 97–101, text-figs 1–2, pl. 29.

HORIZON AND LOCALITY. Upper Permian or Scythian. Madumabisa shales, 82 miles from Kabwe (Broken Hill), Lunsempfwa Valley, Zambia.

DIAGNOSIS. As for the genus *Ischnolepis*.

HOLOTYPE. S.A.M. 9338 with counterpart S.A.M. 9339.

MATERIAL. Photographs of holotype, P.27577–9.

The material in the B.M.(N.H.) consists of two blocks (part and counterpart; P.27577–8) and several fragments (collectively P.27579); all contain specimens of *Ischnolepis* together with an unidentified palaeoniscoid.

DESCRIPTION. *Size* (Fig. 1). The total length from snout tip to the posterior end of the caudal fin in the most complete specimen is 62 mm. The body is fusiform.

Skull (Fig. 2). The overall shape of the skull is very similar to that of *Brookvalia*; it is bullet-shaped and its main features are a large orbit, a moderately oblique opercular series and a slender, curved lower jaw. Almost all the skull bones are ornamented with rugae.

The suprascapular is ornamented with a few tubercles and with elongate rugae which radiate from its antero-dorsal corner. In a specimen on block P.27578, the inner surface of the dermopterotic bears a ventral lamina which runs close to the ventral border of the bone. The posterior end of this lamina appears to be in close association with the dorsal tip of the ascending process of the parasphenoid.

Dorsal to the dermopterotic there are two parietals, the posterior of which is triangular and small, and usually poorly preserved. The anterior extent of the anterior parietal is marked only by a ridge seen in a specimen on block P.27577 (Fig. 3). There is no sign of any extension of the supraorbital canal onto the parietal. The anterior end of the dermosphenotic is very narrow and appears to converge to a point, although its extreme tip is not preserved. Its ventral border is ornamented with four ridges which consist of rows of closely associated rugae. The relationship between the dermosphenotic and the postorbital and suborbital bones is not clear (Fig. 3), the skull roof, including the dermosphenotic, being displaced relative to the cheek bones. In my restoration (Fig. 2) the dermosphenotic has been

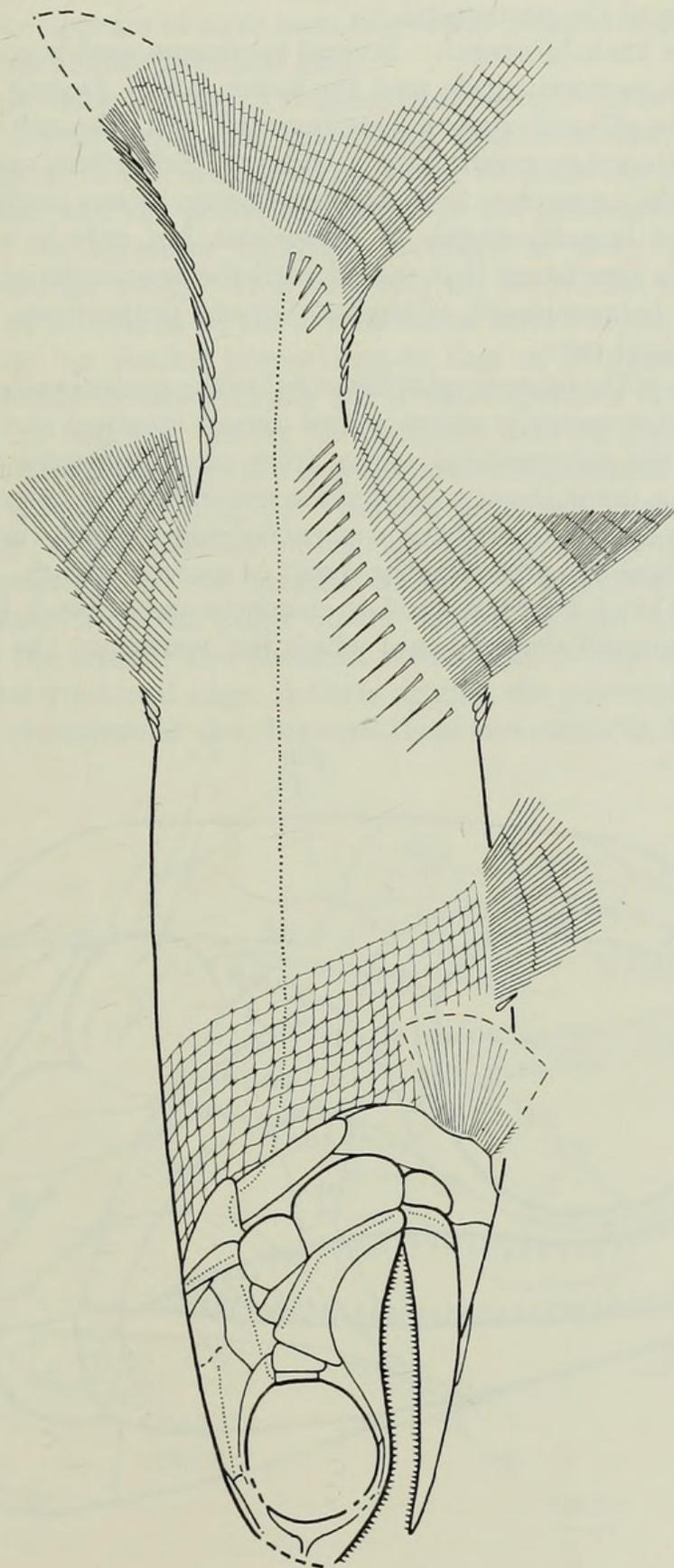


FIG. 1. *Ischnolepis bancrofti* Haughton. Restoration, $\times 2.5$ approx.
Posterior scales omitted.

drawn so that its ventral edge continues the curve of the orbit border suggested by the anterior margin of the postorbital.

There is only one branchiostegal. Several specimens were prepared to reveal the ventral side of the pectoral girdle and the lower jaws. During this preparation, delicate bones of the gill arch system were revealed, and if branchiostegals had been present it is likely that they would have been seen. Schaeffer's opinion (1967 : 334) that *Ischnolepis* lacks a complete branchiostegal series is thus confirmed. Haughton (1934 : 99) observed branchiostegals in *Ischnolepis*, but only in a single fragment; in this context it is significant that mixed with the specimens of *Ischnolepis* there are specimens of a palaeoniscoid, of similar size and proportions, which have eight pairs of branchiostegal rays.

The anterior edge of the subopercular lies at 65° to the ventral margin of the maxilla; the orientation of the opercular series is thus almost identical to that of *Brookvalia*. The ornament on the subopercular varies from small tubercles to elongate rugae which radiate from a point about a third of the way down the anterior edge. As well as rugae, the subopercular bears faint concentric ridges which run parallel with its posterior border; these are probably the result of uneven growth.

In a specimen on block P.27578, and less clearly in one on block P.27577, there is a single plate-like diamond-shaped bone, which lies ventral to the lower jaw ramus.

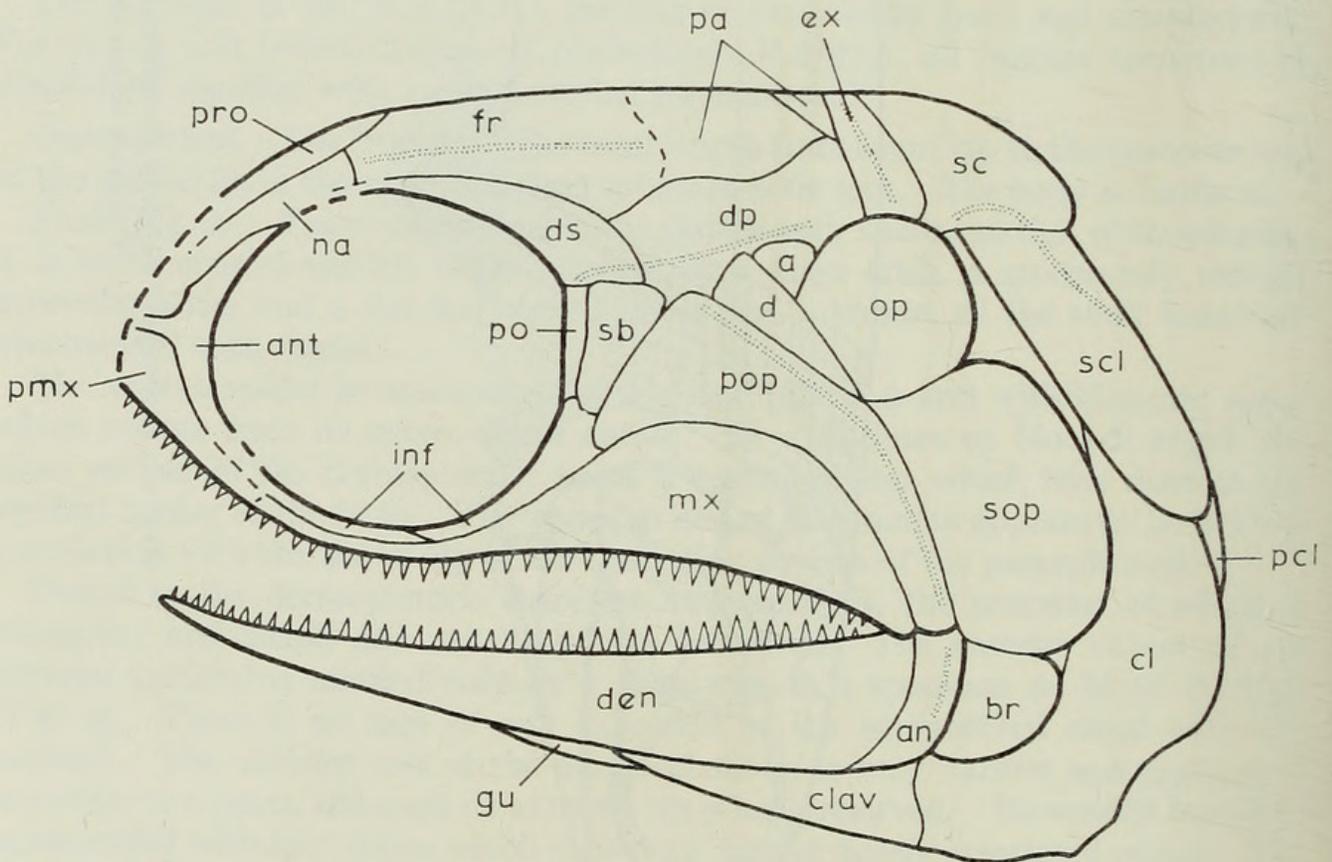


FIG. 2. *Ischnolepis bancrofti* Haughton. Restoration of skull and pectoral girdle, $\times 5.5$ approx.

There are faint traces of grooves running parallel to its anterior margins. Although damaged, this bone appears to have been bilaterally symmetrical, and is therefore a mid-line element; probably a median gular.

In a specimen on block P.27577, a fragment of the right dermohyal is fused, or at least is in close contact, with the underlying hyomandibular. There is a tiny element lying ventral to the dermohyal, inserted between the antero-dorsal corner of the subopercular and the posterior margin of the preopercular. This element corresponds with the accessory opercular recorded in many palaeoniscoids (e.g. *Watsonichthys*, Gardiner 1963). It is seen only on the medial surface of the cheek (Fig. 3), laterally it is covered by the antero-dorsal corner of the opercular.

The preopercular has similar proportions to that of *Brookvalia*, except that its anterior limb extends antero-ventrally for a short distance dorsal to the antero-dorsal border of the maxilla. Along the posterior part of the suture between the preopercular and the maxilla there is a very shallow medial lamina on the preopercular which underlaps the maxilla (Fig. 3). Further anteriorly there is a groove in the antero-dorsal edge of the maxilla which receives the antero-ventral part of the preopercular. Ornament on the maxilla consists of tubercles and some elongate rugae which radiate from the point on its ventral margin which lies below the posterior edge of the orbit. The posterior infraorbital is expanded posteriorly and has a complex postero-dorsal edge: it butts against the postorbital and the antero-ventral tip of the preopercular and, between these two contacts, is notched to receive

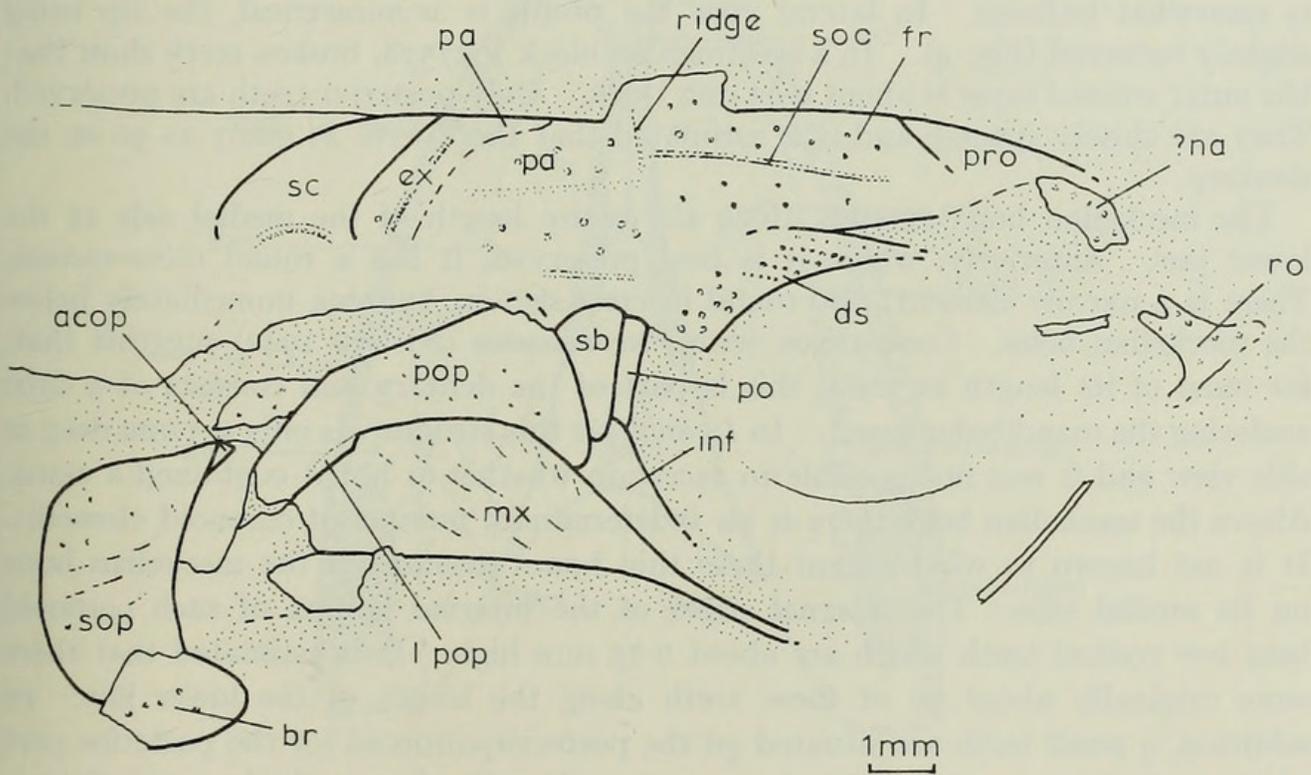


FIG. 3. *Ischnolepis bancrofti* Haughton. P.27577: cheek, left side internal view; roof, impression of left side.

the ventral tip of the suborbital. The anterior infraorbital extends along the ventral border of the orbit and is extremely narrow and, as at this same point the maxilla is narrow, the infraorbital bar is very slender.

The snout is poorly preserved. In a specimen on block P.27578, there is a fragment of bone sutured to the anterior end of the left frontal which is probably part of the nasal. A narrow curved fragment seen in a specimen on block P.27577 (Fig. 3) is probably also nasal. Neither of these fragments gives any indication of the anterior extent of this bone. A postrostral is preserved in the specimen noted above (on P.27578). It is lozenge-shaped, smooth and has a peg-like extension at its anterior end. A poorly preserved rostral (on P.27577, Fig. 3) bears a notch which probably accommodated this peg.

There is clear evidence of only one other bone in the snout region. This is a narrow curved antorbital which borders the anterior margin of the orbit. Midway along its anterior edge there is an anterior process. It is not certain whether a premaxilla is present, although in a specimen on block P.27577, an elongate tooth-bearing element is seen lying medial to the anterior end of the right maxilla. Anteriorly this element is expanded and it is thus unlikely to be entirely composed of maxilla. Comparison with *Brookvalia* suggests that it is premaxilla, but the possibility that it is partly rostral or a rostro-premaxilla must be admitted.

Lower Jaw (Fig. 4). The lower jaw is deep posteriorly and tapers towards the symphysis so that the anterior part is very slender. The dentary is a thin lamina of bone ornamented with elongate rugae. It bears conical teeth which are 0.5 mm high. Halfway up each tooth there is a slight constriction above which the profile is somewhat bulbous. In lateral view the profile is asymmetrical, the tip being slightly recurved (Fig. 4). In a specimen on block P.27578, broken teeth show that the outer enamel layer is about 0.03 mm thick. Only posterior teeth are preserved. They are closely spaced, and it is estimated that there were as many as 50 on the dentary.

The meckelian bone extends along the entire length of the medial side of the lower jaw. Anteriorly, where it is best preserved, it has a round cross-section. There is a narrow element, also round in cross-section, running immediately below the meckelian bone. Comparison with *Pteronisculus* (Nielsen 1942) suggests that, for most of its length at least, this is part of the dentary and consists of a tube enclosing the mandibular canal. In *Ischnolepis* this structure is only 0.3 mm deep in side view and it was not possible to ascertain whether or not it contained a canal. Above the meckelian bone there is an indeterminate number of coronoid elements. It is not known to what extent these thin bones overlapped the meckelian bone on its medial side. The internal edges of the internal lamina of each coronoid bear low conical teeth which are about 0.15 mm high. It is estimated that there were originally about 50 of these teeth along the length of the lower jaw. In addition, 9 small teeth are situated on the posterior coronoid (or the posterior part of the posterior coronoid) which slopes postero-dorsally close to the jaw articulation. Numerous extremely small teeth are scattered on the surface of the internal lamina of the coronoids.

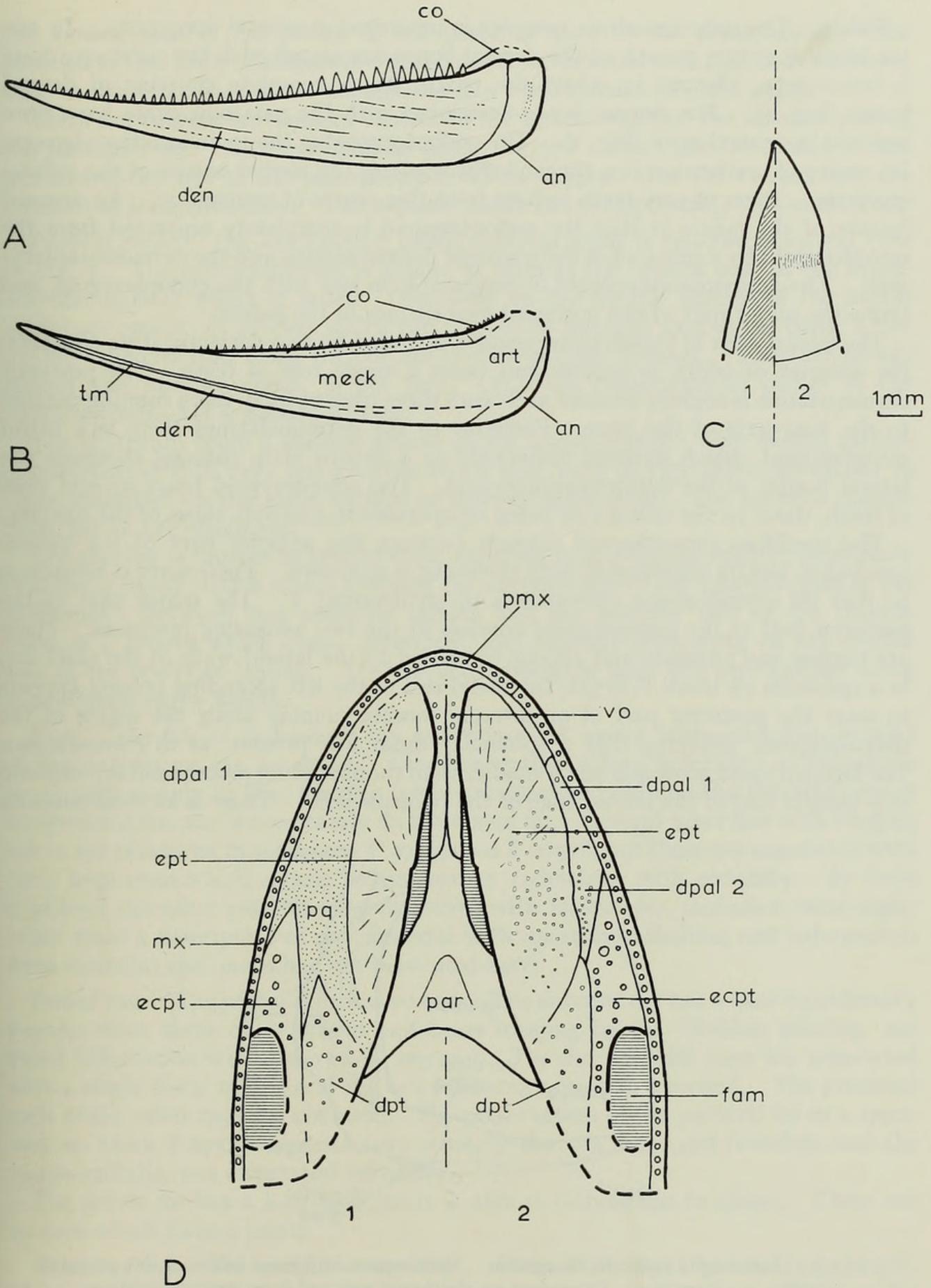


FIG. 4. *Ischnolepis bancrofti* Haughton. (A) Lower jaw. Restoration of right ramus in lateral view, coronoid teeth omitted, $\times 5.5$ approx. (B) Lower jaw. Restoration of left ramus in medial view, dentary teeth omitted, $\times 5.5$ approx. (C) Dentary tooth from P.27578: 1, in section; 2, in lateral view. (D) Restoration of palate in ventral view, $\times 5.5$ approx.; 1, incompletely ossified; 2, completely ossified.

Palate. The palatoquadrate complex is preserved in several specimens. In one (on block P.27577) growth of the dermal bones associated with the palatoquadrate is incomplete, whereas in others the palate has a complete covering of dermal bones (Fig. 4). The dermal bones associated with the palatoquadrate have been restored in ventral view (Fig. 4). The endopterygoid is the main anterior element. Its centre of ossification lies almost halfway along the medial border of the palatoquadrate. Rows of tiny teeth radiate from this centre of ossification. An unusual feature of the palate is that the endopterygoid is completely separated from the ectopterygoid by a junction of the posterior dermopalatine and the dermometapterygoid. The dermometapterygoid is comparable in size with the endopterygoid, and forms the major part of the postero-dorsal surface of the palate.

The lateral edge of the endopterygoid is bounded by two dermopalatine elements, the anterior of which is narrow and bears a single row of teeth. The posterior dermopalatine is slightly broader and bears three rows of small teeth running parallel to the long axis of the bone. Posterior to the dermopalatines there is a broad ectopterygoid, which extends posteriorly as a narrow strip running alongside the lateral border of the dermometapterygoid. The ectopterygoid bears several rows of teeth, those in the centre row being comparable in size with those of the dentary.

The toothless parasphenoid extends between the anterior part of the palatoquadrate, but its relationship with the snout is unknown. Posteriorly it bifurcates so that its overall shape corresponds to an inverted Y. The major part of the posterior half of the parasphenoid consists of the two ascending processes. These are narrow and elongate and appear to extend to the lateral walls of the skull for, in a specimen on block P.27578, the distal end of the left ascending process appears to meet the posterior part of an internal lamina running along the inside of the dermopterotic, implying that a spiracular canal was present, as in *Pteronisculus*. The basipterygoid process is much smaller than the ascending process and is composed of a ventral fold of the lateral edge of the parasphenoid. There is an oval dome on

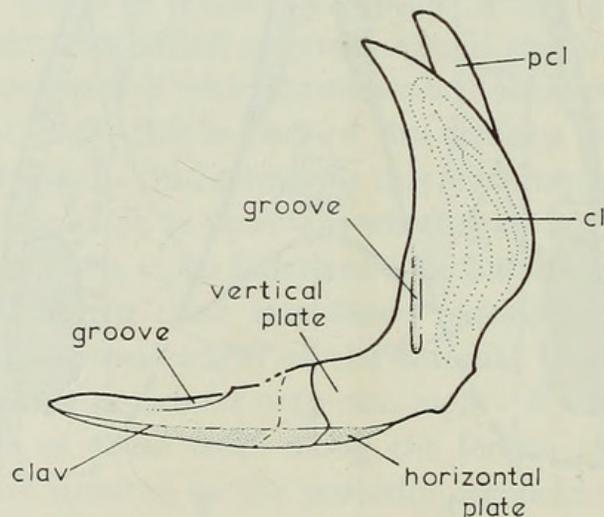


FIG. 5. *Ischnolepis bancrofti* Haughton. Restoration of dermal bones of left pectoral girdle, $\times 4.5$ approx. Ornament on cleithrum restored from internal surface.

the ventral side of the centre of the posterior part of the parasphenoid. The function of this dome is unknown. Its position corresponds with that of a depression seen on the dorsal side of the parasphenoid in *Pteronisculus* (Nielsen 1942).

There are two narrow vomers ventral to the lateral edges of the anterior part of the parasphenoid. In a specimen on block P.27578 a short midline suture is seen at the anterior end of the parasphenoid, which suggests that the vomers met one another, at least anteriorly. The vomers, unlike the parasphenoid, bear small teeth.

Pectoral girdle. The ventral part of the pectoral girdle is restored in lateral view in Fig. 5. The supracleithrum is almost as wide as the ventral part of the suprascapular against which it butts. Ornament on the medial surface of the supracleithrum consists of grooves which run parallel to the long axis of the bone; a row of tiny tubercles runs along the bottom of each of these grooves. These are evenly spaced and number about 30 per mm. Only the postero-dorsal corner of the supracleithrum has a smooth surface.

The cleithrum bears a shallow groove on its lateral surface. Its medial surface is ornamented with very fine grooves which bear rows of tiny tubercles similar to those described on the inner surface of the supracleithrum. The anterior margin is devoid of any ornament.

The clavicle is narrow in lateral view, tapering to a point anteriorly; posteriorly it forms a broad lamina which overlaps the anterior end of the vertical plate of the cleithrum. Between this posterior lamina and the anterior half of the clavicle there is a groove which opens anteriorly, and extends posteriorly on the medial side of the posterior lamina. The clavicles appear to have met one another along almost their entire length.

Fins. The fins of *Ischnolepis* are well preserved, and a fairly complete account of their structure can be given. This description differs from that of Houghton (1934 : 97) mainly in that fringing fulcra are described only on the anterior rays of the pectoral fin, and less certainly on the dorsal fin. Several other fins with fringing fulcra are preserved in specimens P.27577 and P.27578, but these are associated with body fragments which cannot be assigned to *Ischnolepis* with certainty. As there is at least one other palaeoniscoid preserved with *Ischnolepis*, confusion could easily result from a description of any material with uncertain affinities, and information from doubtful specimens has not been used here.

Paired fins. The pectoral fin has 20 rays. The anterior ray has a base considerably broader than those of its fellows and bears fringing fulcra. Neither jointing, nor distal bifurcation was observed in any ray. The five anterior rays are associated with a single distal radial, and the two following rays with a second. The proximal ends of the other rays are not seen. The preservation of the pectoral fin in a specimen on block P.27577 suggests very strongly that its base, and therefore also the margo radialis, was orientated vertically.

The pelvic fin has a long base, so it is almost rectangular in shape. There are 29 rays which have 2 joints.

Unpaired fins. The anal fin is very large. Its base is 20% of the total body length. There are 51 rays, and as the anterior rays are six to seven times as long as the

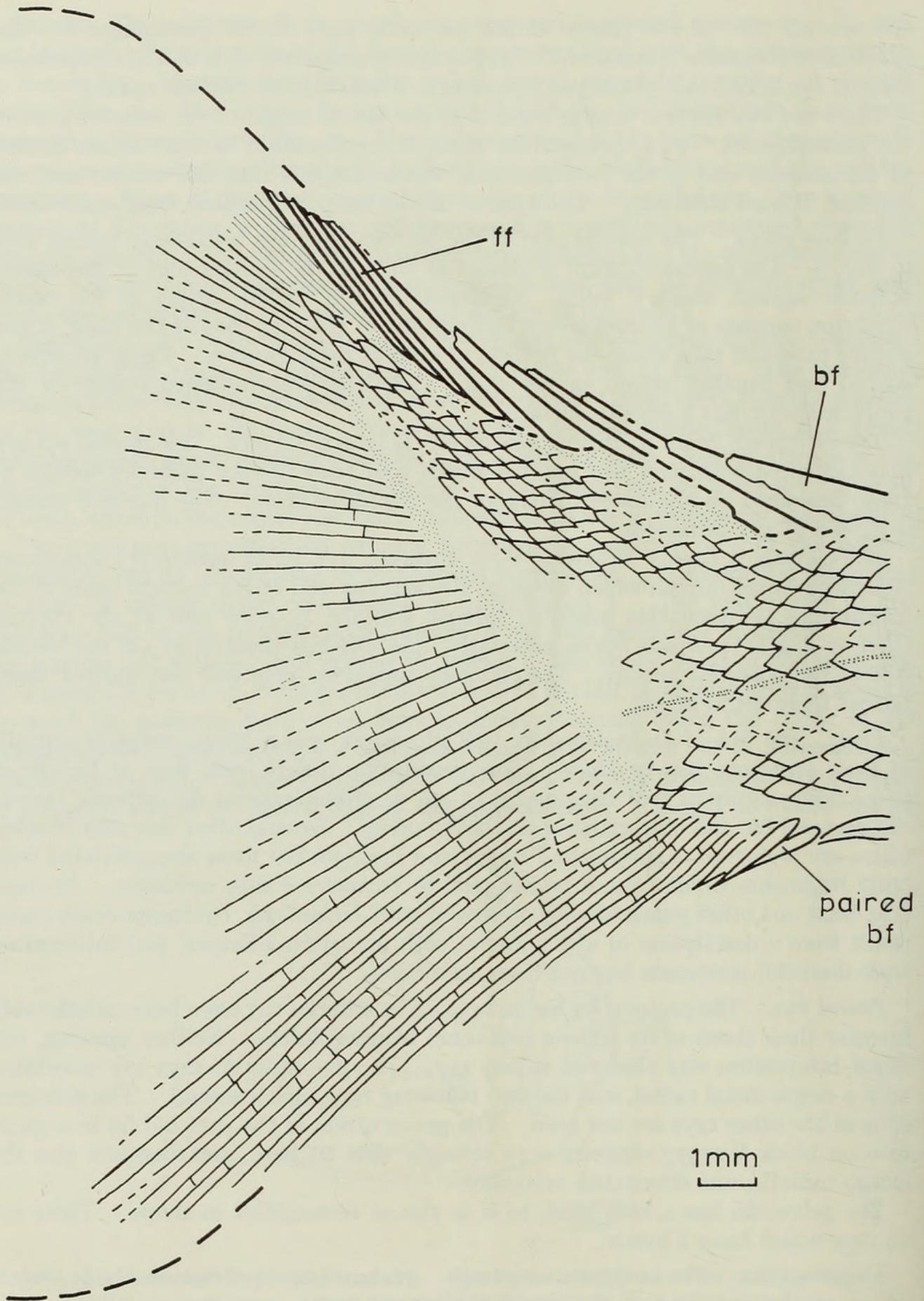


FIG. 6. *Ischnolepis bancrofti* Haughton. Caudal fin, P.27577. Right side.

posterior rays, the fin has an overall triangular appearance. The anterior rays have 8 joints and bifurcate distally, the posterior rays have as few as 2 joints and do not bifurcate.

The dorsal fin has 26 rays which have 5 joints, and which are bifurcated along almost their entire length. In some specimens there are faint traces of fringing fulcra on one of the anterior rays.

The caudal fin is well preserved except for the tip of the dorsal lobe (specimen in block P.27577, Fig. 6). Photographs of the holotype (S.A.M.9338) show that the lobes are equal in size and that the fin is not deeply cleft. The body lobe is long, extending over halfway along the length of the dorsal lobe. There are 66 rays; those of the dorsal lobe have 3 joints, and those of the ventral lobe up to 11 joints. The 7 anterior rays of the dorsal lobe are epaxial in position. Distal bifurcation was not observed in the specimens available for study, although this has been noted in the holotype (Haughton 1934 : 101).

Squamation. The scales are leaf-shaped, the largest flank scales being 0.8 mm long and 0.7 mm deep. They bear an ornament consisting of a row of closely spaced tubercles which form a ridge running postero-ventrally across each scale. There are 50 body transverse scale rows, containing about 30 scales in the region of the dorsal fin. The change in orientation of scales from body to body lobe is achieved gradually, so that there is no hinge line visible at the base of the body lobe.

Genus *ATOPOCEPHALA* Brough 1934

1934 *Atopocephala* Brough: 564.

DIAGNOSIS (emended). Head bluntly pointed. Skull bones ornamented with tubercles. One pair of parietals. Dermopterotic short and deep. Frontal elongate, separated from the orbit edge by dermosphenotic. Snout region poorly known, but appearing to be similar to that of *Brookvalia*. Opercular series almost vertical. Opercular and subopercular of almost equal size, and bearing long spines projecting from their posterior borders. Antopercular with curved posterior border. A single suborbital present. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth pointed and slightly recurved. Lower jaw deep posteriorly, tapering abruptly anteriorly. Lower jaw shorter than the upper jaw margin.

Body fusiform. Pectoral girdle ornamented with tubercles and parallel ridges. Scales rhombic and ornamented with tubercles. Jointing regular on all fin-rays, except the anterior rays of the pectoral fin which are unjointed. Fin-rays with large fulcra. Caudal fin hemiheterocercal and equilobate.

TYPE (and only) SPECIES. *Atopocephala watsoni* Brough.

REMARKS. *Atopocephala*, although a member of the family Brookvaliidae, obviously represents a line which is separate from what may be regarded as typical members of the family—*Ischnolepis* and *Brookvalia*. The main feature of the genus is the shortness of the skull. As a result of this, the skull bones are relatively deeper than those of other brookvaliid genera, although the actual interrelationships of the bones remain unchanged.

Atopocephala watsoni Brough

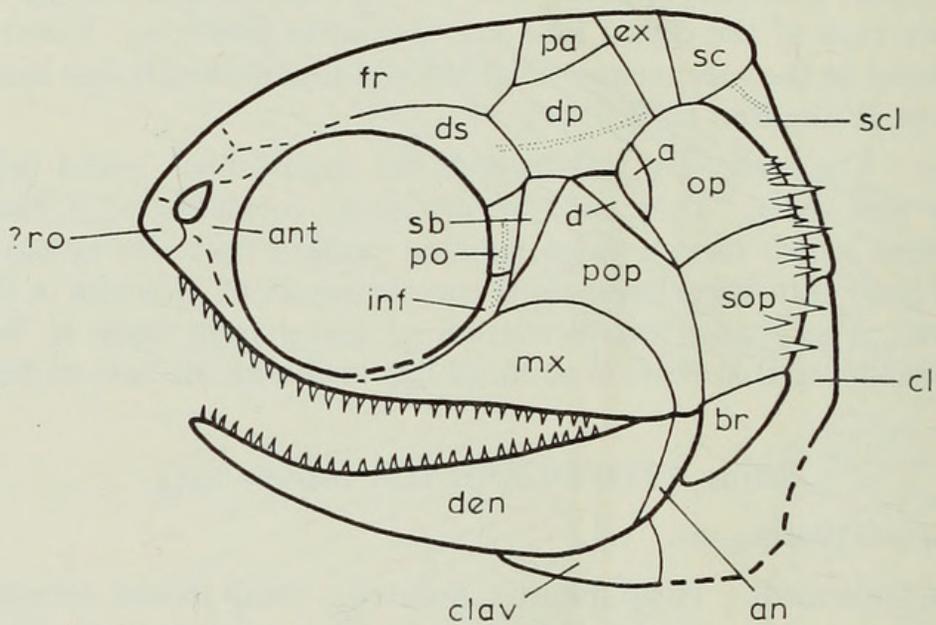
(Fig. 7)

1934 *Atopocephala watsoni* Brough: 564-570, text-figs 2-3, pl. 1, figs 2-3.

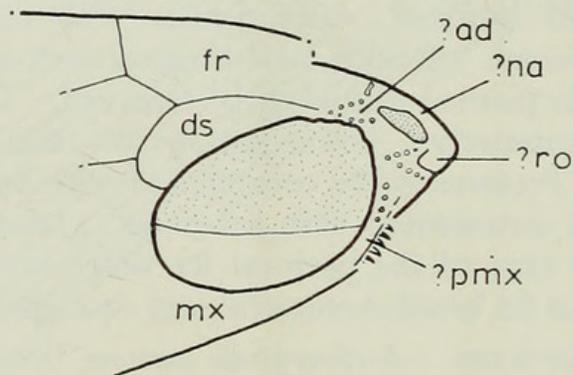
HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As for the genus *Atopocephala*.

HOLOTYPE. P.16079-80. A specimen with counterpart, the only specimen known.



A



B

4mm

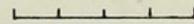


FIG. 7. *Atopocephala watsoni* Brough. (A) Restoration of skull and pectoral girdle, $\times 4.5$ approx. (B) P.16080, impression of left side.

DESCRIPTION. The only additions to the description given by Brough (1934 : 564) are a new interpretation of the snout and of the opercular region (Fig. 7).

The snout region is difficult to interpret. The only certain features are the nostril outline, a suture running from the antero-ventral corner of the nostril to the edge of the snout and the presence of a toothed element on the ventral edge of the snout. The only other indications of the probable pattern of the bones of the snout consist of rows of tubercles. These are almost confluent, and form elongate rugae which may mark the outlines of elements (Fig. 7). The area occupied by the nasal in Brough's figure (1934 : text-fig. 3), contains two elements which are here interpreted as being the adnasal and antorbital. The anterior border of the orbit is formed by the antorbital. This element is separated from the ventral edge of the snout by a narrow (?) premaxilla. Dorsal to the top part of the antorbital there is a diamond-shaped adnasal which just borders the nostril anteriorly and the dermosphenotic posteriorly. The dorsal edge of the nostril is bordered by the nasal, a rectangular element which meets the frontal posteriorly and the rostral anteriorly. There is no postrostral.

Anterior to the opercular there is an antopercular and a dermohyal. The dermohyal is elongate and extends ventrally to the antero-ventral corner of the opercular. The antopercular has a curved posterior margin which fits into a notch in the antero-dorsal corner of the opercular (see Brough 1934 : pl. 1, fig. 3).

A suture between the angular and the dentary is clearly visible.

Genus *BROOKVALIA* Wade 1933

- 1933 *Brookvalia* Wade: 121
 1935 *Brookvalia* Wade; Wade: 20
 1935 *Dictyopleurichthys* Wade; Wade: 35
 1935 *Beaconia* Wade; Wade: 33

DIAGNOSIS (emended). Head bullet-shaped with large orbit anteriorly placed. Skull bones ornamented with tubercles. Posterior parietal triangular. Dermopterotic extensive dorsally and bearing a posterior extension of the supraorbital sensory canal. Frontal curved and elongate, bordering, or almost bordering, part of the dorsal edge of the orbit. Small rostral element at snout tip, probably bordering the anterior edge of the nostril. Opercular series narrow and moderately oblique. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth sharp, conical and numerous. Lower jaw with slight dorsal curve toward the symphysis. Lower jaw shorter than upper jaw margin.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped and ornamented with rugae. Jointing regular on all fin-rays except those of the pectoral fin, in which jointing only occurs distally on the anterior rays. Caudal fin hemiheterocercal and equilobate.

TYPE SPECIES. *Brookvalia gracilis* Wade.

REMARKS. In this revision, five species classified in three genera by Wade (1935) have been reduced to four species, all included in a single genus. *B. parvisquamata* has been made a junior synonym of *B. gracilis* and *Dictyopleurichthys*

latipennis has been included in the genus *Brookvalia*, but retains its identity at the species level because of its slightly different scale ornament. Finally, the identification of an antopercular and of a single branchiostegal in *Beaconia* makes the validity of that genus extremely doubtful, and the one species which it contained has been removed to the genus *Brookvalia*.

The members of *Brookvalia* as here constituted differ significantly from one another only in their overall body shape, in the shape of the caudal fin and in the size, shape and position of the dorsal fin.

***Brookvalia gracilis* Wade**

(Figs 8-12, 14)

1933 *Brookvalia gracilis* Wade: 121-123, text-fig. 1.

1933 *Brookvalia parvisquamata* Wade: 124-125, text-fig. 3.

1935 *Brookvalia gracilis* Wade; Wade: 21-29, text-figs 5-14, pl. 4, fig. 1, pl. 5, fig. 1.

1935 *Brookvalia parvisquamata* Wade; Wade: 31-33, text-fig. 16, pl. 5, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS (emended). Extrascapular pentagonal. Two pairs of parietals, posterior element triangular, anterior element roughly oval and bearing two short parallel sensory canals. Dermopterotic bearing a short posterior extension of the supraorbital sensory canal. Postrostral probably present. Infraorbital elements reduced so that maxilla probably borders ventral edge of the orbit. Enlarged recurved teeth at tip of lower jaw.

Body slender. Scales ornamented with single, or rarely two, elongate rugae. Fringing fulcra not numerous, but present on anterior rays of all fins. Pectoral and pelvic fins equal in size, and fan-shaped with anterior and posterior rays almost equal in length. Dorsal fin originating just anterior to anal fin. Caudal fin deeply forked, with a few bifurcated rays in the lower lobe.

HOLOTYPE. P.15799 and counterpart P.15800.

MATERIAL. Holotype and P.15801-11, P.15813-24, P.15826-33, P.15835-42, P.15844-51, P.15853-6, P.15858, P.15860, P.15872, P.15878-9, P.15905-6, P.15914-5, P.15926, P.15930-1, P.15937, P.15939, P.15942, P.16997-17001, P.17005-17, P.24710-35.

U.S.G.D. 2, 4, 19, 28-9, 40-2, 80, 94, 141, 152, 159, 185-7, 205, 214, 218-19, 238, 244, 269, 272, 274, 277, 350 (at the University Museum of Zoology, Cambridge).

D.M.S.W. 383-8, 390-1 (at the University Museum of Zoology, Cambridge).

F.455 (at the Sedgwick Museum, Cambridge).

L.12143A-G.

DESCRIPTION. *Size* (Fig. 8). The total length from snout tip to the posterior end of the caudal fin varies from 30 mm (P.15810) to 125 mm (U.M.Z.C. un-catalogued). The body is fusiform and slender, its greatest depth occurring just behind the pectoral region.

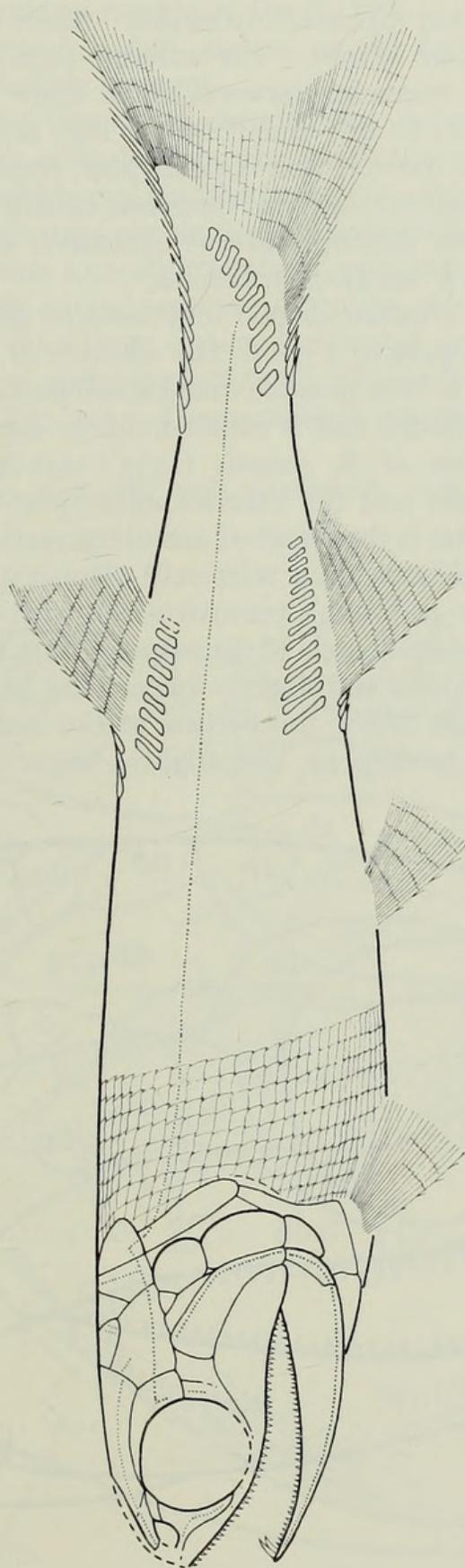


FIG. 8. *Brookvalia gracilis* Wade. Restoration, $\times 3$ approx.
Posterior scales omitted.

Skull (Fig. 9). The frontal is elongate, wide posteriorly and tapering towards the snout. It is sparsely covered with small tubercles. There are two pairs of parietals (parietal and postparietal of Wade). The anterior parietal is roughly oval, and bears three short rows of tubercles between which there were probably a pair of short sensory canals (U.S.G.D. 218 and P.15813, Fig. 10). The posterior parietal is larger than the anterior parietal and is triangular, coming to a point ventrally. In lateral aspect this element is small, but its dorsal extent is in fact quite large. It bears small tubercles. The dermopterotic is extensive, forming the main lateral element of the skull roof; it too bears tubercles.

The dermosphenotic is crescent-shaped and borders the postero-dorsal part of the orbit. Anteriorly it tapers to a point, but whether or not it meets the adnasal cannot be determined. It is thus possible that a small part of the frontal borders the dorsal edge of the orbit, though this is rather unlikely (see P.24730, Fig. 12).

In Wade's reconstruction of *B. gracilis* (1935 : text-fig. 5) the opercular lies ventral to the suprascapular and the extrascapular (post-temporal and tabular of Wade). This reconstruction is the result of misinterpretation of specimens in which opposite sides of the skull have been relatively displaced. In fact the opercular lies further anteriorly than in Wade's reconstruction with the result that the skull appears shorter, and the inferred angle of the suspensorium appears steeper (P.15813, Fig. 10). The opercular is oval and slightly longer than broad. It bears a series of low concentric ridges which follow the outline of the bone. The subopercular is elongate, being 1.5 times as deep as, and slightly longer than, the opercular. It

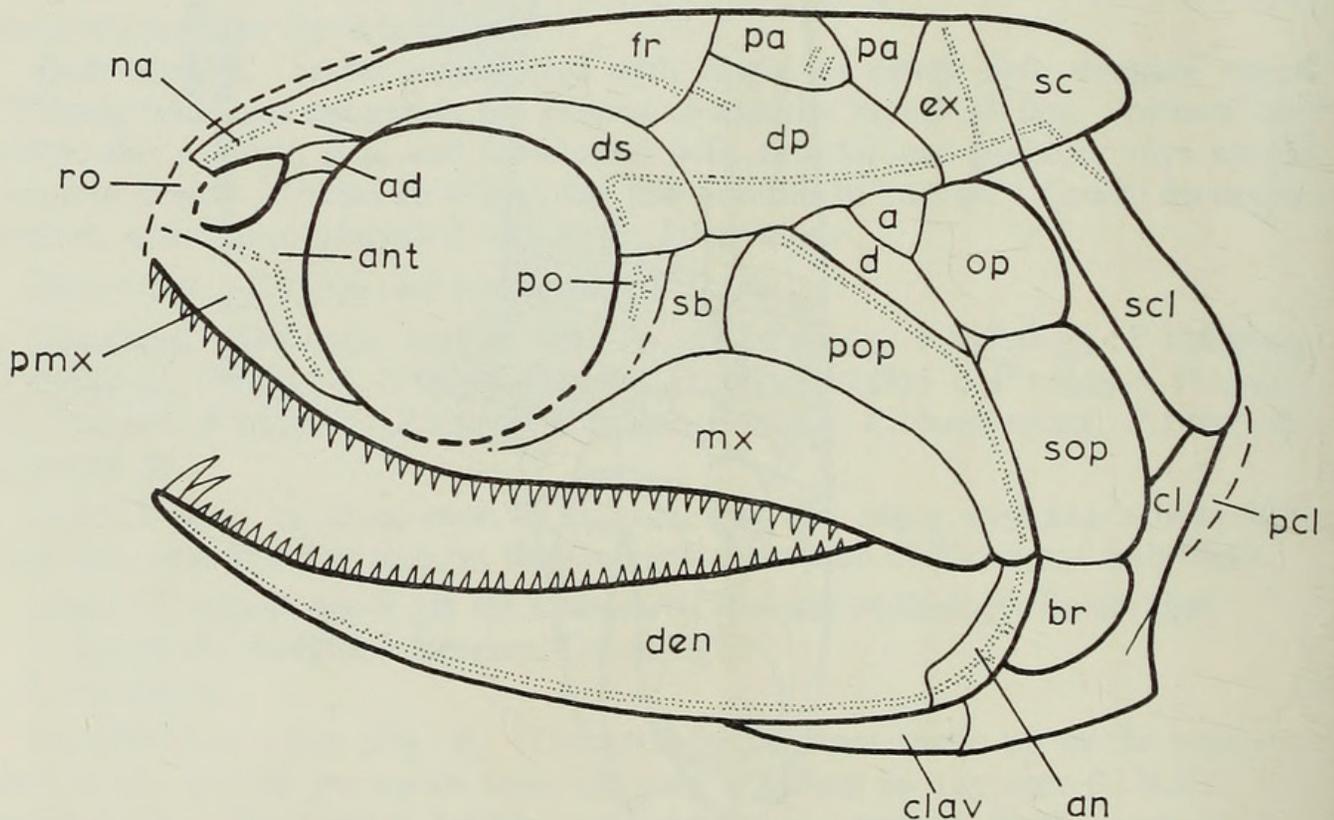


FIG. 9. *Brookvalia gracilis* Wade. Restoration of skull and pectoral girdle, $\times 5.5$ approx.

bears a similar series of concentric ridges. The anterior edge of the subopercular lies at about 65° to the ventral margin of the maxilla. There is a single triangular branchiostegal element which is half as long as the supopercular. Together, the opercular bones form a shallow crescent.

Anterior to the opercular there is an antopercular and a dermohyal. The dermohyal is wedge-shaped and extends along the whole anterior edge of the opercular. It bears elongate rugae which run parallel to its long axis (P.24723).

The preopercular is definitely not as deep as indicated by Wade (1935 : text-fig. 5); its shape is clearly seen in a disarticulated specimen (P.24734). The maxilla is characterized by a long curved anterior extension which appears to border the ventral edge of the orbit for a short distance, although no specimen shows this area clearly. It bears about 35 sharp conical teeth which are up to 1 mm high in large specimens (e.g. P.15813, Fig. 10). The maxilla is ornamented with elongate ridges (U.M.Z.C. uncatalogued).

The postorbital region is rarely well preserved, but specimen P.24734 shows

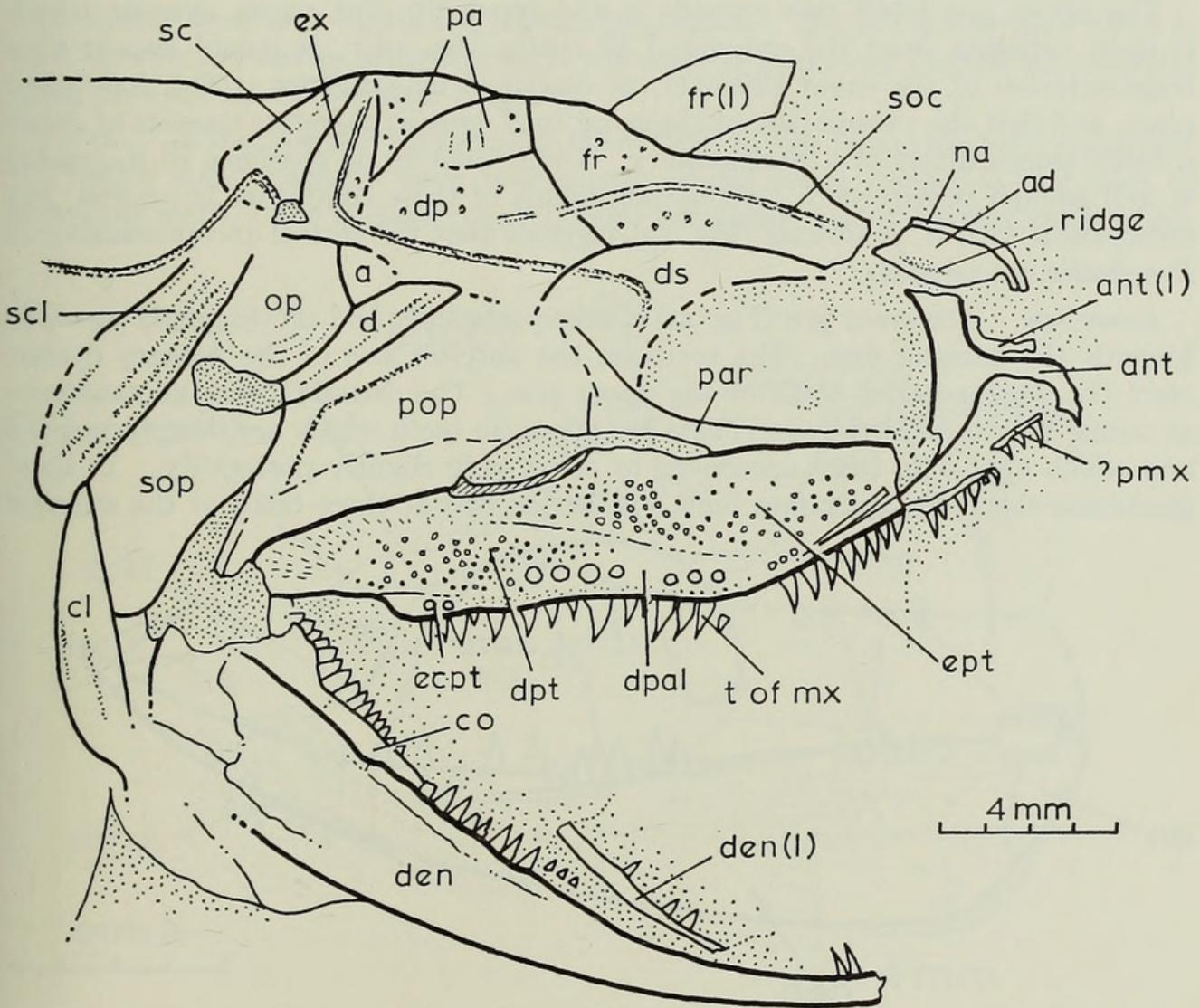


FIG. 10. *Brookvalia gracilis* Wade. P.15813: right side unless otherwise indicated.

that the preopercular was separated from the postorbital by a single element.

The snout is badly crushed in all specimens, but most of the elements can be identified with a high degree of confidence. The anterior edge of the orbit is bordered by two elements (P.15813, Fig. 10). The antorbital is the larger, more ventral of these elements, and is a long curved bone which sutures obliquely with the maxilla. Midway along its anterior border there is an anterior extension, which carries the infraorbital sensory canal forwards, and which borders the ventral edge of the nostril. This extension is similar to the rostral process described by Gardiner in the Lower Carboniferous palaeoniscoid *Nematoptychius greenocki* (1963 : 280). The anterior end of this extension is not preserved in *B. gracilis*. Dorsally, the antorbital meets the adnasal, a small diamond-shaped element which bears a single elongate ridge. The suture between the frontal and nasal is never very clear, but appears to be oblique, running antero-dorsally from near the orbit edge (P.24722). There is no evidence that the nasals met at the midline; they are always preserved as separate elements, and it is inferred that they, and possibly the anterior ends of the frontals, were separated by a median postrostral.

The upper jaw tooth row extends to the snout tip, but on an element which is quite separate from the antorbital (P.15813, Fig. 10). It would appear that fragmentation of the snout elements, as described by Gardiner (1963), has taken place, and that the ventral part of the snout in *B. gracilis* therefore consists of either a rostro-premaxillary or a premaxillary. Unfortunately no specimen of *B. gracilis* is well enough preserved to demonstrate which of these conditions is present, but comparison with *B. propennis* (Fig. 13) suggests that the rostral and premaxilla in *Brookvalia* are separate.

Lower jaw. The lower jaw (Fig. 11) is deep posteriorly and curves gently upwards towards the anterior end. The teeth on the anterior end of the dentary do not meet the most anterior teeth of the upper jaw. The dentary bears an ornament of strong longitudinal ridges. There are about 40 teeth which are sharply pointed and which appear in some specimens to curve very slightly posteriorly. In large specimens the teeth are 1 mm high, except for two or three teeth at the anterior

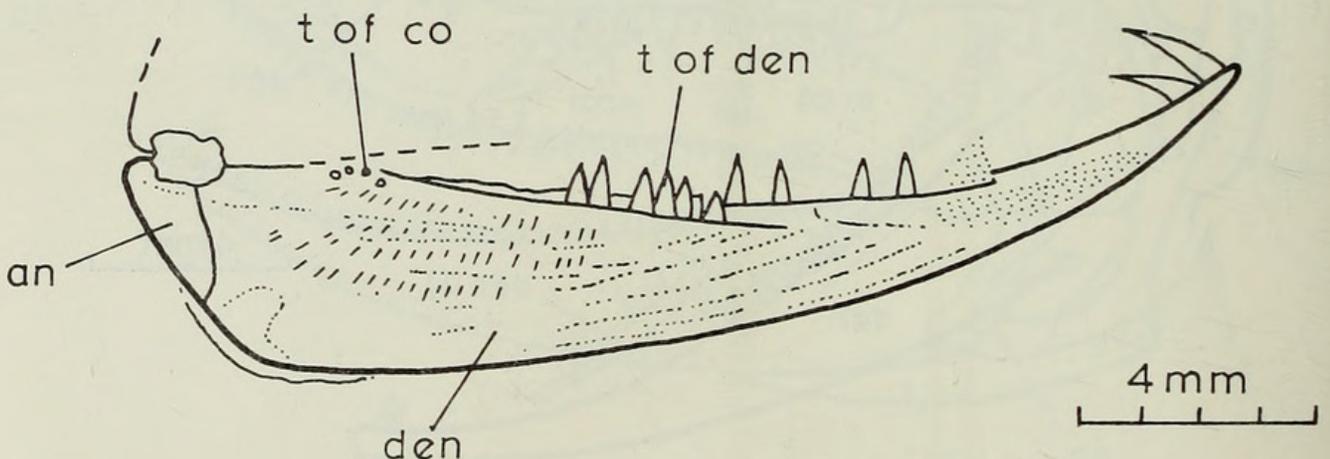


FIG. 11. *Brookvalia gracilis* Wade. P.15858: right side.

tip of the dentary which are twice as long as any other and which are sharply re-curved (P.15858, Fig. 11). In lateral view the posterior coronoid curves dorsally along the dentary margin. This too bears numerous teeth which are up to 0.5 mm high, and which appear to overlap one another in lateral aspect (P.15813, Fig. 10).

Sensory canal system. Part of the ethmoid commissure is represented on the anterior process of the antorbital by two groups of three or four shallow pits, similar to those seen on the infraorbitals of *Aestuarichthys fulcratus* (Gardiner 1969 : 437). No trace can be seen of the anterior branch of the infraorbital sensory canal on the dermosphenotic figured by Wade (1935 : text-fig. 5). The supraorbital sensory canal is not of the normal palaeoniscoid pattern: it runs across the nasal and frontal, but posteriorly it passes onto the dermopterotic (Fig. 10). Often the canal is displaced slightly at the suture between the frontal and dermopterotic. In no specimen was the supraorbital canal observed to join the infraorbital canal on the dermopterotic (c.f. Wade 1935 : text-fig. 5). In some (e.g. P.15827 and P.24730, Fig. 12), there is apparent joining of the supraorbital and infraorbital canals, because canals from both sides of the skull are preserved and the canal which appears to run into a right infraorbital canal is in fact a left supraorbital canal. The left infraorbital canal is seen about a millimetre below the right infraorbital canal and the left supraorbital canal does not reach the latter (Fig. 12).

Palate. In specimens P.15827 and P.15813 (Fig. 10) the palate has been preserved. Its visible upper surfaces have been partly eroded away, revealing the roots of numerous teeth. The endopterygoid is wide anteriorly, and bears tiny teeth which

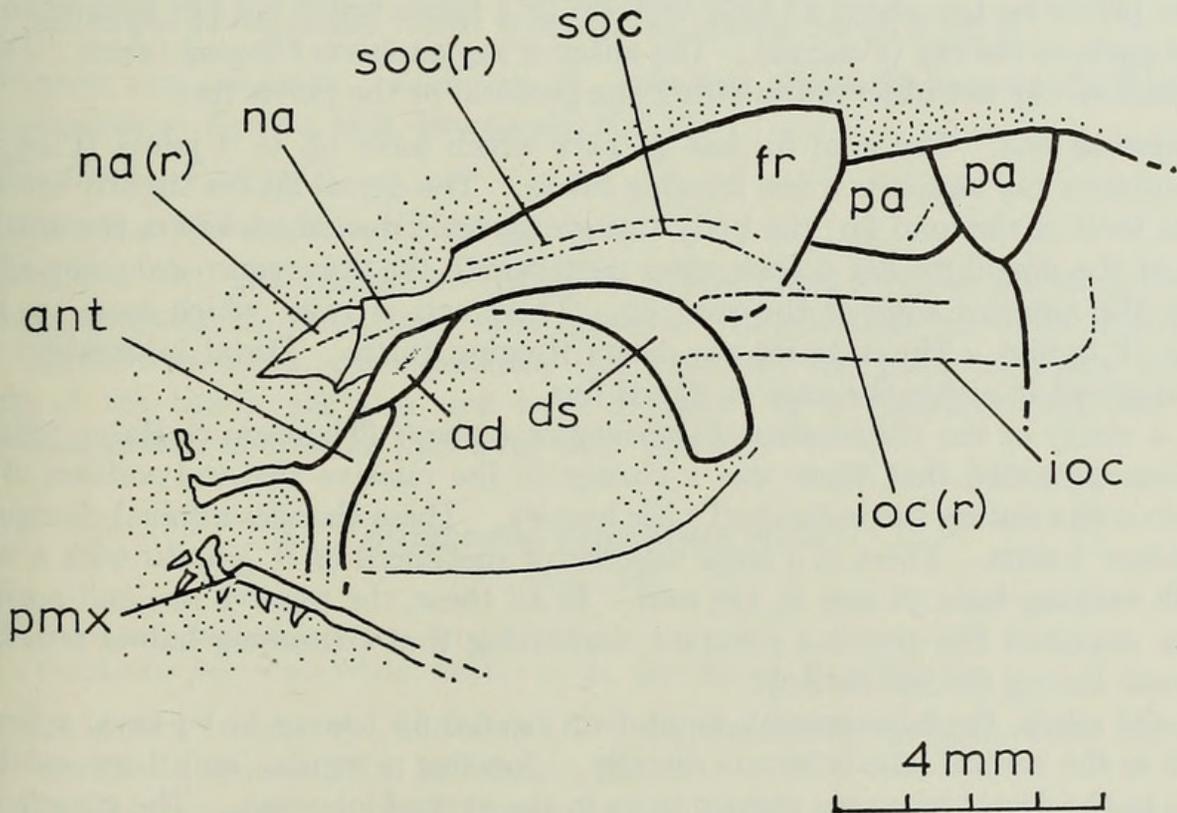


FIG. 12. *Brookvalia gracilis* Wade. P.24730: right side unless otherwise indicated.

are less than 0.1 mm in diameter, and which are arranged in rows which radiate from a point about halfway along its median edge. Lateral to the anterior edge of the endopterygoid is a dermopalatine element which is poorly preserved but which bears several teeth. Posterior to the dermopalatine is the ectopterygoid which bears numerous small teeth in addition to a row of six or seven larger ones. An area posterior to the ectopterygoid is very indistinct and presumably marks the position of the fossa for the adductor mandibulae. The dermometapterygoid sutures anteriorly with the ectopterygoid and endopterygoid. It bears numerous teeth which radiate from a point midway along its lateral border. Posteriorly there is a ridge and groove along the medial border of the palate; this was probably closely associated with the base of the hyomandibular. It is not clear whether this groove is in the endopterygoid or the dermometapterygoid.

Pectoral girdle. The supracleithrum is roughly oval in outline and extends ventrally to a point almost halfway down the posterior edge of the subopercular. It bears an ornament of three or four well developed concentric ridges (P.15827). The cleithrum is lanceolate dorsally, but wider ventrally. Just below the posterior margin of the lower jaw there is a clear suture between the cleithrum and clavicle (P.15853). The clavicle extends anteriorly below almost a third of the length of the lower jaw. Both the cleithrum and clavicle are ornamented with strong ridges. A postcleithrum is probably present, lying posterior to the dorsal half of the cleithrum (P.24713).

Paired fins. The pectoral fin has 17 rays (U.S.G.D. 269) which have one or two distal joints. The anterior ray supports fringing fulcra.

The pelvic fin has about 21 rays with up to 4 joints which are not limited to the distal parts of the ray (P.24722). The anterior ray supports fringing fulcra. Distal bifurcation was not observed in either the pectoral or the pelvic fins.

Unpaired fins. The anal fin has 42 rays which have up to 7 joints (P.25799). The anterior ray supports a few fringing fulcra. The dorsal fin lies slightly anterior to the level of the anal fin; the body transverse scale row which meets the anterior edge of the dorsal fin lies 9 scale rows posterior to the transverse scale row which meets the anterior edge of the anal fin. There are 32 rays, which have up to 6 joints (P.15799). The anterior ray bears fringing fulcra. Distal bifurcation was not observed in either the anal or dorsal fins.

In a study of the rhipidistian *Eusthenopteron foordi* (Thomson & Hahn 1968) it was demonstrated that there was a change in the relative size and position of the unpaired fins during the individual's life history. These changes implied changes in the fishes' habits. There is a large number of specimens of *B. gracilis* with a total length varying from 30 mm to 125 mm. In all these, the relative size and position of the unpaired fins remains constant, indicating that swimming habits remained constant during the life history.

In the adult, the heterocercal, equilobate caudal fin has up to 63 rays, a few of which in the ventral lobe bifurcate distally. Jointing is regular, and there are three joints in the dorsal lobe rays and up to 11 in the ventral lobe rays. The growth and development of the tail in *B. gracilis* is discussed below (see p. 328).

Fin skeleton. Young specimens of *B. gracilis* are incompletely scaled, and in some of these specimens parts of the fin skeletons are visible. Little detail can be made out, but it is clear that radial elements are fewer than the rays which they support. The anal fin has 14 radials which support 42 rays (P.15802), the dorsal fin at least 9 supporting 32 rays (P.15800) and the caudal fin at least 10, which extend along the ventral margin of the body lobe and support 33 rays.

Squamation. The scales are rhomboidal. They are exceptionally well preserved in specimen U.S.G.D. 218 (a specimen about 90 mm long) in which the largest scales are 0.8 mm long and 1 mm deep. There are 50 body transverse scale rows, containing about 30 scales in the region of the dorsal fin.

Each scale bears a ridge, or ruga, which bifurcates anteriorly, and which runs from the antero-dorsal to the postero-ventral corner of the scale. A few anterior flank scales bear two rugae.

Wade (1935 : 27) has described the gradual appearance of adult squamation in the growth series represented by large numbers of specimens of *B. gracilis*. In addition, it may be noted that young scales first appear as oblique 'scale buds': these approximate to the rugae seen in fully developed scales. In larger individuals the scales appear leaf-shaped, and it is only in the largest specimens that the scales fit closely together or overlap slightly, to give the appearance of a pattern of repeated rhomboidal shapes.

Brookvalia parvisquamata Wade

1933 *Brookvalia parvisquamata* Wade: 124-125, text-fig. 3.

1935 *Brookvalia parvisquamata* Wade; Wade: 31-33, text-fig. 16, pl. 5, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

HOLOTYPE. P.15798.

MATERIAL. Holotype and P.15843.

REMARKS. All the characters listed by Wade (1935 : 31) in his diagnosis of *B. parvisquamata* are found also in *B. gracilis*. In addition, all other characters that can be seen in *B. parvisquamata* (for example, the pattern of the sensory canals of the head) are also seen in *B. gracilis*. It is therefore proposed that *B. parvisquamata* is a junior synonym of *B. gracilis*.

Brookvalia propennis Wade

(Fig. 13)

1933 *Brookvalia propennis* Wade; 124, text-fig. 2.

1935 *Brookvalia propennis* Wade; Wade: 29-31, text-fig. 15, pl. 4, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS (emended). Skull incompletely known; discernible features as in *B. gracilis*.

Body slender, with caudal peduncle slightly deeper than in *B. gracilis*. Scales ornamented with two, or rarely three, elongate rugae. Fringing fulcra on anterior rays of all fins. No distal bifurcation in any fin-ray. Fins triangular with anterior rays 3-4 times as long as the posterior rays. Pectoral fin base 1.5 times as long as that of the pelvic fin, and composed of laterally expanded rays, with joints only at distal end of anterior rays. Anterior edge of dorsal fin lying just posterior to the level of the anterior edge of the pelvic fin. Caudal fin not deeply forked.

HOLOTYPE. U.S.G.D. 203.

MATERIAL. Holotype and P.15825 with counterpart P.15868, P.15850, P.24699 and P.24710.

DESCRIPTION. *Size*. The best preserved specimen of *B. propennis* is P.15825. Its length, measured from snout tip to the posterior end of the caudal fin, is 61 mm. The body is fusiform, its greatest depth occurring at the pectoral region. The body of *B. propennis* is very similar to that of *B. gracilis* except that the caudal peduncle in the former species is slightly deeper.

Skull. The skull in all specimens is badly crushed and few sutures can be seen. The anterior parietal appears to be slightly larger than in most specimens of *B. gracilis*, but this is not very significant because the apparent size and shape of the parietals in *B. gracilis* was seen to depend considerably upon the mode of preservation of each specimen. The extrascapular extends slightly further anteriorly than in *B. gracilis*, but the other skull bones show no significant differences from that species: they are ornamented with a similar pattern of tubercles; an antopercular and a dermohyal are present (P.15850); the ventral margin of the maxilla has the same characteristic convex curve below the orbit, followed by an upward curve towards the snout.

The snout is badly crushed, but in specimens P.15825 and its counterpart P.15868 (Fig. 13) there are two short tooth-bearing elements which run to the snout tip, between which there is a triangular element which bears numerous tooth-like denticles. These elements can be identified as premaxillae and rostral respectively. The more dorsal snout elements cannot be identified with certainty.

The lower jaw is characterized by the upturned tip seen in *B. gracilis* and the teeth, where preserved, are sharp and conical.

Pectoral girdle. Only the cleithrum is preserved. It is slender ventrally and ornamented with elongate ridges.

Paired fins. The pectoral fin is triangular and has 19 rays which are very broad, being composed of a median spine with flat lateral extensions. There are faint signs of two or three distal joints on the anterior rays (P.15850) but the other rays are unjointed. The anterior ray bears numerous fringing fulcra, and there is no distal bifurcation. Although composed of fewer rays, the pectoral fin is as large as the dorsal fin, and its base is 1.5 times as long as that of the pelvic fin.

The pelvic fin lies rather closer to the anal fin than to the pectoral fin. It is small and triangular. There are 24 rays, which are flattened laterally in a similar way to those of the pectoral fin, though to a lesser extent. There are up to 4 joints evenly

distributed along the rays. A few fringing fulcra may be present on the anterior ray (P.15850), but poor preservation does not allow certain identification. There is no distal bifurcation.

Unpaired fins. The rays of the unpaired fins are not expanded laterally to the extent seen in the paired fins. The anal fin is the same shape as, but larger than, the pelvic fin. It has 21 rays, which have up to 8 joints. Each joint of the anterior rays bears a single fringing fulcrum. There is no distal bifurcation.

The dorsal fin is almost the same shape and size as the anal fin, and lies completely in front of the anal fin. The body transverse scale row which meets the anterior ray of the dorsal fin, meets the anterior ray of the anal fin. There are 27 rays which have up to 7 joints. The anterior rays bear fringing fulcra and there is no distal bifurcation.

The caudal fin is equilobate but is not as deeply forked as it is in *B. gracilis*. The upper lobe has 28 rays, 7 of which are epaxial in position. The rays have up to 15 joints, and those bordering the anterior edges of the dorsal and ventral lobes bear fringing fulcra. There is no distal bifurcation. The posterior basal fulcrum on the dorsal side of the tail is inserted just anterior to the posterior tip of the body lobe. This condition is seen in *B. gracilis*, but only in juvenile (i.e. incompletely scaled) specimens.

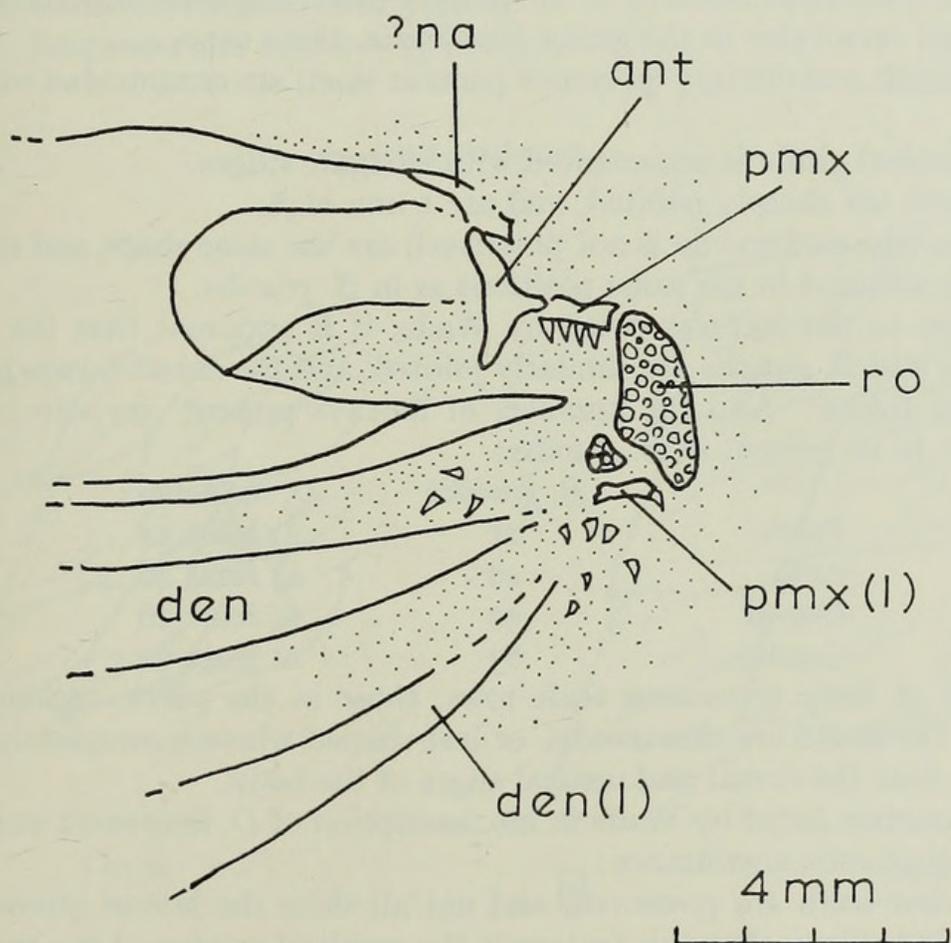


FIG. 13. *Brookvalia propennis* Wade. P.15868: right side unless otherwise indicated.

Squamation. The scales are leaf-shaped, but in the flank region they overlap and are rhomboidal in appearance. The largest scales are 0.8 mm long and 0.75 mm deep (P.15868) and are ornamented with two or more horizontal rugae. There are 40 body transverse scale rows, each calculated to contain up to 20 scales.

Brookvalia latipennis (Wade) comb. nov.

(Fig. 14)

1935 *Dictyopleurichthys latipennis* Wade: 35-37, pl. 7, fig. 1.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. Incompletely known. Discernible features as in *B. gracilis*, except that scales on the anterior flank region bear complex ornament of three or four rugae of variable length.

HOLOTYPE. P.15883, the only specimen known.

REMARKS. *B. latipennis* is represented by a single fossil. The body is complete, but only the posterior part of the skull is present, and this is badly crushed so that sutures are not visible. The length of the body from the posterior edge of the pectoral girdle to the caudal peduncle is 65 mm.

Most of the characters listed by Wade in the generic diagnosis of *Dictyopleurichthys* (1935 : 35-36) occur also in the genus *Brookvalia*, these are:

1. The maxilla and dentary (posterior parts at least) are ornamented with elongate ridges.
2. The pectoral girdle is ornamented with elongate ridges.
3. The teeth are sharply pointed, and are 1 mm high.
4. The fins (the pectoral fin is not preserved) are the same shape and relative size, and are situated in the same positions as in *B. gracilis*.

In addition to the features noted by Wade, it is apparent that the fin-rays in *D. latipennis* and *B. gracilis* are similarly jointed, and the anterior rays in each case bear fringing fulcra. Also the numbers of fin-rays present compare closely with those known to be present in *B. gracilis*:

	<i>B. gracilis</i>	<i>D. latipennis</i>
Pelvic	21	at least 14
Anal	42	at least 40
Dorsal	32	at least 26
Caudal	63	at least 62

There are 48 body transverse scale rows, those in the pelvic region containing 32 scales. The scales are rhomboidal, or leaf-shaped where incompletely developed scales occur near the dorsal and ventral edges of the body.

Other characters listed by Wade in his description of *D. latipennis* would seem to be of little diagnostic significance:

1. Very few teeth are preserved, and not all show the lateral groove described by Wade. It is likely that this feature is the result of erosion of the tooth surface.
2. Wade (1935 : 36) describes the dorsal fin of *D. latipennis* as being 'almost

completely anterior to the anal fin'. In fact, the anterior edge of the dorsal fin lies only 4 mm anterior to the level of the anal fin. The body transverse scale row which meets the anterior dorsal fin-ray lies 9 scale rows posterior to the row which meets the anterior ray of the anal fin; exactly the same condition is seen in *B. gracilis*.

3. The body is fusiform as in *B. gracilis*. The maximum body depth occurs immediately behind the pectoral girdle and measures 28 mm, which is over 25% of the estimated length between the snout tip and caudal peduncle. This implies that the body is deeper than in *B. gracilis*, in which the maximum body depth is just under 25% of the body length. This difference is not significant, however, because the ratio is variable in *B. gracilis* itself and, more importantly, the apparently increased depth may be due to compression during fossilization. The effect of compression is to exaggerate the body depth relative to body length in larger specimens, and *D. latipennis* is larger than any known specimen of *B. gracilis* (see Schaeffer, 1955 : 7-8 for a discussion of a similar situation).

The maximum body depth is 2.5 times the depth of the caudal peduncle, as is the case in *B. gracilis*.

4. As mentioned above, only the crushed remains of the posterior part of the head are preserved, and sutures are not visible. The following characters of the skull listed by Wade (1935 : 35) cannot be regarded as reliable:

1. Large orbits anteriorly placed.
2. Suspensorium moderately oblique.

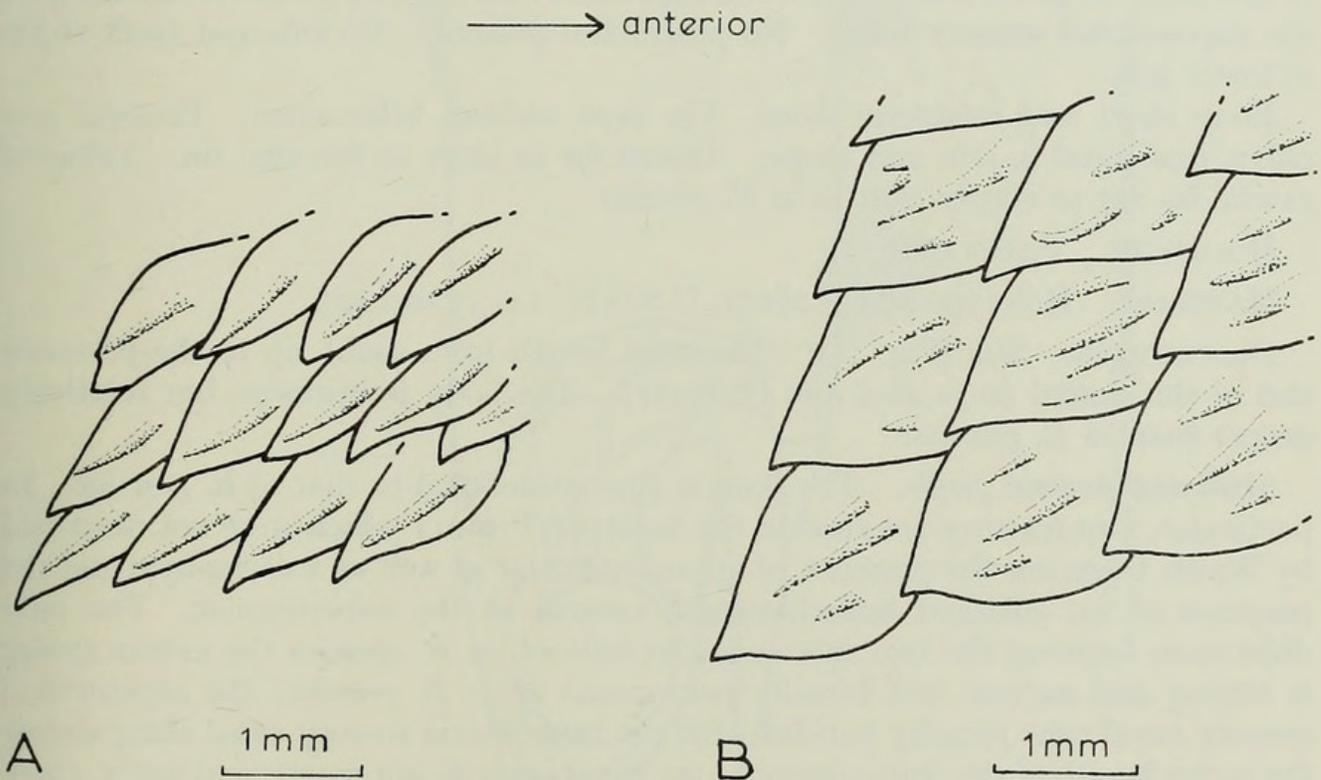


FIG. 14. Anterior flank scales. (A) *Brookvalia gracilis* Wade. P.15827.
(B) *Brookvalia latipennis* (Wade). P.15883.

3. Gape wide.
4. Operculum small, quadrangular.
5. Maxilla greatly expanded behind orbit.

There is only one character which is clear in *D. latipennis* and which is not seen in any specimen of *B. gracilis*. In the former species, most scales bear a single, or very occasionally two, rugae orientated obliquely, as is the case in *B. gracilis*. However, in the antero-dorsal region of the body of *D. latipennis* the scales are ornamented with three or four similar rugae—a condition never seen in *B. gracilis* (Fig. 14). There are enough similarities between *D. latipennis* and *Brookvalia* to justify the inclusion of *D. latipennis* in the genus *Brookvalia*, but the presence of the more complex scale ornament in *D. latipennis* warrants separation at the specific level. It is therefore proposed that *Dictyopleurichthys latipennis* be included in the genus *Brookvalia*, but that it should retain its specific name.

Brookvalia spinosa (Wade) comb. nov.

(Fig. 15)

1935 *Beaconia spinosa* Wade: 33–35, text-fig. 17, pl. 6, figs 1–2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. Extrascapular narrow. Two pairs of parietals; anterior element having long contact with dermopterotic, and bearing a pair of short sensory canals in the shape of an inverted “v”. Dermopterotic bearing long posterior extension of the supraorbital sensory canal. No postrostral present. No enlarged teeth at tip of lower jaw.

Body short and relatively deep. Fin rays without bifurcation. Pectoral and pelvic fins equal in size and shape. Dorsal fin as large as the anal fin. Lobes of caudal fin not as deeply cleft as in *B. gracilis*.

HOLOTYPE. P.16211.

MATERIAL. Holotype and P.16212, U.S.G.D. 14, 33 and 105.

DESCRIPTION. *Size* (Fig. 15). The total length from snout tip to the posterior end of the caudal fin is 46.5 mm (P.16211). The body is fusiform, but relatively deeper than in *B. gracilis*.

Skull and pectoral girdle. The skull is almost identical to that of *B. gracilis*. In particular, two features are seen in the holotype P.16211 which were not described by Wade; these are the presence of an antopercular as well as a dermohyal and the presence of an enlarged branchiostegal ventral to the subopercular. The only differences between the two species are as follows: in *B. spinosa* the extrascapular is oblong and narrow, not broadly pentagonal as in *B. gracilis*; the supraorbital sensory canal runs roughly parallel with the infraorbital sensory canal along almost the entire length of the dermopterotic (the two canals do not meet); and lastly, there are no enlarged teeth at the anterior tip of the lower jaw. The shape of the anterior parietal is slightly different from that of most specimens of *B. gracilis*, but is identical

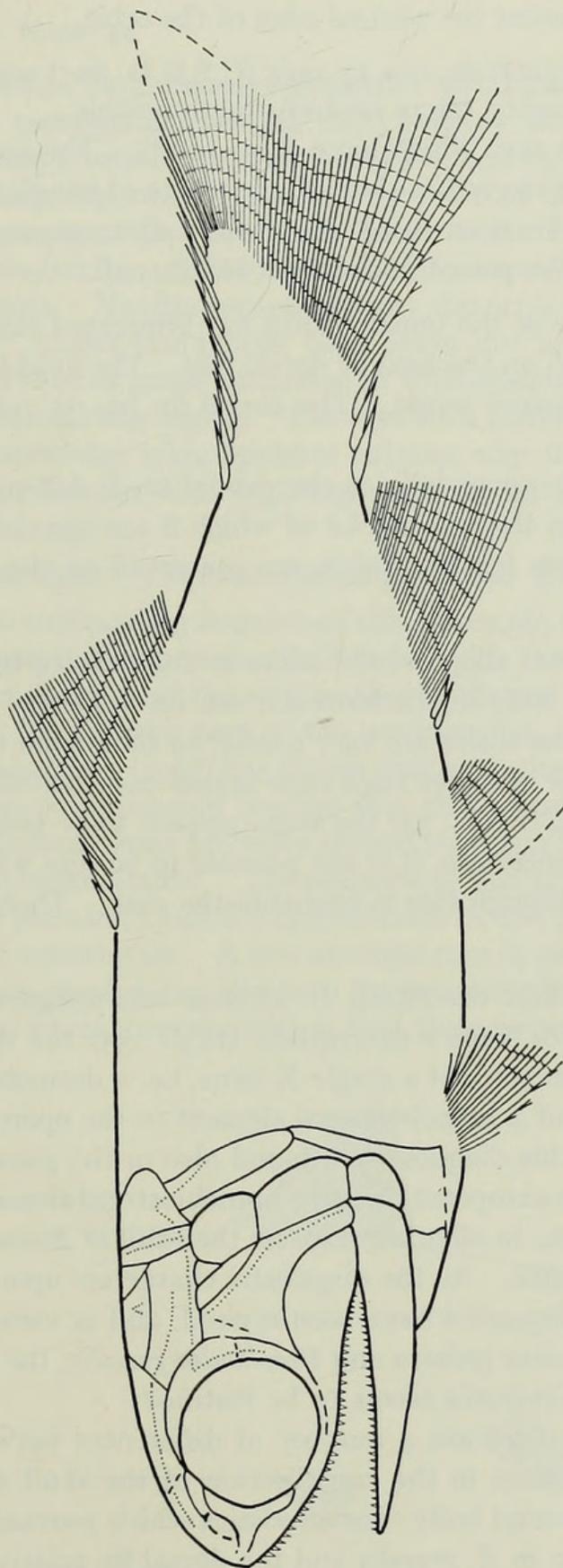


FIG. 15. *Brookvalia spinosa* (Wade). Restoration, $\times 3.5$ approx. Scales omitted.

with that of *B. propennis*. No postrostral is visible; also it is uncertain whether infraorbital elements border the ventral edge of the orbit.

Paired fins. The pectoral fin has 17 rays (U.S.G.D. 105) which have one or two distal joints. A few fringing fulcra are indistinctly visible.

The pelvic fin has 22 rays which have three joints. The anterior margin of the fin is not well enough preserved to show the presence of fringing fulcra. The pelvic fin lies close to the anal fin, there being only three body transverse scale rows between the two. The rays of the paired fins are not bifurcated.

Unpaired fins. None of the unpaired fins has bifurcated rays, nor are there any fringing fulcra preserved on the anal or dorsal fins. The anal fin has 31 rays which have up to 6 equally spaced joints. The dorsal fin has 35 rays which have up to 3 joints.

The distal end of the upper lobe of the caudal fin is not preserved. There are 49 rays, including 29 in the upper lobe of which 8 are epaxial. The longest rays have 10 joints, and a few fringing fulcra are preserved on the anterior edge of the ventral lobe.

Squamation. The exact shape of the scales in fully scaled individuals is difficult to determine. Young individuals, however, are incompletely scaled (U.S.G.D. 14 and 105) and in these the scales are very similar to those seen in young individuals of *B. gracilis*. A single elongate ruga runs across each leaf-shaped scale. In the fully scaled specimen (U.S.G.D. 33) the rugae appear to be paired, but because the outline of the scales is uncertain, it is not possible to be sure whether pairs of rugae occur on single scales, though this is probably the case. There are 40 body transverse scale rows.

DISCUSSION. When first described, *B. spinosa* was assigned to a new genus—*Beaconia*. According to Wade's description (1936 : 33) the diagnostic characters of the genus were the presence of a single X bone, i.e. a dermohyal, but no antopercular, and the absence of a branchiostegal element in the opercular series. All the other features listed in his diagnosis are found also in the genus *Brookvalia*.

It is now clear that an antopercular and a branchiostegal element are in fact present in *B. spinosa*. Moreover, in all other respects the skull of *Beaconia* is almost identical with that of *Brookvalia*. As the diagnostic characters upon which the validity of the genus *Beaconia* depended have been revised, and in view of the general close similarity between *Beaconia spinosa* and *Brookvalia gracilis*, the removal of *Beaconia spinosa* to the genus *Brookvalia* seems to be justified.

At the specific level there are a number of differences between *B. spinosa* and *B. gracilis*. The differences in the construction of the skull are described above. In addition there are several body characteristics which warrant mention: the body is relatively deeper than in *B. gracilis* and the dorsal fin relatively larger and more anterior in position (cf. Figs 8 and 15).

Genus *PHLYCTAENICHTHYS* Wade 19351935 *Phlyctaenichthys* Wade: 42.

DIAGNOSIS (emended). Skull bones ornamented with tubercles. Posterior parietal triangular, anterior rectangular, bearing short sensory canals in the shape of an inverted "v". Dermopterotic shallow and elongate, bearing long posterior extension of the supraorbital sensory canal. Frontal curved and elongate, separated from orbit edge by dermosphenotic. Opercular bones wider than in *Brookvalia*, and orientated almost vertically. Preopercular with no contact with dermopterotic. Six suborbital elements. Maxilla separated from the orbit by narrow infraorbitals. Postrostral present. Lower jaw shorter than upper jaw margin.

Body fusiform. Pectoral girdle ornamented with discontinuous, elongate rugae. Scales very deep in lateral line region. Fin rays with many joints. Anal fin small. Dorsal fin with anterior edge lying opposite anterior edge of pelvic fin. Tail hemiheterocercal, deeply bilobate, with high aspect ratio; anterior rays of dorsal lobe bifurcated twice.

TYPE (and only) SPECIES. *Phlyctaenichthys pectinatus* Wade.

DISCUSSION. The outstanding features of this genus are the near vertical suspensorium and the presence of numerous suborbitals. The suborbitals are presumably the product of fragmentation of the single suborbital seen in other redfieldiiforms, and possibly also of the anterior part of the preopercular. These two features are probably related. Gardiner (1967) has shown that with the acquisition of a vertical suspensorium in some palaeoniscoid families (e.g. the Aeduelliidae and the Boreosomidae) the adductor mandibulae probably shifted its origin from the palatoquadrate to the front of the hyomandibular. The pressure of this muscle, together with that of the levator arcus palatini, caused fragmentation of the anterior part of the preopercular and of the suborbitals. A less extreme case is seen in *Perleidus* in which several suborbitals are present, but in which the preopercular is not greatly reduced. The possible explanation of this condition is that the preopercular is prevented from

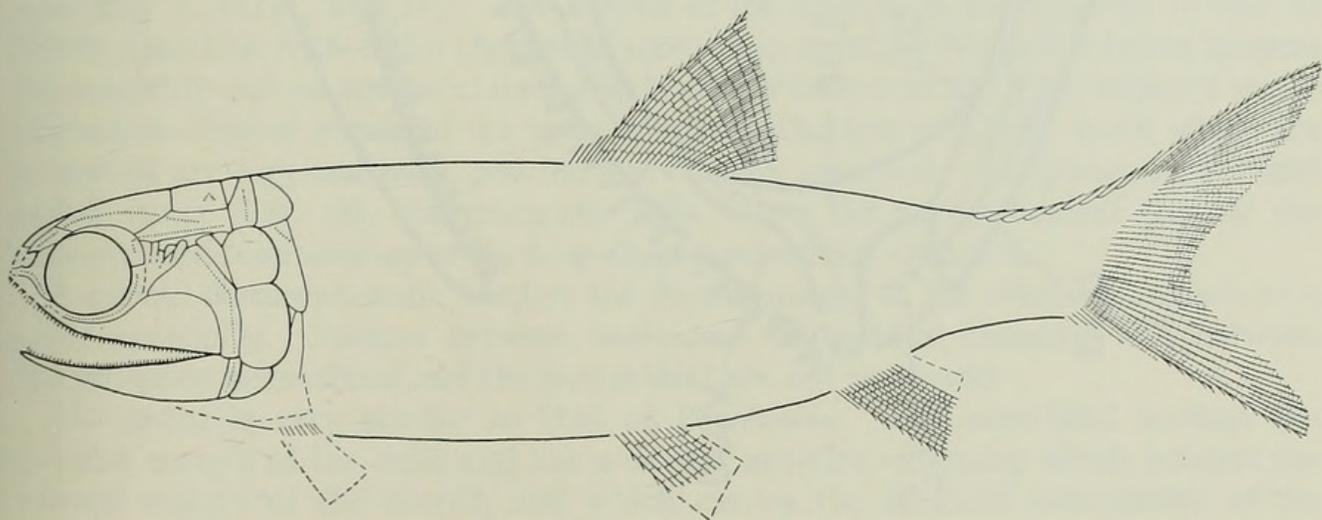


FIG. 16. *Phlyctaenichthys pectinatus* Wade. Restoration, $\times 1$ approx. Scales omitted.

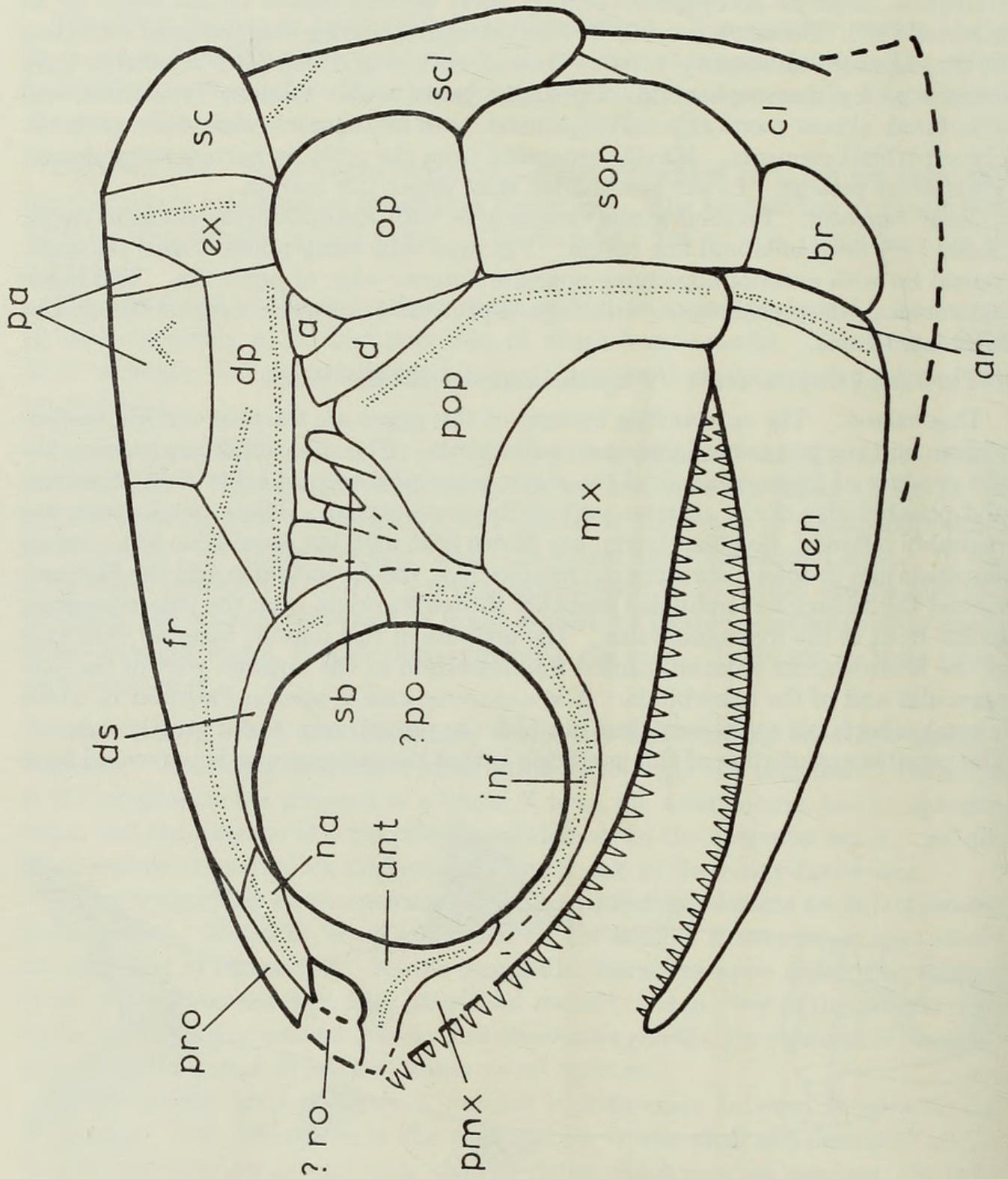


FIG. 17. *Phlyctaenichthys pectinatus* Wade. Restoration of skull and pectoral girdle. X 7. approx.

more complete fragmentation because part of the adductor mandibulae remains inserted on its interior face. This latter condition is also seen in the Peltopleuriformes, Platysiagiformes and Cephaloxeniformes (Gardiner 1967 : 200). If such a condition does exist in *Phlyctaenichthys*, this genus provides an example of the evolution of such a jaw musculature quite independently within the family Brookvaliidae.

Phlyctaenichthys pectinatus Wade

(Figs 16-18)

1935 *Phlyctaenichthys pectinatus* Wade: 42-44, text-fig. 20, pl. 10, fig. 1.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Phlyctaenichthys*.

HOLOTYPE. U.S.G.D. 200.

MATERIAL. Holotype and U.S.G.D. 183, L.12141 and P.16205-6.

DESCRIPTION. *Size*. (Fig. 16). The total length from snout tip to the posterior end of the caudal fin is 137 mm (U.S.G.D. 200). The body is fusiform, its greatest depth occurring between the posterior edge of the head and the level of the dorsal fin.

Skull. (Fig. 17). All the skull bones bear an ornament of numerous small tubercles. Two parietals are present; the posterior element is triangular and overlaps the anterior edge of the extrascapular. The dermopterotic is shallow and elongate, and tapers greatly anteriorly. The infraorbital sensory canal runs close to its ventral edge, and does not join the supraorbital sensory canal.

The opercular series is steeply inclined, the anterior edge of the subopercular lying at 75° to the ventral margin of the maxilla. The opercular is slightly deeper than it is long. The supopercular is 1.3 times as deep and almost exactly the same length as the opercular. An antopercular and a dermohyal lie anterior to the opercular (L.12141, Fig. 18). The outline of the maxilla is more similar to that of North American redfieldiids (Schaeffer 1967) than to other Brookvale forms because the smoothly curved outline of its dorsal border is broken at the point where it meets the antero-ventral corner of the preopercular. The few maxillary teeth which are preserved are 0.75 mm high, pointed and slightly recurved. In specimens P.16206 and L.12141 (Fig. 18), the triangular area below the antero-ventral part of the dermopterotic contains up to six drop-shaped suborbital elements.

A curved dermosphenotic borders the dorsal margin of the orbit, and tapers to a point anteriorly. Sutures between individual infraorbital elements and between the posterior infraorbital and the postorbital are not preserved.

The snout is very similar to that of *Brookvalia*. The antorbital borders the anterior margin of the orbit and has a narrow anterior extension which borders the ventral margin of the nostril, and which carries the ethmoid commissure of the infraorbital sensory canal. Dorsally the antorbital appears to meet the anterior tip of the dermosphenotic, but comparison with other redfieldiiforms suggests that there

could be an adnasal in this area. If this is true of *Phlyctaenichthys*, the suture between the antorbital and the adnasal is not preserved.

The snout tip is not preserved, but there was presumably a rostral element which bordered the anterior part of the nostril. Ventral to the anterior extension of the antorbital there is a small knob of bone bearing two teeth (L.12141, Fig. 18); this may be part of the premaxilla which is in evidence further ventrally, and which bears large denticles on its lateral surface, and teeth along its ventral margin. The suture between the premaxilla and the maxilla is not preserved, but its position is indicated by a change in surface ornament from denticles (premaxilla) to smaller tubercles (maxilla).

Lower jaw. The lower jaw tapers anteriorly and its end is upturned. Fifteen teeth only are preserved which are almost 0.75 mm high (P.16205). They appear to be blunt, but this may be due to poor preservation. The tip of the lower jaw does not extend as far as the tip of the snout.

Pectoral girdle. The supracleithrum extends ventrally to a point almost midway down the posterior edge of the subopercular, and bears an ornament of sinuous ridges, which are broken to form discrete rugae on its postero-dorsal part. Except for the dorsal part of the cleithrum, which is narrow, the rest of pectoral girdle is not preserved.

Paired fins. Nothing is known of the pectoral fin except that it has 8 rays. The

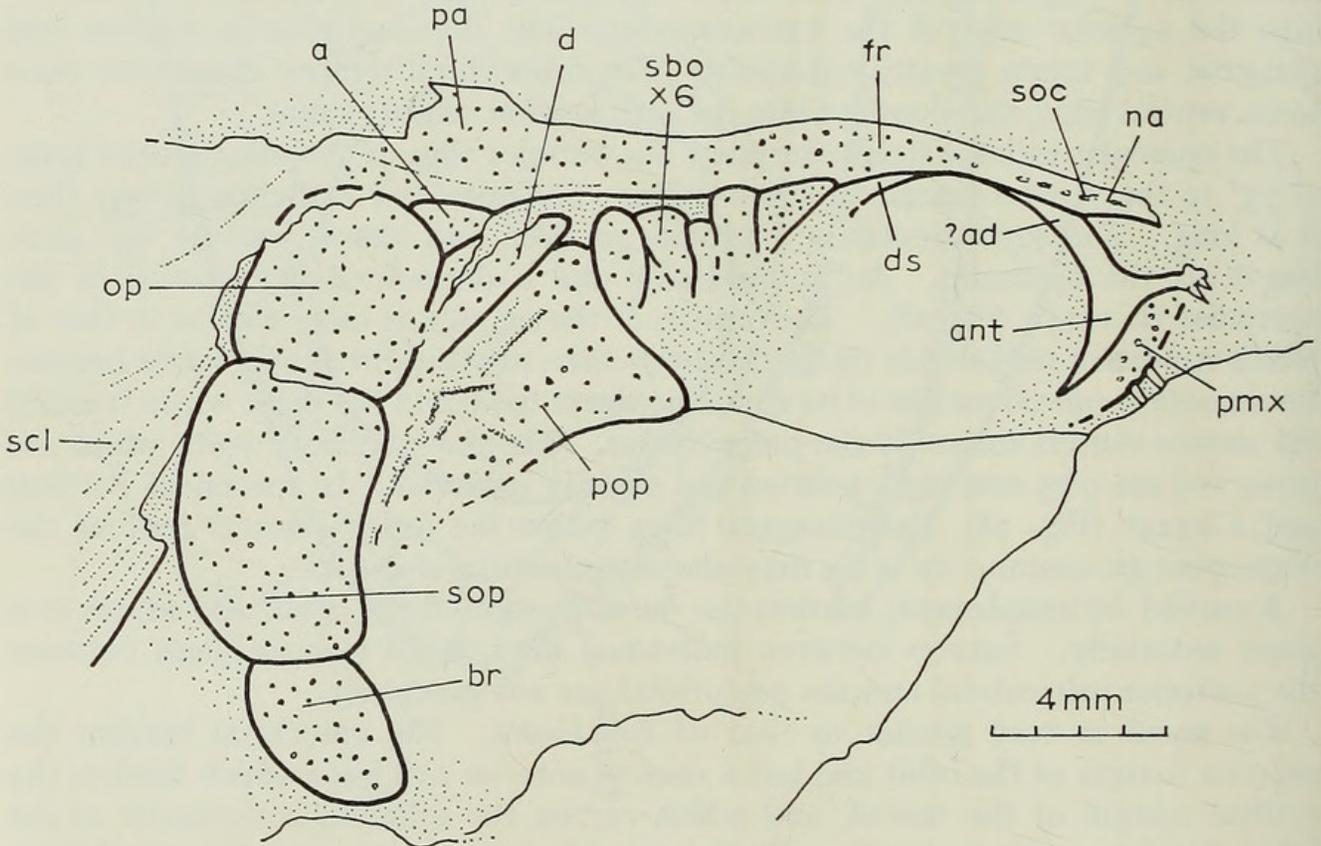


FIG. 18. *Phlyctaenichthys pectinatus* Wade. L.12141: impression of left side.

pelvic fin is also incompletely preserved. It has at least 10 rays which have 5 joints. The anterior ray bears fringing fulcra. There is no distal bifurcation.

Unpaired fins. The anal fin is small and has at least 15 rays which have up to 15 joints. The joints are closely spaced and equal the number of fulcra on the distal parts of the anterior rays. There is no distal bifurcation. The dorsal fin has 25 rays which have up to 12 joints. The anterior rays bear fringing fulcra, and the central rays bifurcate along half their length. The caudal fin is deeply cleft and has a high aspect ratio. There are 43 rays, 27 in the dorsal lobe, and the longest rays have at least 50 joints. The anterior rays on both lobes of the tail bear fringing fulcra. In the dorsal lobe the first 9 rays are epaxial in position. All the caudal fin-rays bifurcate; in addition, the anterior rays of the dorsal lobe bifurcate a second time at their distal ends.

Squamation. The body scales, except for those in the lateral line region, are leaf-shaped, but overlap to give a rhomboidal pattern. The largest flank scales are 1.6 mm long and 4 mm deep (U.S.G.D. 183) but nearer the dorsal and ventral edges of the body the scales are equidimensional. There are 40 body transverse scale rows.

Family **REDFIELDIIDAE** Berg 1940

DIAGNOSIS. Orbit small. One pair of parietals usually present, but sometimes three or four (one pair + one, or two pairs) present. Dermosphenotic equal in size to dermopterotic. Posterior extension of supraorbital sensory canal, if present, on parietal. Dermosphenotic rectangular, widely separating frontal from dorsal orbital edge. Snout composed of rostral and paired antorbitals and nasals. Snout elements ornamented with large tubercles, presumably specialized for support of fleshy lip. Postrostral usually present, but reduced or lost in some Upper Triassic genera. Antorbital broad, bordering anterior edge of orbit; posterior, ventral, and sometimes anterior, edges of nostril; and ventral edge of snout. No premaxilla. Large adnasal with broad contact with antorbital and dermosphenotic. A single dermohyal present. No antopercular, except in two species of one genus (*Helichthys*). Maxilla narrow anteriorly and separated from orbital edge by complete infraorbital series. Gular plate present. Lower jaw deep, short and either straight or curved dorsally towards the symphysis.

Elements of pectoral girdle generally broad. Fulcra usually well developed on all fins. Scales rhomboidal to leaf-shaped, often with denticulated posterior borders. Hinge line at base of body lobe of tail not marked by abrupt change in orientation of scale rows.

Genus **DAEDALICHTHYS** Brough 1931

1931 *Daedalichthys* Brough: 245.

DIAGNOSIS (emended). Head bullet-shaped with snout extended to form a pronounced rostrum. Skull bones ornamented with large tubercles and with posterior margins frequently denticulated. A single pair of parietals. Dermoptero-

tic rhombic. Frontal rectangular and elongate, separated from the orbit edge by a deep dermosphenotic. Adnasal almost square with broad contact with dermosphenotic. Nasals elongate. Rostral bordering the anterior edge of the nostril, and forming an overhanging rostrum at snout tip. Postrostral present. Opercular series moderately oblique. A single suborbital present. Maxilla deep posteriorly, antero-dorsal edge overlapped by broad infraorbital elements. Teeth pointed and slightly recurved. Lower jaw stout and straight.

Posterior margins of suprascapular and supracleithrum denticulate. Scales rhombic, ornamented with ridges, and with denticulated posterior borders. Fin-rays with large fulcra. Paired fin-rays stout, unjointed and few in number. Unpaired fin-rays numerous, delicate and with regular jointing. Caudal fin hemiheterocercal.

TYPE (and only) SPECIES. *Daedalichthys higginsi* Brough.

REMARKS. Apart from the presence of two branchiostegals, *Daedalichthys* is remarkable for its similarities with North American redfieldiids of the Upper Triassic (Schaeffer 1967). The characteristic arrangement of the bones of the snout and cheek appears to have changed very little during the Triassic, and enables the family Redfieldiidae to be easily recognized and defined.

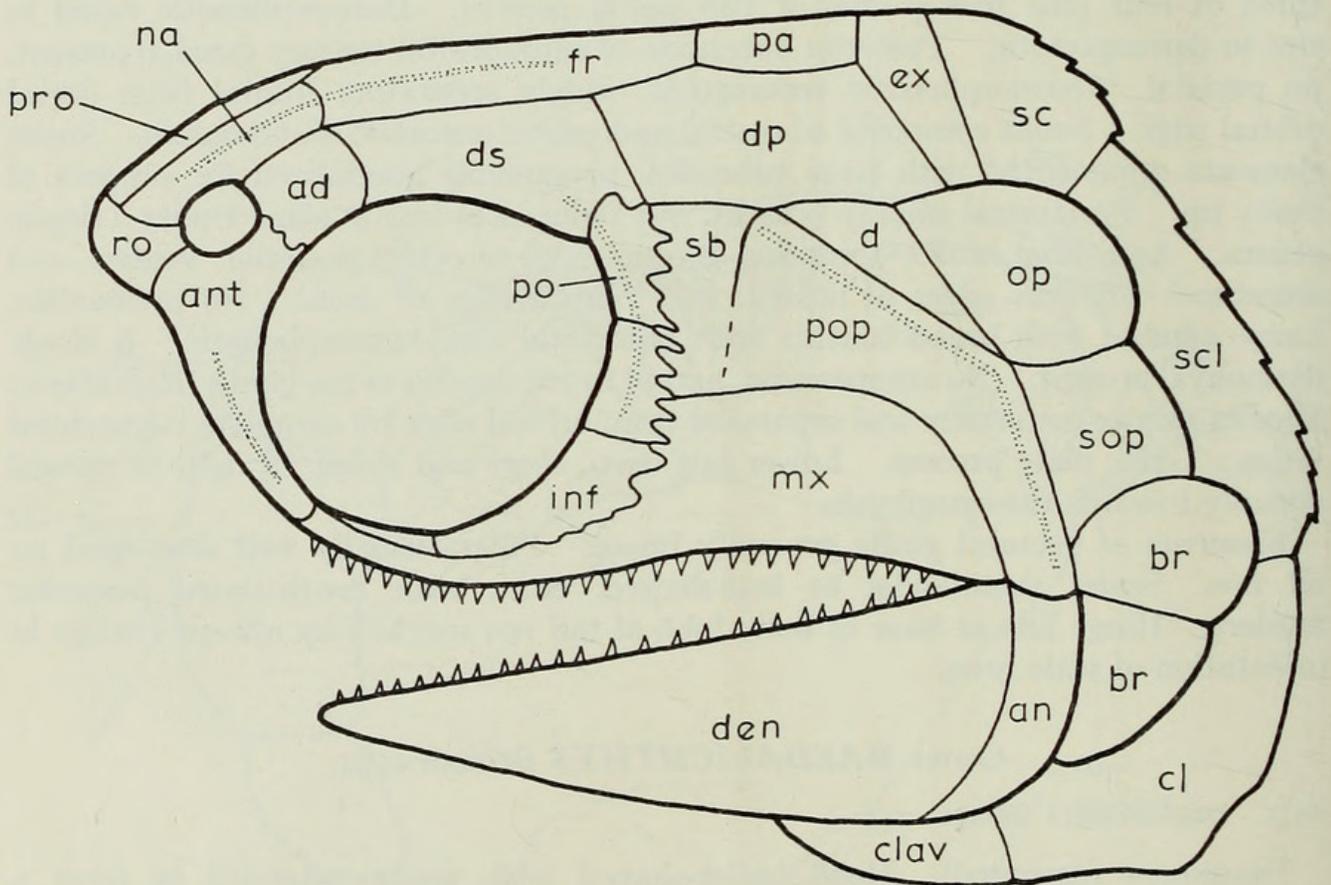


FIG. 19. *Daedalichthys higginsi* Brough. Restoration of skull and pectoral girdle, $\times 5.5$ approx.

Daedalichthys higginsi Brough

(Figs 19-20)

1931 *Daedalichthys higginsi* Brough: 245-246, text-fig. 3, pl. 1, fig. 4.1934 *Daedalichthys higginsi* Brough; Brough: 559-564, text-fig. 1, pl. 1, fig. 1.

HORIZON AND LOCALITY. Scythian. Lower Cynogathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As for the genus *Daedalichthys*.

HOLOTYPE. G.N. 301.

MATERIAL. Holotype, P.17532-3 and P.17538.

DESCRIPTION. Study of specimens G.N. 301 and P.17532-3 enables some additions and some corrections to be made to the otherwise complete description of *D. higginsi* (Brough 1934).

The area occupied by the nasal in Brough's figure (1934 : text-fig. 1) in fact contains two elements, the adnasal and antorbital. The antorbital forms the anterior border of the orbit as it does in other redfieldiiforms; its identification is confirmed by the presence of pits leading into the infraorbital sensory canal. In specimen G.N. 301 (Fig. 20) the ventral parts of both antorbitals are damaged, revealing tubes along which the sensory canal itself ran. The adnasal is also clearly seen in specimen G.N. 301.

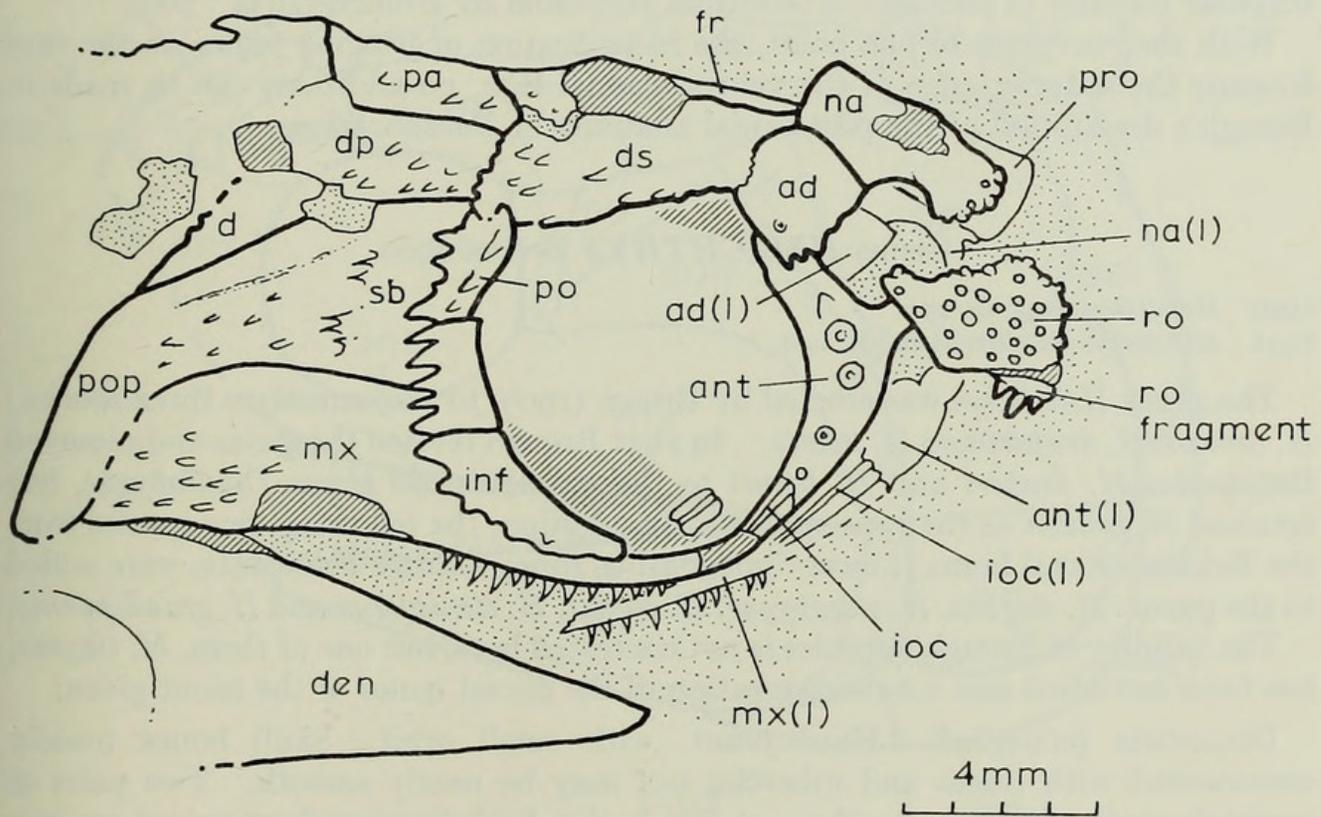


FIG. 20. *Daedalichthys higginsi* Brough. G.N. 301: right side unless otherwise indicated.

Identification of the antorbital and adnasal in *D. higginsi* necessitates re-interpretation of the other snout elements, and makes a new restoration of the whole skull possible (Fig. 19). A curved nasal (second postrostral of Brough) lies anterior to the frontal. It forms the dorsal border of the nostril. Between the nasals there is a postrostral which extends posteriorly between the anterior ends of the frontals. The snout tip is formed by an ornamented rostral which gives the snout its singular profile. In specimen G.N. 301 (Fig. 20) there is a fragment of bone lying ventral to the main part of the rostral, and separated from it by an area of crushed bone. At first this appeared to be a premaxilla, mainly because teeth seemed to be present on its ventral border. Closer inspection, however, shows that these tooth-like projections are identical with the tubercles found on other parts of the snout, and differ from the maxillary and dentary teeth in that they are neither as pointed, nor are they slightly recurved. It is therefore concluded that this fragment represents the ventral part of the rostral, and that there is no premaxilla in *Daedalichthys*.

The only other additions to Brough's description of *D. higginsi* are the identification of a single wedge-shaped dermohyal lying anterior to the opercular, and a suture between the angular and dentary. Modifications of Brough's restoration are seen in a slight change in the angle of the suture which subdivides the branchiostegal (a variable feature in the genus), and in the identification of only a single suborbital (second postorbital of Brough). Brough (1934 : 563) has already noted that there is some variation in the sutural pattern between elements of the opercular series. There was no sign, in the specimens studied, of subdivision of the extrascapular (tabular of Brough), a condition suggested by Brough (1934 : 560).

With the exception of one point, the identification of fringing fulcra on the rays forming the anterior edge of the ventral caudal lobe, no additions can be made to Brough's description of the postcranial anatomy of *Daedalichthys*.

Genus *HELICHTHYS* Broom 1909

1909 *Helichthys* Broom: 254.

1931 *Helichthys* Broom; Brough: 246.

The genus *Helichthys* was erected by Broom (1909) to accommodate three species; *H. browni*, *H. draperi* and *H. tenuis*. In 1931 Brough revised the genus and removed the species *H. draperi* and *H. tenuis* to the palaeoniscoid genus *Dicelopygiae*, but retained *H. browni* as the type species. In addition, the following new species from the Bekker's Kraal fauna (Lower Cynognathus zone), Orange Free State, were added to the genus: *H. elegans*, *H. stegopygae*, *H. obesus*, *H. ctenipteryx* and *H. grandipennis*.

The validity of Brough's species is not contested here, but one of them, *H. elegans*, has been restudied and a new restoration of the dorsal bones of the snout given.

DIAGNOSIS (emended). Head blunt, with small orbit. Skull bones usually ornamented with ridges and tubercles but may be nearly smooth. Two pairs of parietals similar in shape to those of *Brookvalia*, both bearing short paired sensory canals. Dermopterotic roughly rectangular, but narrow posteriorly. Frontal elongate. Adnasal deep with broad contact with dermosphenotic. Nasal short.

Rostral bordering anterior edge of nostril. Postrostral present. Opercular series moderately oblique. Subopercular and branchiostegal divided by a straight suture. Antopercular may or may not be present. A single suborbital present. Teeth conical and sharply pointed. Lower jaw stout and straight.

Body fusiform. Pectoral girdle large and ornamented with strong ridges. Scales rhombic to leaf-shaped, unornamented. Fin-rays with large fulcra. Pectoral fin-rays stout, jointed distally or not at all, other fin-rays with regular jointing. Caudal fin hemiheterocercal and equilobate.

TYPE SPECIES. *Helichthys browni* Broom.

Helichthys elegans Brough
(Figs 21-22)

1931 *Helichthys elegans* Brough: 248-252, text-figs 4-5, pl. 2, figs 1-2.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As in Brough (1931 : 248). Only one alteration need be made to

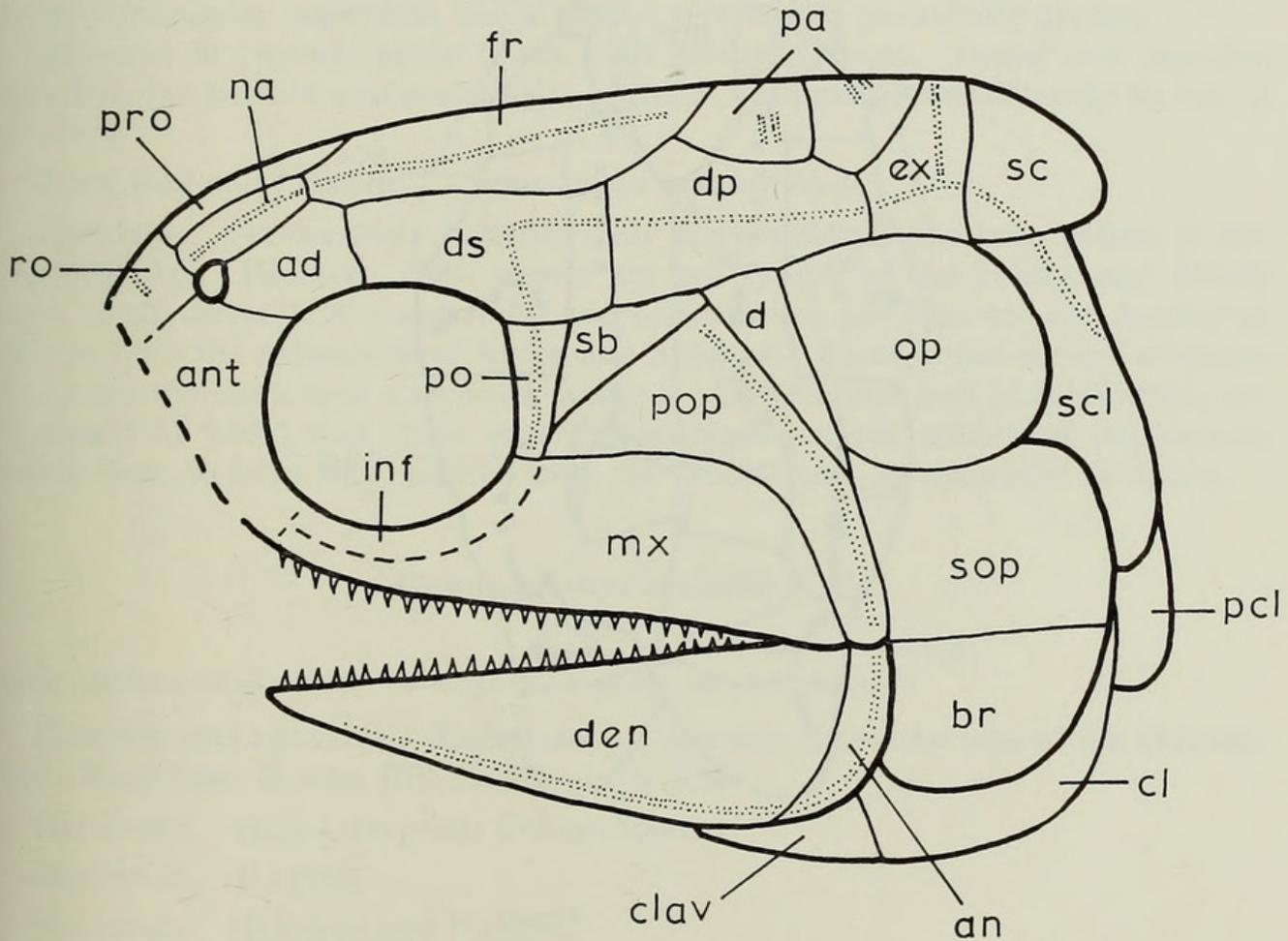


FIG. 21. *Helichthys elegans* Brough. Restoration of skull and pectoral girdle, $\times 6$ approx.

Brough's diagnosis; restoration of the snout region shows that the orbit can no longer be regarded as having ' . . . an extreme anterior position in the head'.

HOLOTYPE. A specimen in the D. M. S. Watson collection (missing from the Cambridge University Zoology Department collection).

MATERIAL. G.N. 316.

DESCRIPTION. Brough did not describe the snout region in any species of *Helichthys*. In an attempt to remedy this omission, Schaeffer has made a new restoration of the skull of *Helichthys* based upon material in the A.M.N.H. (1967 : text-fig. 17B). This restoration is slightly inaccurate however, mainly because the adnasal is figured without contact with the nostril border. An almost perfectly preserved skull roof of *H. elegans* from the Cambridge University Zoology Department collection (G.N. 316, fig. 22) makes an accurate restoration of most of the snout of *Helichthys* possible (Fig. 21). Specimen G.N. 316 shows that the dorsal

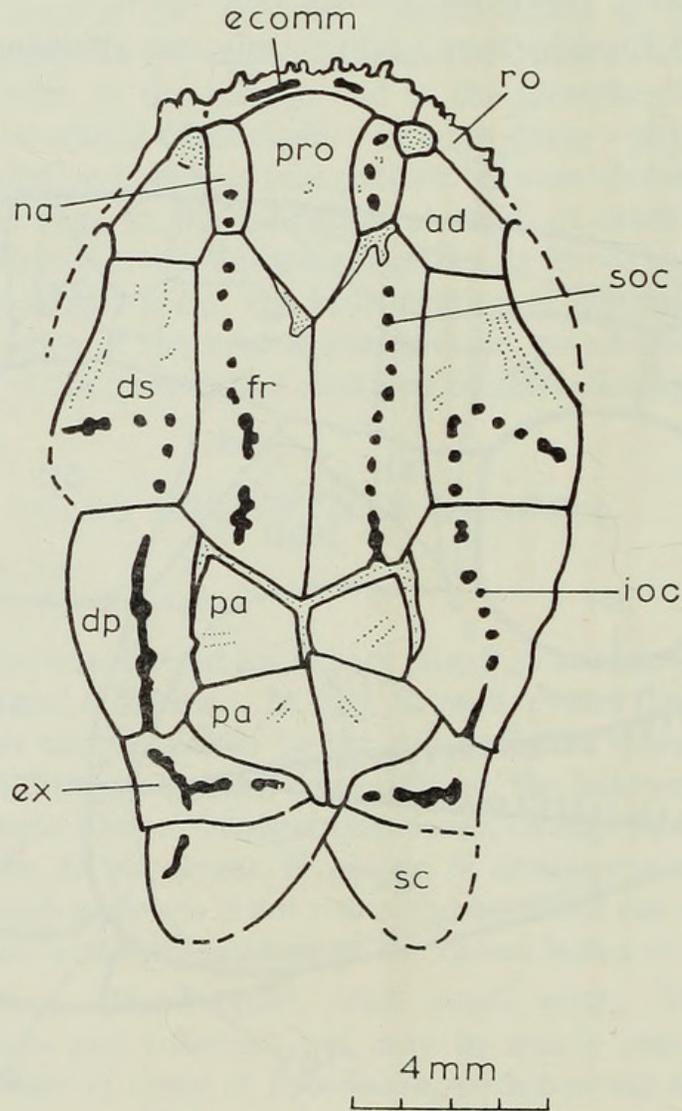


FIG. 22. *Helichthys elegans* Brough. G.N. 316: dorsal view.

part of the snout in *Helichthys* is almost identical to that of *Cionichthys* and *Redfieldius* (Schaeffer 1967). The difference between *Cionichthys* and *Redfieldius* is that in the latter genus the adnasal extends considerably further posteriorly than does the nasal, whereas in *Cionichthys* these two bones extend posteriorly to the same level. *Helichthys* shows an intermediate condition in that the adnasal extends only slightly further posteriorly than does the nasal.

The only other major difference between Brough's figures of *Helichthys* and the restoration given here is that the sensory canal on the preopercular is not joined to the infraorbital sensory canal on the dermopterotic.

Genus *GEITONICHTHYS* Wade 1935

1935 *Geitonichthys* Wade: 37.

DIAGNOSIS (emended). Skull deep, orbit small. Dermopterotic deep and oblong. Frontal not as elongate as in *Molybdichthys*. Dermosphenotic deep, with ornament of ridges on its ventral edge. Antorbital wide, bordering the whole of the ventral border of the nostril. Opercular deeper than long. Opercular series narrow, inclined steeply. Preopercular with short contact with dermopterotic. A single narrow triangular suborbital, and a narrow rectangular postorbital present.

Elements of pectoral girdle broad. All fin-rays jointed. Dorsal and anal fins opposite one another and posterior in position. Bifurcation visible only in caudal fin-rays.

TYPE (and only) SPECIES. *Geitonichthys ornatus* Wade.

REMARKS. *Geitonichthys*, together with *Molybdichthys*, has been placed in the Redfieldiidae. However, these genera are not typical of the family, and details such as the shape of the antorbital and of the lower jaw separate the Australian genera from the redfieldiids of Africa and America. There is not enough evidence to justify the erection of a separate family for *Geitonichthys* and *Molybdichthys*, but it should be noted that these genera probably represent redfieldiid populations which were, in some way, isolated from the 'mainstream' of redfieldiid evolution.

Geitonichthys ornatus Wade

(Figs 23-24)

1935 *Geitonichthys ornatus* Wade: 37-39, text-fig. 18, pl. 8, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Geitonichthys*.

HOLOTYPE. P.15859.

MATERIAL. Holotype and P.15880.

DESCRIPTION. *Size*. The total length of the holotype (the larger of the two specimens) is estimated to be 120 mm. The body is fusiform, its greatest depth

occurring midway between the posterior edge of the operculum and the anterior edge of the dorsal fin.

Skull (Fig. 23). The postero-dorsal part of the skull and parts of the snout tip are missing in both specimens. The frontal is deep and rectangular. The large dermosphenotic bears four ridges ventrally which follow the outline of the dorsal margin of the orbit. The dorsal edge of the dermosphenotic is clear but, below this, the bone surface is eroded and the anterior extension of the infraorbital sensory canal figured by Wade (1935 : text-fig. 18) cannot be seen. In specimen P.15880 (Fig. 24) the dermosphenotic is displaced ventrally, relative to the adnasal, by about 1 mm; its probable position has been restored in Fig. 23. The dermopterotic is also extensive and is roughly rectangular. The suprascapular and extrascapular are either missing (P.15880) or poorly preserved (P.15859) and, although their outlines cannot be traced, numerous elongate tubercles are seen where they occur.

The anterior edge of the subopercular lies at 68° to the ventral margin of the maxilla. A single triangular branchiostegal ray is present, fitting closely to the posterior edge of the lower jaw. A single wedge-shaped dermohyal lies anterior to the opercular. The preopercular is 'r'-shaped and has point contact with the dermopterotic. There is a single triangular suborbital.

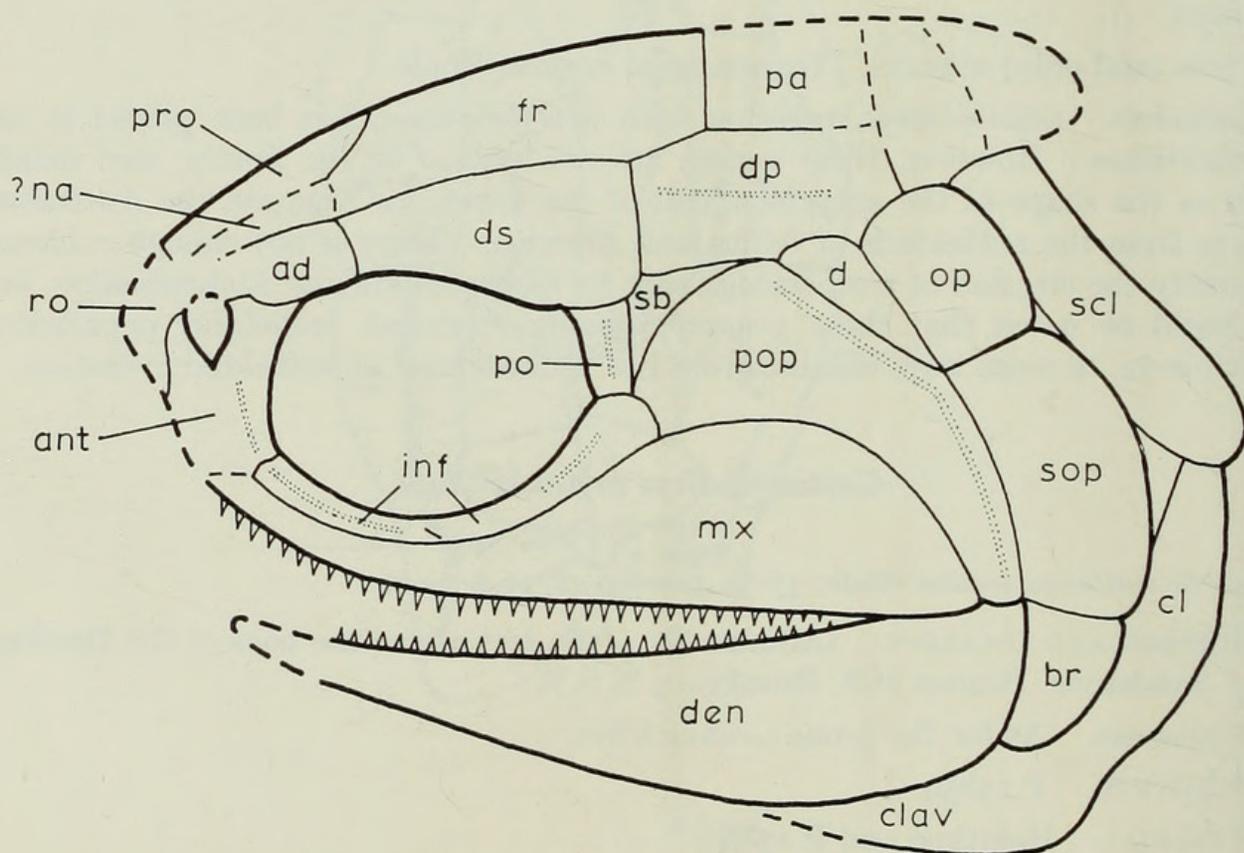


FIG. 23. *Geitonichthys ornatus* Wade. Restoration of skull and pectoral girdle, $\times 5$ approx.

Few teeth are preserved, but those present are pointed and 0.5 mm high (P.15859). In specimen P.15880 (Fig. 24) numerous palatine teeth 0.1 mm in diameter are visible in cross section near the ventral edge of the maxilla.

A curved bone lies anterior to the frontal. Its anterior extent is seen in P.15859 where it is disarticulated from whatever element lay further anteriorly. It bears a ridge which runs antero-ventrally towards the nostril (P.15880, Fig. 24), but whether this is associated with a sensory canal is not clear. The most likely interpretation of this region is that this is a postrostral and that it has been displaced ventrally, thus obscuring a narrow nasal. Anterior to the dermosphenotic, and bordering the orbit between the dermosphenotic and the antorbital, is an adnasal. Its anterior extent is not known. Its ventral margin bears a low ridge which follows the outline of the bone and curves dorsally for a short distance between the orbit and the nostril. If the anterior edge of the adnasal follows this ridge dorsally, the adnasal does not reach the nostril border. This restoration would imply that the nasal ran behind the nostril to meet the dorsal edge of the antorbital. An alternative restoration can be made in which the adnasal extends antero-ventrally to the posterior edge of the nostril. Comparison with *Molybdichthys* and Upper Triassic redfieldiids from N. America suggests that the latter interpretation is more likely to be correct.

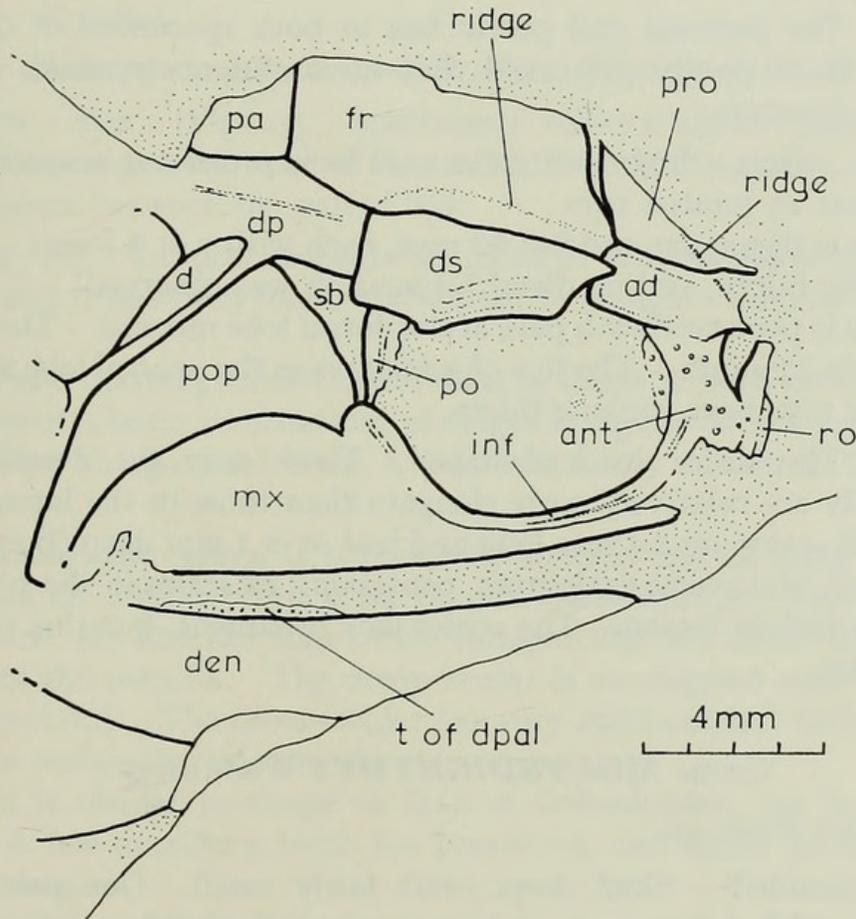


FIG. 24. *Geitonichthys ornatus* Wade. P.15880: right side.

The nostril is an inverted drop shape. The antorbital is wide and bears numerous tooth-like denticles. The snout tip is missing and in consequence the exact anterior extent of the maxilla is not known; also it is not known if a premaxilla was present. There is a ridge running from the anterior edge of the nostril ventrally, and this may mark the anterior end of the antorbital, but there is no suture visible. There was presumably a rostral on the snout tip, and its presence is suggested by a few traces of tubercles in that area (Fig. 24), but its extent, and thus the profile of the snout, is unknown.

Lower jaw. The dentary bears an ornament of fine elongate ridges. Teeth on the lower jaw are not clearly preserved.

Sensory canal system. The infraorbital sensory canal is clearly seen on the dermopterotic (P.15880, Fig. 24) but its anterior extension on the dermosphenotic, figured by Wade (1935 : text-fig. 18), cannot be traced. As mentioned above, in specimen P.15880 the dermosphenotic has been displaced ventrally, but the probable original position of its dorsal edge is represented by a shallow ridge running along the ventral edge of the frontal. In Wade's figure this ridge has been misinterpreted as a sensory canal. There are no clear traces of the supraorbital sensory canal.

Pectoral girdle. The bones of the pectoral girdle all bear an ornament of well defined, elongate rugae. The supracleithrum extends to a point more than midway along the posterior edge of the subopercular. No postcleithrum is visible.

Paired fins. The pectoral and pelvic fins in both specimens of *G. ornatus* are either missing or so poorly preserved that no useful observations can be made regarding their structure.

Unpaired fins. Only a fragment of the anal fin is preserved in specimen P.15859. There are at least 15 jointed rays.

The dorsal fin is triangular and has 22 rays, each with 7 or 8 joints. The anterior rays bear fringing fulcra, and no distal bifurcation was observed.

The caudal fin is preserved with part of the dorsal lobe missing. There are at least 40 rays with up to 17 joints. The tips of some rays in the ventral lobe are bifurcated, and the anterior rays bear fringing fulcra.

Squamation. The scales are leaf-shaped. Those near the dorsal and ventral edges of the body are relatively more elongate than those in the lateral line region. The largest flank scales are 1.5 mm long and just over 1 mm deep (P.15859). There are about 50 body transverse scale rows, containing 22 scales in the pectoral region, and 19 in the dorsal fin region. The scales lack ornament, but this may be due to poor preservation.

Genus *MOLYBDICHTHYS* Wade 1935

1935 *Molybdichthys* Wade: 39.

DIAGNOSIS (emended). Skull deep, orbit fairly small. One pair of parietals, roughly square, and bearing a pair of sensory canals in the shape of an inverted 'v'. Dermopterotic moderately deep anteriorly, narrower posteriorly. Frontal long and

deep. Dermosphenotic deep, with ornament of ridges on its ventral edge. Nasal narrow and rectangular. Antorbital wide, bordering the postero-ventral edge of the nostril. Opercular longer than deep. Opercular series broad, orientated almost vertically. Preopercular with short contact with the dermopterotic. Maxilla deeper than in *Geitonichthys* posteriorly. Single large suborbital. Postorbital region wide.

Elements of pectoral girdle extremely broad. Fin-rays bifurcated and with many joints. Dorsal and anal fins opposite one another and posterior in position.

TYPE (and only) SPECIES. *Molybdichthys junior* Wade.

REMARKS. *Molybdichthys* is very similar to *Geitonichthys*, and differences can be related mainly to the presence of a more upright suspensorium.

Molybdichthys junior Wade

(Figs 25-27)

1935 *Molybdichthys junior* Wade: 40-42, text-fig. 19, pl. 7, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Molybdichthys*.

HOLOTYPE. P.16204.

MATERIAL. Holotype and P.16207-8, P.16822, P.24695-6, U.S.G.D. 43, 146, 216.

DESCRIPTION. *Size*. (Fig. 25). Specimen P.16822 is almost complete; its length from snout tip to the posterior end of the caudal fin is about 145 mm. The maximum body depth occurs between the paired fins.

Skull. (Fig. 26). In most respects the skull of *Molybdichthys* resembles that of *Geitonichthys* and it has been found convenient to compare the two in the following description.

The frontal and dermosphenotic are similar in shape in both genera; also, in both the dermosphenotic bears an ornament of ridges along the dorsal border of the orbit. In *Molybdichthys* the parietal bears a pair of sensory canals in the shape of an inverted 'v'.

In *Molybdichthys* the opercular is relatively shorter, and all three elements of the opercular series are considerably wider than in *Geitonichthys*. The opercular series is nearer vertical; the anterior edge of the subopercular lies at 80° to the level of the ventral edge of the maxilla. The preopercular is overlapped anteriorly by a large triangular suborbital. The preopercular has very short contact with the dermopterotic. A single wedge-shaped dermohyal is present.

The maxilla is similar in shape to that of *Geitonichthys*, but is slightly deeper posteriorly. A few maxillary teeth are preserved, and about 50 are calculated to have been present.

The posterior edge of the orbit is bordered by a postorbital element which is somewhat wider than that of *Geitonichthys*. The anterior edge of the orbit is bordered

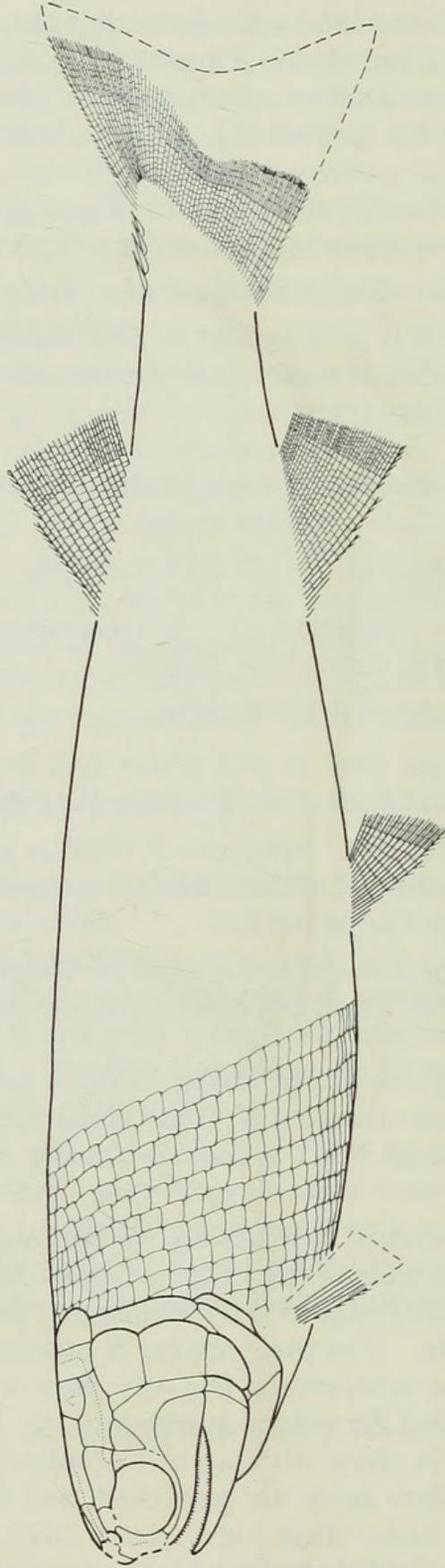


FIG. 25. *Molybdichthys junior* Wade. Restoration, $\times 1$ approx.
Posterior scales omitted.

by an antorbital which bears tooth-like denticles. Its ventral edge is not completely clear so that it is not possible to determine the exact relationship between the antorbital and the maxilla. The antero-dorsal edge of the antorbital borders part of the posterior edge of the nostril. Dorsal to the antorbital there are traces of an adnasal which also borders the nostril, and probably part of the orbit.

The rest of the snout has been restored from the crushed remains of specimens P.16822 and U.S.G.D. 43. In P.16822 (Fig. 27) there is a large postrostral which caps the snout. Lateral to this is a rectangular nasal which bears the anterior extension of the supraorbital sensory canal (only the right nasal is preserved in P.16822). The postrostral has been crushed ventrally onto the rest of the snout. The snout tip is completed by a rostral which is incompletely preserved; it bears tooth-like denticles.

Lower jaw. The dentary is deep posteriorly and tapers anteriorly. Some variation in the maximum depth of the dentary was observed in several specimens of *M. junior* but as no other details of the skull could be observed in these, it could not be definitely established whether this variation represented distinction at the specific

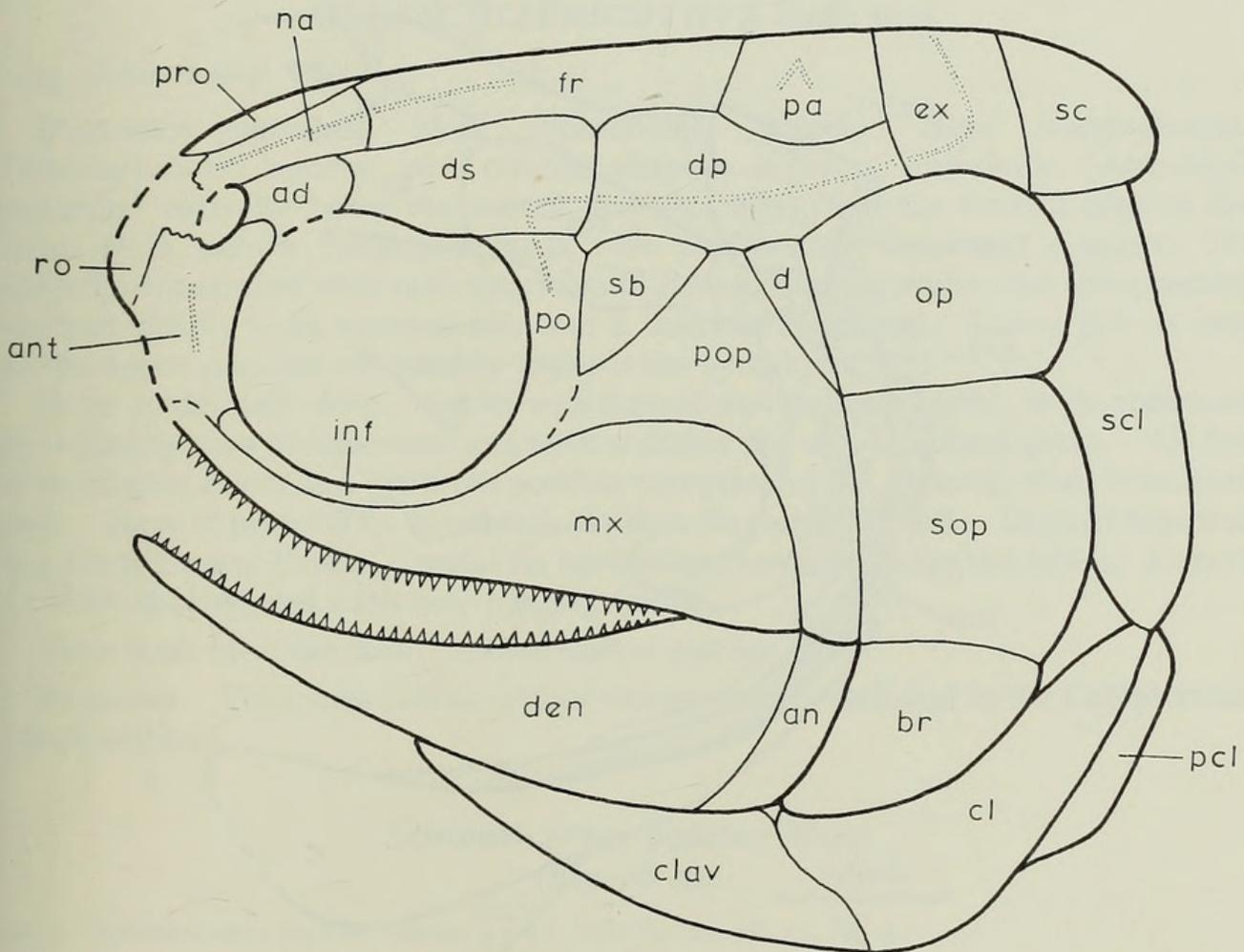


FIG. 26. *Molybdichthys junior* Wade. Restoration of skull and pectoral girdle, $\times 4.5$ approx.

level. Provisionally therefore, all the known specimens are retained in a single species.

The dentary bears an ornament of elongate ridges. About 50 conical teeth are calculated to have been present.

Pectoral girdle. The supracleithrum extends to a point two-thirds of the way along the posterior edge of the subopercular. It bears an ornament of parallel ridges, as does the cleithrum. The cleithrum and clavicle are broad and the latter extends at least halfway along the ventral edge of the lower jaw. An elongate, ornamented postcleithrum is present.

Paired fins. A fragment of the pectoral fin is preserved in specimen U.S.G.D. 216. Little can be determined except that at least 6 rays are present. They appear to be unjointed, fringing fulcra are present and there is distal bifurcation of at least one ray.

The pelvic fin has at least 14 stout rays, with 6-7 joints. The anterior rays bear fringing fulcra and there is distal bifurcation.

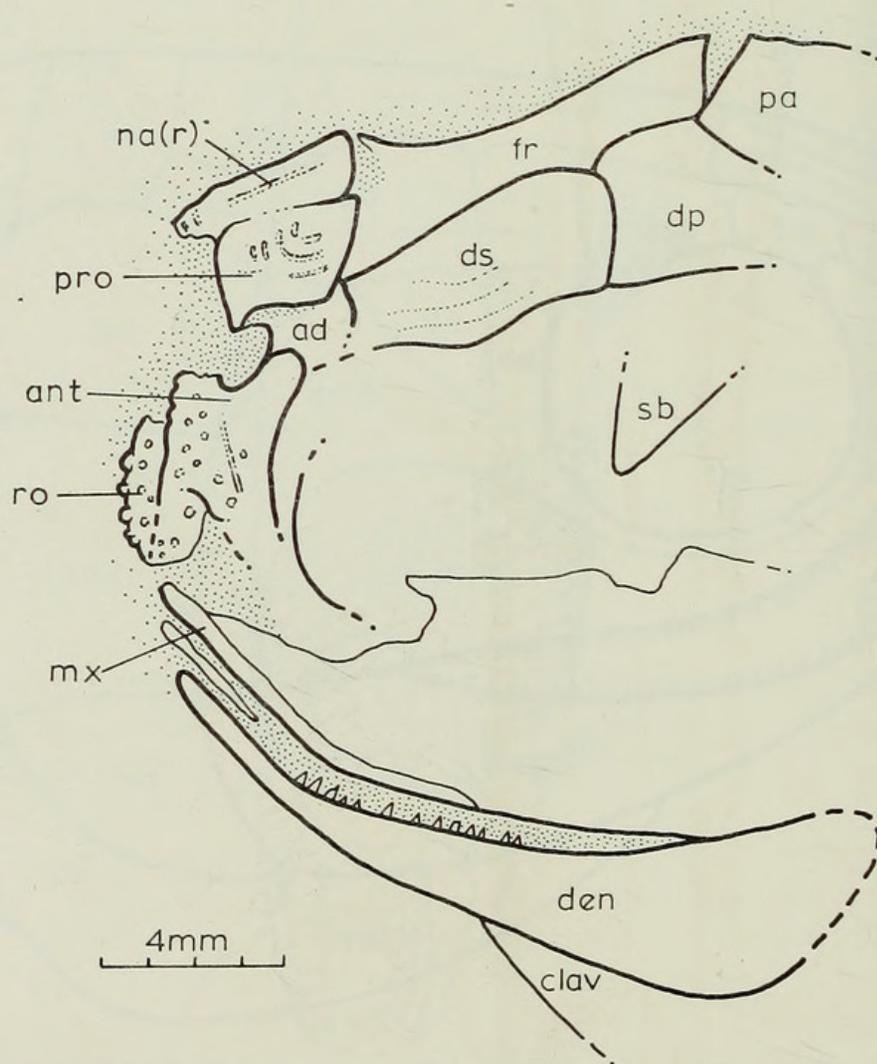


FIG. 27. *Molybdichthys junior* Wade. P.16822: left side unless otherwise indicated.

Unpaired fins. All the unpaired fin-rays bifurcate distally and the leading rays have fringing fulcra. The anal fin has 30 rays, the longest of which have 20 joints.

The dorsal fin lies just anterior to the level of the anal fin. There are 17 rays which have up to 15 joints.

The distal part of the ventral lobe of the caudal fin is missing. There are 26 rays in both the dorsal and ventral lobes, with at least 19 joints. In the dorsal lobe the rays bifurcate first at the 13th joint and again at about the 19th joint.

Squamation. The scales are very variable in shape. Anteriorly they are rhomboidal, up to 2.8 mm long and 3.5 mm deep in the lateral line region; towards the dorsal and ventral margins the scales are less than 1 mm deep while remaining up to 2 mm long. Posteriorly the scales are leaf-shaped and are 2 mm long and 1.5 mm deep. No ornament is preserved. There are 44 body transverse scale rows which contain up to 20 scales.

Family **SCHIZURICHTHYIDAE** nov.

DIAGNOSIS. As for the genus *Schizurichthys*.

Genus **SCHIZURICHTHYS** Wade 1935

1935 *Schizurichthys* Wade: 44.

DIAGNOSIS (emended). Skull incompletely known. Head wedge-shaped. Dermosphenotic narrow and crescent-shaped, tapering anteriorly. Antorbital expanded ventrally below the nostril, but separated from the ventral edge of the snout by a narrow toothed element. No postrostral. Opercular elements 'D'-shaped, ornamented with radiating rows of tubercles. Opercular and subopercular inclined steeply. An antopercular and a dermohyal present. Lower jaw as long as the upper jaw, curved dorsally towards the symphysis.

Body moderately deep. Scales equidimensional to rectangular, with ornament of radiating rows of tubercles, and with a dorsal peg and a ventral notch. All fins with fringing fulcra and (with the possible exception of the pectoral) with bifurcated rays. Rays of pectoral fin unjointed, of pelvic fin partly jointed. Rays of unpaired fins jointed many times. Caudal fin hemiheterocercal, with epaxial lobe of six rays of which the first and sixth bear fringing fulcra.

TYPE (and only) SPECIES. *Schizurichthys pulcher* Wade.

REMARKS. The genus *Schizurichthys* was previously included in the Catopteridae (Redfieldiidae).

Schizurichthys pulcher Wade

(Figs 28-30)

1935 *Schizurichthys pulcher* Wade: 44-46, text-fig. 21, pl. 10, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Schizurichthys*.

HOLOTYPE. P.15892.

MATERIAL. Holotype, P.15891 and U.S.G.D. 305.

DESCRIPTION. *Size*. (Fig. 28). The best preserved specimen of *S. pulcher* is U.S.G.D. 305. Its total length from snout tip to the posterior end of the caudal fin is about 235 mm. The body is fairly deep, its greatest depth occurring between the paired fins.

Skull. (Fig. 28). In lateral view the skull is wedge-shaped, tapering anteriorly to a blunt snout. The outlines of the dorsal bones immediately anterior to the suprascapular cannot be distinguished. A narrow frontal is incompletely preserved.

The opercular and subopercular bones are 'D'-shaped. A single branchiostegal is present (P.15891) and has similar dimensions to the opercular. The opercular series is moderately oblique; the anterior margin of the subopercular lies at 65° to the ventral margin of the maxilla. All the opercular bones are ornamented with lines of rugae which radiate from a point close to the antero-dorsal corner of each element. The presence of antopercular and dermohyal elements is inferred from two indentations in the ventral margin of the dermopterotic. The cheek region is poorly preserved. The maxilla is similar in shape to that of *B. gracilis*, but its narrow anterior portion is badly crushed, and it cannot be determined whether it borders the ventral margin of the orbit or if it is separated from the latter by infra-orbital elements. The maxilla bears about 50 conical teeth, which are up to 1.5 mm high.

The postero-dorsal edge of the orbit is bordered by a curved dermosphenotic which appears to taper to a point anteriorly (U.S.G.D. 305, Fig. 29). Its posterior edge is not preserved. The antero-dorsal edge of the orbit appears to be bordered by a narrow diamond-shaped adnasal, but this too, is poorly preserved. The nostril, visible as a notch in the antorbital, is large; dorsally it is bordered by a narrow nasal which bears traces of part of the supraorbital sensory canal (U.S.G.D. 305, Fig. 29). Ventral to the nostril the antorbital is deep, and further ventrally a tooth-bearing element extends to the snout tip, but it cannot be determined whether this is a premaxilla or the anterior part of the maxilla.

Pectoral girdle. The supracleithrum extends ventrally to a point halfway down the posterior edge of the subopercular. The dorsal part of the cleithrum is slender and lanceolate. Both bones are ornamented with numerous ridges which run parallel to the edges of the bones. The suture between the cleithrum and clavicle is not visible.

Paired fins. The pectoral fin has at least 12 stout rays (P.15891). Joints are not visible and distal bifurcation is not preserved. The anterior ray bears numerous fringing fulcra. The pelvic fin has 25 stout rays which bifurcate about midway along their length. Up to 3 joints are visible on the proximal parts of the anterior rays. Fringing fulcra are borne by the anterior rays.

Unpaired fins. All the rays of the unpaired fins are bifurcated, and all bear tiny tubercles on their proximal parts. The anal fin is large. There are at least 41 stout

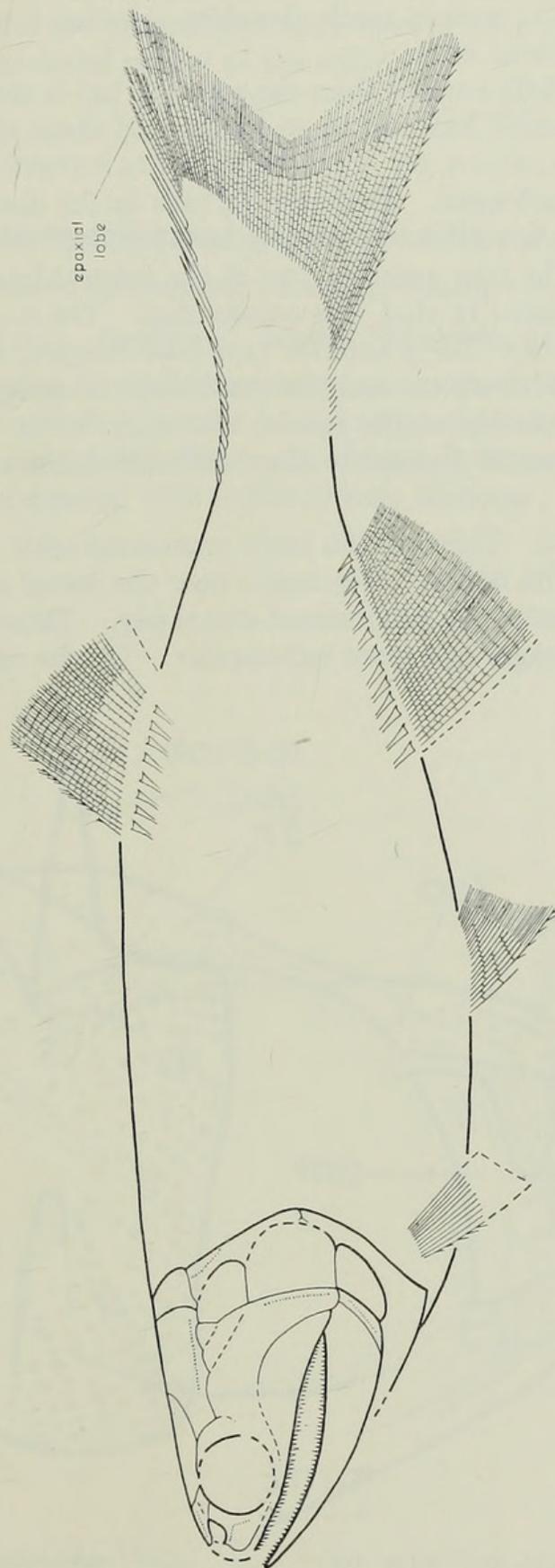


FIG. 28. *Schizurichthys pulcher* Wade. Restoration, $\times 0.75$ approx.

rays with up to 14 joints. The anterior rays are not preserved. The anal fin is supported by at least 14 radials (each therefore associated with three rays) which have wide, spatulate distal ends.

The dorsal fin is slightly smaller than the anal fin, but is similar in shape. There are at least 22 rays, which have up to 20 joints, and those along the anterior edge bear fringing fulcra.

The caudal fin is equilobate. There are 34 rays in the dorsal lobe and 35 in the ventral lobe. All the rays bifurcate distally for up to half their length, and have as many as 35 joints. The four anterior rays of the ventral lobe bear fringing fulcra. The dorsal lobe is unusual in that it is subdivided. The 6 anterior rays originate from an epaxial position. The 3 anterior rays bear fringing fulcra, the fourth (and possibly also the fifth) bifurcates and the sixth bears fringing fulcra. The seventh ray has its origin at the tip of the caudal lobe (i.e. lies in the position normally occupied by the first caudal fin-ray in other redfieldiiforms) and also bears fringing fulcra.

Squamation (Fig. 30). There are 60 body transverse scale rows, each containing 30 scales in the dorsal fin region. The scales near the dorsal and ventral margins of the body are subcircular with a pronounced dorsal peg. Those nearer the lateral line become progressively larger and more rectangular. On the ventral side of the inner

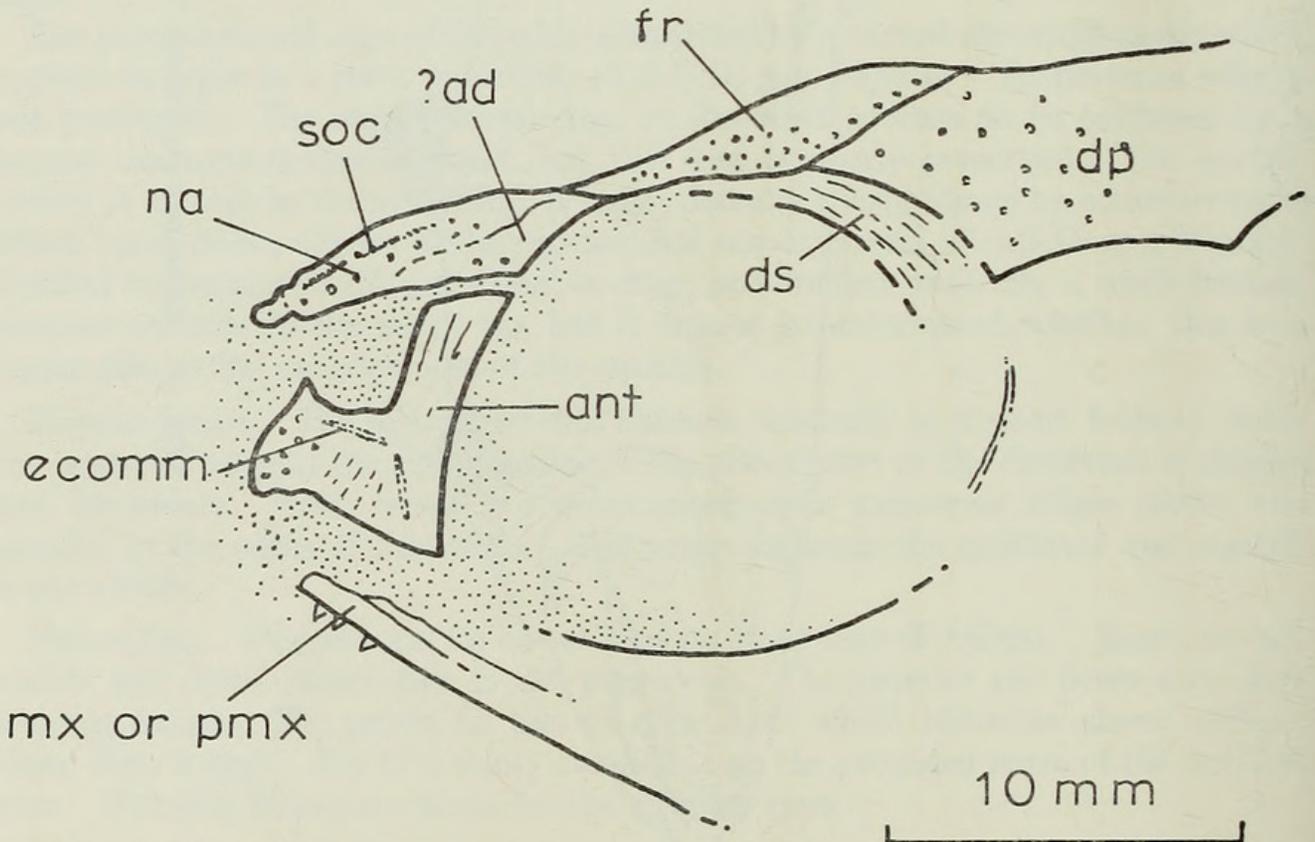


FIG. 29. *Schizurichthys pulcher* Wade. U.S.G.D. 305: left side.

surface of each scale there is a socket, into which the dorsal peg of the next ventral scale fits. All the scales are ornamented with rows of tubercles which radiate from a point near the antero-dorsal corner of the scale.

GENERA PROVISIONALLY ASCRIBED TO REDFIELDIIFORMES

Sakamenichthys germaini Lehman *et al.*

1959 *Sakamenichthys germaini* Lehman *et al.*: 179-184, text-figs 1-2, pls 1-2.

HORIZON AND LOCALITY. Scythian. Middle Sakamena group, Madagascar.

REMARKS. The reasons for including this genus in the order Redfieldiiformes are slight. The opercular series appears to consist of an opercular, a subopercular and a single branchiostegal element, but this is one of the only known features of *Sakamenichthys* which can be compared with redfieldiiform anatomy.

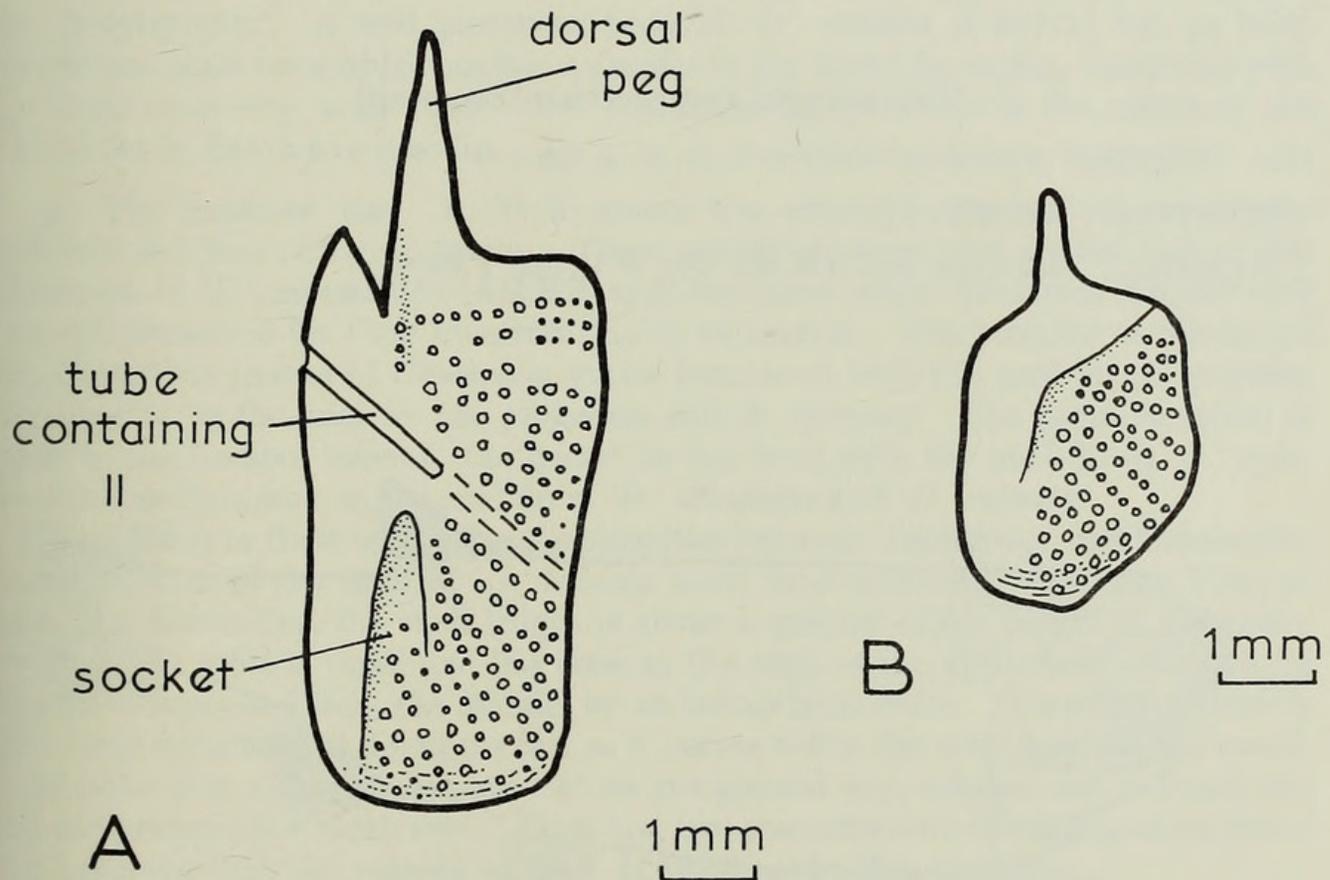


FIG. 30. *Schizurichthys pulcher* Wade. (A) P.15892: scale from anterior lateral line region, right side, internal surface. (B) P.15892: scale from ventral side of body, left side, external surface.

Sinkiangichthys longipectoralis Liu

1958 *Sinkiangichthys longipectoralis* Liu: 149-150, pl. 1.

HORIZON AND LOCALITY. Triassic. Chang-P'eng-Kon, Chitai, Sinkiang, China.

REMARKS. This genus is represented by a single specimen 98 mm long. It is poorly preserved, and the only characters noted by Liu which show that it could be a redfieldiiform are: eye forward in position; maxilla low anteriorly with a high postorbital part; heterocercal tail; no branchiostegal rays. With the exception of the last, which could be the result of poor preservation, all these characters could equally be found in other chondrosteian orders.

'Dictyopyge' robusta Woodward

(Fig. 31)

1890 *'Dictyopyge' robusta* Woodward: 20, pl. 3, figs 4-5

HOLOTYPE. AM.MF 170.

MATERIAL. Holotype and AM.MF 169, P.6271a and b, and P.18110.

'Dictyopyge' symmetrica Woodward

1890 *'Dictyopyge' symmetrica* Woodward: 17, pl. 4, figs 5-6.

HOLOTYPE. AM.MF 173.

MATERIAL. Holotype and AM.MF 167, F.13394, P.6270.

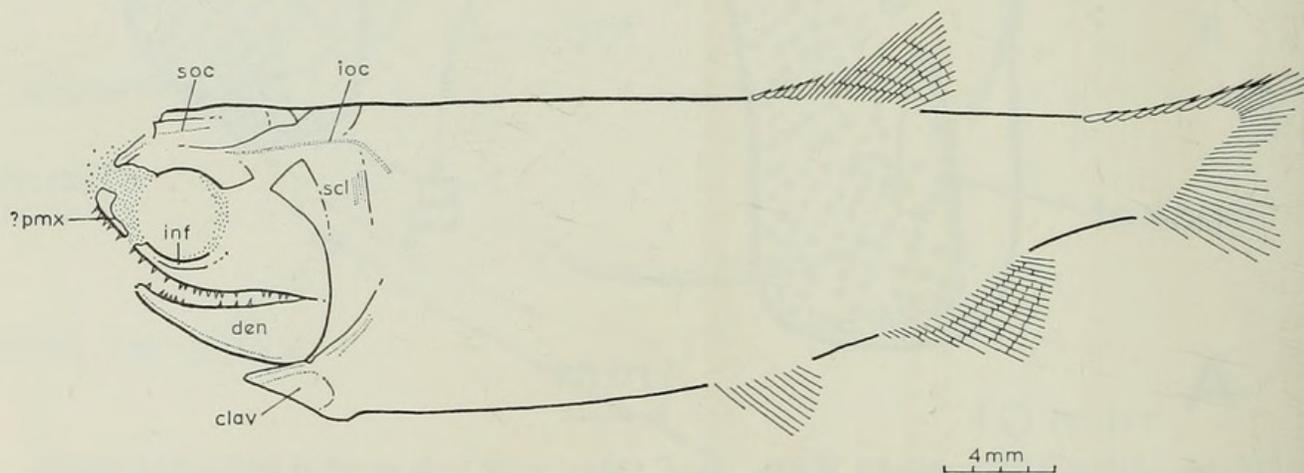


FIG. 31. *Dictyopyge robusta* Woodward. P.6271a: left side, scales omitted.

'*Dictyopyge*' *illustrans* Woodward

1890 '*Dictyopyge*' *illustrans* Woodward: 18, pl. 4, figs 7-9.

HOLOTYPE. In the collection of the Australian Museum, Sydney (but possibly lost. Pickett, pers. comm.).

MATERIAL. AM.MF 171, 172, F.13343, P.6269, P.18111 and P.33239.

HORIZON AND LOCALITY. Of all three species; Scythian or Anisian. Band of shale 6 feet thick at the top of the Narrabeen Shales, Gosford, N.S.W.

REMARKS. All the specimens of '*Dictyopyge*' from Gosford are poorly preserved and little can be added to Woodward's description of the three species (1890; 16-22). In particular, the skulls have been badly crushed and any comparison with any other fish, including the type species of the genus *Dictyopyge*, *D. macrura*, must be based almost entirely on features such as body form and the nature of the scales and fins.

Some characters of the Gosford 'dictyopygids' are seen also in the genus *Brookvalia*. These are:

1. Body shape. In both genera the body is fusiform. Most species are slender, with one exception, '*D.*' *robustus*.

2. Scales. Leaf-shaped as in *Brookvalia*, though there appear to be fewer scales in 'dictyopygids'. A well preserved body of '*D.*' *robusta* (P.6271a) has 33 body transverse scale rows which contain 13 scales in the dorsal fin region, compared with 50 body transverse scale rows which contain about 30 scales in the region of the dorsal fin in *Brookvalia gracilis*.

3. The unpaired fins. In both genera the unpaired fin-rays are repeatedly jointed and bear fringing fulcra. There are bifurcating rays in the tail of the holotype of '*D.*' *symmetrica* (AM.MF 173) but most other specimens are not well enough preserved for their identification to be certain. The position of the dorsal fin in various species of *Brookvalia* varies from level with the anal fin (*B. gracilis*) to anterior to the anal fin (*B. propennis* and *B. spinosa*). The same variation is seen in the Gosford species; the dorsal fin lies level with the anal fin in '*D.*' *symmetrica*, and anterior to the anal fin in '*D.*' *illustrans* and '*D.*' *robusta*.

In addition to these very general similarities between '*Dictyopyge*' and *Brookvalia*, some features of the skull of '*D.*' *robusta* merit brief mention. Specimen P.6271a (Fig. 31) shows that the skull length is about a quarter of the length of the entire body. The orbit is small and lies close to the edge of the upper jaw, although its border is separated from the maxilla by an infraorbital series. A notable feature is the steep upturning of the upper jaw as it curves below the orbit towards the snout. The lower jaw, although damaged at its symphysial end, appears not to reach the tip of the upper jaw tooth row. These last two characters are the strongest evidence for believing that '*D.*' *robusta*, at least, is allied to the Brookvaliidae.

In conclusion, therefore, there is some slight evidence to support Wade's opinion (1940 : 208) that the Gosford 'dictyopygids' are related to *Brookvalia* or a similar genus.

Pseudobeaconia bracaccinii Bordas

1944 *Pseudobeaconia bracaccinii* Bordas: 454-455, pl. 1.

Pseudobeaconia elegans Bordas

1944 *Pseudobeaconia elegans* Bordas: 456, pl. 1.

HORIZON AND LOCALITY. Of both species, Triassic bituminous rocks, Santa Clara, Mendoza and San Juan provinces, Argentina.

REMARKS. *Pseudobeaconia* is now known to be an advanced perleidiform genus (Hutchinson, in press).

Rushlandia gilli Bock

1959 *Rushlandia gilli* Bock: 113-120, text-figs 49-51, pls 20-21.

HORIZON AND LOCALITY. Carnian or Norian. Lockatong formation (Newark), Fairview Village and Rushland, Pennsylvania, U.S.A.

REMARKS. The general body shape, and the structure and position of the fins of *Rushlandia* do not exclude this genus from membership of the Redfieldiiformes, nor do they exclude it from possible membership of several other sub-holostean or holostean groups. The shape of the maxilla in *Rushlandia* is reminiscent of that seen in redfieldiiforms.

AN UN-NAMED SPECIMEN IN THE COLLECTION OF THE INDIAN STATISTICAL UNIT
CALCUTTA

An un-named sub-holostean has been reported from the Maleri formation of India (Jain, Robinson & Chowdhury, 1964 : 118) which is possibly a redfieldiiform. This species has not yet been described. There is one fragment showing part of the posterior region of the head. This shows an opercular, a 'considerably larger' subopercular and part of the upper jaw (Jain, pers. comm.).

Order PERLEIDIFORMES

DIAGNOSIS. See Berg 1958 : 131-132.

Family COLOBODONTIDAE Stensiö 1916

DIAGNOSIS. See Schaeffer 1955 : 19, except than an antorbital is present.

Genus *MEIDIICHTHYS* Brough 1931

1931 *Meidiichthys* Brough: 261.

DIAGNOSIS. See Brough (1931 : 261-262). Two slight amendments can be made to Brough's diagnosis. Firstly the opercular is shorter than the subopercular and has a convex ventral border, and the two bones consequently do not form 'one continuous quadrangular plate'. Secondly, the suture between the maxilla and preopercular is curved, hence the maxilla does not in effect come to an 'apex situated just behind the orbit'.

TYPE (and only) SPECIES. *Pholidophorus browni* Broom.

REMARKS. There is little doubt that *Meidiichthys* is closely related to forms such as *Perleidus* (Stensio 1932; Lehman 1952). Specializations of the genus include the presence of a forwardly directed suspensorium and a large flat post-rostral (Brough 1931 : 262). Also the small number of branchiostegals in *Meidiichthys* should be noted here. One feature, however, suggests that the genus is close to the basal stock of all perleidids; this is the presence of a clavicle (G.N. 312, Fig. 33). In many perleidids the clavicle is small or absent.

***Meidiichthys browni* (Broom)**
(Figs 32-33)

1909 *Pholidophorus browni* Broom: 267-268, pl. 13, fig. 10

1931 *Meidiichthys browni* (Broom) Brough: 262-266, text-figs 11-12, pl. 4, fig. 1.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As for the genus *Meidiichthys*.

HOLOTYPE. S.A.M. 6030.

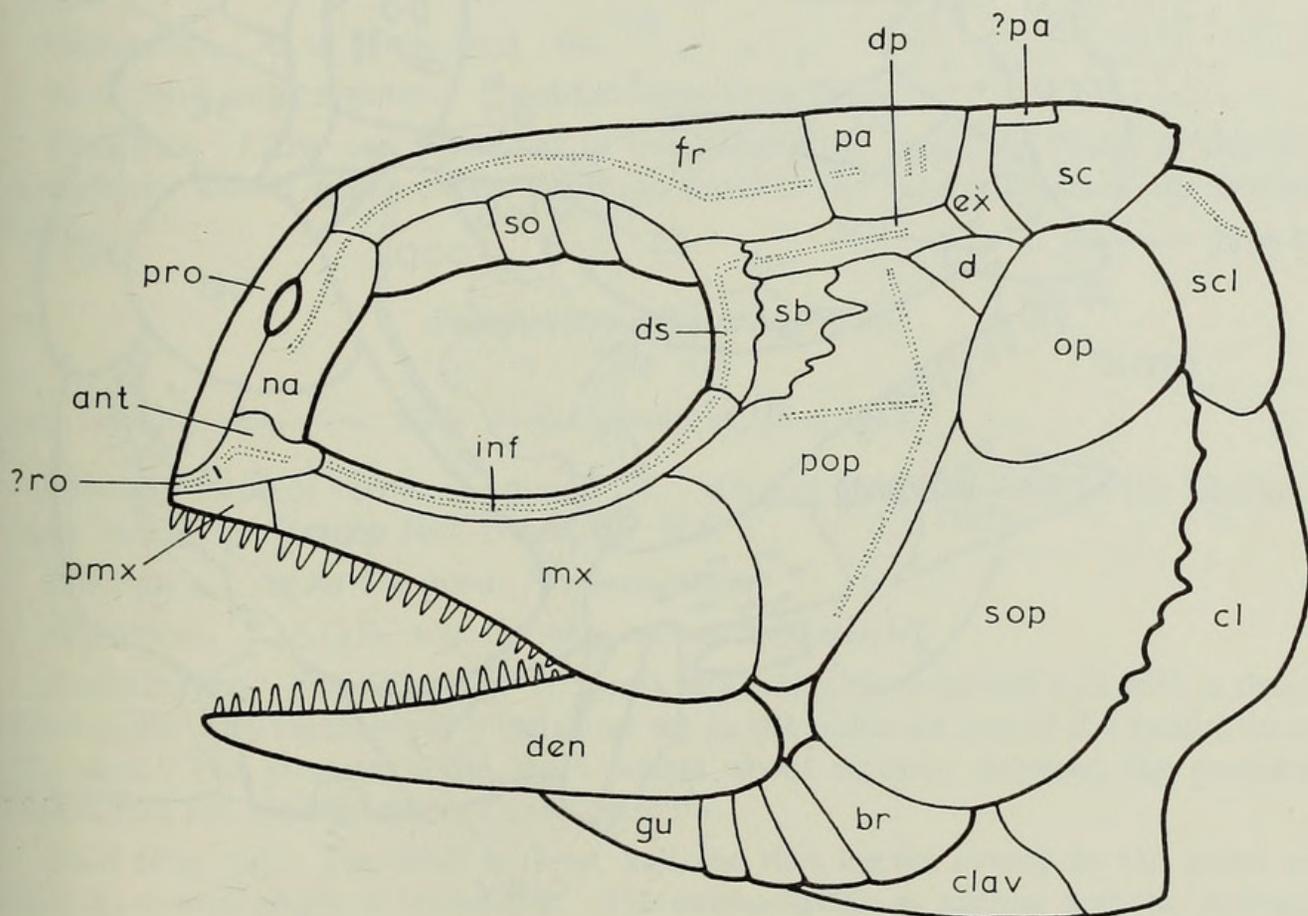


FIG. 32. *Meidiichthys browni* (Broom). Restoration of skull and pectoral girdle, $\times 5$ approx.

MATERIAL. P.16074, P.16075, G.N. 304 and counterpart 318, 305, 311-314, 317, 348 and counterpart 355.

DESCRIPTION. *M. browni* has been described by Brough (1931 : 262-266). A new restoration of the skull is given here (Fig. 32) to include additions and amendments.

The opercular has a curved ventral border (G.N. 312, Fig. 33); the posterior border of the subopercular is pectinated and its surface ornamented with small spines. The preopercular has a more strongly concave antero-ventral border than is shown in Brough's figure (1931 : text-fig. 11). In addition to the usual preopercular sensory canal, there is a long horizontal branch extending across that bone (P.16075). The single triangular suborbital and the rectangular dermosphenotic have pectinated posterior borders. The dorsal side of the orbit is bordered by four supraorbital elements (G.N. 304). These are deep and appear considerably foreshortened in the restoration.

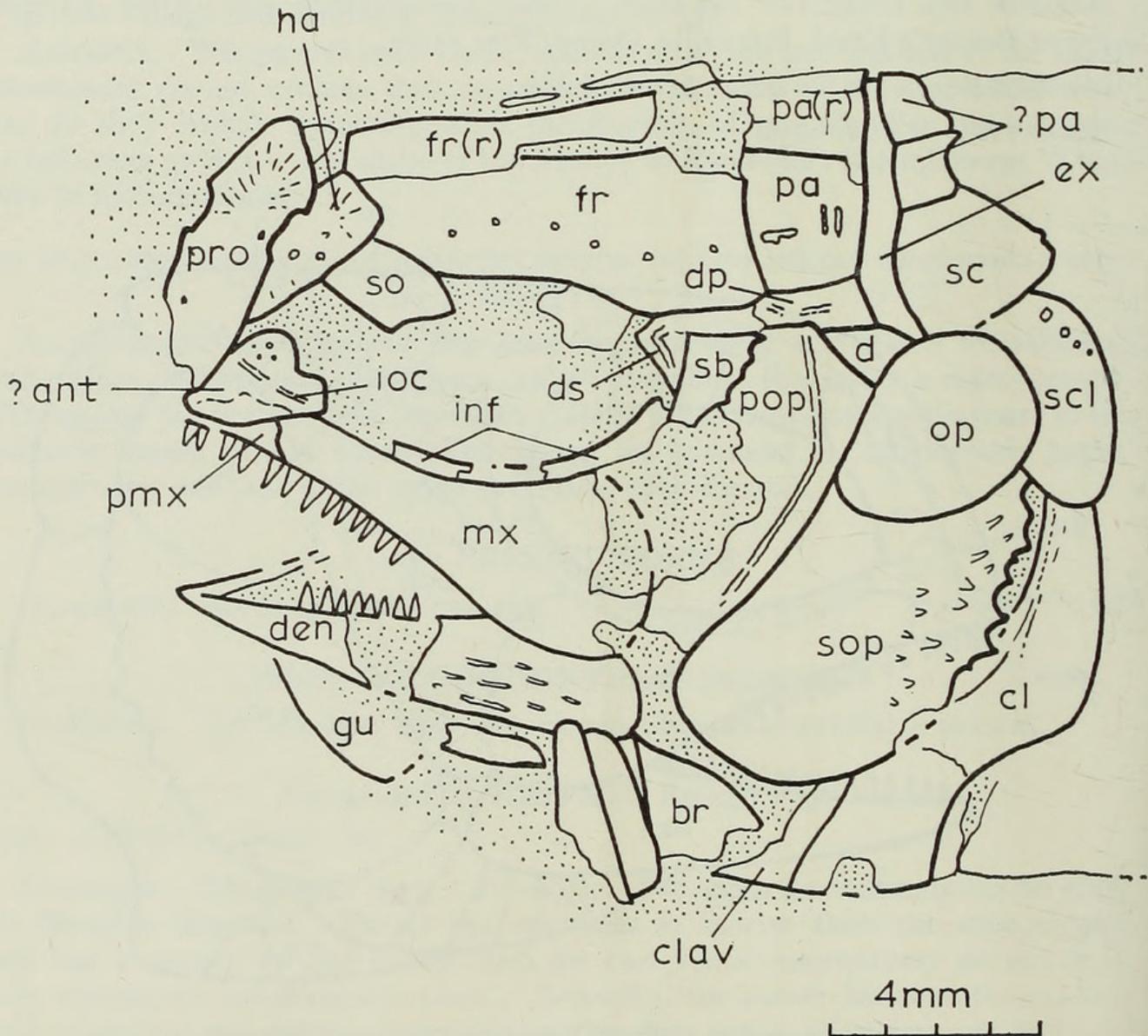


FIG. 33. *Meidiichthys browni* (Broom). G.N. 312: left side unless otherwise indicated.

The nasals are long and separated by a large postrostral (G.N. 312, Fig. 33). The nostrils lie between the anterior edges of the nasals and the lateral edges of the postrostral. The ventral part of the snout consists of an element which bears part of the infraorbital sensory canal (G.N. 312, Fig. 33) and the ethmoid commissure (P.16075). There is some indication in specimen P.16075 that the anterior part of this element is a separate bone, but this cannot be confirmed in other specimens. It is therefore uncertain whether the ventral part of the snout consists of a rostrantorbital or of separate rostral and antorbital bones.

The anterior end of the upper jaw is composed of small wedge-shaped premaxillae. There are four branchiostegal rays.

The suprascapulars are the normal 'D' shape, but do not meet in the midline and are separated by a pair of small square elements (G.N. 312, Fig. 33). The identity of these elements is uncertain, although they are similar in shape to the posterior parietals seen in some specimens of *Perleidus piveteaui* (Lehman 1952 : text-fig. 88B). The suture between the cleithrum and clavicle is seen in specimen G.N. 312 (Fig. 33).

Genus *PROCHEIRICHTHYS* Wade 1935

1935 *Procheirichthys* Wade: 62.

DIAGNOSIS. As in Wade 1935 : 62.

TYPE (and only) SPECIES. *Procheirichthys ferox* Wade.

REMARKS. Little can be added to the description made by Wade of this incompletely known genus except that the nasal is not separated from the orbital border.

Procheirichthys ferox Wade

(Fig. 34)

1935 *Procheirichthys ferox* Wade: 62-64, text-fig. 31, pl. 9, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Procheirichthys*.

HOLOTYPE. U.S.G.D. 209, the only known specimen.

DESCRIPTION. *Size* (Fig. 34). *P. ferox* is a fairly deep-bodied fish with a deep, short skull. Its total length from snout tip to the posterior end of the caudal fin is 163 mm. The greatest body depth occurs about midway between the pectoral region and the anterior edge of the dorsal fin.

Skull (Fig. 34). The skull is deep, and the roof curves evenly to the snout so that its overall shape is triangular. The extrascapular is narrow and the parietal rectangular, being deeper than long. The frontal is extremely deep and fairly short. Neither the suture between the dermopterotic and the extrascapular, nor that between the anterior end of the dermopterotic and the dermosphenotic are

preserved. The suture between the opercular and subopercular is indistinct, but appears to divide the opercular plate so that the subopercular is almost twice as deep as the opercular. The angle between the anterior margin of the opercular series and the ventral margin of the maxilla is 72° , but in fact the opercular series is orientated almost vertically and the ventral edge of the maxilla slopes anterodorsally towards the snout tip. The preopercular appears to be broad, and dermohyal, suborbital and infraorbital elements are either absent or not preserved. The dorsal side of the orbit is bordered by three small supraorbitals.

The snout is not complete, but appears to be similar to that of *Mendocinia* (Schaeffer 1955). The nasal is rectangular and is not separated from the anterior border of the orbit as suggested by Wade (1935 : text-fig. 31). There is a fragment of bone lying anterior to the dorsal end of the nasal which is probably part of the post-rostral. The ventral part of the snout is divided by a vertical suture which runs from the ventral side of the nasal to the margin of the upper jaw. Crossing this suture there is a short sensory canal. Although no more of the snout is preserved, it is probable that there were antorbital and rostral elements lying ventral to the nasal, separated by this vertical suture. Further ventrally, the vertical suture probably separates premaxilla from maxilla. Thus the known facts are quite consistent with a snout pattern similar to that of *Mendocinia*.

The lower jaw is extremely deep, its length being only 2.5 times its maximum depth. The teeth are large, conical and pointed.

Pectoral girdle. The dorsal part of the pectoral girdle is not well preserved but there are indications that the suprascapular elements are well separated and do not meet in the midline. The cleithrum is ornamented with fine parallel ridges.

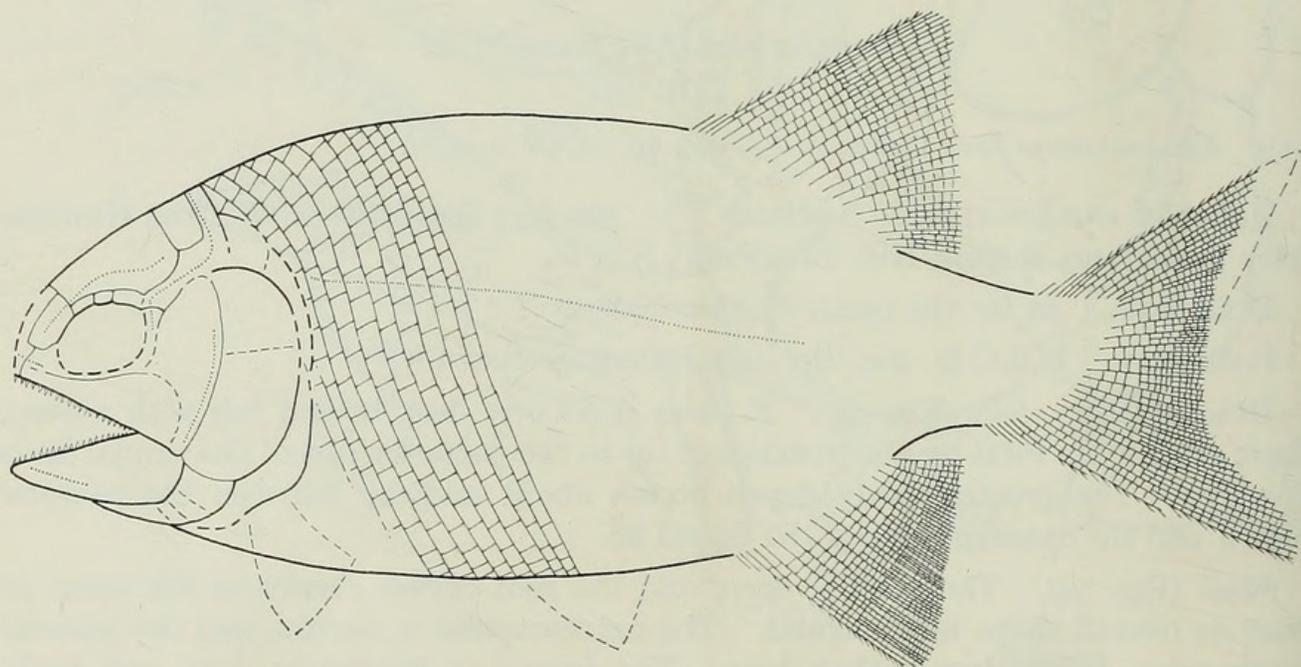


FIG. 34. *Procheirichthys ferox* Wade. Restoration, $\times 0.8$ approx.
Posterior scales omitted.

Paired fins. The paired fins are not preserved in *Procheirichthys*.

Unpaired fins. All the unpaired fin-rays bifurcate distally, and the leading rays bear fringing fulcra. The anal fin has 18 rays which bifurcate twice, and there are up to 23 joints.

The dorsal fin contains 20 rays which bifurcate once. The anterior rays bear fringing fulcra and there are up to 18 joints.

The body lobe of the tail is very abbreviated. The caudal fin has 34 rays, 18 in each lobe. Ten rays in the dorsal lobe are epaxial in position. Most bifurcate twice and there are up to 30 joints.

Squamation. The scales are smooth and rhombic. There are 42 transverse body scale rows, not including any in the region immediately posterior to the cleithrum, where none are preserved.

Genus *MANLIETTA* Wade 1935

1935 *Manlietta* Wade: 58.

DIAGNOSIS (emended). Skull short and deep, 25% of total body length with head. Skull bones smooth or ornamented with fine granular tubercles. Rostrum sloping as in *Mendocinia*. No postrostral. Nasals forming anterior border of orbit and meeting in the midline. Nostril at ventral border of nasal. Snout composed of rostral, paired antorbitals and probably premaxillae. Frontals three times as long as the square parietals. Dermopterotic narrow and elongate. Suspensorium steeply inclined. Wedge-shaped dermohyal present. Preopercular divided into two ossifications, lower element with infraorbital process. No suborbital. Opercular equal in size to subopercular. Three or four branchiostegals present. Gular almost as long as lower jaw. Mandible stout and tapering anteriorly. Teeth large and well separated.

Body deeply fusiform, with greatest depth immediately behind pectoral girdle. Paired fins poorly preserved but pectoral fin containing at least 8 rays, and pelvic fin at least 6 rays. Unpaired fins with fringing fulcra, bifurcating rays and basal fulcra. Anal and dorsal fins posterior in position, dorsal fin slightly in advance of anal. Anal fin with 9 long rays, dorsal fin with 17 rays. Caudal fin hemiheterocercal, slightly cleft, equilobate and with 17 rays. Scales smooth with straight posterior borders.

TYPE (and only) SPECIES. *Manlietta crassa* Wade.

REMARKS. *Manlietta* is extremely similar to *Mendocinia* from Argentina. Of the characters listed by Schaeffer (1955 : 4) in the generic diagnosis of *Mendocinia*, the following important similarities with *Manlietta* may be noted: rostrum sloping rather than blunt; nasal bones forming anterior border of orbit; paired dentigerous premaxillaries; dermopterotic narrow and elongated; preopercular with infraorbital process; teeth conical; dorsal fin remote, origin midway between origin of pelvic and anal fins; caudal fin hemiheterocercal, moderately cleft and equilobate; anterior scales thin, smooth with straight posterior border, decreasing in depth posteriorly. Many of these features are common to all perleidids but, overall, the

similarity between the two genera is impressive (cf. Fig. 35 and Schaeffer 1955 : text-fig. 1). The differences between the cheek regions of *Manlietta* and *Mendocinia* can be related to the fact that the suspensorium is more vertical in the latter. This difference is accompanied by a reduction in the width of the preopercular, and considerable reduction of the posterior part of the maxilla. Other changes can be seen in the anatomy of the fins. In *Manlietta* the unpaired fins bear fringing fulcra, but these are lost in *Mendocinia*; also, whereas in *Manlietta* the basal fulcra of the anal and dorsal fins do not exceed the length of the proximal lepidotrichia, in *Mendocinia* they extend almost to the distal ends of the anterior rays.

There are several reasons for supposing that, although closely related, *Manlietta* is not ancestral to *Mendocinia*. The preopercular of *Manlietta* is subdivided and there is no postorbital element, and the anal fin-rays are unusually long. More important is the anatomy of the snout. In *Manlietta* the postrostral has been lost and the nasals meet in the midline. In consequence the nostril cannot lie at the anterior margin of the nasal, and is situated at the ventral edge of the nasal. This condition is paralleled in *Birgeria* and *Haplolepis*, although in these forms the postrostral is still present, and reasons for migration of the nostril from the position more typical of lower actinopterygians are obscure.

***Manlietta crassa* Wade**

(Figs 35-37)

1935 *Manlietta crassa* Wade: 59-62, text-figs 29-30, pl. 9, fig. 1.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Manlietta*.

HOLOTYPE. U.S.G.D. 213.

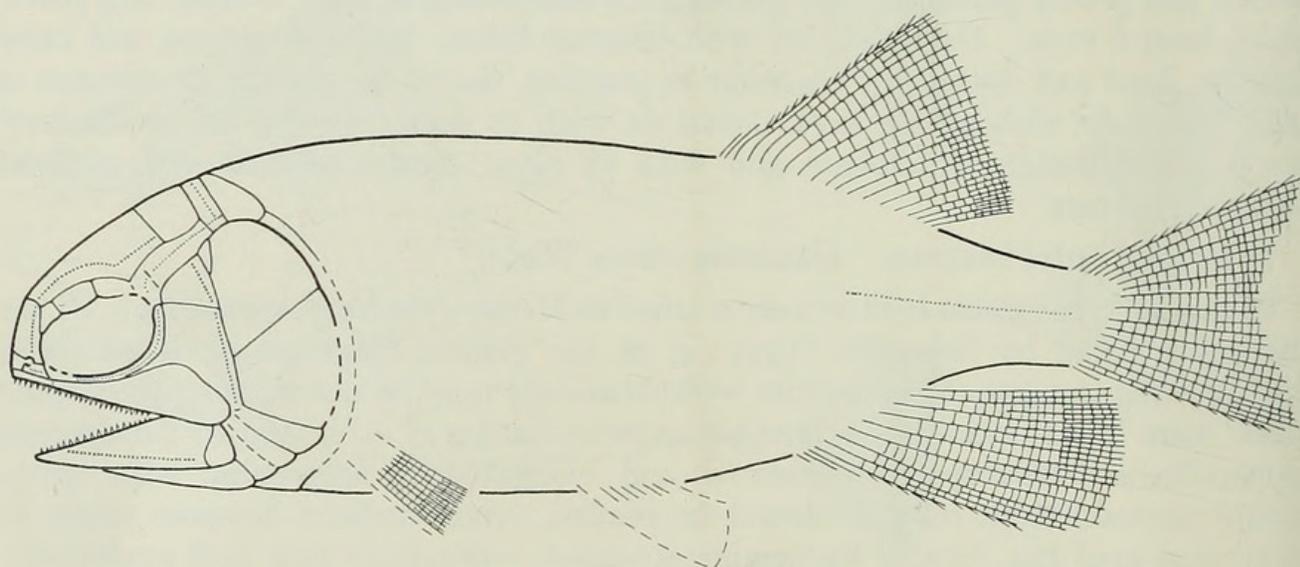


FIG. 35. *Manlietta crassa* Wade. Restoration, $\times 2$ approx. Scales omitted.

MATERIAL. Holotype and P.15881 and counterpart P.16825.

DESCRIPTION. *Size* (Fig. 35). The total length from snout tip to the posterior end of the caudal fin is 77 mm (P.15881). The greatest body depth occurs immediately behind the pectoral region.

Skull (Fig. 36). The skull is similar to that of *Mendocinia brevis* from the Triassic of Argentina (Schaeffer 1955 : text-fig. 4). The edge of the frontal which borders the dermopterotic is concave in *Manlietta* (U.S.G.D. 213, Fig. 37), whereas it is convex in *Mendocinia*. The supraorbital sensory canal closely follows the ventral edge of the frontal and is straight posteriorly and curved over the orbital region. The dermopterotic is shallow and rectangular, and does not extend dorsally between

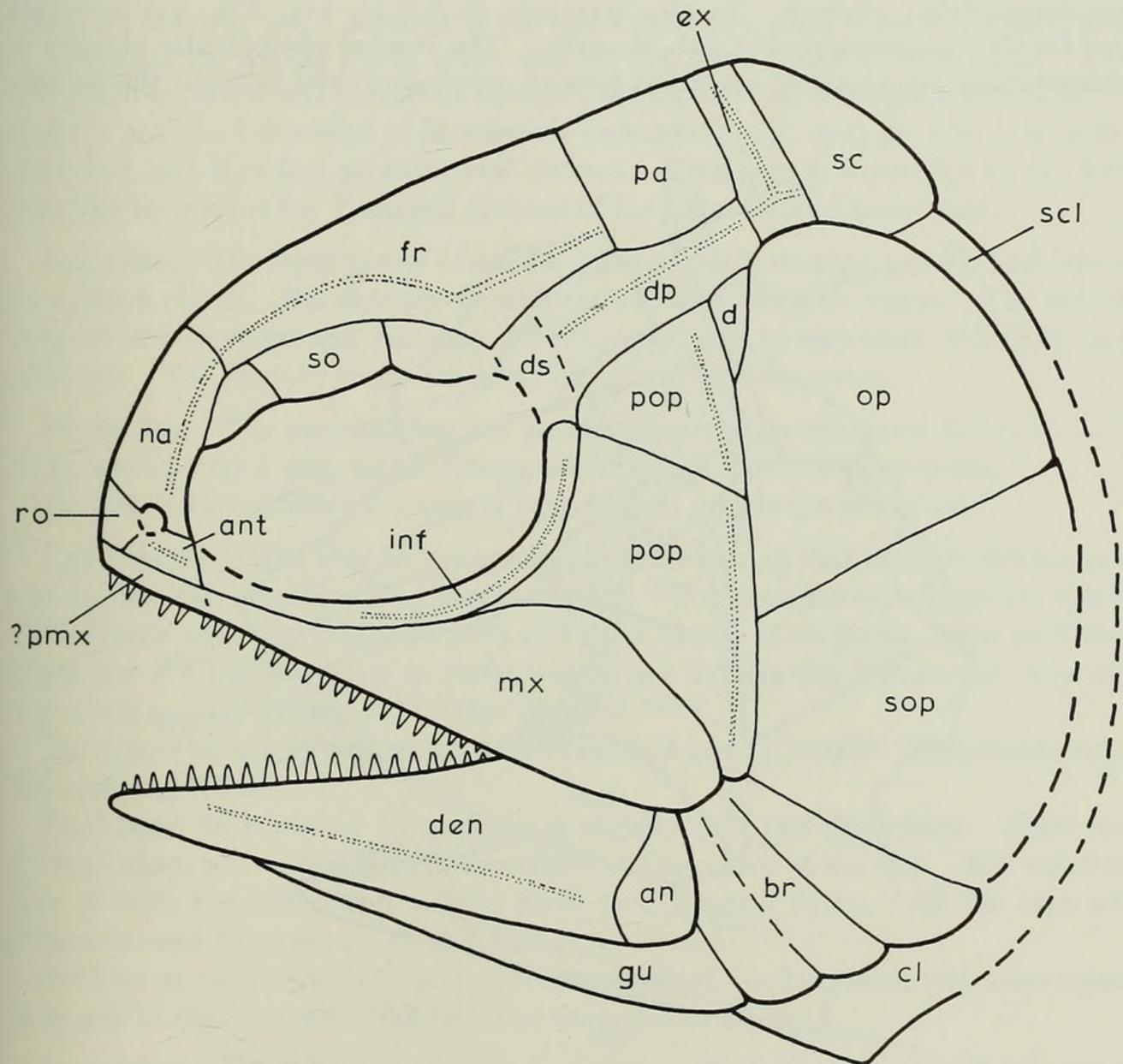


FIG. 36. *Manlietta crassa* Wade. Restoration of skull and pectoral girdle, $\times 7$ approx.

the frontal and parietal. There is no evidence that the skull roof in *Manlietta* is separate from the cheek region along the ventral edge of the dermopterotic as it is in *Mendocinia*. The dermosphenotic is not preserved. The overall shape of the opercular plate is similar to that of *Mendocinia*. In *Manlietta*, however, the suture dividing the opercular and subopercular slopes postero-dorsally so that the two bones have a similar surface area. The angle between the anterior edge of the opercular series and the ventral border of the maxilla is 82° in *Mendocinia*, and 64° in *Manlietta*. A wedge-shaped dermothyal is present in *Manlietta* (U.S.G.D. 213, Fig. 37) but this does not extend as far ventrally along the anterior margin of the opercular as it does in *Mendocinia*. In *Manlietta* there are three branchiostegal rays. The gular plate is extremely long and extends below the entire length of the lower jaw.

In *Manlietta* the preopercular is broad and there is no sign of any suborbital (supraspiracular) element. In one specimen (U.S.G.D. 213, Fig. 37) a suture divides the preopercular into two elements. The ventral preopercular element is characterized by a narrow extension passing antero-ventrally between the maxilla

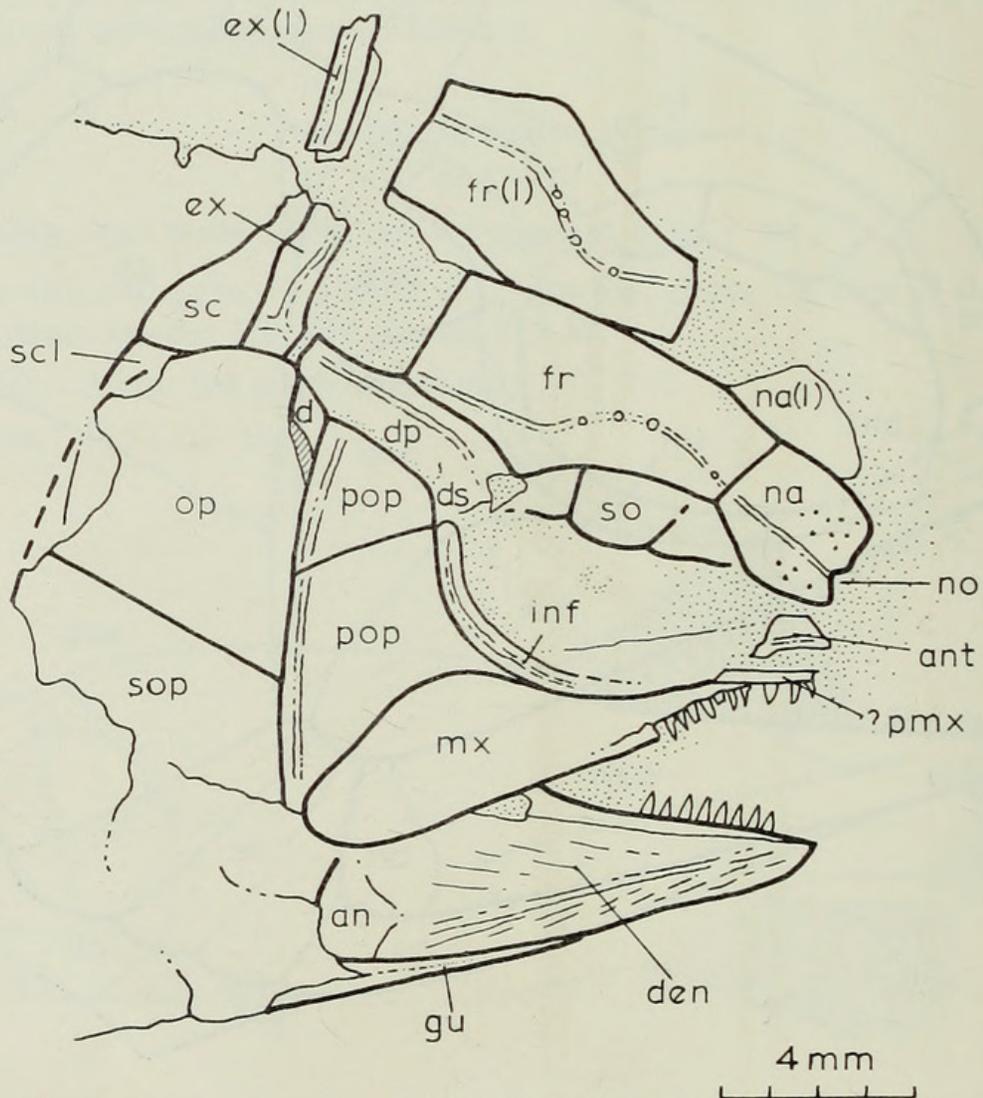


FIG. 37. *Manlietta crassa* Wade. U.S.G.D. 213: right side unless otherwise indicated.

and the infraorbital elements. The length of the cheek region is greater in *Manlietta* than in *Mendocinia* so that the posterior part of the maxilla in the former genus appears to be much more shallow. In fact the dorsal extent of the maxilla is similar in both genera. In specimen U.S.G.D. 213 (Fig. 37) there is a break at a point where the suture between the maxilla and a premaxilla may well have been present. The teeth of the upper jaw are large and somewhat blunt.

The infraorbital elements are narrow. The dorsal side of the orbit is bordered by three irregularly shaped supraorbitals, the centre member being the largest.

The snout region of *Manlietta* is not only different from that of *Mendocinia*, but also from all other perleidids in which this region is known. The nasals are ornamented with fine tubercles, are broad and meet in the midline, there being no postrostral. The nostril is situated on the ventral margin of the nasal (P.16825 and U.S.G.D. 213, Fig. 37). Ventral to the nasal there is a small rostral (P.16825) and a tetragonal antorbital which bears part of the infraorbital sensory canal. The fact that the rostral and antorbital elements are separate in *Manlietta* makes it likely that the anterior infrorbital of *Mendocinia* (Schaeffer 1955 : text-fig. 4 B), is wrongly identified, and is in fact an antorbital element. This view is supported by the fact that this bone bears the Y-shaped division of the infraorbital sensory canal.

Lower jaw. The lower jaw of *Manlietta* is stout. It is deep posteriorly and tapers to a blunt point. The dentary is ornamented with elongate rugae. The suture between the dentary and the angular is clearly seen in specimen U.S.G.D. 213 (Fig. 37). The dentary teeth are large, blunt and well separated.

Paired fins. The pectoral fins are poorly preserved in specimen U.S.G.D. 213. There are at least 8 rays which bifurcate and which have up to 11 joints.

The pelvic fin consists of at least 6 rays, but no details are preserved.

Unpaired fins. The anal fin has 9 rays which are so long that they extend posteriorly beyond the anterior edge of the caudal fin. The posterior rays bifurcate twice. The anterior rays bear fringing fulcra and there are up to 21 joints. The proximal joints are 4-5 times as long as those lying more distally (in *Mendocinia* they are 6-7 times as long and extend further distally).

The dorsal fin has 17 rays which have between 8 and 15 joints. The anterior rays bear fringing fulcra.

The caudal fin is almost homocercal, is slightly cleft and equilobate. There are 17 rays which are widely spaced, especially at the centre of the tail. The anterior rays of both the dorsal and ventral lobes bear fringing fulcra. All the rays are bifurcated and there are up to 20 joints.

Anterior to each unpaired fin there are basal fulcra, the longest of which are equal in length to the most proximal joints of the anterior fin-ray.

Squamation. The scales in the anterior part of the body are not well preserved but appear to be rhomboidal. Further posteriorly they become leaf-shaped. There is no surface ornament. There are about 36 body transverse scale rows.

Family **CLEITHROLEPIDIDAE** Wade 1935

DIAGNOSIS. Head deep posteriorly. Bones ornamented with tubercles. Parietal square. Frontal elongate and moderately deep. Accessory dermopterotic present. Opercular series vertical or almost vertical. Opercular smaller than subopercular. Small triangular dermohyal present. Quadratojugal present. Ventral end of preopercular narrow above quadratojugal. Preopercular with antero-ventral process. Three supraorbital elements present. Paired nasals separated by a postrostral. Nasal probably separated from the orbit margin. Paired 'Y'-shaped rostro-antorbitals or, possibly, separate rostrals and antorbitals. Premaxillae probably always present. Lower jaw slender and finely tapered. Teeth very small or absent.

Body deep, dorsal side with marked hump, ventral side strongly convex. Suprascapular absent. Accessory dermopterotic separating the extrascapular from the dorsal border of the opercular. Postcleithrum probably present. Rays of paired fins jointed or unjointed, sometimes bifurcated. Unpaired fin-rays jointed many times, bifurcating. Anterior rays of each fin bearing fulcra and more numerous than their endoskeletal supports, posterior rays more widely spaced. Dorsal and anal fins situated close to the caudal fin so that their anterior rays lie well posterior to the deepest part of the body. Short body lobe in tail. Scales elongate and ornamented with fine tubercles. Scales in pectoral region orientated antero-ventrally.

Genus **CLEITHROLEPIDINA** Berg 1940

1940 *Cleithrolepidina* Berg: 405.

The genus *Cleithrolepidina* was erected by Berg (1940 : 405) to include *Cleithrolepis minor* Broom, which he thought had a more vertical suspensorium than other members of the genus *Cleithrolepis*. The cheek region of *C. minor* has been re-examined and there appears to be no significant difference between the two genera in this respect. However, there are three other differences between the two genera. In *Cleithrolepidina* the maxilla is extremely shallow anteriorly, the snout is only moderately deep and the extrascapular is undivided. In *Cleithrolepis*, on the other hand, the maxilla is very deep throughout its length, the snout is extremely deep and the extrascapular is divided. Thus the genus *Cleithrolepidina* is valid, but not on Berg's grounds.

DIAGNOSIS (emended). Deep-bodied fish similar to *Cleithrolepis*, but in which the skull is moderately deep. The maxilla tapers anteriorly, and its anterior half is extremely shallow. Premaxilla very small or absent. Snout moderately deep, so that the nasal is roughly 3 times as deep as it is long. Postrostral half as long as the frontal. Extrascapular undivided.

TYPE SPECIES. *Cleithrolepis minor* Broom.

Cleithrolepidina minor (Broom)
(Figs 38-39)

1909 *Cleithrolepis minor* Broom: 266, pl. 13, fig. 9.

1931 *Cleithrolepis minor* Broom; Brough: 267-270, text-fig. 13.

1940 *Cleithrolepidina minor* (Broom) Berg: 405.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS (emended). Parietal almost rectangular with straight ventral edge. Dermopterotic narrow and rectangular. Opercular with straight ventral edge. About five branchiostegal rays. Preopercular rounded dorsally, the dermohyal and suborbital being small. Anterior process of preopercular overlapped by postero-dorsal border of maxilla. Maxilla with a postero-dorsal extension running behind posterior infraorbital. Posterior supraorbital equidimensional. Teeth probably absent.

Supracleithrum in contact dorsally with accessory dermopterotic and with extrascapular.

HOLOTYPE. S.A.M. 6037.

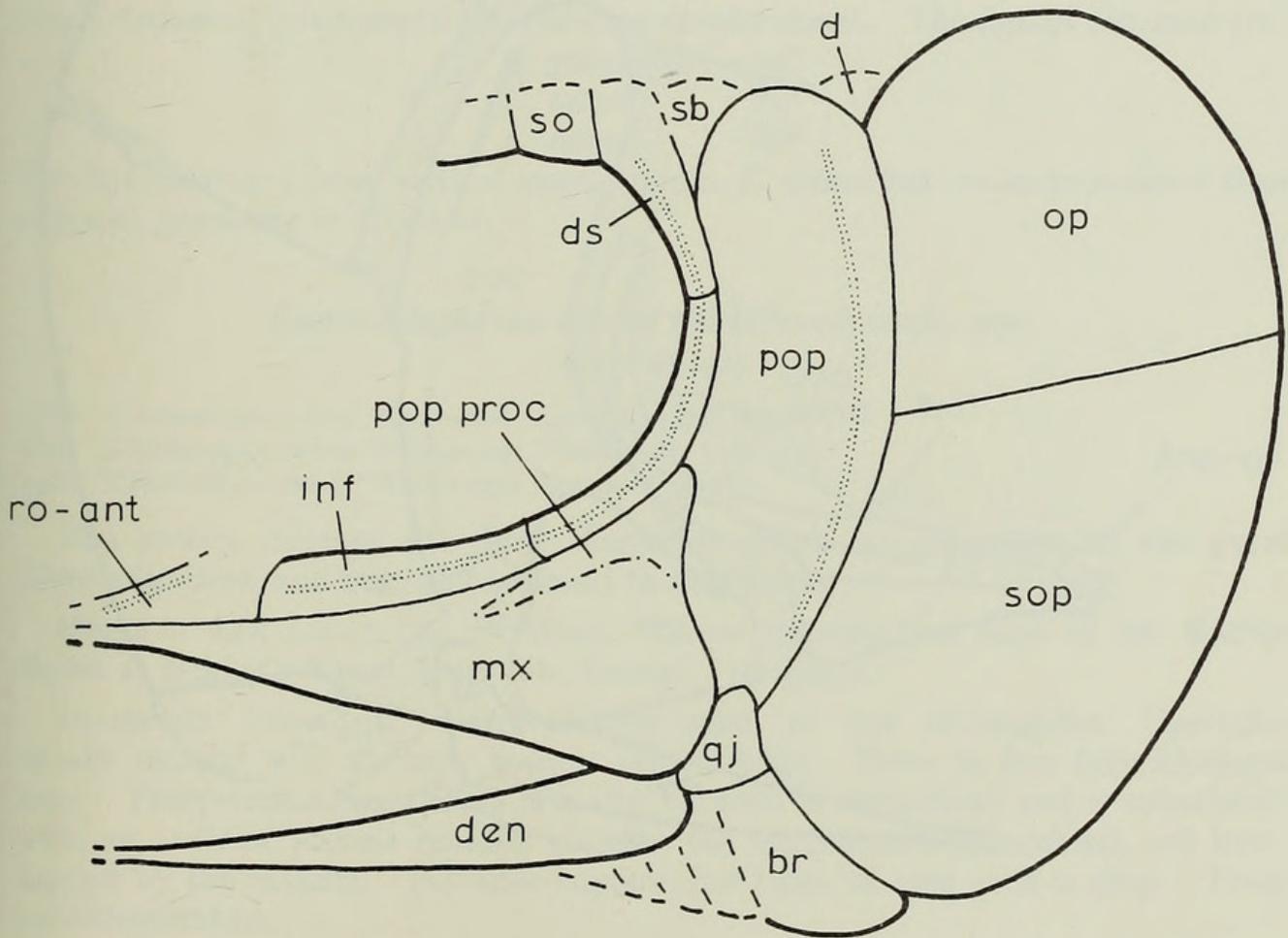


FIG. 38. *Cleithrolepidina minor* (Broom). Restoration of jaws, cheek and opercular regions, $\times 8$ approx.

MATERIAL. P.12594, P.16048-51, P.16067, P.16068 and counterpart P.16069. G.N. 293, 194, 328, 330 and counterpart 331.

DESCRIPTION. This species has been well described by Brough (1931 : 267-270) and little can be added here. However, the species has been placed in a new genus *Cleithrolepidina* by Berg (1940 : 405) because it was thought to have a vertical rather than an inclined supensorium. A description of the cheek region of *C. minor* is therefore given here in order to assess the validity of this taxonomic change.

Cheek region (Fig. 38). The maxilla, preopercular and opercular bones are well preserved in specimens G.N. 330 (Fig. 39) and its counterpart G.N. 331. The opercular is as long as it is broad. The suture between it and the subopercular is straight and slightly inclined postero-dorsally. The subopercular is almost 1.5 times the depth of the opercular. Four or five branchiostegal rays are present. The angle

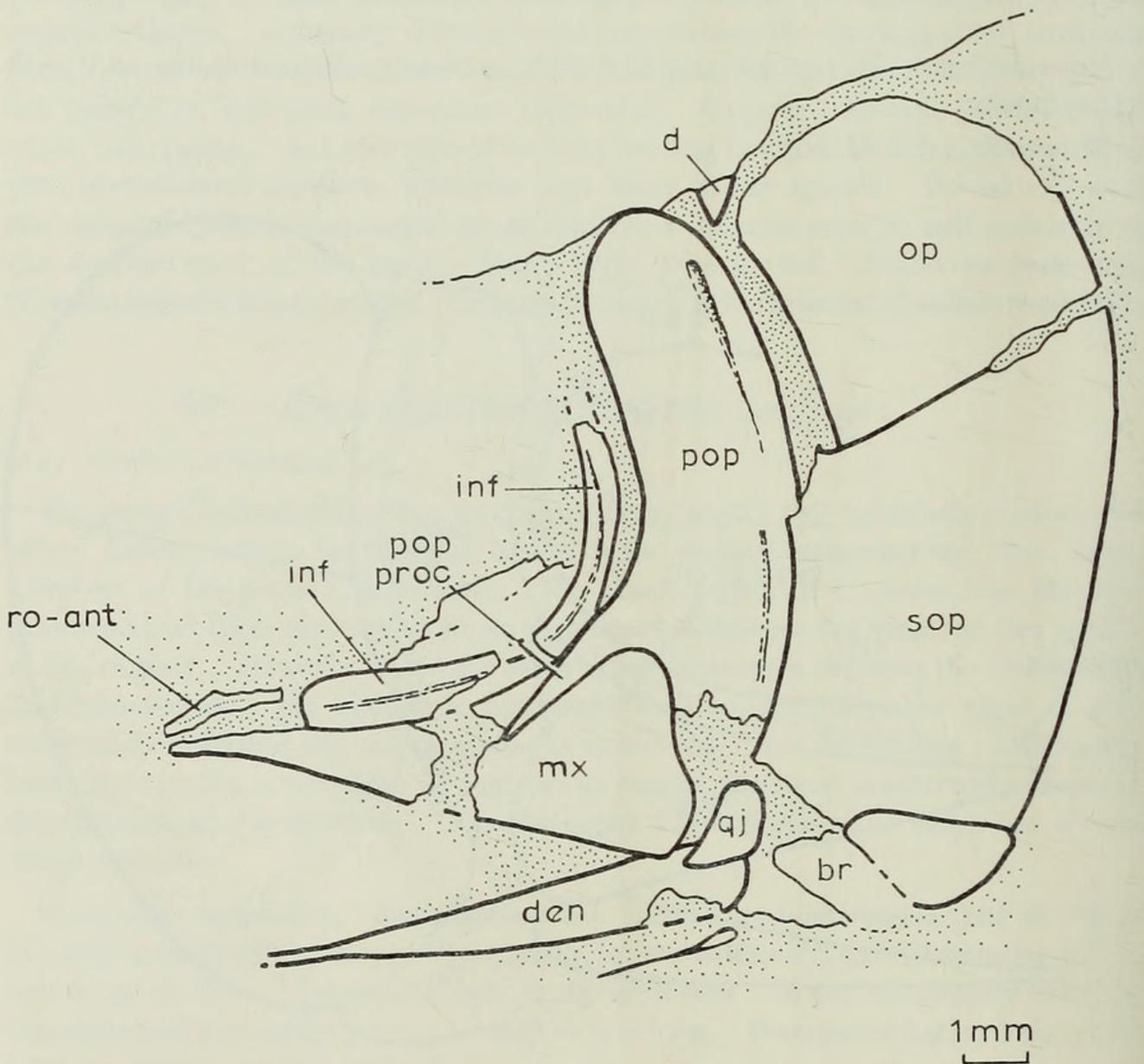


FIG. 39. *Cleithrolepidina minor* (Brough). G.N. 330: right side, internal surface.

between the anterior edge of the opercular series and the ventral edge of the maxilla is 86° .

The preopercular is kidney-shaped. Its posterior edge is convex, fitting closely to the anterior margin of the opercular series; its dorsal end is rounded and not constricted between the suborbital and dermohyal as it is in *C. extoni* and *C. granulata*, although dermohyal and suborbital are present (G.N. 331, P.16048 and P.12594). Its anterior edge is concave, the dorsal part bordering the posterior infraorbital and the ventral part having long sinuous contact with the maxilla. The preopercular has an antero-ventrally directed process which lies below the postero-dorsal part of the maxilla. The maxilla is deep posteriorly and tapers sharply anteriorly. There is a roughly triangular quadratojugal ossification, between the maxilla and the antero-ventral corner of the subopercular (G.N. 330, Fig. 39).

REMARKS. The above description shows that Berg's (1940 : 405) separation of *C. minor* from members of the genus *Cleithrolepis* on account of its more vertical suspensorium is unjustified. An accurate measurement of the angle between the anterior margin of the opercular series (a line joining the antero-dorsal corner of the opercular with the antero-ventral corner of the subopercular) and the ventral border of the maxilla may not be a measurement of the actual angle of the suspensorium, but it is closely related to that feature and, as long as the maxilla does not show too much variation, it is a useful comparative measurement. The figures obtained are:

<i>C. granulata</i>	93°
<i>C. extoni</i>	89°
<i>C. minor</i>	86°

Far from having a more vertical suspensorium, *C. minor* has one more inclined than either *C. granulata* or *C. extoni*.

Cleithrolepidina extoni (Woodward) comb. nov.

(Figs 40-42)

1888 *Cleithrolepis extoni* Woodward: 141-143, pl. 6, figs 6-7.

1895 *Cleithrolepis extoni* Woodward; Woodward: 156-157.

1909 *Cleithrolepis extoni* Woodward; Broom: 264-266.

This species displays the three characters which are diagnostic of the genus *Cleithrolepidina*, and has been removed to that genus.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS (emended). Dermopterotic more or less rectangular. Opercular almost circular with strongly convex ventral edge. Three to five branchiostegal rays. Preopercular constricted dorsally between a dermohyal and a suborbital; with an anterior process running between the maxilla and infraorbital, not overlapped by the maxilla. Posterior supraorbital twice as long as it is deep. Teeth probably absent.

Supracleithrum in contact dorsally with accessory dermopterotic only.

HOLOTYPE. P.5455.

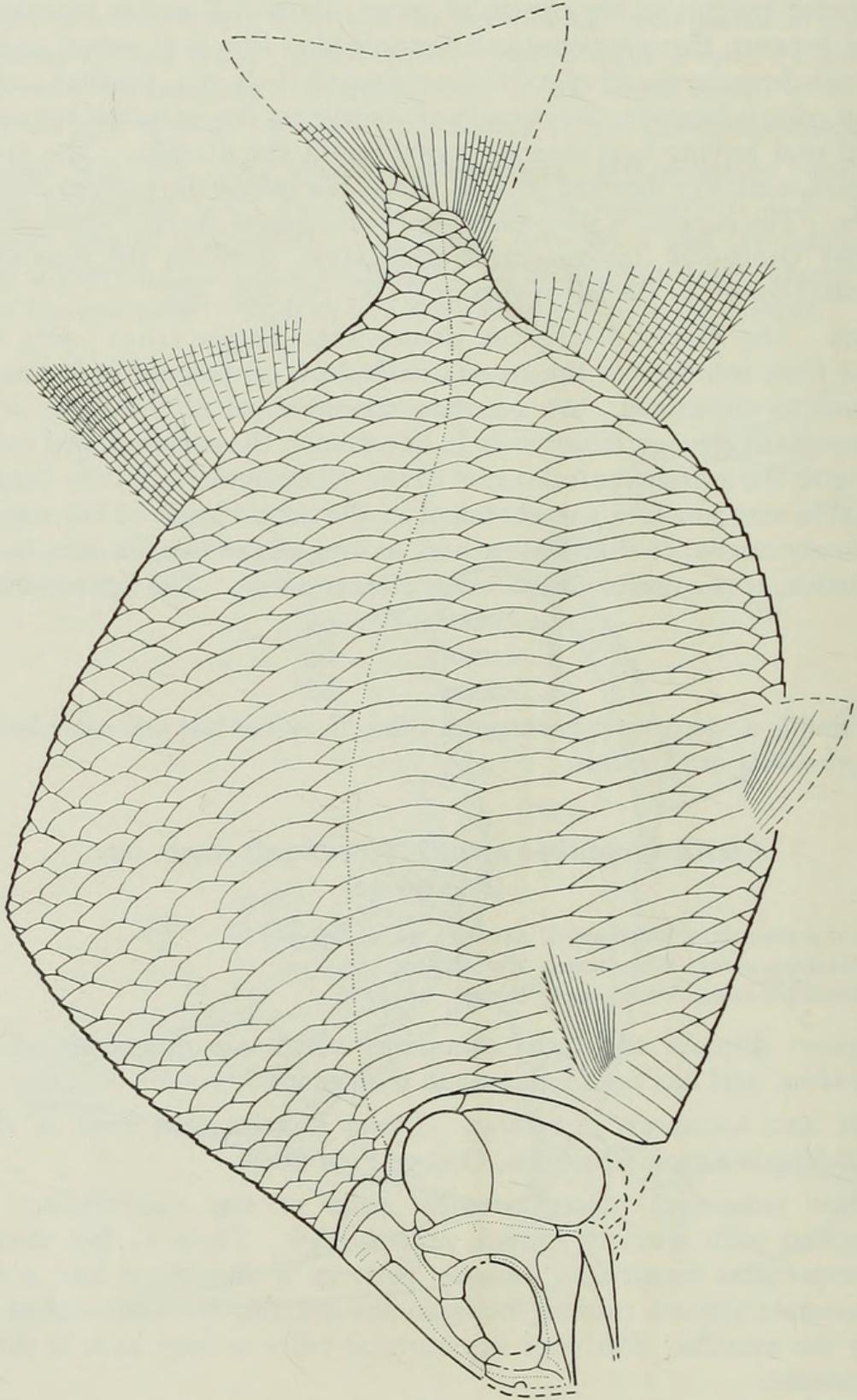


FIG. 40. *Cleithrolepidina extoni* (Woodward). Restoration, $\times 1.5$ approx.

MATERIAL. Holotype and P.5455a, P.16043 and counterpart P.16044, P.16045, P.16105 and counterpart P.16106.

DESCRIPTION. *Size* (Fig. 40). The holotype is about 120 mm long, measured from snout tip to the posterior end of the caudal fin, and 68 mm at its greatest depth. The body is similar in shape to *Cleithrolepis granulata* (Fig. 43) in that the dorsal side of the body is humped, with a distinct point separating the anterior part of the body outline, which is convex and faces antero-dorsally, from the posterior part which is also convex and which faces postero-dorsally. The maximum body depth is almost eight times the depth of the caudal peduncle.

Skull (Fig. 41). All the dermal elements of the skull are ornamented with numerous, well defined tubercles. The head is roughly triangular, the skull roof sloping

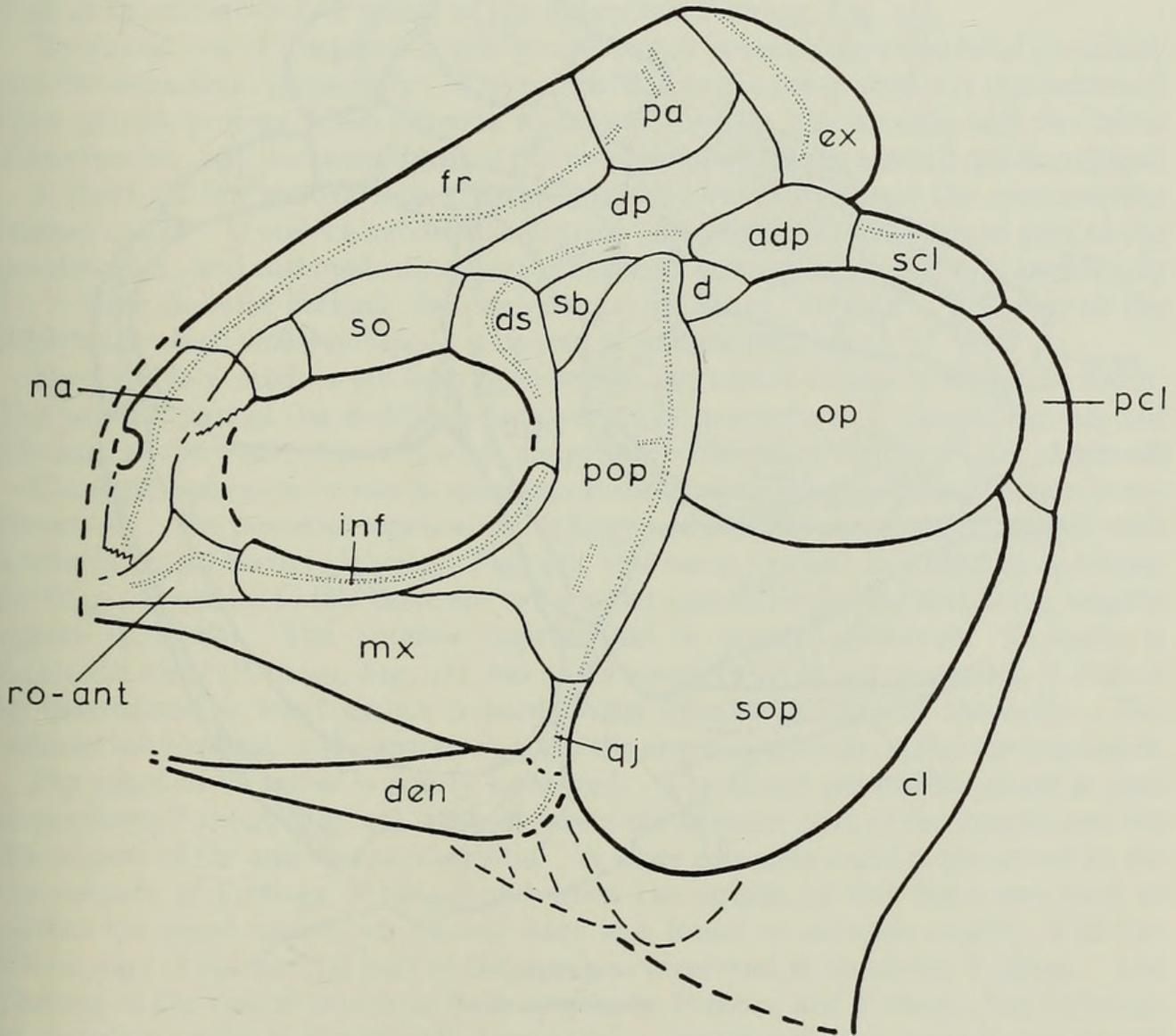


FIG. 41. *Cleithrolepidina extoni* (Woodward). Restoration of skull and pectoral girdle, $\times 4.5$ approx.

steeply towards the snout. The supraorbital sensory canal is enclosed in a massive tube which runs along the entire length of the frontal bone. Anteriorly it is curved so that it runs parallel with the ventral border of the frontal, posteriorly it just extends on to the parietal (P.5455a). Posterior to the parietal there is a deep, narrow bone which is 'D'-shaped. This element is similar in shape to the suprascapular of many actinopterygians, but is identified as an extrascapular because it bears

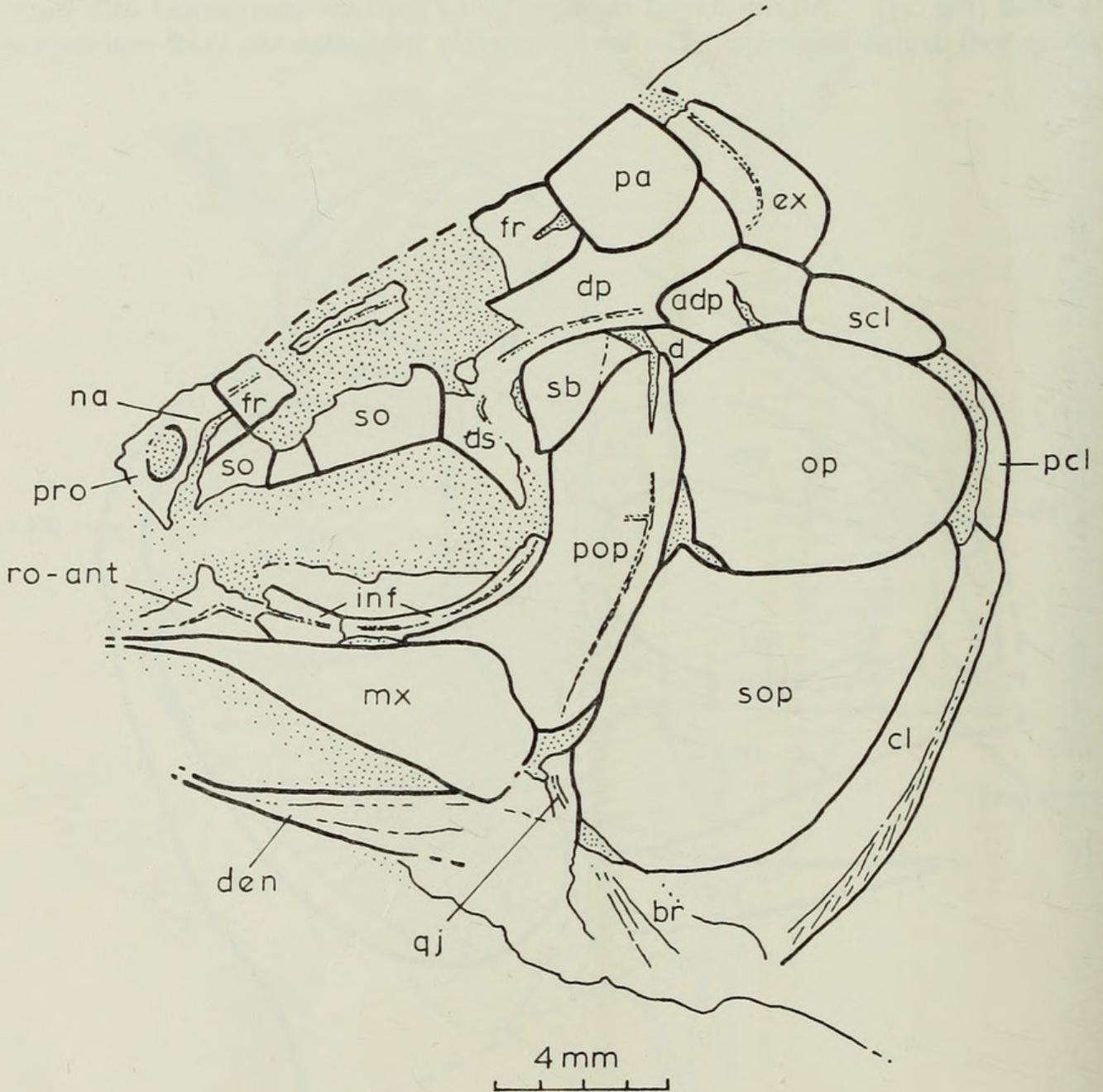


FIG. 42. *Cleithrolepidina extoni* (Woodward). P.16045: left side. Ornament of fine tubercles omitted.

a vertical branch of the temporal sensory canal (P.16045, Fig. 42). The dermopterotic is elongate and narrow, except posteriorly where it extends dorsally between the parietal and the extrascapular.

The remaining element of the skull roof is roughly oval in shape. Dorsally it meets the postero-ventral edge of the dermopterotic and the ventral edge of the extrascapular, ventrally it meets the dorsal edge of the dermohyal (P.16045, Fig. 42). Posteriorly this element butts against the supracleithrum. In *C. minor* an element with exactly these spatial relationships bears part of the infraorbital sensory canal and is there identified as an accessory dermopterotic (see discussion of the family Cleithrolepididae, p. 338).

The opercular is slightly longer than deep and is 'D'-shaped. The subopercular is 1.3 times as deep and almost exactly the same width as the opercular. In specimen P.16045 (Fig. 42) branchiostegal rays are very poorly preserved, but there appear to be only three or four such elements. There is a small triangular dermohyal at the antero-dorsal corner of the opercular (P.16045, Fig. 42).

The dorsal end of the preopercular is constricted between the suborbital anteriorly and the dermohyal posteriorly. The ventral end of the preopercular is characterised by a narrow process which extends anteriorly between the maxilla and the infraorbital series. At the ventral end of the preopercular there is a small quadratojugal.

A short pit-line groove runs parallel with the ventral part of the preopercular sensory canal. There is a suborbital element lying anterior to the dorsal part of the preopercular, and although its external shape is triangular, it extends posteriorly for a short distance beneath the preopercular (P.16045, Fig. 42). The part of the suborbital which was overlapped is devoid of surface ornament.

The maxilla is moderately deep posteriorly, and tapers evenly towards the snout. The anterior part of the maxilla is bent ventrally in specimen P.16045 (Fig. 42) but this may be the result of post mortem distortion. Maxillary teeth were not observed.

The dermosphenotic is seen in specimen P.16043 although its ventral portion is not preserved. The posterior supraorbital is large and roughly rectangular, though with a convex dorsal border (P.16045, Fig. 42); this same element is broken in specimen P.16043. Anterior to this there are two smaller supraorbitals, the first being roughly square (P.16043). The anterior supraorbital is poorly preserved. Dorsally it meets the nasal (P.16045, Fig. 42), but as its ventral part is not preserved, it cannot be determined to what extent it borders the anterior margin of the orbit. The anterior infraorbital, or the anterior part of the anterior element, is slightly expanded.

The snout of *C. extoni* is poorly preserved. The dorsal part of the nasal is seen in specimen P.16045 (Fig. 42) where it meets the anterior part of the frontal and the dorsal part of the anterior supraorbital. A more complete nasal is preserved in the counterpart of P.16043, P.16044, and when the outline of this bone was used to restore the snout region, its ventral edge was found to coincide exactly with the dorsal edge of the ventral part of the snout as preserved in specimen P.16045. The position of the nostril is seen in both specimens P.16044 and P.16045, but although its anterior border is presumably formed by a postrostral, this bone is not clearly preserved in any specimen.

Only a single element of the ventral part of the snout can be determined. It is

poorly preserved but is roughly triangular, its posterior part meeting the anterior infraorbital, and its ventral part lying above the anterior tip of the maxilla. As noted above, restoration of the snout suggests that the dorsal margin of this element was in contact with the nasal. This bone bears the anterior part of the infraorbital sensory canal, and is probably the rostro-antorbital (see Gardiner 1963 : 312).

The lower jaw is slender and probably toothless.

Pectoral girdle. The pectoral girdle is best preserved in specimen P.16045 (Fig. 42). There is no suprascapular. The supracleithrum is small and lies almost horizontally above the opercular. Anteriorly it butts against the accessory dermopterotic. The supracleithrum does not meet the cleithrum; between these bones there is a post-cleithrum which is curved and which follows the posterior outline of the opercular. Only the dorsal part of the cleithrum is preserved. The posterior border of the cleithrum is ornamented with deep parallel ridges which run along the long axis of the bone. The major part of the cleithrum, however, is smooth. The clavicles, if present, are not preserved.

Paired fins. The pectoral fin contains 12 rays, the first of which bears fringing fulcra. No specimen showed any evidence of jointing or bifurcation of the rays. The pectoral fin does not lie close to the ventral margin of the body, and its base is orientated so that the insertion of the anterior ray lies antero-dorsally relative to that of the posterior ray.

The pelvic fin is poorly preserved and only 9 rays are present, showing neither trace of jointing or bifurcation, nor the presence of fringing fulcra.

Unpaired fins. In both the dorsal and anal fins the rays bifurcate, and the anterior rays bear fringing fulcra and are almost four times the length of the posterior rays. The posterior rays are more widely spaced than are the anterior rays. The dorsal fin-rays number about 20 and bear up to 17 joints, and the anal fin-rays number about 18 and bear up to 15 joints. In both fins the proximal joints are long compared with the more distal ones.

The proximal part of the caudal fin is preserved in a single specimen (the holotype, P.5455). There are about 26 rays.

Squamation. There are 36 transverse body scale rows. The scales are very deep, especially in the lateral line region where their depth is up to 6 times their length (this ratio takes into account only that part of the scale which is not overlapped by adjoining scales). Each scale bears a ridge along its posterior border and a surface ornament consisting of numerous tubercles. In general the transverse body scale rows pass postero-ventrally across the body; there are three exceptions, however: at the antero-ventral corner of the body, posterior to the cleithrum, there are about 9 scales orientated postero-dorsally; at the base of the dorsal fin the body scale rows become inclined so that scales immediately at the fin base, when viewed from above, run parallel to the long axis of the body. In a similar way the scale rows become anteriorly directed as they approach the base of the anal fin.

Genus *CLEITHROLEPIS* Egerton 1864

- 1864 *Cleithrolepis* Egerton: 3.
 1890 *Cleithrolepis* Egerton; Woodward: 37.
 1895 *Cleithrolepis* Egerton; Woodward: 154.
 1931 *Cleithrolepis* Egerton; Brough: 266.
 1935 *Cleithrolepis* Egerton; Wade: 49.
 1940 *Cleithrolepis* Egerton; Berg: 405.

The genus *Cleithrolepis* has been diagnosed twice in recent years, but the diagnosis of Brough (1931: 266-267) was based on a single species, *Cleithrolepis minor*, now thought to be a member of the genus *Cleithrolepidina* (see above) while that of Wade (1935: 49) was based on *Cleithrolepis granulata*. *Cleithrolepis granulata* has many features in common with both species of *Cleithrolepidina* (*C. minor* and *C. extoni*), but differs in three important respects. The emended diagnosis of *Cleithrolepis* emphasizes these latter points.

DIAGNOSIS (emended). Deep-bodied fish similar to *Cleithrolepidina*, but in which the skull is extremely deep. The maxilla tapers slightly anteriorly, but is deep throughout its length. A large triangular premaxilla present. Snout extremely deep so that the nasal is roughly 4.5 times as deep as it is long. Postrostral as long as the frontal. Extrascapular divided into four elements.

TYPE (and only certain) SPECIES. *Cleithrolepis granulata* Egerton.

In 1941 Wade compared *Cleithrolepis granulata* with *Cleithrolepis* (now *Cleithrolepidina*) *minor* (Wade 1941b: 391-2). It is important to examine the differences which he thought existed between these two forms because he concluded that the two were quite distinct. Wade did not attempt to separate *C. granulata* and *C. minor* into separate genera, even though he concluded that, whereas *C. minor* was a typical perleidid, *C. granulata* was quite distinct from that family. The differences noted by Wade will now be listed and examined.

1. The dorsally angulated body of *C. minor* has become more gently curved in *C. granulata*.

This difference, although present, is very slight and would not seem to warrant distinction between the two forms at anything above the species level, being of the same order as variation of skull length relative to that of the body.

2. The temporal region of *C. minor* is shallow, and that of *C. granulata* is deep.

3. The simple tabulars of *C. minor* are divided in *C. granulata*.

Both these differences are certainly present but cannot be regarded as having great significance as they can be simply related to the acquisition of a deeper skull in *C. granulata*.

4. In *C. granulata* (but not in *C. extoni* or *C. minor*) there is a second preoperculum bearing a preopercular sensory canal.

The second preoperculum referred to by Wade is here called a quadratojugal (see Westoll 1944: 73). This bone has been identified in both *C. minor* and *C. extoni* as well as *C. granulata*. Wade's suggestion that there was a functional relationship between the presence of a second preoperculum (quadratojugal) and the development of a preopercular peg or process which articulated with the maxilla

may well be correct. In *C. extoni*, which has a relatively small quadratojugal, the preopercular process is short and is not overlapped by the maxilla. The presence of a quadratojugal and a preopercular process in *C. minor*, *C. extoni* and *C. granulata* serves to unite rather than to separate the three species.

5. There are few branchiostegals in *C. minor* but about a dozen in *C. granulata*. Branchiostegals are reduced in most perleidiforms; the presence of a large number in *C. granulata* may show that the genus did not evolve directly from *C. minor*, but it certainly does not imply that the two taxa should be placed in separate families.

6. The circumorbital bones are well developed in *C. granulata* and narrow in *C. minor*.

This difference in fact applies only to the supraorbital bones, and even these are not as narrow in *C. minor* as Brough's reconstruction suggests. In *C. extoni* the supraorbitals are even deeper than in *C. granulata*.

7. The suture between the maxilla and the preopercular in *C. minor* runs diagonally across the cheek to a point behind the orbit. In *C. granulata* this suture runs to a point below the orbit.

This difference is valid, but its taxonomic importance is lessened by the fact that *C. extoni* displays an intermediate condition in this respect.

In conclusion, the differences between *C. minor* and *C. granulata* noted by Wade do not indicate that the two forms have affinities with different families. Many characteristics of *C. granulata* such as the divided extrascapular and the deep dermopterotic can be related to the fact that in *C. granulata* the skull in general and the maxilla in particular are unusually deep. These differences serve to separate *Cleithrolepidina minor* and *Cleithrolepidina extoni* from *Cleithrolepis granulata* and to justify separation at the generic level only. The genera *Cleithrolepis* and *Cleithrolepidina*, however, share some very unusual features and must be regarded as members of one family (see discussion on the classification of the Perleidiformes, p. 335).

Cleithrolepis granulata Egerton

(Figs 43-44)

1864 *Cleithrolepis granulatus* Egerton: 3, pl. 1.

1890 *Cleithrolepis granulatus* Egerton; Woodward: 39-42, text-fig., pl. 7, figs 1-7, pl. 8, figs 2-3.

1895 *Cleithrolepis granulatus* Egerton; Woodward: 155-156.

1908 *Cleithrolepis granulatus* Egerton; Woodward: 25.

1935 *Cleithrolepis granulata* Egerton; Wade: 49-57, text-figs 22-26, pl. 6, fig. 3.

HORIZONS AND LOCALITIES. Triassic of Cockatoo Island, near Sydney, N.S.W.; Scythian or Anisian Narrabeen shales at Gosford, N.S.W.; Ladinian (?) Hawkesbury Sandstone at Beacon Hill, Brookvale, N.S.W.; and Wianamatta shales at St. Peters, N.S.W.

DIAGNOSIS (emended). Parietal equidimensional with convexo-concave ventral edge. Dermopterotic deep posteriorly. Opercular with slightly convex ventral edge. Thirteen branchiostegal rays and gular plate present. Preopercular constricted dorsally between a dermohyal and a suborbital, with an anterior process

overlapped by postero-dorsal border of maxilla. Posterior supraorbital equidimensional. Small teeth present at anterior tip of lower jaw.

Supracleithrum in contact dorsally with accessory dermopterotic and with extrascapular.

HOLOTYPE. A specimen in the Australian Museum; see Egerton 1864 : pl. 1, fig. 3.

MATERIAL. P.15752 and counterpart P.15753, P.15754-6, P.15759, P.15761, P.15766-70, P.15773, P.24674, P. 24675.

G.N. 419, 422 and counterpart 438.

U.S.G.D. 91, 167, 217, 203 (at the University Museum of Zoology, Cambridge).

All the specimens studied were from the Brookvale locality.

DESCRIPTION. The species has been described in detail by Wade (1935 : 49-57) and a full description will not be repeated here. However, there are several differences between Wade's restoration of the species and that given here, and these are noted in the description below.

Size (Fig. 43). The body shape is similar to that of *Cleithrolepidina extoni* (see Fig. 40); however, the head, as noted by Wade, is significantly larger than in *C. extoni*.

Skull (Fig. 44). The frontal is long and somewhat deeper than in *C. extoni*. The supraorbital sensory canal does not appear to extend onto the parietal. Posterior to the parietal, the extrascapular is divided into four elements which become

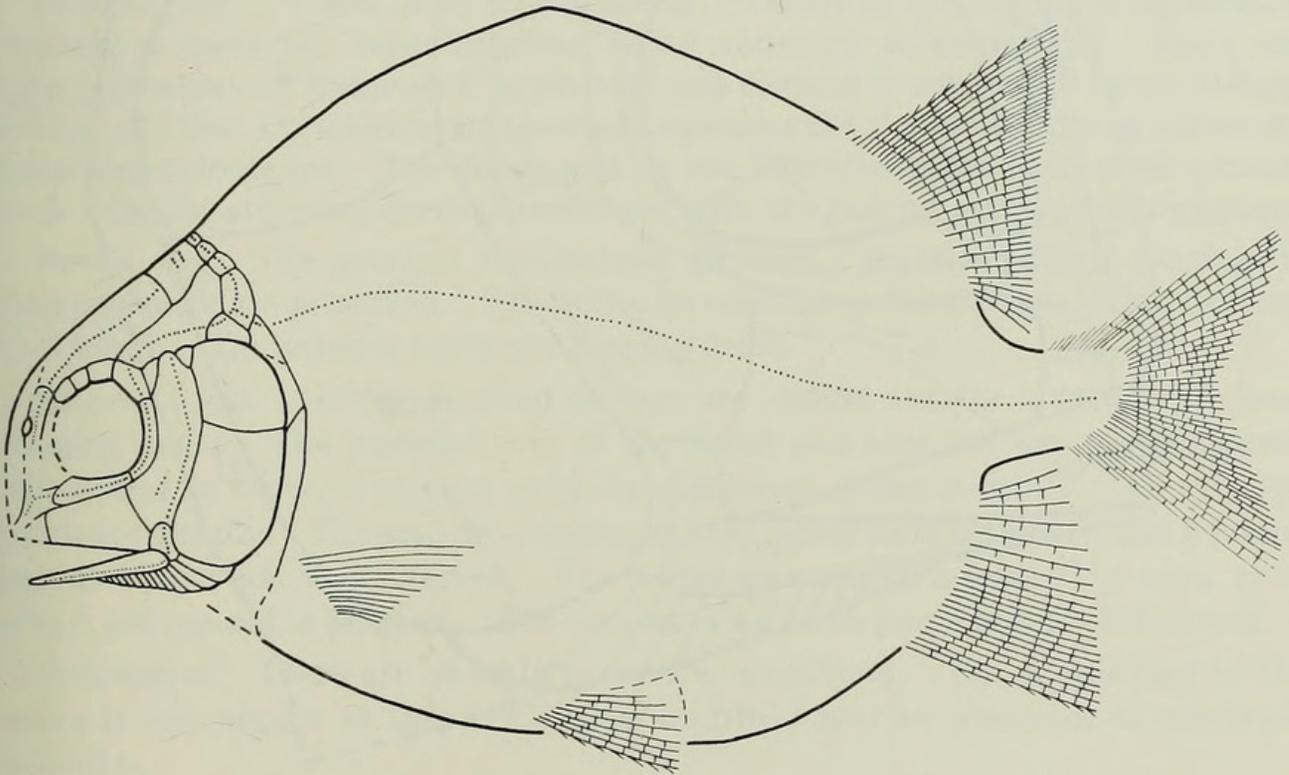


FIG. 43. *Cleithrolepis granulata* Egerton. Restoration, $\times 1.5$ approx.
Scales omitted.

progressively larger ventrally. The dermopterotic is similar in shape to that in *C. extoni*, except that it is deeper, especially posteriorly. The infraorbital sensory canal runs roughly through the centre of the dermopterotic, and is not limited to the ventral edge of this bone. There is no sign of subdivision of the dermopterotic as figured by Wade (1935 : text-fig. 23); however, there is a lozenge-shaped element lying between the ventral edge of the extrascapular and the dorsal edge of the opercular (P.15754). Comparison with *C. extoni* suggests that this bone is an accessory dermopterotic.

The opercular series is inclined antero-ventrally at an angle similar to that seen in *C. extoni*. The opercular is 'D'-shaped, and there is a triangular dermothal at its

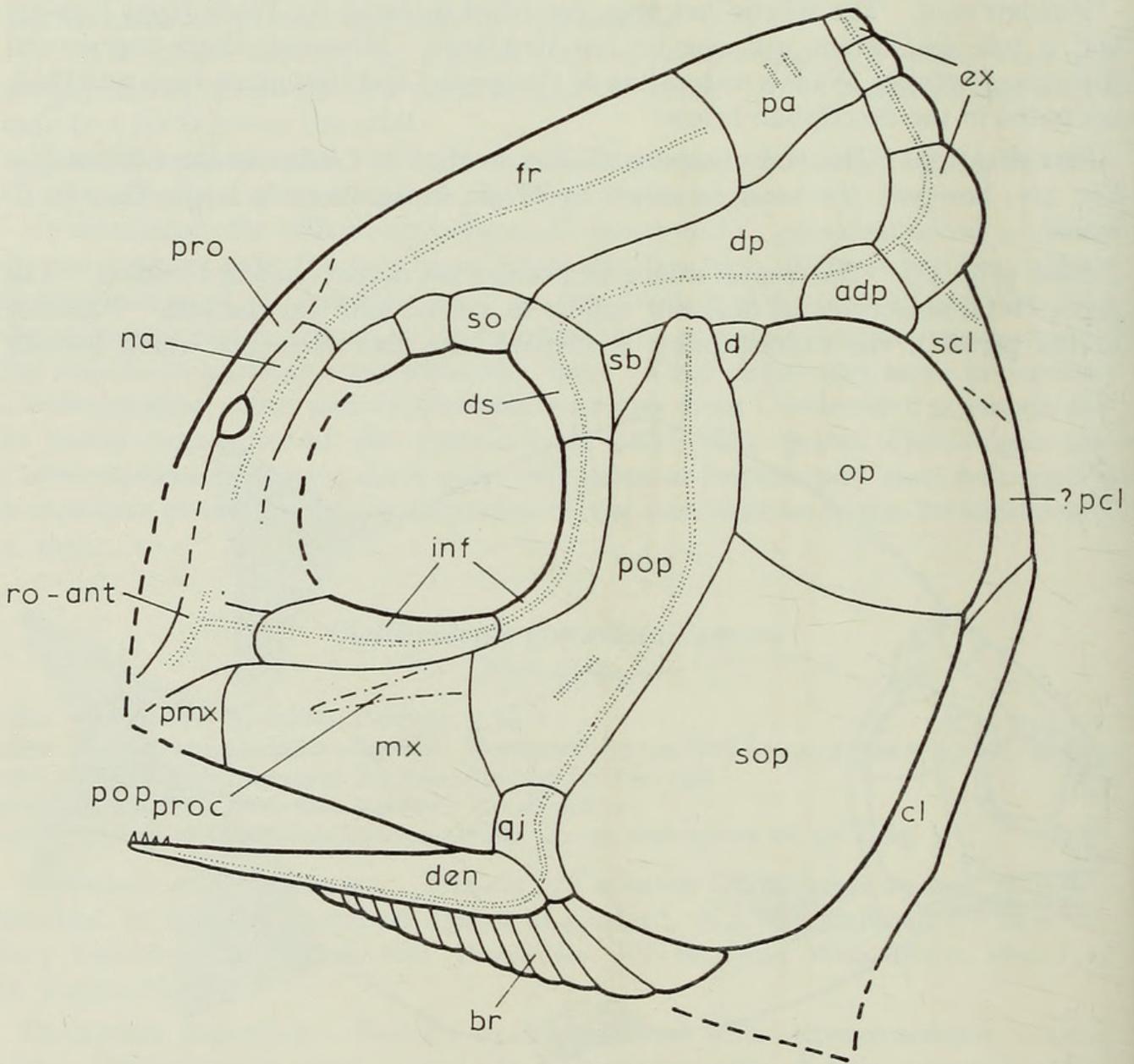


FIG. 44. *Cleithrolepis granulata* Egerton. Restoration of skull and pectoral girdle, $\times 4.5$ approx.

antero-dorsal corner (G.N. 419). The subopercular is deeper than that of *C. extoni*, and is roughly rectangular in shape, being wide ventrally.

The preopercular differs from that of *C. extoni* in that its depth is greater and its ventral part extends further anteriorly, so that the suture between it and the maxilla lies almost below the centre of the orbit. Also, the antero-ventral process of the preopercular does not extend between the maxilla and infraorbitals as is the case in *C. extoni*, but is completely overlapped by the maxilla so that it is not visible in lateral view (G.N. 419, Fig. 43). At the ventral end of the preopercular there is a quadratojugal.

The maxilla is quite different from that of *C. extoni* in that it is deep throughout its length.

Three supraorbital elements border the dorsal part of the orbit (G.N. 419). The anterior of these elements does not appear to extend ventrally to border the anterior part of the orbit, although Wade (1935 : 51) has noted the occurrence of such an element in a single specimen, U.S.G.D. 135 (this specimen was not available for study).

The snout of *C. granulata* appears to be similar to that of *C. extoni* except that the nasal and postrostral elements are considerably elongated, the skull being much higher at this point. There is a premaxilla at the ventral tip of the snout. A rostral is not preserved, and it is possible that there has not been any fragmentation of the rostro-antorbital (see Gardiner 1963 : 312).

The lower jaw is straight and extremely slender. In specimens P.13953 and P.24675 three or four tiny teeth are preserved at the extreme tip of the lower jaw.

Pectoral girdle. There is no suprascapular. Dorsal to the cleithrum an element extends to meet the bone identified as an accessory dermopterotic. There are faint indications in specimen P.15761 that this element is subdivided by an oblique suture, and that a postcleithrum therefore separates the cleithrum from an extremely small supracleithrum. The dorsal end of the supracleithrum is in close contact both with the accessory dermopterotic and with the ventral extrascapular element.

Paired fins. The pectoral fin contains 12 rays. No bifurcation, jointing or fringing fulcra are preserved. The pelvic fin contains at least 8 rays which have up to 8 joints. The anterior ray bears fringing fulcra.

Unpaired fins. All the unpaired fin-rays are jointed and the anterior rays bear fringing fulcra. The posterior rays of the dorsal and anal fins are widely spaced. The dorsal fin contains 26 rays which have between 3 and 10 joints. All the rays bifurcate distally. The anal fin contains 24 rays which have between 3 and 9 joints, but no bifurcation was observed. The caudal fin contains a total of 37 rays, 12 of which are epaxial in position. The rays have up to 10 joints and are bifurcated.

Squamation. There are 40 body transverse scale rows. The morphology of the scales is very similar to that of *C. extoni* and they bear an ornament of numerous tubercles.

A description of the axial skeleton, and of variation of morphological details during development in *C. granulata*, has been given by Wade (1935 : 53-56).

Family **HYDROPESSIDAE** nov.

DIAGNOSIS. - As for the genus *Hydropessum*.

Genus **HYDROPESSUM** Broom 1909

1909 *Hydropessum* Broom: 266.

DIAGNOSIS (emended). Head deep posteriorly. Bones of the skull roof ornamented with tubercles, those of the opercular series with rugae. Parietal short and deep. Frontal extremely deep. No accessory dermopterotic present. Opercular series forming a 'D'-shaped plate. The suture dividing the opercular and subopercular oblique, so that the anterior margin of the subopercular is shorter than that of the opercular and the posterior margin of the opercular is shorter than that of the subopercular. The ventral border of the subopercular is concave. No dermohyal present. About seven branchiostegals present. Preopercular without anteroventral process seen in *Cleithrolepis*. Ventral end of preopercular broad, and extending anteriorly to a point almost level with the midpoint of the orbit. A large element, probably an accessory preopercular, extending dorsally over halfway along anterior edge of subopercular, and anteriorly almost halfway along upper jaw margin. Only anterior part of upper jaw margin formed by maxilla. Infraorbitals narrow. Two supraorbitals present. Nasal bordering anterior margin of the orbit. Snout consisting of paired nasals separated by a postrostral and, probably, paired rostral-antorbitals and paired premaxillae. Lower jaw short and stout. Teeth probably absent.

Body deep, diamond-shaped with corners at the head and tail, and midway along the dorsal and ventral sides. Maximum body depth equal to length from snout tip to end of caudal lobe. Suprascapular large and 'D'-shaped. Scales deep and ornamented with elongate rugae. Scales in pectoral region orientated parallel to those on the rest of body. Dorsal and anal fins situated with their anterior rays inserted at the deepest part of the body. Pelvic fins probably lost.

TYPE (and only) SPECIES. *Hydropessum kannemeyeri* Broom.

REMARKS. The genus *Hydropessum* was previously included in the Cleithrolepididae (Wade 1935, Berg 1940, Gardiner 1967).

Hydropessum kannemeyeri Broom

(Figs 45-47)

1909 *Hydropessum kannemeyeri* Broom: 266-267, pl. 12, fig. 5.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As for the genus *Hydropessum*.

HOLOTYPE. S.A.M. 1334.

MATERIAL. P.16042, P.16180 and counterpart P.16181. G.N. 358.

DESCRIPTION. *Size* (Fig. 45). The total length of the best preserved specimen, P.16180, is estimated to have been about 95 mm. It is 77 mm at its greatest depth. The body is diamond-shaped.

Skull (Fig. 46). The bones of the skull roof are ornamented with tubercles, and those of the cheek and opercular regions with rugae.

The frontal is an extremely broad bone having its widest point about midway along its length (P.16181, Fig. 47). The opercular and subopercular are extremely

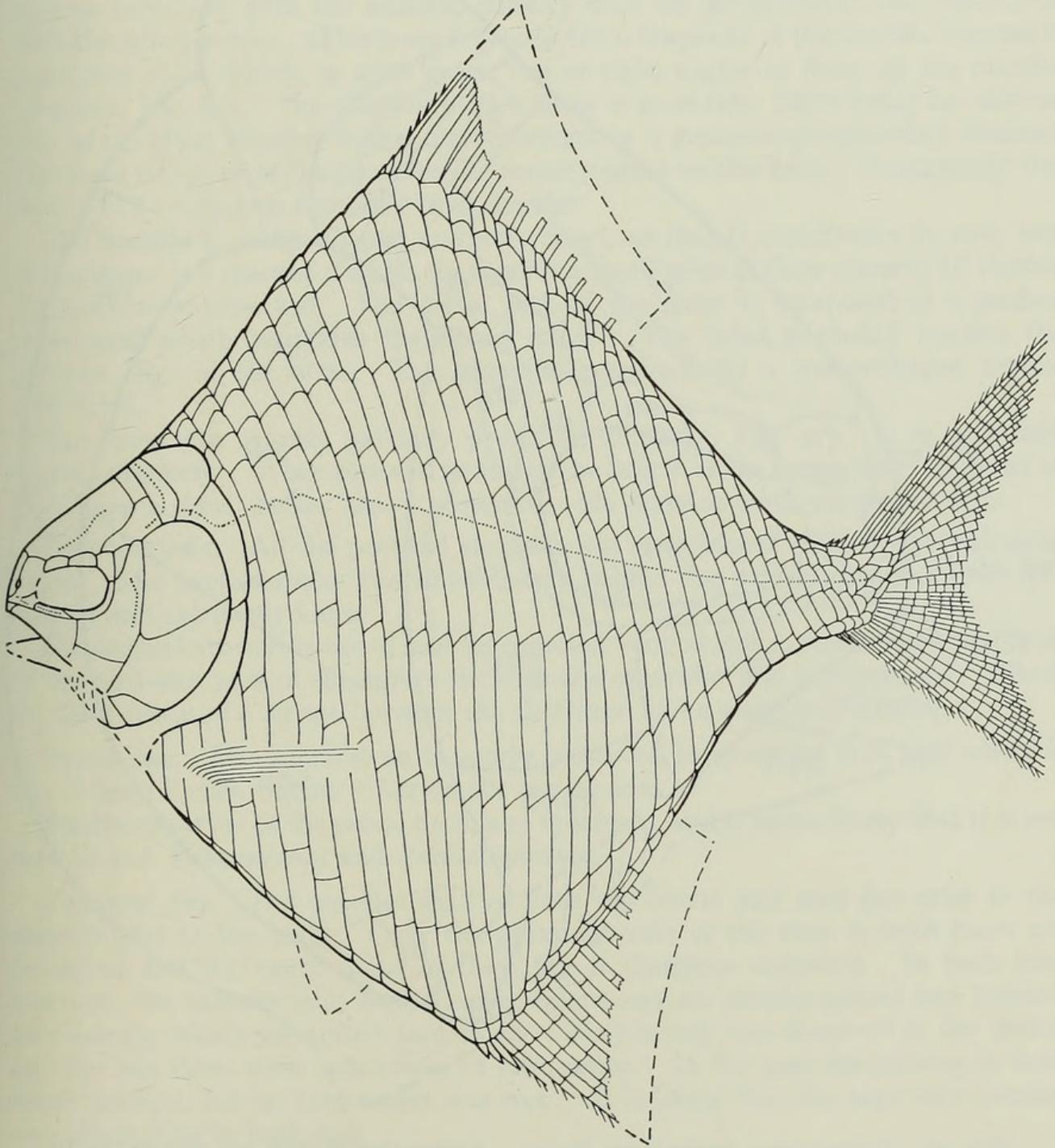


FIG. 45. *Hydropessum kannemeyeri* Broom. Restoration. $\times 1.5$ approx.

large. Together they form a 'D'-shaped plate which extends to a point well below the level of the snout tip. In consequence, the upper jaw margin slopes anterodorsally from the antero-ventral corner of the subopercular. The angle between the anterior edge of the opercular series and the ventral edge of the maxilla is 62° . On the medial surface of the antero-dorsal corner of the opercular there is a deep notch which received the opercular process of the hyomandibular (G.N. 358). The opercular is ornamented with elongate rugae which radiate from its antero-dorsal

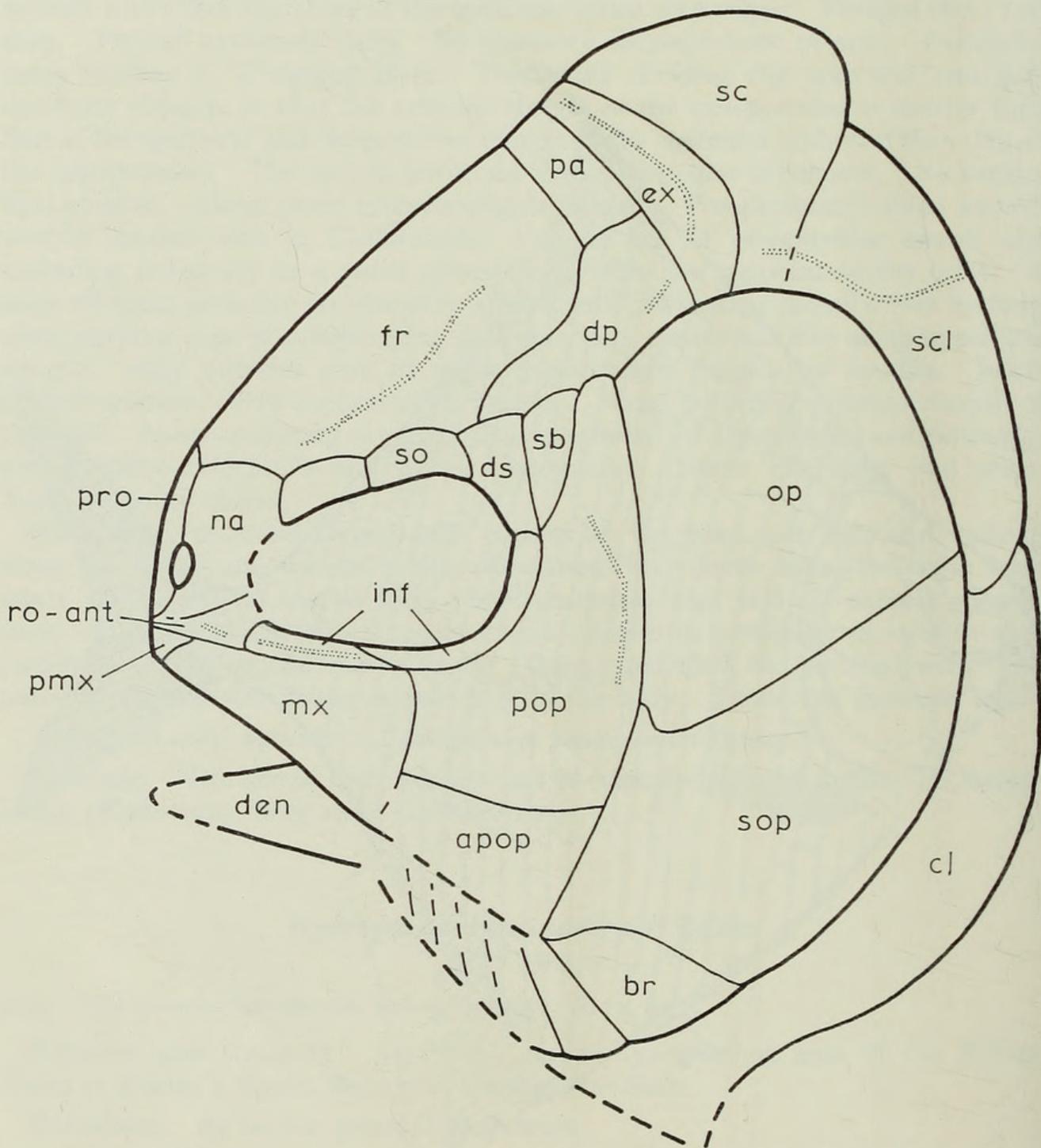


FIG. 46. *Hydropessum kannemeyeri* Broom. Restoration of skull and pectoral girdle, $\times 5.5$ approx.

corner and the subopercular with rugae which radiate from its antero-ventral corner. Six or seven branchiostegal rays are present.

The preopercular is 'L'-shaped. Its dorsal part is narrow and constricted anteriorly by a single triangular suborbital. The preopercular sensory canal does not extend to the dorsal tip of the preopercular, but turns antero-dorsally at a level just below that of the centre of the opercular. There is no dermohyal. The lower part of the preopercular is deep. It extends anteriorly so that the vertical suture between it and the maxilla lies below the centre of the orbit. The ventral part of the preopercular is separated from the upper jaw margin by a rectangular bone which sutures anteriorly with the maxilla, dorsally with the preopercular and posteriorly with the subopercular. This bone is clearly not a fragment of the maxilla because it bears fine striae which, in some cases, run at right angles to those on the maxilla (P.16181, Fig. 47). The identity of this bone is uncertain, there being no obvious way of deciding whether it is a quadratojugal or a separate preopercular element. There are no traces of the preopercular sensory canal on this bone. Tentatively this bone will be called an accessory preopercular.

The maxilla is wedge-shaped and very short, so that it contributes to only half of the upper jaw margin. At its tip there is a small premaxillary element (P.16180). No teeth were observed. The dorsal part of the snout is composed of a median postrostral which separates the broad nasals. The nasal probably borders the anterior edge of the orbit. The snout is completed by a wedge-shaped rostro-antorbital.

The lower jaw is only partially preserved (P.16181, Fig. 47). It is deep and tapers anteriorly. When restored to match the length of the upper jaw, it appears to have been a short, rather heavy structure. No dentary teeth were observed.

Pectoral girdle. All the pectoral elements are ornamented with elongate sinuous rugae. The suprascapular lies immediately behind the extrascapular, and is 'D'-shaped and extremely large.

The supracleithrum is broad and its rounded ventral end extends below the level of the posterior part of the suture between the opercular and subopercular. There are faint traces of a suture between the cleithrum and a clavicle (P.16180).

Paired fins. The pectoral fin is poorly preserved in specimen G.N. 358 where it has at least 8 rays, but no other details can be seen.

There is no trace of the pelvic fin in any specimen, and it seems likely that it is not present (c.f. *Bobasatrania* and *Amphicentrum*).

Unpaired fins. The anterior rays of both the dorsal and anal fins arise at the deepest part of the body. Only the proximal ends of the rays in both cases are preserved and the exact shape of these fins is therefore unknown. In both fins, however, the anterior rays bear fringing fulcra and are closely spaced and become increasingly widely separated posteriorly. No jointing was observed in the dorsal fin-rays but there were indications of bifurcation. In the anal fin jointing is definitely present, but no bifurcation was seen. It is likely that the rays were jointed and bifurcating in both fins.

The caudal fin is borne on a short body lobe. There are 30 rays, 10 of which are

epaxial in position. The anterior rays of both the dorsal and ventral lobe are closely spaced, bear fringing fulcra and are long. The tail has a high aspect ratio. All the caudal fin-rays are bifurcated, the longest rays twice.

Squamation. There are 34 body transverse scale rows. There is no reversal of the scale rows below the pectoral fin as is seen in *Cleithrolepis*. The scales are deepest in the lateral line region where the depth of some is almost 10 times their length (this ratio takes into account only that part of the scale which is not overlapped by adjoining scales). The scales close to the dorsal and ventral edges of the body

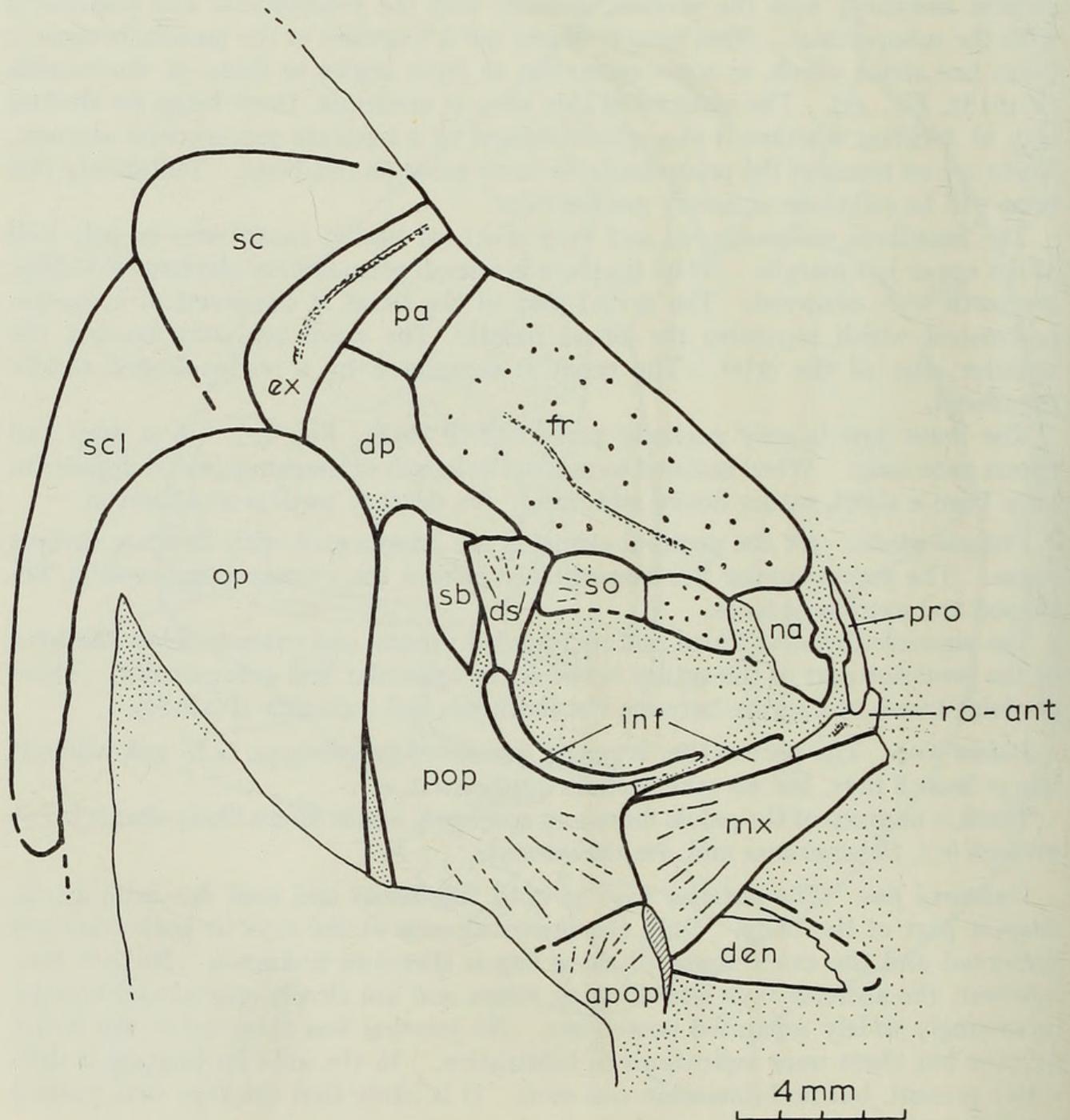


FIG. 47. *Hydropsessum kannemeyeri* Broom. P.16181: impression of left side.

are almost equidimensional, those close to the base of the anal fin being particularly small. The flank scales bear an ornament of long rugae, while those at the dorsal and ventral edges of the body have short sinuous rugae.

GENERA PROVISIONALLY ASCRIBED TO PERLEIDIFORMES

Cleithrolepis cuyana Bordas

1944 *Cleithrolepis cuyana* Bordas: 457-458, pl. 2.

HORIZON AND LOCALITY. Triassic. Bituminous rocks, Santa Clara, Mendoza and San Juan provinces, Argentina.

REMARKS. This form is deep-bodied and has a skull with a blunt snout and large orbits. The bones of the skull, however, have not been preserved well enough to allow any description. Thus the inclusion of this form in the genus *Cleithrolepis*, or even the order Perleidiformes, remains provisional.

Dipteronotus cyphus Egerton

1854 *Dipteronotus cyphus* Egerton: 369-371, pl. 11, figs 1-2.

1910 *Dipteronotus cyphus* Egerton; Woodward: 322-323.

HORIZON AND LOCALITY. Lower Keuper, Bromsgrove, Worcestershire.

HOLOTYPE. G.S.M. 18188 and counterpart 18189, the only specimen known.

REMARKS. The body shape of *D. cyphus* is extremely similar to that of *Cleithrolepis* and *Cleithrolepidina* in that there is a dorsal 'hump' occurring almost halfway along the body. The dorsal and anal fins lie posterior to the deepest part of the body, but do not appear to extend as close to the caudal fin as they do in *Cleithrolepis* and *Cleithrolepidina*. The anterior dorsal fin identified by Egerton (1854: 370) in fact consists of a group of displaced body scales. Little of the skull anatomy can be determined except that the orbit is large and anteriorly placed, and the opercular series orientated vertically. The scales do not bear any ornament and are deep, but not as deep as in known cleithrolepids.

III. DISCUSSION

(a) Classification of the Redfieldiiformes.

(i) *Brookvaliidae* and *Redfieldiidae*.

The differences between the families *Brookvaliidae* and *Redfieldiidae* are as follows:

Brookvaliidae

1. Orbit large.
2. Dermosphenotic narrow and crescent-shaped, tapering to a point anteriorly.

Redfieldiidae

- Orbit small.
- Dermosphenotic deep and roughly rectangular.

- | | |
|--|--|
| 3. Infraorbitals narrow, reduced in some genera. | Infraorbitals never reduced. |
| 4. Antorbital excluded from snout margin by toothed element (probably a premaxilla). | Antorbital bordering ventral margin of snout. No premaxilla. |
| 5. Adnasal absent or small, having, at most, point contact with dermosphenotic. | Adnasal large with broad contact with dermosphenotic. |
| 6. Four parietals (except <i>Atopocephala</i> which has two). | Two parietals (except <i>Helichthys</i> which has four, and <i>Redfieldius</i> which has three or four). |
| 7. Posterior part of supraorbital sensory canal, if present, on dermopterotic. | Posterior part of supraorbital sensory canal, if present, on parietal. |
| 8. Antopercular present. | No antopercular (except in two species of <i>Helichthys</i>). |
| 9. Lower jaw slender, long and curved dorsally towards the symphysis. | Lower jaw deep, short, and either straight or curved dorsally towards the symphysis. |

In order to compare the orbit size in the various redfieldiiform genera, measurements were taken from restorations in this study, from Schaeffer (1967) and in one case (*Dictyopyge decipiens*) from Brough (1931). A vertical line was drawn which passed halfway between the anterior and posterior edges of the orbit. The height of the orbit, and of the head, was measured along this line and the ratios between these two measurements calculated (Table 1).

TABLE 1

The relative orbit size in redfieldiiform genera.

Genus	Vertical	Vertical	A
	height of orbit in mm	height of skull in mm	—
	A	B	B
Brookvaliidae			
<i>Ischnolepis</i>	51.5	69	0.75
<i>Atopocephala</i>	38	52	0.73
<i>Brookvalia</i>	43	59.5	0.72
<i>Phlyctaenichthys</i>	43	60.5	0.71
Redfieldiidae			
<i>Daedalichthys</i>	45	73	0.62
<i>Helichthys</i>	31	58	0.53
<i>Geitonichthys</i>	34.5	71.5	0.48
<i>Molybdichthys</i>	42.5	78	0.54
<i>Dictyopyge (decipiens)</i>	14	34	0.41
<i>Cionichthys</i>	20.5	34.5	0.59
<i>Redfieldius</i>	18.5	34	0.54
<i>Lasalichthys</i>	20	35.5	0.56
<i>Synorichthys</i>	20.5	36.5	0.56

The value of this data by itself might be regarded as slight, but significantly, the

relative orbital sizes can be correlated with the shape of the dermosphenotic. In the brookvaliids this element is curved and narrow, tapering to a point anteriorly, whereas in redfieldiids it is deep and rectangular except that its ventral edge is excavated where it borders the orbit.

The snout of the North American redfieldiids is now well known (Schaeffer 1967). The antorbital is a large element bordering the anterior edge of the orbit, the ventral edge of the snout and the ventral edge of the nostril. There is a large adnasal between the dorsal part of the antorbital and the anterior end of the dermosphenotic. The dorsal part of the nostril is bordered by a narrow nasal, and the postrostral may or may not be present. The snout tip is capped by a rostral and there is no premaxilla.

The Lower Triassic African redfieldiids, *Daedalichthys* and *Helichthys*, have an identical snout pattern to that just described. The Middle Triassic Australian genera, *Geitonichthys* and *Molybdichthys* are also very similar, differing only in the shape of the antorbital which is rectangular and extends so far anteriorly that it borders the anterior as well as the posterior edge of the nostril. Participation of the antorbital in the infraorbital bar is limited.

The snout of brookvaliids is rarely well preserved, but enough of its structure is now known to suggest important differences between the two families. In the Brookvaliidae, a toothed element excludes the antorbital from the ventral margin of the snout. The antorbital is a narrow crescent-shaped element bordering the anterior edge of the orbit. Its anterior part is limited to a narrow projection which borders the ventral edge of the nostril, and which carries the ethmoid commissure. The adnasal is either a small diamond-shaped element having point contact or no contact with the dermosphenotic (*Brookvalia*), or is lacking altogether (*Ischnolepis* and probably *Atopocephala* and *Phlyctaenichthys*).

The cheek region in both families is variable but differences can be related to the evolution of a more upright suspensorium, a trend which occurred independently in various genera.

(ii) *Schizurichthyidae*.

Schizurichthys is known by a single species, *S. pulcher*, which is incompletely preserved, but which has several characteristics unique among the Redfieldiiformes. It obviously represents a group quite isolated from other known members of the order, and therefore a new family, Schizurichthyidae, is proposed to include the genus.

The unique characters of the Schizurichthyidae are seen in the configuration of the snout elements, the length of the lower jaw and the structure of the caudal fin and scales.

The dermosphenotic is similar to that of the Brookvaliidae in that it is crescent-shaped and comes to a point anteriorly. The antorbital borders the anterior edge of the orbit, but is excluded from the ventral edge of the snout by a toothed element. Unlike the Brookvaliidae, however, the antorbital is deep ventrally, so that its shape resembles that of an inverted hatchet. The profile of the snout as a whole differs

from that of both the Brookvaliidae and Redfieldiidae in that the upper jaw runs smoothly to the snout tip, and is not sharply upturned just below the orbit.

The lower jaw is moderately deep and curves dorsally towards the symphysis. It is unique in that it extends to the level of, or even beyond, the snout tip.

The tail has a structure unknown in any redfieldiiform, and is probably unlike that of any known actinopterygian. The 6 anterior rays of the upper caudal fin lobe originate on the dorsal side of the body lobe. The first and sixth rays bear fringing fulcra. The seventh ray, which originates at the tip of the body lobe, also bears fringing fulcra (Fig. 28).

The scales of brookvaliids and redfieldiids vary in shape from rhombic to leaf-shaped. They are smooth, or bear ornament consisting of one to four elongate rugae. In *Ischnolepis* the rugae are seen to consist of single rows of closely associated tubercles. The posterior margins of the scales of *Daedalichthys* are denticulated, but their overall shape is still rhombic. The scales of *Schizurichthys* vary in shape from subcircular to rectangular (Fig. 30). They bear pronounced pegs on their dorsal edges and sockets on their ventral edges, and they are ornamented with rows of tubercles which radiate from a point close to the antero-dorsal corner of the scale. In these three characteristics, the scales of *Schizurichthys* are unique within the Redfieldiiformes.

(iii) *Redfieldiiformes*—discussion

Orbit and dermosphenotic. Brough (1936 : 400) has suggested that during the evolution of the Redfieldiiformes (his Catopteridae) the orbit became smaller. This view is difficult to substantiate. In the first instance, the series showing supposed reduction of the orbit (Brough 1936 : text-fig. 10) is not arranged in strict stratigraphic order; secondly, genera considered here to belong to separate families were then discussed together. The fact that redfieldiids, which have small orbits, were more abundant than brookvaliids during the Upper Triassic, gave apparent support to the incorrect hypothesis that there was an evolutionary trend in the Redfieldiiformes towards a decrease in orbit size. There is, in fact, little evidence of any change in orbit size in either the redfieldiids or the brookvaliids: *Helichthys* has an orbit comparable with those of Upper Triassic redfieldiids, and the earliest known brookvaliid, *Ischnolepis*, has an orbit very similar to that of *Brookvalia*.

Schaeffer (1967 : 331) is of the opinion that the narrowness of the dermosphenotic in *Atopocephala* is related to the large size of the orbit, but in *Brookvalia* to posterior expansion of the frontal. The second interpretation was necessary because in Wade's figure of *Brookvalia* (1935 : text-fig. 5) the vertical height of the orbit is underestimated. In fact, the orbit in *Brookvalia* is large, and there seems to be no reason to suppose that the narrowness of the dermosphenotic is related to any factor other than the large orbit.

Infraorbitals. Brough (1936 : 401) remarks that loss of infraorbitals (his sub-orbital bones) constitutes 'one of the clearest trends to be observed in the family'. In view of his opinion that another trend was towards reduction of orbital size, this opinion seems, on theoretical grounds, surprising. Once again, there is no evidence of any particular evolutionary trend with regard to the infraorbitals. What is

apparent is that the infraorbitals are narrow or reduced in the brookvaliids, and slightly broader in redfieldiids. This slight difference is almost certainly related to the difference in orbital size between the two families.

Cheek region. In refuting Brough's opinion (1936 : 390) that there was a trend within the Redfieldiiformes from oblique to vertical orientation of the suspensorium, Schaeffer (1967 : 335) states that, with the exception of *Brookvalia*, there is little change in this character from early to late Triassic times. I cannot agree with this latter opinion. The angle between the anterior edge of the subopercular and the ventral region of the maxilla (an angle more easily measured than the true angle of the suspensorium, and certainly related to it) varies as much as 10° within the families Brookvaliidae and Redfieldiidae (cf., for example, *Ischnolepis* with *Phlyctaenichthys*, and *Geitonichthys* with *Cionichthys*). As few of the known redfieldiiform genera are closely related to one another, this variation implies that the angle of the suspensorium was becoming steeper in several phylogenetic lines within the order.

Pectoral girdle and fins. Watson (1925 : 824) has shown that the palaeoniscoid pectoral fin is primitively broad based with an insertion which runs parallel to the body axis. In later palaeoniscoids the base of the pectoral fin became narrower (White 1939 : text-fig. 12) and its orientation relative to the rest of the body also changed. Westoll (1944 : 83) has shown that the base of the pectoral fin in haplolepidids, and probably in most palaeoniscoids, is inserted so that the anterior end of the fin base is slightly raised. The functional explanation for this orientation is that in this position the pectoral fin acts as a hydrofoil providing lift at a point anterior to the centre of gravity of the fish; this counteracts the lift created by the swimming movement of a heterocercal tail.

In *Ischnolepis* the pectoral fin appears to be inserted on a vertical margo radialis, and it is possible that the pectoral fin in the other Redfieldiiformes was similarly orientated.

The function of a vertically orientated pectoral fin is to act as a brake, a function found almost exclusively in teleosts. If the pectoral fin of Redfieldiiformes functioned in a similar way it would appear to have lost its original hydrodynamic function. One of the most distinctive characteristics of Redfieldiiformes (exclusive of the Schizurichthyidae) is the upturned snout. This snout is probably an adaptation to special feeding habits, but it quite possibly could have performed a secondary, hydrodynamic function, and allowed other selective pressures to influence the orientation of the pectoral fin.

When a fin acts as a brake rather than as a hydrofoil, it is subjected to direct water pressure, and so must be fairly rigid. The pectoral fins of Redfieldiiformes (and to a lesser extent the pelvic fins) are remarkable in that their structure is modified to a considerably greater extent than is the structure of the other fins (Brough 1936 : 391). The rays have few joints or are unjointed, and are stout compared with other fin-rays.

(b) A functional analysis of the redfieldiiform skull.

The redfieldiiform skull resembles that of most other palaeoniscoids in that the maxilla is firmly fused to the preopercular and to the infraorbital bones. The

orientation of the suspensorium varies from oblique to vertical. There are, however, several anatomical features which indicate that the Redfieldiidae, at least, had a specialized feeding mechanism. That this mechanism was efficient is indicated by the ubiquity of the family at a time when forms with the holostean feeding mechanism were rapidly replacing the more primitive palaeoniscoids.

Two important functions of the fish skull are, firstly, to provide a flow of water over the gills, and secondly, to contain an efficient feeding mechanism. These will now be discussed in turn with reference to the Redfieldiiformes.

(i) *Gill ventilation.*

Hughes and Shelton (1958) have emphasized that gill ventilation depends upon the operation of two pumps; the buccal cavity which, when adducted, acts as a force pump; and the opercular cavities which, on abduction of the operculars, act as suction pumps. Abduction of the operculars closely follows adduction of the buccal cavity so that a more or less continuous flow of water overcomes the resistance of the gill. Moreover, 'Depending upon the relative size of the cavities and on the extent of their volume change, it is possible for either the buccal pressure pump or the opercular suction pump to become the dominant ventilating mechanism in different species' (Hughes & Shelton 1958 : 822).

There are three indications that the redfieldiiform opercular pump was weak. In most genera the opercular series is remarkably narrow, in consequence the underlying opercular cavity could not have been very large. Also the presence of only one branchiostegal ray must, as noted by Schaeffer (1967), have restricted the opercular opening to the side of the head. Thirdly, evidence from *Ischnolepis* and *Brookvalia* shows that the hyomandibular did not articulate with the opercular at a point close to the latter's antero-dorsal corner. As a result, contraction of the dilator operculi could only have had a limited effect on the opercular, and it seems likely that abduction of the opercular was neither extensive nor powerfully executed. If the opercular pump was weak, it follows that the buccal pump was correspondingly powerful, for there is no reason to suppose that the Redfieldiiformes could ventilate their gills by continuous swimming as do some teleosts. A result of having a powerful buccal pump is that an unusual feeding mechanism in the Redfieldiidae was made possible.

(ii) *Feeding*

The main differences between the three redfieldiiform families appear to be broadly related to different methods of feeding. *Schizurichthys* is similar to many palaeoniscoids in which the upper and lower jaw tooth rows are long, with the lower jaw extending to a point level with the tip of the snout, and in which the suspensorium is oblique. These characters indicate that *Schizurichthys* was probably a predator in which feeding consisted of simply seizing food in the jaw and swallowing small prey whole, or biting pieces off a larger mass.

The brookvaliids show few departures from this method of feeding, and were probably quite versatile in their habits. The fact that the lower jaw is slightly shorter than the upper jaw indicates that these genera probably fed on the bottom

for at least some of the time, and stomach contents in *Brookvalia gracilis* which appear to consist of small molluscs (P.15847, P.15848, P.17013, P.24711 and P.24712) support this hypothesis.

The redfieldiids were also bottom feeders, and Schaeffer (1967) has suggested that they scooped detritus from the river or lake bottom. Whilst agreeing in general with this hypothesis, I believe there is good evidence that the redfieldiids were active suction feeders.

In teleosts the buccal cavity is an effective suction pump not only because it is capable of extreme expansion, but also because this expansion is supplemented by the upper and lower jaws which can be thrust anteriorly to form a protrusible tube. Such a mechanism is not possible in redfieldiids because the gape of the jaws is long, and abduction of the lower jaw would cause immediate loss of negative pressure created by abduction of the branchial basket. However, it is quite likely that considerable negative pressure in the buccal cavity could be achieved by independent abduction of the branchial basket. In this connection it should be noted that in all redfieldiid genera, the lower jaw is consistently shorter than the upper jaw. The length of the lower jaw cannot be correlated with forward shift of the jaw articulation for, even in a genus such as *Daedalichthys* which has an oblique suspensorium, the tip of the lower jaw falls well short of the level of the snout tip. In consequence the redfieldiid buccal cavity may have opened ventrally through a crescent-shaped gap, even when the jaws were closed.

The mechanism by which the branchial basket is abducted in actinopterygians has been described by Schaeffer and Rosen (1961). First the ventral part of the pectoral girdle is pulled postero-ventrally by the ventro-lateral muscles inserted on the cleithrum, then the anterior part of the copula and of the hyoid bar is pulled postero-ventrally by the sternohyoid muscle which extends from the cleithrum to the hyoid bar. If, as I suggest, such expansion of the buccal cavity in the Redfieldiidae was capable of producing a suction powerful enough to be used as a feeding device, one would expect the development of an unusually extensive ventro-lateral and sternohyoid musculature. Such development would be reflected by the size of the copula and of the ventral part of the pectoral girdle. Unfortunately, copulae are not preserved in any redfieldiid, but comparison with the Brookvaliidae shows that the cleithrum in the Redfieldiidae is an exceedingly large and robust element.

As well as the muscles described above, the levator arcus palatini assisted expansion of the buccal cavity by pulling the ventral part of the hyomandibular forwards (Gardiner 1967b). Normally this muscle is considered to have had its origin on the lateral wall of the braincase, as it does in *Polypterus* (Edgeworth 1935), and pressure of this muscle on the overlying dermal bones is held to be responsible for fragmentation of the suborbital in many palaeoniscoids. With the possible exception of *Redfieldius*, all redfieldiid genera are characterized by a large unfragmented suborbital. As one would expect the levator arcus palatini to be well developed in any suction feeder, spread of the origin of this muscle onto the inner surface of the suborbital is likely, thus explaining the latter's size and undivided state. Supporting this reconstruction is the fact that in redfieldiids the suture between the suborbital

and the anterior part of the preopercular is always orientated at right angles to the line of action of the levator arcus palatini. Such an alignment would ensure most efficient resistance to stresses created by contraction of the levator arcus palatini.

The most convincing evidence that the redfieldiids were suction feeders is the structure of the snout. As noted above, the ventral edge of the snout extends well beyond the tip of the mandible. The antorbital is large and extends posteriorly along the infraorbital bar. Both the antorbital and the rostral bear tubercles which, as suggested by Schaeffer (1967), would have helped support a fleshy lip. Such a lip would function to control the flow of water into the buccal cavity during abduction of the branchial basket.

In conclusion, various modifications of the redfieldiid skull are readily interpreted as adaptations towards suctorial feeding. Although the jaw gape was long, the mouth could function as a terminal suctorial organ when abduction of the branchial basket was achieved independently of abduction of the lower jaw.

Although small pieces of food were sucked into the buccal cavity, more conventional methods of feeding were also employed by the redfieldiids. The presence of teeth on the posterior border of the maxilla indicates that the lower jaw could be abducted to accommodate larger food masses. Adduction of the lower jaw is achieved by contraction of the adductor mandibulae. This muscle was completely enclosed by the dermal cheek elements, and the presence of an internal flange on the preopercular of *Ischnolepis* indicates that at least part of the adductor mandibulae had its origins on this bone in some redfieldiiforms.

One final redfieldiiform character remains to be considered, the presence of a single branchiostegal. The loss of the branchiostegal series in redfieldiiforms cannot be correlated with a forward shift of the jaw articulation for, as noted above, some genera have an oblique suspensorium. Loss of branchiostegals may possibly have allowed greater flexibility of the buccal floor, an important consideration in fish in which the buccal pump is more important than the opercular pump in maintaining a respiratory current. The single branchiostegal which is retained almost certainly acted to tie the ventral end of the opercular series to the throat region.

(c) Growth of the tail in *Brookvalia*, and some notes on palaeoniscoid body lobe squamation.

Wade (1935 : 27) has described the gradual appearance of scales in a growth series of *B. gracilis*. Here, a closer examination is made of the growth and development of the caudal region in that species. Four stages in the development of the tail in *B. gracilis* are represented by the following specimens: P.15810 (total length 31.5 mm); P.24710 (66 mm); U.S.G.D. 42 (76 mm); and an uncatalogued specimen in the University Museum of Zoology, Cambridge (115 mm); (Fig. 48).

In P.15810 the body, including the body lobe, is scaleless. The body lobe axis lies at 14° to the body axis, a lower angle than in larger specimens in which this angle is 26° . The dorsal border of the body lobe bears at least 11 paired basal fulcra which are short and broad (P.15810 and P.15807). There are 44 rays, 32 of which are contained in the ventral lobe. They are all unjointed and unbifurcated. Two

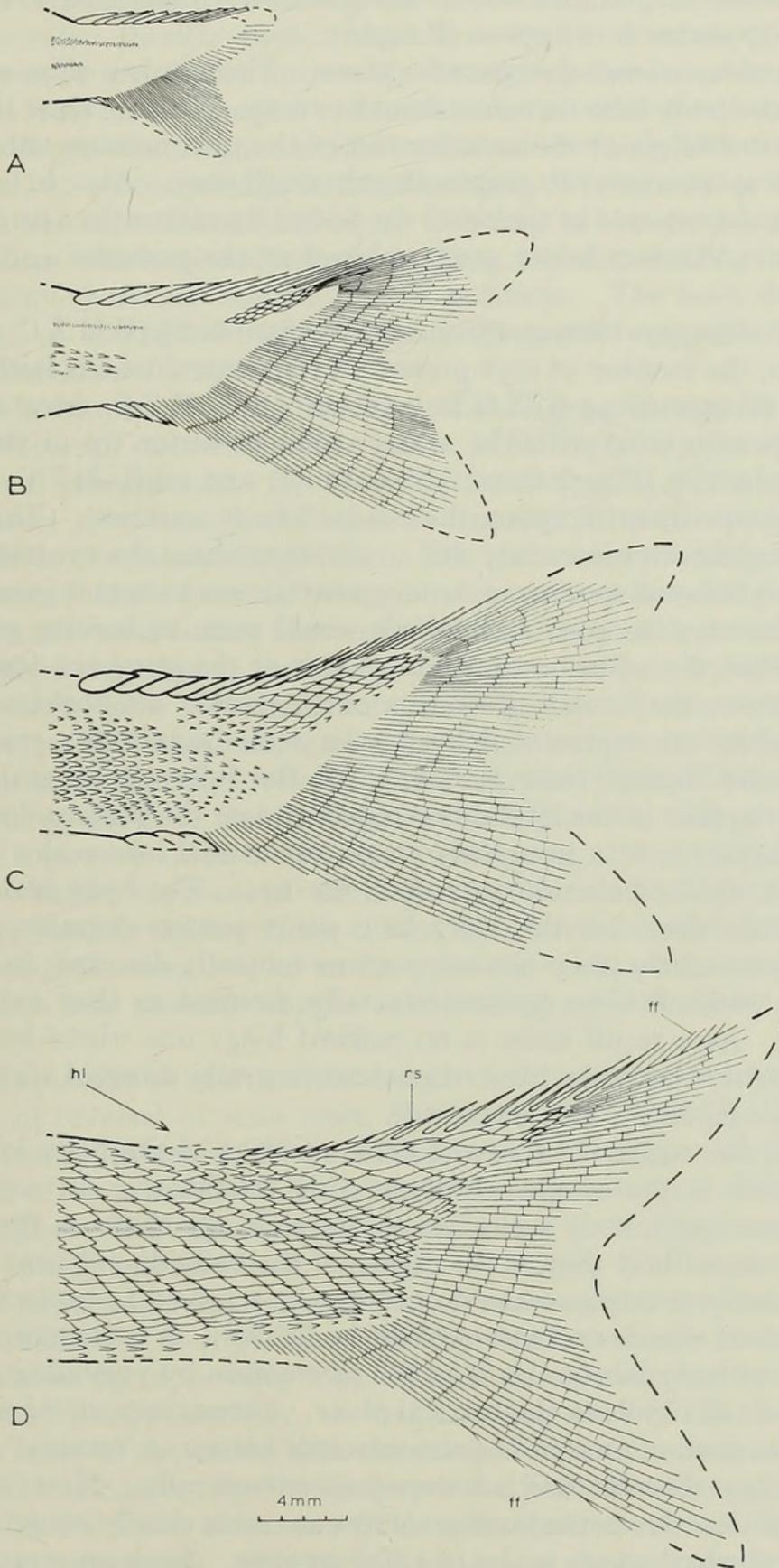


FIG. 48. *Brookvalia gracilis* Wade. Series showing growth and development of caudal fin. (A) P.15810; (B) P.24710; (C) U.S.G.D. 42; (D) U.M.Z.C. uncatalogued.

bands of carbonaceous granules extend along the body flank and it is between these bands that body scales first appear (P.24710).

As the tail grows, several changes take place. The number of basal fulcra on the dorsal side of the body lobe increases from 11 to 15. This increase is certainly due to development of fulcra at the anterior end of the row, because anterior fulcra are smaller in large specimens of *B. gracilis* than in small ones. Also, in large specimens, posterior fulcra are inserted at the tip of the body lobe rather than further anteriorly, indicating that additional fulcra are developed at the posterior end of the row as well.

The number of fin rays increases from 44 (P.15810) to 63 (U.M.Z.C. uncatalogued). In spite of this, the number of rays present in the ventral lobe is fairly constant; 32 (P.15810), 38 (P.24710), 34 (U.S.G.D. 42) and 37 (U.M.Z.C. uncatalogued). The number of rays associated with the scales at the posterior tip of the body lobe is also fairly constant; 9 (P.24710), 10 (U.S.G.D. 42) and 11 (U.M.Z.C. uncatalogued) (in the smallest specimen, P.15810, the caudal lobe is scaleless). Thus the increase in the number of fin-rays is mainly due to addition along the ventral margin of the body lobe. In almost all specimens the long ventral rays have nine joints, and increase in length of the rays in larger individuals would seem to involve growth between joints, rather than the addition of new segments at the proximal end of the ray.

As noted above, very small specimens of *B. gracilis* are scaleless. When they first appear, scales are represented by narrow scale buds which gradually become broader until the characteristic leaf-shape of the fully grown scale is apparent. Scale buds first appear in the lateral line region and on the postero-dorsal part of the body lobe (P.24710). At a very early stage, the caudal lobe scales become closely associated with eight or nine dorsal caudal fin-rays. The body scales are directed posteriorly, while those on the body lobe point postero-dorsally. As the body scales extend posteriorly, they become postero-ventrally directed; in a similar way, the body lobe scales become postero-ventrally directed as they extend anteriorly (U.S.G.D. 42). As a result there is no marked hinge line where body and caudal scales meet; rather there is a band of postero-ventrally directed scales crossing the caudal peduncle (U.M.Z.C. uncatalogued).

Smith (1956) has suggested that the main function of the body lobe squamation in palaeoniscoids is protection. I doubt this conclusion. In some forms, e.g. *Birgeria* (Nielsen 1949), body scales are absent although those on the body lobe are retained. It seems likely that, if the organs of the body do not need the protection afforded by a scaly covering, scales would not be retained to protect the relatively unimportant blood vessels and nerves of the body lobe. It is far more likely that the main function of body lobe scales is to aid locomotion by providing an exoskeleton which holds the tail rigidly in the vertical plane. Strong supporting evidence of this view is the phenomenon present in palaeoniscoids known as 'reversal' of caudal scale rows. The body scale rows of all fish slope postero-ventrally. Kerr (1952) has shown that in *Lepisosteus* scales in the same scale row are more closely bound to one another by connective tissue than are scales of adjacent rows. Such an arrangement allows lateral flexibility of the body. In fish with heterocercal tails, efficient locomotion demands that the body lobe be laterally flexible whilst remaining rigid in the vertical

plane, and this is achieved by close association of body lobe scales in rows which run antero-ventrally (Smith 1956). Antero-ventrally orientated, or reversed, body lobe scale rows are almost universally found in palaeoniscoids, and it is concluded that this is so for mechanical rather than for protective reasons.

Returning to *B. gracilis*, the mechanical function of the body lobe scales is stressed by the fact that, at an early stage in development, the posterior scales are closely associated with the dorsal caudal fin-rays. Rigidity of the caudal lobe is assisted by the basal fulcra which extend anteriorly along the dorsal side of the body lobe as far as the 'hinge' which crosses the caudal peduncle. The early development of basal fulcra and of caudal lobe squamation in *B. gracilis* suggests that these fish were active swimmers early in life.

Study of the development of the squamation in *B. gracilis* suggests very strongly that so called 'reversal' of caudal scale rows is, in this species at least, an apparent rather than a real phenomenon. As noted by Smith (1956 : 10), when scales meet 'heel to toe', scale rows can be regarded as running antero-ventrally or postero-ventrally. Such is the case in *B. gracilis*. The main reason for regarding postero-ventrally orientated scale rows as being homonomous (*sensu* Simpson 1961 : 93) with the body scale rows, is that the angle between body scale rows and the body axis (40°) is exactly the same as that between postero-ventral caudal scale rows and the axis of the caudal lobe. The difference in orientation of scale rows on body and body lobe is thus readily explained, not by reversal of scale rows, but by the fact that the 'tail does not at first during development turn upwards' (Moy-Thomas 1939 : 109), an occurrence noted above in the development of *B. gracilis*. Also it may be noted here that there is no reversal of direction of overlapping of scales on the caudal lobe of *B. gracilis*. Varied mechanical demands, for lateral flexibility at the caudal peduncle and for verticle rigidity of the caudal lobe, have therefore been met, not by reversal of caudal scale rows, but by variation in the orientation of individual scales within rows which bear constant angular relationships with the body and body lobe axes.

If the caudal squamation of *B. gracilis* can be readily interpreted without recourse to the concept of reversal of scale rows, it is likely that the squamation of other palaeoniscoids can be interpreted in a similar way. I believe this to be possible, even in the case of forms in which the hinge line marks a sudden change from body to body lobe scales. The tails figured here (Fig. 49) do not represent changes in squamation in closely related forms, but they do suggest how apparent reversal of body lobe scale rows may have taken place. *Paramesolepis tuberculata* (Fig. 49A) is clearly unspecialized in that postero-ventrally orientated scale rows ran from the body to the posterior tip of the body lobe. The scale rows become more horizontally orientated as they pass posteriorly, so that the long axes of the diamond-shaped posterior scales come to lie parallel with the caudal lobe axis. Such an arrangement gives the body lobe maximum rigidity in the vertical plane (Smith 1956). To achieve the same effect in *Turseodus dolorensis* (Fig. 49B), the ventral half of a single scale row (arrowed) is bifurcated. Similar bifurcation of body scale rows frequently occurs near the bases of the anal and dorsal fins in palaeoniscoids. In high aspect ratio tails, the need for such bifurcation is greater because the scale rows on the caudal

peduncle must be turned through a larger angle if the posterior scale rows are to achieve the orientation which gives maximum rigidity to the caudal lobe. In *Pteronisculus stensioei* (Fig. 49C), one scale row has bifurcated twice (large arrow), and another only once. If such bifurcation takes place frequently, the postero-ventral orientation of the scale rows becomes obscured and the postero-dorsal rows of adjacent scales becomes more apparent. The illusion of scale row reversal is thus due to repeated bifurcation of postero-ventrally orientated scale rows. Finally, if repeated bifurcation only takes place posterior to a particular scale row, a distinct

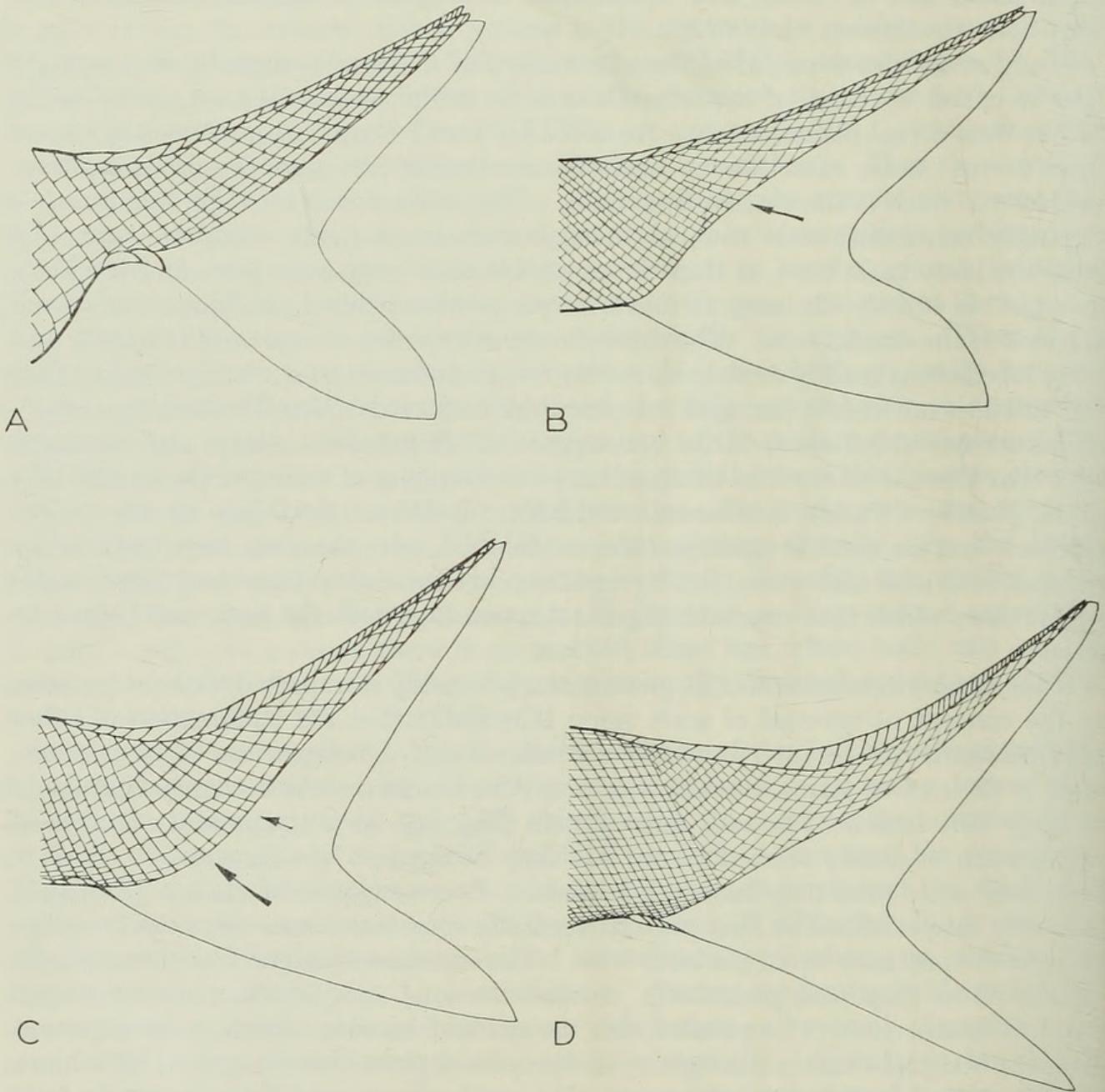


FIG. 49. The squamation of the body lobe in different palaeoniscoids. (A) *Paramesolepis tuberculata* (Moy-Thomas and Dyne 1938). (B) *Turseodus dolorensis* (Schaeffer 1967). (C) *Pteronisculus stensioei* (Nielsen 1942). (D) *Pygopterus nielsenii* (Aldinger 1937).

boundary, or hinge line, between body and body lobe scales occurs at that scale row (e.g. *Pygopterus nielsenii* Fig. 49D). Associated with the formation of a hinge line is the development of specially shaped transitional scales (see Smith 1956 : text-fig. 5).

The contrary view to that outlined above has recently been expressed by Patterson (1968 : 231), who argues: 'That this (reversal of caudal scale rows) is a real change in orientation of the scales is shown by the reversed direction of the overlapping of the scales and of the keels and peg-and-socket joints on the inner surface of the caudal scales'. The change in direction of overlapping in caudal scales noted by Patterson occurs in *Pholidophorus falcifer* (Schultze 1966 : text-fig. 11b). However, as the mechanical function of caudal scales has been relieved in pholidophorids by anterior development of the uroneurals (Patterson 1968), it is possible that their condition is recently evolved, and has little relevance to the condition seen in the Chondrostei.

(d) Classification of the Perleidiformes.

(i) *Colobodontidae*.

Of the genera included in this family (see Gardiner 1967 : 200), the following are sufficiently well known to provide a useful basis for discussion; *Colobodus*, *Dollopterus*, *Manlietta*, *Meidiichthys*, *Mendocinia*, *Meridensia*, *Perleidus*, *Pristisomus* and *Procheirichthys*. Several authors have indicated the various characters which these genera share (e.g. Brough 1931 and Schaeffer 1955) and it is generally accepted that they should be included in a single family. Whether or not the cleithrolepids should be included with these genera has been a more controversial topic and is discussed below. The most recent diagnosis of the family is that of Schaeffer (1955 : 19), to which nothing can be added here except that, in my opinion, it is doubtful that the antorbital is absent in colobodontids, as he suggests.

Although many characters are shared by various colobodontids, I cannot agree with Schaeffer (1955 : 15) that 'the known perleidids . . . have a relatively stable pattern'. For example, whereas *Colobodus koenigi* has twelve branchiostegal rays (Stolley 1920 : pl. 11, fig. 5), *Meidiichthys browni* has only three (Fig. 32). Again, *Manlietta crassa*, unlike other known genera, has no postrostral, the nasals meeting in the midline (Fig. 35). Whenever such variation occurs, it is usually possible to identify the more primitive condition by making comparisons with the condition typically found in palaeoniscoids. By employing such methods, a picture of the skull of a hypothetical colobodontid ancestor has been constructed (Fig. 50). This hypothetical fish will be called Y. Although Y has many characteristics typical of palaeoniscoids, it would nevertheless fall within the definition of the family Colobodontidae. Y will now be described briefly, so that the different ways in which known colobodontids have diverged from this type may be appreciated.

In Y the skull roof slopes gently towards the snout and is composed of three pairs of bones; narrow extrascapulars, square parietals and elongate frontals which are broad posteriorly and which are excavated along their ventral edges where they pass

above the orbit. The dermopterotic is rectangular. In all colobodontid genera except *Meidiichthys* and *Meridensia* the skull roof is steeply inclined towards the snout, and in *Perleidus* the extrascapular is fairly broad. In *Meidiichthys* and *Perleidus* the dermopterotic is narrow.

In Y the opercular series is moderately inclined, and is composed of an opercular and a subopercular which are roughly equal in size. There are at least thirteen branchiostegal rays. In *Colobodus*, *Dollopterus*, *Manlietta* and *Mendocinia* the opercular and subopercular bones are also equal in size, but in *Meridensia* the opercular is slightly larger than the subopercular, and in all other genera the opercular is smaller than the subopercular. In *Colobodus* and *Meridensia* there are about eleven branchiostegals, but in all other genera there are six or fewer.

The cheek region in Y consists of a broad, high, 'r'-shaped preopercular, and a triangular dermohyal and suborbital. Variations of this pattern in colobontid genera include the loss of the dermohyal in *Meridensia* and probably also in *Procheirichthys*, subdivision of the preopercular in *Manlietta*, and fragmentation of the dorsal border of the preopercular in *Perleidus* to give two or three spiracular elements. In

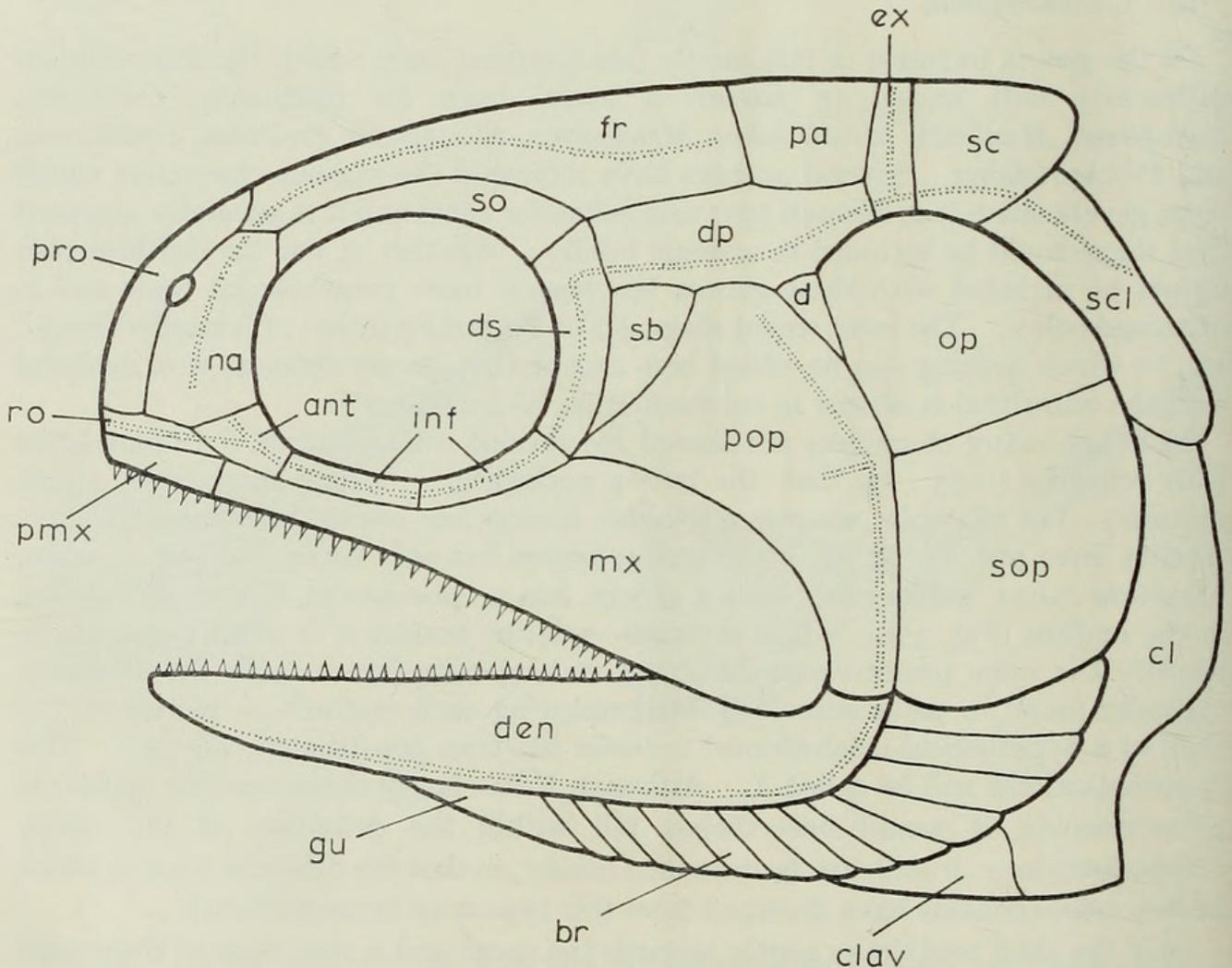


FIG. 50. Restoration of the skull and pectoral girdle of a hypothetical colobodontid ancestor.

all colobodontids the exact shapes of the preopercular and of the posterior part of the maxilla vary with the angle of the opercular series (cf. for example *Manlietta* with *Mendocinia*).

In Y the snout is composed of paired nasals which border the anterior orbital edge, and which are separated by a postrostral. The ventral part of the snout probably consists of paired rostrals, antorbitals and premaxillae, but this restoration is quite hypothetical because the ventral part of the snout in known colobodontids is rarely preserved. In *Meidiichthys* the postrostral is large and flat and gives the snout a profile with a blunt appearance which is unique amongst the colobodontids. In *Manlietta* the postrostral is lost and the nasals meet in the midline. As a result the nostrils have migrated to the ventral edge of the nasals and so parallel the condition seen in haplolepidids (Westoll 1944).

The circumorbital bones are fairly stable in colobodontids. Y is figured with a single supraorbital element bordering the dorsal edge of the orbit. This is probably the condition seen in *Colobodus* and *Dollopterus*, while in other genera this bone has fragmented, usually into three elements. In *Meridensia* the supraorbitals are reduced so that the frontal borders the orbit for a short distance.

The pectoral girdle in Y consists of four paired dermal elements, 'D'-shaped suprascapulars, supracleithra, cleithra and clavicles. This same condition is seen only in *Meidiichthys*; in all other colobodontids the clavicles are either lost or fused to the cleithra. *Perleidus* and *Procheirichthys* are unusual in that their suprascapulars are widely separated, a condition which was probably present in the colobodontid ancestor of the Cleithrolepididae.

From the above comparisons it is clear that it is almost impossible to postulate phyletic lines within the family which include more than one known genus. The only exception to this may be the case of *Manlietta* and *Mendocinia* which are extremely similar in many respects. All genera have characteristics which may be thought of as being primitive in terms of the family as a whole, but no genus is consistently more primitive than any other genus. It may be concluded, therefore, that there may have been as many separate phyletic lines within the Colobodontidae as there are known genera. If this is so, the known genera represent but a small sample of a radiation which must have taken place in Triassic times.

(ii) *Cleithrolepididae* and *Hydropessidae*

The family Cleithrolepididae was erected by Wade (1935 : 47) to include three genera, *Cleithrolepis*, *Dipteronotus* and *Hydropessum*. To these can be added a fourth, *Cleithrolepidina*, erected in 1940 by Berg.

The phylogenetic relationship between the Cleithrolepididae and other chondrosteian families is uncertain. Early views on this topic have been summarized by Brough (1931 : 269) and Wade (1935 : 47). In 1931 Brough, in a discussion of the systematic position of *Cleithrolepis minor* (now *Cleithrolepidina minor*, see above), says: 'The acceptance of the view that *Cleithrolepis* is a Platysomid derivative would involve the institution of a new family and, considering the doubt, it is better at present to regard it as a deep-bodied Perleidid' (1931 : 270). Four years later Wade did erect a new family saying ' . . . it is in the highest degree probable that

Cleithrolepis is derived, not directly from the Palaeoniscoids, but from the Platyosomids, and that it should, therefore, be placed in a new family, the Cleithrolepidae . . . ' (1935 : 48). In 1941 Wade modified this opinion somewhat. After a discussion in which he compared the species *Cleithrolepis minor* and *Cleithrolepis granulata*, he concluded that the two forms were different and that *C. minor* was a typical perleidid whereas *C. granulata* was quite distinct from the Perleididae (Colobodontidae). He continued ' . . . we must conclude that if *C. minor* is a member of the Cleithrolepidae, this family must have arisen from some ancestor common to both Perleididae and Cleithrolepidae' (Wade 1941 : 392). Similar doubts about inclusion of *C. granulata* and *C. minor* in the same genus were expressed by Berg (1940), who separated them into distinct taxa, *Cleithrolepis* and *Cleithrolepidina*. However, he included both these genera in the family Cleithrolepidae [sic].

Most recent reviewers of actinopterygian classification have assumed that the Cleithrolepididae is a valid taxon and have favoured close association between it and colobodontids; Berg, Cleithrolepidae in Perleidiformes (1940 : 405); Lehman, *Cleithrolepis*, *Dipteronotus* and *Hydropessum* in Perleididae (1966 : 115-116); Gardiner, Cleithrolepididae in Perleidiformes (1967c : 190).

Five questions arise from this brief review of recent literature on cleithrolepids:

- (1) Do *C. granulata* and *C. minor* represent separate genera?
- (2) If so, can *Cleithrolepis* and *Cleithrolepidina* be included in one family, the Cleithrolepididae?
- (3) If so, can other genera hitherto regarded as being similar to *Cleithrolepis* be included in the Cleithrolepididae, and if not, to what family do they belong?
- (4) What are the evolutionary relationships of Cleithrolepididae?
- (5) What are the evolutionary relationships of genera hitherto regarded as similar to *Cleithrolepis* but not included in the Cleithrolepididae?

These questions are discussed in turn here and at the beginning of the next section.

(1) Descriptions given above of *C. granulata*, *C. minor* and *C. extoni* show that two genera are present. *C. granulata* is included in the genus *Cleithrolepis* and *C. minor* and *C. extoni* in the genus *Cleithrolepidina*. The differences between these genera are not, however, those suggested by Berg (1940 : 405).

(2) Granted that *Cleithrolepis* and *Cleithrolepidina* are valid genera, can they be included in one family? Wade implied that this was not possible (Wade 1941b : 391-2) but his arguments have been discussed above with the conclusion that the differences noted by Wade merited at most generic status, and do not therefore merit separation of *Cleithrolepis* and *Cleithrolepidina* into separate families. Far more significant than the few differences between *Cleithrolepis* and *Cleithrolepidina*, are the large number of similarities between the two genera. The more important of these are:

1. The nasal is probably separated from the orbital edge.
2. The opercular is smaller than the subopercular.
3. A small triangular dermohyal present.
4. A slender lower jaw.
5. An accessory dermopterotic which lies ventral to the extrascapular.
6. The lack of a suprascapular.

7. The body shape—the dorsal side is strongly convex and forms a hump.
8. The unpaired fins have their origins close to the caudal fin and well posterior to the deepest part of the body.
9. The scales covering the pectoral region are orientated antero-ventrally.

This suite of characters strongly suggests that *Cleithrolepis* and *Cleithrolepidina* can be united within a single family.

(3) Before a diagnosis for the family Cleithrolepididae was constructed, other genera hitherto regarded as being similar to *Cleithrolepis* were examined to discover whether they share the suite of characters listed above. There are two such genera, *Dipteronotus* and *Hydropessum*.

Dipteronotus is poorly preserved. Its only characters which can be distinguished and which are found in the list above are: the body shape, the dorsal side is strongly convex, forming a hump, and the ventral side is also fairly strongly convex; and the positions of the unpaired fins, the dorsal and anal fins lie close to the caudal fin, well posterior to the deepest part of the body. No features can be discerned which suggest that *Dipteronotus* is not related to *Cleithrolepis* and *Cleithrolepidina*. *Dipteronotus* therefore may be provisionally viewed as being related to the cleithrolepids, but there is little strong evidence in support of this view.

Hydropessum is fairly well preserved and a new description has been given above. When the known features of this genus are compared with those of the cleithrolepids, many differences are at once apparent.

Cleithrolepis and *Cleithrolepidina*

Nasal probably separated from orbital border.

Opercular smaller than subopercular.

A dermohyal present.

Lower jaw slender.

Accessory dermopterotic ventral to extra-scapular.

Suprascapular absent.

Dorsal side of body strongly convex and humped, ventral side convex.

Unpaired fins close to caudal fin, lying well posterior to deepest part of body.

Scales covering pectoral region orientated antero-ventrally.

Hydropessum

Nasal bordering orbital border.

Opercular larger than subopercular.

No dermohyal.

Lower jaw robust.

No accessory dermopterotic.

Suprascapular present.

Body diamond-shaped with roughly straight antero-dorsal, postero-dorsal, antero-ventral and postero-ventral sides.

Unpaired fins distant from caudal fin, lying with their anterior edges at the deepest part of the body.

Scales covering pectoral region orientated postero-ventrally.

It is therefore clear that, although *Hydropessum* is superficially similar to the cleithrolepids, there are enough differences between the two forms to warrant separation at familial level. The diagnosis of the Cleithrolepididae has been emended to include only the genera *Cleithrolepis*, *Cleithrolepidina* and *Dipteronotus*, and a new family, Hydropessidae, erected to include the genus *Hydropessum*.

(e) Evolution of the Perleidiformes.

The evolution of the Colobodontidae has been discussed above (p. 333). The relationships of the Cleithrolepididae and the Hydropessidae with the Colobodontidae will now be discussed in turn.

(i) *Cleithrolepididae*.

Early discussions on the origin of the cleithrolepids have emphasized the similarities of body shape between *Cleithrolepis* and *Platysomus* (Egerton 1864 : 3 and Woodward 1890 : 38). More recently, advocates of cleithrolepid-platysomid relationship have been Brough (1931 : 270) and Wade (1935 : 48). Some of the points of similarity between the two groups, such as the postero-dorsal slope of the skull roof and the presence of a hump anterior to the dorsal fin (Wade 1935) could be expected in any deep-bodied form whatever its ancestry, and therefore have little or no importance in this context. Another supposed point of similarity, the peculiar position of the post-temporal (suprascapular) (Brough 1931 : 270) can be discounted because the suprascapular is in fact lost in cleithrolepids. The bone identified by Brough as post-temporal in *C. minor* is here identified as an accessory dermopterotic. Lastly, because *Cleithrolepis granulata* has radials in advance of the anterior edge of the dorsal fin, Wade has suggested that its ancestor had a long dorsal fin, and that *Hydropessum* was this ancestor, linking *Cleithrolepis* with *Platysomus* (Wade 1935 : 48). This theory can now be shown to be untenable because the new description here of *Hydropessum* demonstrates that this genus differs from *Cleithrolepis* and must have had an entirely separate ancestry.

Although the case for platysomid and cleithrolepid relationship is weakened by evidence included here, there is, in my opinion, positive evidence which shows that cleithrolepids could not have evolved from platysomids. In *Cleithrolepidina* the maxilla is shallow, the infraorbital series narrow and the anterior border of the orbit close to the snout tip—all palaeoniscoid characters. The earliest representatives of the two platysomid families are Lower Carboniferous (Tournaisian) in age (e.g. *Paramesolepis* and *Platysomus*—Platysomidae, and *Cheirodopsis*—Amphicentridae) (Gardiner 1967a). In all these forms the maxilla is deep and triangular, the infra-orbital deep and the snout tip elongated into a beak which extends a considerable distance antero-ventrally from the anterior orbital border (Moy-Thomas & Dyne 1938). Thus platysomids, as soon as they appear in the fossil record, have specialized features which preclude them from direct ancestry to the cleithrolepids.

Having ruled out the platysomids as possible cleithrolepid ancestors, it remains to discuss a more likely candidate. Brough (1931 : 269) admits that cleithrolepids have many features in common with colobodontids, but doubted that these were of phylogenetic significance because he was unable to point to any form with a body shape intermediate between the fusiform type seen in typical colobodontids and the deep type seen in cleithrolepids. However, there do not seem to be valid reasons for this doubt. The earliest cleithrolepids occur in rocks of Lower Triassic age. It is likely, therefore, that their ancestors were alive in Upper Permian times. But there are no known Upper Permian colobodontids, because their record, too, does not begin until Lower Triassic times. It is therefore impossible with the present state of

knowledge to point to an actual cleithrolepid ancestor among the colobodontids. However, this does not disprove relationship between the two groups, and it remains possible that the two are descended from a common Permian ancestor. This possibility will now be examined.

Cleithrolepids and colobodontids such as *Meidiichthys* share a large number of features. The most primitive known cleithrolepid is *Cleithrolepidina*, and a list of features common to *Cleithrolepidina extoni* and *Meidiichthys browni* is impressive and certainly suggests common ancestry. They are:

1. A skull roof containing square parietals, a long narrow dermopterotic and a long frontal which is excavated above the orbit.
2. An upright opercular series containing an opercular which is smaller than the subopercular.
3. A single triangular dermohyal.
4. A single suborbital.
5. A preopercular bearing a horizontal sensory canal and with an antero-ventral process which extends between the maxilla and the infraorbital series.
6. The dermosphenotic, supraorbital and infraorbital elements are shaped similarly in the two forms.
7. A large, similarly shaped antorbital, anteriorly placed.
8. A snout composed of rectangular nasals, separated by a long postrostral, and paired antorbitals.
9. An essentially palaeoniscoid maxilla.
10. Unpaired fins with jointed, bifurcating rays which bear fringing fulcra.

There are, of course, differences between the two forms. Characters developed in *Cleithrolepidina extoni* but not in *Meidiichthys browni* can, in the main, be related to the evolution of a laterally compressed body and of a deep skull. These are:

1. A postero-dorsally sloping skull roof.
2. The absence of the suprascapular.
3. The development of an accessory dermopterotic.
4. The insertion of a postcleithrum in the pectoral girdle.

These characters are specifically related to the evolution of a greatly increased depth of the posterior part of the skull. In palaeoniscoids the dorsal part of the pectoral girdle must have been braced against the posterior part of the braincase through the suprascapular. This arrangement presumably remained unchanged throughout most of palaeonisciform history, for the 'D'-shaped suprascapular is one of the most conservative elements of the order. With the evolution of deep-skulled forms such as *Platysomus*, the suprascapular became enlarged so that the pectoral girdle could retain contact at its dorsal end with the braincase. A similar need in cleithrolepids appears to have been satisfied in a novel way. The suprascapular, instead of being enlarged, is lost entirely. This loss has been accompanied by the development of a new association, that between the dorsal end of the supracleithrum and an element here called an accessory dermopterotic. The accessory dermopterotic lies ventral to the extrascapular, unlike the suprascapular which lay posterior to it. Thus in cleithrolepids the pectoral girdle remains braced against the posterior

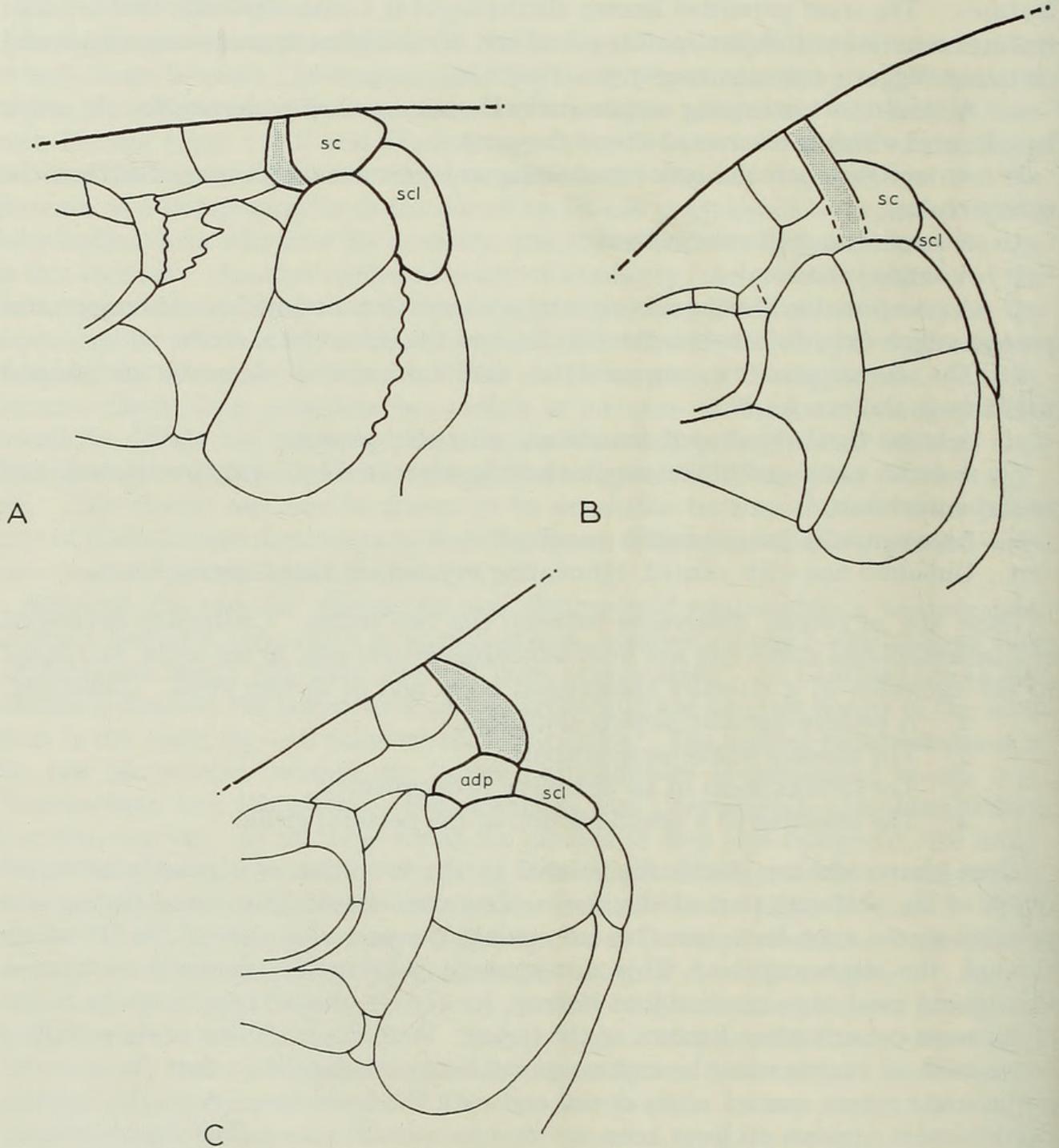


FIG. 51. Series showing the possible change in function of the extrascapular (stippled), during the evolution of a cleithrolepid from a colobodontid ancestor. The skulls are drawn to standard length, and orientated to the same base line to demonstrate the accompanying change of inclination of the skull roof. (A) *Meidiichthys browni* (Broom). (B) *Procheirichthys ferox* Wade. (C) *Cleithrolepidina extoni* (Woodward).

part of the skull, but in such a way as to allow dorsal extension of the dermal skull roof to evolve, in order to accommodate an increase in the depth of the body, without disturbing the pectoral girdle.

It is tempting to suppose that the accessory dermopterotic in cleithrolepids is homologous with the postspiracular seen in *Perleidus piveteaui* (Lehman 1952 : text-fig. 86) but the presence of part of the infraorbital sensory canal on the former bone in *Cleithrolepis granulata* makes this unlikely, and is the reason for identifying it as a fragment of the dermopterotic.

The change from the palaeoniscoid pectoral girdle to that of cleithrolepids involved not only rearrangement and loss of elements, but also a change in direction of the thrust acting through the supracleithrum. In palaeoniscoids the head of the supracleithrum butts against the roughly horizontal ventral edge of the suprascapular—the condition also seen in most colobodontids. In cleithrolepids the supracleithrum butts against the posterior edge of the accessory dermopterotic which faces posteriorly. Unfortunately there is no intermediate form known which shows how this change of structural organization took place. The nature of such an intermediate form is, however, suggested by the condition seen in *Procheirichthys* (Fig. 34) and *Perleidus* (Lehman 1952 : text-fig. 86) which have fairly deep skulls, though not as markedly deep as in cleithrolepids. In these genera the suprascapular elements are widely separated and probably occupied an area which bordered equally the ventral part of the extrascapular posterior margin and the postero-dorsal part of the opercular. Such an arrangement would cause the suture between the supracleithrum and the suprascapular to become more ventrally directed. It would probably also bring the dorsal end of the supracleithrum close to the posterior part of the dermopterotic. Once a firm connection was established between these two elements, the suprascapular would be deprived of its function and would be lost (Fig. 51).

The presence of a postcleithrum in *Cleithrolepidina extoni* is probably also related to the evolution of greater depth of the posterior part of the skull; its presence enables the pectoral girdle to span an increased distance effectively without excessive elongation of the cleithrum. Finally, in *Cleithrolepis granulata*, which has an even deeper skull than is seen in *Cleithrolepidina*, the extrascapular has fragmented into four separate elements.

There are a few other features seen in cleithrolepids but not in colobodontids, but they do not appear to discount relationship between the two groups. These are: a slender, toothless or almost toothless, lower jaw; a quadratojugal at the jaw articulation.

The first is of minor significance. Obviously, loss of teeth implies adoption of specialized feeding habits, but the type of lower jaw seen in cleithrolepids could readily be derived from that seen in colobontids (or almost any palaeoniscoid).

The development of a quadratojugal in cleithrolepids is perhaps more surprising. There is little evidence that such a bone is present in all palaeoniscoids, although it has been reported in *Cheirolepis* (Westoll 1937a) and *Pteronisculus* (Nielsen 1942). It would appear therefore that the quadratojugal in cleithrolepids has evolved *de novo*. An exact parallel in this respect is seen in the Haplolepididae (Westoll 1944).

One final difference between cleithrolepids and colobodontids is the probable

presence in the former of an element which excludes the nasal from the orbital border. This is not a very significant difference because the cleithrolepid condition can readily be derived from that seen in colobodontids. In most of the cleithrolepid specimens studied, sensory canals were filled with calcite and so were readily visible. In no specimen was any trace of a sensory canal seen in the region immediately anterior to the orbit. It therefore seems likely that if a bone was in fact present in this area, it would probably consist of a supraorbital bone which had expanded ventrally, rather than an antorbital which had expanded dorsally.

It has been noted above that if the cleithrolepids are related to colobodontids, then their common ancestor was likely to have lived during Upper Permian times. The presence of a large number of branchiostegal rays in *Cleithrolepis granulata* supports this conclusion because all known colobodontids have a reduced number of branchiostegals and, if the ancestor to cleithrolepids was a colobodontid, it would need to be a primitive form which still retained about 13 branchiostegal rays. It may be noted here that the skull pattern seen in cleithrolepids could readily be derived from the hypothetical colobodontid ancestor Y (Fig. 50).

In conclusion therefore, the Cleithrolepididae, as defined here, is a family which shares many characters with colobodontids, and there is good evidence that the two groups had a common ancestor which, though not known, probably lived during Upper Permian times.

(ii) *Hydropessidae*.

Differences between *Hydropessum* and the cleithrolepids have been listed in the discussion of the Cleithrolepididae and Hydropessidae. The main reasons for concluding that *Hydropessum* merits recognition at familial level are as follows. The posterior part of the skull of *Hydropessum* is deep, but the supracleithrum retains contact with an enlarged suprascapular and is not modified as it is in cleithrolepids. More important, the bones of the cheek and upper jaw are specialized in shape and unlike those of any cleithrolepid, colobodontid or palaeoniscoid. Thus, although the condition of the pectoral girdle in *Hydropessum* suggests that it could be a primitive cleithrolepid, it is excluded from such a position by displaying other characters which are more advanced than those found in cleithrolepids. *Hydropessum* therefore is a representative of a phylogenetic line in which a deep body evolved, which is quite independent from that leading to cleithrolepids, and it remains to investigate the probable origin of the family.

Four families of deep-bodied fish should first be investigated in order to determine whether they may be related to the Hydropessidae; they are the Amphicentridae, Platysomidae, Dorypteridae and Bobasatraniaidae. The first two of these families cannot be regarded as ancestral to the Hydropessidae because of the specialized nature of their snouts. *Hydropessum* has narrow infraorbitals and its snout retains proportions normally associated with unspecialized palaeoniscoids. In a similar way, relationship between the Dorypteridae or Bobasatraniaidae and the Hydropessidae seems most unlikely. Both these families have specializations, such as heavy maxillae with crushing dentitions, which are not seen in the Hydropessidae.

One is therefore forced to look for possible ancestors of *Hydropessum* among fish

with fusiform bodies, and once again, the colobodontids appear to be the most satisfactory. A comparison between *Hydropessum* and *Meidiichthys* produces the following list of similarities:

A single suborbital.

Similarly shaped dermosphenotic, supraorbital and infraorbital elements.

A similarly shaped orbit.

A snout consisting of paired nasals separated by a postrostral and bordering the orbital border; paired antorbitals or rostro-antorbitals and paired premaxillae.

This list is not as impressive as a list of similarities between cleithrolepids and colobodontids, but it should be emphasized that *Hydropessum* displays characters so aberrant that comparison with any other known form is not likely to produce convincing evidence of phylogenetic relationship. The difficulty of assessing the taxonomic position of *Hydropessum* is increased by lack of knowledge of the jaw articulation. Only part of the lower jaw of *Hydropessum* is preserved, and it is not clear whether it articulates with the quadrate near the posterior part of the maxilla or near the postero-ventral corner of the accessory preopercular. If the former condition is present, the unusual shape of the preopercular is readily interpreted as a means by which the jaw articulation has been brought forward. If this were so, it would be tempting to assume that there is a coronoid process on the lower jaw, but once again there is no evidence on this point.

In conclusion, therefore, there is a little evidence which suggests that *Hydropessum* evolved from colobodontids but, if this did indeed happen, there is good evidence suggesting that the phyletic line leading from colobodontids to *Hydropessum* was quite independent of that leading from colobodontids to cleithrolepids.

(f) Origin of the Redfieldiiformes and Perleidiformes.

Early members of these orders are very similar to one another, and it is not surprising that genera from both were, until 1931, included in a single family, the Catopteridae (see Schaeffer 1967 : 329 for earlier classifications of these forms). Recent authors are of the opinion that there are few differences between the Redfieldiiformes and Perleidiformes. According to Schaeffer (1955) and Gardiner (1967c) these are the presence in the Redfieldiiformes of a single branchiostegal ray and an excess of fin-rays over radials in the dorsal and anal fins. In addition, Lehman (1952) notes the presence in perleidiforms of triturating teeth. There are in fact other valid differences between the orders, some of which were mentioned by Brough (1931 : 288). The most important of these is the presence of an unusual snout in the Redfieldiiformes, and the probable evolution of this feature will now be discussed in order to assess whether its presence gives any indication of the relationships of the group.

The redfieldiiform snout differs from that of palaeoniscoids in two important respects: the anterior orbital edge is bordered by the antorbital, not by the nasal, and there is a single large nostril, not two. Moreover, in the snout of the Brookvaliidae the antorbital is separated from the upper jaw margin by a premaxilla, while in the Redfieldiidae there is no premaxilla and the upper jaw margin is formed by the antorbital. The evolution of the brookvaliid and redfieldiid snouts from the

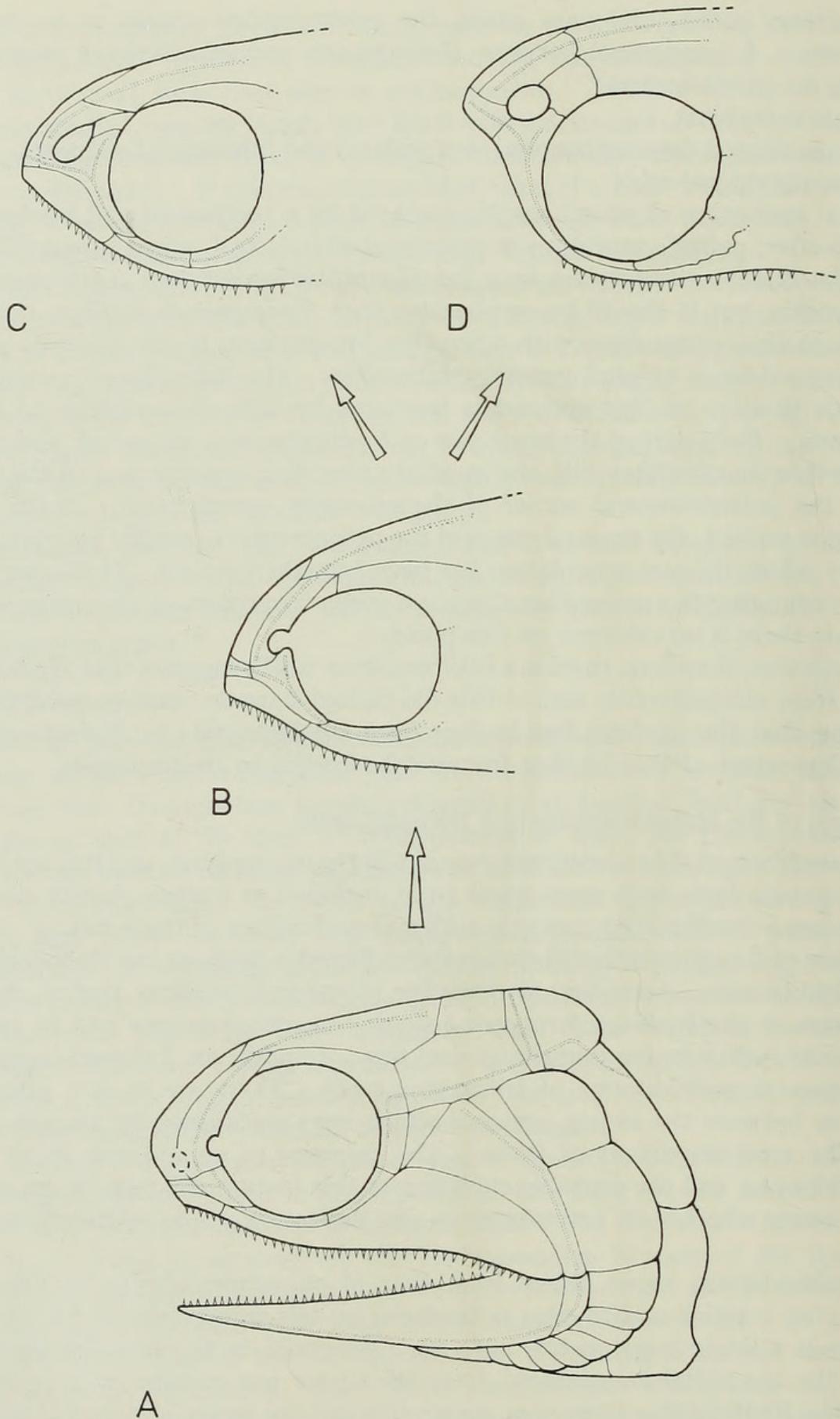


FIG. 52. The probable evolution of the redfieldiiform snout. (A) Hypothetical redfieldiiform ancestor. (B) Intermediate form in which dorsal extension of the dermosphenotic (or adnasal) begins to exclude the nasal from the anterior orbital border. (C) Brookvaliid type snout. (D) Redfieldiid type snout.

palaeoniscoid type is reconstructed in Fig. 52. The hypothetical snout (Fig. 52A) is typical of almost all palaeonisciform families, the anterior orbital edge being bordered by long nasals which are separated in the midline by a postrostral. Complete fragmentation of the rostro-premaxillo-antorbital is assumed to have taken place, for I have not seen any evidence which supports Gardiner's claim that 'the rostro-premaxillo-antorbital is still a single bone in the primitive members' (of the Redfieldiiformes) (1967 : 193). In the intermediate form (Fig. 52B) three changes may be noted:

(1) The anterior end of the dermosphenotic has begun to extend ventrally, excluding the dorsal part of the nasal from the orbital edge. (Fragmentation of the anterior end of the dermosphenotic, to give the redfieldiiform adnasal, may have been a synchronous event).

(2) The antorbital has begun to extend dorsally, thus excluding the ventral part of the nasal from the orbital edge, and is also beginning to take part in the posterior margin of the nostril. Such dorsal development of the antorbital has occurred several times during actinopterygian evolution, eg. in *Lawnia taylorensis* (Wilson 1953 : text-fig. 6), *Watsonulus eugnathoides* (Lehman 1952 : text-fig. 106), *Paracentrophorus madagascariensis* (Gardiner 1960 : text-fig. 66) and *Ichthyokentema purbeckensis* (Griffith & Patterson 1963 : text-fig. 6).

(3) The anterior nostril has either been lost or it has migrated around the ventral border of the nasal, and become confluent with the posterior nostril. Again, the latter event has been demonstrated in other actinopterygians (Gardiner 1963 : 315-318). Its occurrence in redfieldiids could possibly account for the large size of the nostril. Migration of the anterior nostril is usually correlated with loss of the postrostral, but this cannot be true in the case of the Redfieldiiformes, because the postrostral is almost invariably retained.

The intermediate form just described would readily give rise to the brookvaliid type of snout (Fig. 52C) if dorsal expansion of the antorbital continued until it met the adnasal, and to the redfieldiid type (Fig. 52D) if the same events were accompanied by the loss of the premaxilla. In both cases the nasal is reduced in size and becomes orientated so that it lies almost horizontally. As a result the nostril, which in most palaeoniscoids is ventral in position, assumes an unusually high position on the snout.

In a functional analysis of the redfieldiiform snout I have suggested that in both the brookvaliids and the redfieldiids many features can be related to bottom feeding. The changes which I now suggest must have taken place at an early stage, to produce the kind of snout seen in the Redfieldiiformes, may be related to this same habit. If the snout is frequently in contact with muddy river or lake bottoms, there would be an advantage in having the external nostril in a high position on the snout. This position has been achieved by shortening the nasal and by a change in its orientation so that its long axis lies roughly continuous with that of the frontal. Such alteration in the size and orientation of the nasal would lead to distortion of the orbit, and so would have necessitated the formation of a new anterior orbital edge; this has been achieved by dorsal growth of the antorbital.

Returning to the broader aspects of redfieldiiform relationships, it is likely that,

although the redfieldiiform snout is unusual, it can be simply derived from a common palaeoniscoid pattern, and its presence does not debar close relationship of the order with the Perleidiformes. The hypothetical ancestor of the Redfieldiiformes (Fig. 52A) is very similar to that constructed for the Perleidiformes (Fig. 50); the only differences between the two are that in the latter the preopercular is broad, and the dermosphenotic borders the dorsal, rather than the posterior orbital edge. It may be concluded that it is quite likely that the two orders have origins in closely related palaeoniscoid groups.

Brough (1936 : 403) has suggested that the redfieldiiforms, at least, may be derived from a palaeoniscoid found in the Bekker's Kraal fauna, *Dicelloypyge*. However, the holotype of *D. macrodentata*, the type species of the genus (Fig. 53), shows that this is unlikely for two reasons. Firstly, the area postero-dorsal to the orbit is covered, not by a single element (cf. Brough 1936 : text-fig. 1), but by a narrow dermosphenotic which is separated from the orbital edge by an equally narrow infraorbital-supraorbital element; secondly, an accessory opercular is present.

Gardiner (1967c) has suggested that a Carboniferous family, the Gonatodidae, is a probable ancestral group to the Redfieldiiformes and Perleidiformes. However, *Gonatodus* itself is an unlikely ancestral form for the Redfieldiiformes at least,

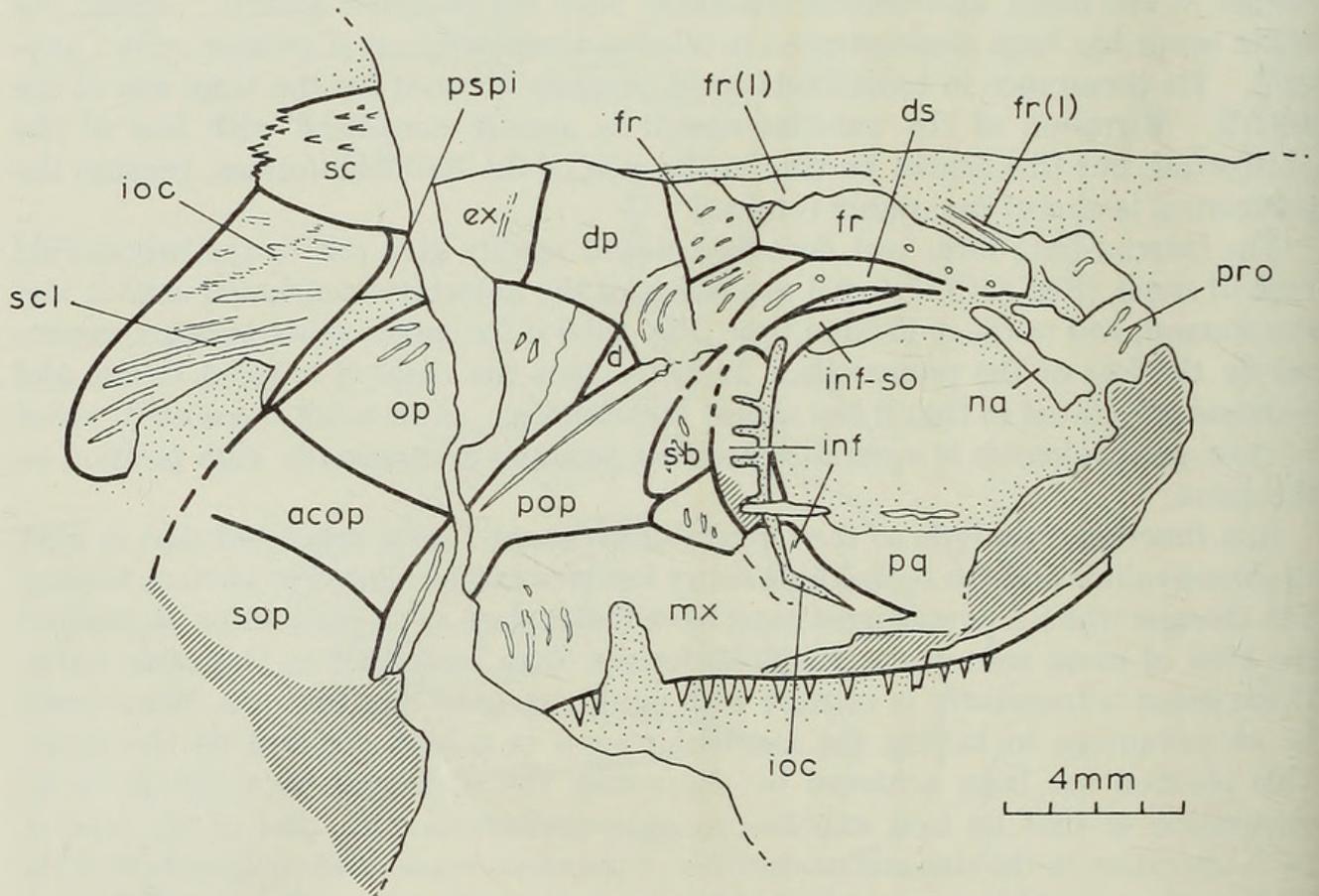


FIG. 53. *Dicelloypyge macrodentata* Brough. G.N. 322: right side unless otherwise indicated.

because the posterior part of the maxilla is already shorter than in forms such as *Ischnolepis* and *Brookvalia*. I believe that the ancestry of both the Redfieldiiformes and the Perleidiformes will eventually be found among the Elonichthyidae, Acrolepididae, Rhadinichthyidae complex of families.

IV. SUMMARY

1. The Redfieldiiformes and Perleidiformes from Triassic localities at Bekker's Kraal (Scythian of South Africa) and Brookvale (probable Ladinian of New South Wales) are redescribed. In addition, *Ischnolepis*, a redfieldiiform from Zambia, is redescribed.
2. The order Redfieldiiformes is divided into three families; the Brookvaliidae, the Redfieldiidae and the Schizurichthyidae *nov.*
3. The Brookvaliidae contains the following well known genera: *Ischnolepis*, *Atopocephala*, *Brookvalia* and *Phlyctaenichthys*. They are characterized by large orbits, narrow crescent-shaped dermosphenotics, a snout in which the antorbital is excluded from the upper jaw margin by a toothed element, and by a slender lower jaw. *Dictyopleurichthys* and *Beaconia* are synonymized with *Brookvalia*, and *Brookvalia parvisquamata* is shown to be a junior synonym of *B. gracilis*.
4. The Redfieldiidae contains the following well known genera: *Daedalichthys*, *Helichthys*, *Geitonichthys*, *Molybdichthys*, *Redfieldius*, *Cionichthys*, *Synorichthys* and *Lasalichthys*. They are characterized by small orbits, deep rectangular dermosphenotics, a snout in which there is no premaxilla and in which the antorbital borders the upper jaw margin, and by a short, robust lower jaw.
5. A new family, the Schizurichthyidae, is erected to contain the genus *Schizurichthys* which, although superficially similar to the brookvaliids, is unique in having scales which articulate with one another with peg-and-socket joints, and a caudal fin which has a separate epaxial lobe.
6. The order Perleidiformes is divided into four families; the Aetheodontidae (which is not discussed here), the Colobodontidae, the Cleithrolepididae and the Hydropessidae *nov.*
7. The Colobodontidae contains the following well known genera: *Dollopterus*, *Colobodus*, *Mendocinia* and *Perleidus* which are not found at either Bekker's Kraal or Brookvale, and *Meidiichthys*, *Procheirichthys* and *Manlietta*. Each colobodontid genus represents a separate phyletic line of a radiation which had Permian origins.
8. The Cleithrolepididae contains two well known genera, *Cleithrolepidina* and *Cleithrolepis*. *Cleithrolepis* differs from *Cleithrolepidina* in having an extremely deep snout and maxilla, and a fragmented extrascapular. *Cleithrolepis extoni* is shown to be a member of *Cleithrolepidina*.
9. A new family, the Hydropessidae, is erected to contain the genus *Hydropessum* which differs from the cleithrolepids in the structure of its skull and pectoral girdle, in the position of its unpaired fins, and in the orientation of the scales in its pectoral region.

- 10. The interrelationships between the redfieldiiform and perleidiiform families are summarized in Fig. 54.
- 11. A functional analysis is made of the redfieldiiform skull, and it is concluded that in the Redfieldiidae food was obtained by using the buccal cavity as a suction pump.
- 12. The growth and development of the tail in *Brookvalia gracilis* is described,

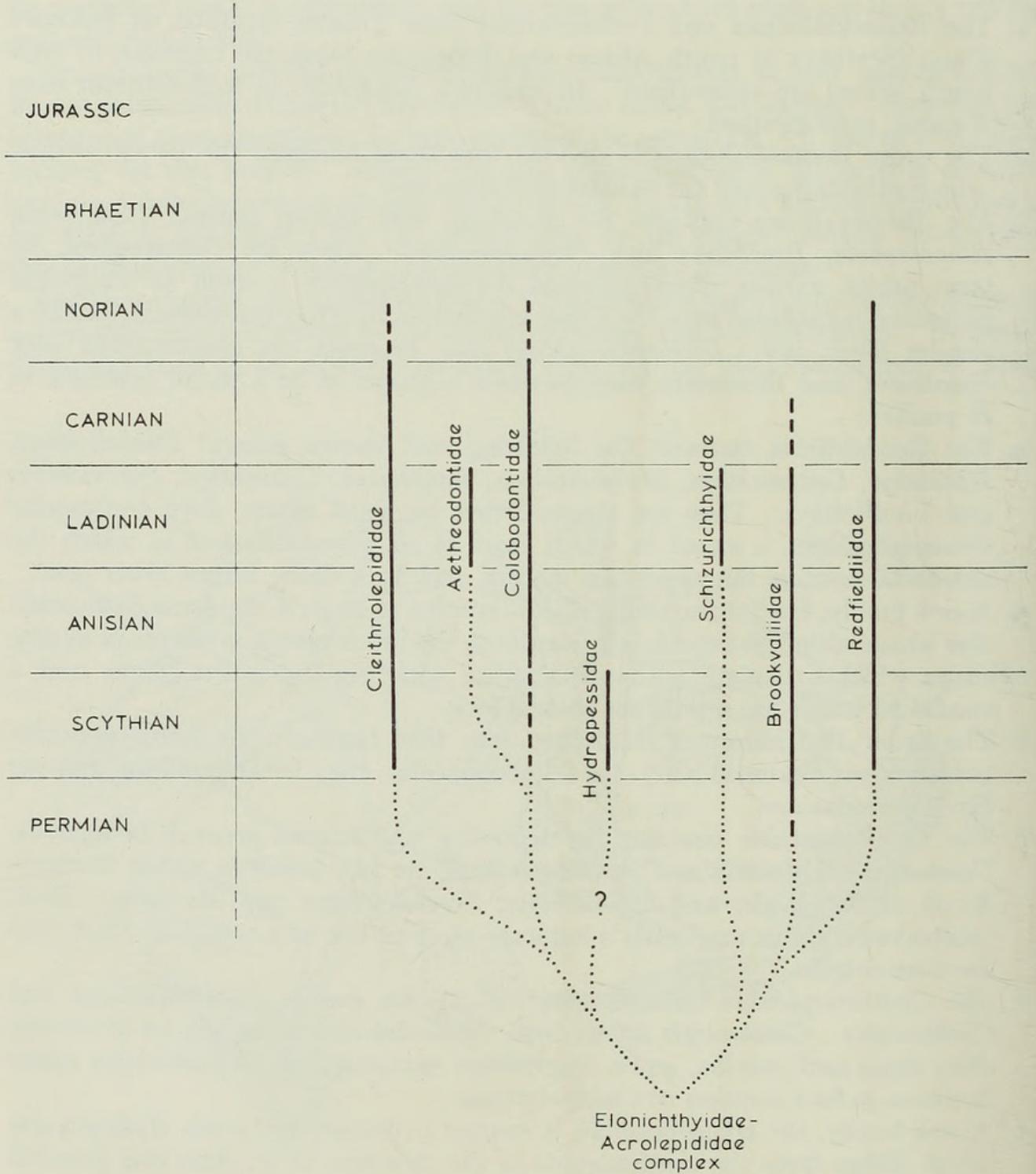


FIG. 54. Probable phylogenetic relationships between the redfieldiiform and perleidiiform families.

and the caudal lobe squamation in palaeoniscoids is discussed. It is concluded that reversal of caudal lobe scale rows does not occur in palaeoniscoids, and that the formation of a hinge line across the base of the caudal peduncle is the result of bifurcation of scale rows in the ventral region of the caudal lobe.

V. ACKNOWLEDGEMENTS

This paper represents part of a review of the Bekker's Kraal and Brookvale faunas completed for a Ph.D. degree in the University of London. I would like to thank my supervisor, Dr C. B. Cox of the Zoology Department, King's College, for his advice and criticism, and the following for allowing me to borrow so freely from the collections in their charge: Mr G. Z. Foldvary of the University of Sydney; Dr R. M. C. Eagar of the Manchester Museum; Dr T. S. Kemp of the University Museum of Zoology, Cambridge; Dr J. W. Pickett of the Geological Survey of New South Wales; and Mr H. A. Toombs and Dr C. Patterson of the British Museum (Natural History). I have learnt much about the preparation of fossil material from Mr C. I. Macadie of the Australian Museum, Sydney, and about other palaeoichthyological matters from Dr B. G. Gardiner of Queen Elizabeth College, London, and Dr J. Griffith of Westfield College, London. I would also like to thank Miss D. G. Thomas and Mrs M. Owens for typing the various drafts of this work, and finally Mr H. Friedhoff for much kindness and generosity.

VI. ABBREVIATIONS

The following abbreviations either indicate the name of an institution, or are used by the institution indicated as a prefix to the catalogue numbers of specimens in their collections:

AM.MF	The Australian Museum, Sydney.
A.M.N.H.	The American Museum of Natural History, New York.
B.M.(N.H.)	British Museum (Natural History), London.
D.M.S.W.	D. M. S. Watson collection (housed at the University Museum of Zoology, Cambridge).
F.	The Australian Museum, Sydney, unless otherwise indicated. (Some specimens at the Sedgwick Museum, Cambridge bear F.—catalogue numbers.)
G.N.	University Museum of Zoology, Cambridge.
G.S.M.	Institute of Geological Sciences, London.
L.	Manchester Museum.
P.	British Museum (Natural History), London.
S.A.M.	South African Museum, Cape Town.
S.U.P.	University of Sydney, Geology Department.
U.M.Z.C.	University Museum of Zoology, Cambridge.
U.S.G.D.	University of Sydney, Geology Department, unless otherwise indicated. (Some specimens at the University Museum of Zoology, Cambridge, bear U.S.G.D.-catalogue numbers.)

ABBREVIATIONS USED IN THE FIGURES

a	antopercular	iop	interopercular
acop	accessory opercular	(l)	left side
ad	adnasal	ll	lateral line
adp	accessory dermopterotic	lpop	lamina of the preopercular
an	angular	meck	meckelian bone
ant	antorbital	mx	maxilla
apop	accessory preopercular	na	nasal
art	articular	no	nostril border or nostril
b	branchial arch element	op	opercular
bf	basal fulcra	pa	parietal
br	branchiostegal ray	par	parasphenoid
cl	cleithrum	pcl	postcleithrum
clav	clavicle	pmx	premaxilla
co	coronoid	po	postorbital
d	dermohyal	pop	preopercular
den	dentary	pq	palatoquadrate
dp	dermopterotic	pro	postrostral
dpal	dermopalatine	proc	process
dpt	dermometapterygoid	pspi	postspiracular
ds	dermosphenotic	qj	quadratojugal
ecomm	ethmoid commissure	(r)	right side
ecpt	ectopterygoid	ro	rostral
ept	endopterygoid	ro-ant	rostro-antorbital
ex	extrascapular	ro-pmx	rostro-premaxillary
fam	foramen for the adductor mandibulae	rs	ridge scale
ff	fringing fulcra	sb	suborbital
fr	frontal	sc	suprascapula
gu	gular plate	scl	supracleithrum
hl	hinge line	so	supraorbital
hym	hyomandibular	soc	supraorbital sensory canal
inf	infraorbital	t	teeth
inf-so	infraorbital-supraorbital	tm	tube containing mandibular canal
ioc	infraorbital sensory canal	vo	vomer

VII. REFERENCES

- ALDINGER, H. 1937. Permische Ganoidfische aus Ostgrönland. *Meddr Grønland*, Kjøbenhavn, **102**, 3 : xlv + 392 pp., 44 pls.
- BALME, B. E. 1969. The Permian-Triassic boundary in Australia. *Spec. Publ. geol. Soc. Aust.*, **2** : 99-112, 3 tables.
- BANKS, M. R. *et al.* 1969. Correlation charts for the Carboniferous, Permian, Triassic and Jurassic Systems in Australia. 467-482 in *Gondwana Stratigraphy*. I.U.G.S. Symposium, Buenos Aires, 1-15 Oct. 1967. xvi + 1173 pp.
- BERG, L. S. 1940. Classification of fishes, both recent and fossil. *Trudy zool. Inst., Leningr.*, **5**, 2 : 517 pp. 190 figs.
- 1958. *System der rezenten und fossilen Fischartigen und Fische*. xii + 311 pp., 263 figs Deutscher Verlag, Berlin.
- BLOT, J. 1966. Étude des palaeonisciformes du Bassin de Commeny. *Cah. de Paléontologie*, Paris, 99 pp., 18 pls.
- BOCK, W. 1959. New eastern American Triassic fishes and Triassic correlations. *Geol. Cent. Res. Ser.*, Philadelphia, **1** : 184 pp.

- BOND, G. 1965. Some new fossil localities in the Karroo system of Rhodesia. *Arnoldia*, (Rhodesia), **11**, 2 : 1-4.
- BORDAS, A. F. 1944. Pesces triásicos de la Quebrada de Santa Clara (Mendoza y San Juan). *Physis B. Aires.*, **19** : 454-460.
- BROOM, R. 1909. The fossil fishes of the Upper Karroo beds of South Africa. *Ann. S. Afr. Mus.*, Cape Town, **7**, 3 : 251-269, 2 pls.
- BROUGH, J. 1931. On fossil fishes from the Karroo System, and some general considerations of the bony fishes of the Triassic period. *Proc. zool. Soc. Lond.* : 235-296, 4 pls.
- 1934. On the structure of certain catopteryd fishes. *Proc. zool. Soc. Lond.* : 559-571, 1 pl.
- 1936. On the evolution of bony fishes during the Triassic period. *Biol. Rev.*, Cambridge, **11** : 385-405, 12 figs.
- 1939. *The Triassic fishes of Besano, Lombardy*. ix+117+xiv pp., 7 pls. Brit. Mus. (Nat. Hist.), London.
- DRYSDALL, A. R. & KITCHING, J. W. 1963. A re-examination of the Karroo succession and fossil localities of part of the upper Luangwa valley. *Mem. Dep. geol. Surv. N. Rhod.*, Lusaka, **1** : 1-72, 7 pls.
- EASTMAN, C. R. 1905. A brief general account of fossil fishes. The Triassic fishes of New Jersey. *Geol. Surv. New Jersey*, Ann. Rept. for 1904: 29-102.
- 1911. Triassic fishes of Connecticut. *Bull. Conn. St. geol. nat. Hist. Surv.*, **18** : 1-75.
- EDGEWORTH, F. H. 1935. *The Cranial Muscles of Vertebrates*. ix+493 pp., 841 figs. Cambridge.
- EGERTON, P. G. 1854. On a fossil fish from the Upper Beds of the New Red Sandstone at Bromsgrove. *Q. Jl geol. Soc. Lond.*, **10** : 367-371, 2 figs.
- 1864. On some Ichthyolites from New South Wales, forwarded by the Rev. W. B. Clarke. *Q. Jl geol. Soc. Lond.*, **20** : 1-5, 1 pl.
- GAIR, H. F. 1960. The Karroo system of the Western end of the Luano valley. *Rep. geol. Surv. Dep. N. Rhod.*, Lusaka, **6** : 1-40, pls 1-3, 2 maps.
- GARDINER, B. G. 1960. A revision of certain Actinopterygian and Coelacanth fishes, chiefly from the Lower Lias. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **4** : 239-384, 8 pls.
- 1962. *Namaichthys schroederi* Gürich and other Palaeozoic fishes from South Africa. *Palaeontology*, London, **5** : 9-21, pl. 6.
- 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **8** : 255-325, 2 pls.
- 1967a. Chondrostei, Holostei and Halecostomi. 644-654 in *The Fossil Record*. Edit. W. B. Harland *et al.* Geol. Soc., London.
- 1967b. The significance of the preoperculum in actinopterygian evolution. *J. Linn. Soc. (Zoology)*, London, **47** : 197-209, 8 figs.
- 1967c. Further notes on palaeoniscoid fishes with a classification of the Chondrostei. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **14** : 143-206, 3 pls.
- 1969. New Palaeoniscoid fish from the Witteberg series of South Africa. *J. Linn. Soc. (Zoology)*, London, **48** : 423-452, 2 pls.
- GRIFFITH, J. & PATTERSON, C. 1963. The structure and relationships of the Jurassic fish *Ichthyokentema purbeckensis*. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **8** : 1-43, 4 pls.
- HAUFF, B. 1953. *Ohmdenia multidentata* nov. gen. et nov. sp. Ein neuer grosser Fischfund aus dem Posidonien-schiefern des Lias. *Neues Jb. Miner. Geol. Päläont.*, Stuttgart, **97** : 39-50, pls. 4-5.
- HAUGHTON, S. H. 1934. On some Karroo fishes from central Africa. *Ann. S. Afr. Mus.*, Cape Town, **31**, 3 : 97-104, pls 29-31.
- HAY, O. P. 1889. On some changes in the names, generic and specific, of certain fossil fishes. *Am. Nat.*, Lancaster, Pa., **33** : 783-792.
- HELBY, R. 1966. Triassic plant microfossils from a shale within the Wollar sandstone, N.S.W. *J. Proc. R. Soc. N.S.W.*, Sydney, **100** : 61-73.

- HILLS, E. S. 1958. A brief review of Australian fossil vertebrates. 86-107 in *Studies on fossil vertebrates*. Edit. T. S. Westoll. xii + 263 pp. London, The Athlone Press.
- HUGHES, G. M. 1960. A comparative study of gill ventilation in marine teleosts. *J. exp. Biol.*, London, **37** : 28-45, 10 figs.
- HUGHES, G. M. & SHELTON, G. 1958. The mechanism of gill ventilation in three freshwater teleosts. *J. exp. Biol.*, London, **35** : 807-23, 1 pl.
- HUTCHINSON, P. 1972. In press.
- JAIN, S. L., ROBINSON, P. L. & CHOWDHURY, T. K. 1964. A new vertebrate fauna from the Triassic of the Deccan, India. *Q. Jl geol. Soc. Lond.*, **120** : 115-124, 3 figs.
- KERR, T. 1952. The scales of primitive living Actinopterygians. *Proc. zool. Soc. Lond.*, **122** : 55-78, 2 pls.
- LEHMAN, J.-P. 1952. Étude complémentaire des poissons de l'Eotrias de Madagascar. *K. svenska VetenskAkad. Handl.*, Stockholm (4) **2**, 6 : 201 pp., 48 pls.
- 1966. Actinopterygii. In *Traité de paléontologie*, **4**, 3. Edit. J. Piveteau. Paris, Masson et Cie, 1-242, figs 1-211.
- LEHMAN, J.-P., CHATEAU, C., LAURIAN, M. & NAUCHE, M. 1959. Paléontologie de Madagascar. 27. Les poissons de la Sakemena Moyenne. *Annls Paléont.*, Paris, **45** : 177-219, 19 pls.
- LIU, H. T. 1958. On a new Triassic dictyopygid fish from Sinkiang, China. *Vertebr. palasiat.*, Peking, **2** : 149-150, 1 pl.
- LUND, R. 1967. An analysis of the propulsive mechanisms of fishes, with reference to some fossil actinopterygians. *Ann. Carneg. Mus.*, Pittsburgh, **39** : 195-218, 12 figs.
- LYELL, C. 1847. On the structure and probable age of the coal field of the James River, near Richmond, Virginia. *Q. Jl geol. Soc. Lond.*, **3** : 263-280, pls 8-9.
- MACADIE, C. I. 1967. Ultrasonic probes in palaeontology. *J. Linn. Soc. (Zoology)*, London, **47**, 311 : 251-253, 1 fig.
- MOY-THOMAS, J. A. 1939. *Palaeozoic fishes*. ix + 149 pp., 33 figs. Methuen, London.
- MOY-THOMAS, J. A. & DYNE, M. B. 1938. Actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Trans. R. Soc. Edinb.*, **59** : 437-480, 2 pls.
- MOY-THOMAS, J. A. & WHITE, E. I. 1939. Notes on some Carboniferous Palaeoniscoids. *Ann. Mag. nat. Hist.*, London, (11), **3** : 622-625.
- MCALLISTER, D. E. 1968. The evolution of branchiostegals and associated opercular, gular and hyoid bones, and the classification of Teleostome fishes, living and fossil. *Bull. natn. Mus. Can.*, Ottawa, **221** : xiv + 239 pp. 21 pls.
- NIELSEN, E. 1936. Some few preliminary remarks on Triassic fishes from East Greenland. *Meddr Grønland*, Kjøbenhavn, **112**, 3 : 53 pp., 19 figs.
- 1942. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus*. *Meddr Grønland*, Kjøbenhavn, **138** : 403 pp., 30 pls.
- 1949. Studies on Triassic fishes from East Greenland. II. *Australosomus* and *Birgeria*. *Meddr Grønland*, Kjøbenhavn, **146** : 309 pp., 20 pls.
- OERTLE, G. F. 1931. *Cleithrolepsis* [sic] *brückneri* n. sp., der erste Vertreter der Gattung aus der europäischen Trias. *Zentbl. Miner.*, Stuttgart, B, **6** : 297-300, 1 fig.
- PATTERSON, C. 1968. The caudal skeleton in Lower Liassic Pholidophorid fishes. *Bull. Br. Mus. nat. Hist. (Geol.)*, London, **16** : 203-239, 5 pls.
- ROMER, A. S. 1945. *Vertebrate Paleontology*. 2nd ed. ix + 687 pp., 377 figs. Chicago University Press.
- 1947. Review of the Labyrinthodontia. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **99** : 368 pp., 48 figs.
- 1966. *Vertebrate Paleontology*. 3rd ed. ix + 468 pp., 443 figs. Chicago University Press.
- SCHAEFFER, B. 1952. The Palaeoniscoid fish *Turseodus* from the Upper Triassic Newark group. *Am. Mus. Novit.*, New York, **1581** : 24 pp., 8 figs.
- 1955. *Mendocinia*, a Subholostean fish from the Triassic of Argentina. *Am. Mus. Novit.*, New York, **1737** : 23 pp., 8 figs.

- SCHAEFFER, B. 1956. Evolution in the subholostean fishes. *Evolution, Lancaster, Pa.*, **10**, 2 : 201-212, 2 figs.
- 1967. Late Triassic fishes from the Western United States. *Bull. Am. Mus. nat. Hist.*, New York, **135** : 285-342, 22 pls.
- SCHAEFFER, B. & ROSEN, D. E. 1961. Major adaptive levels in the evolution of the Actinopterygian feeding mechanism. *Am. Zoologist*, Utica, **1**, 2 : 187-204, 7 figs.
- SCHAEFFER, B. & MANGUS, M. 1970. *Synorichthys* sp. (Palaeonisciformes) and the Chinle-Dockum and Newark (Upper Triassic) fish faunas. *J. Paleont.*, Tulsa, **44** : 17-22, pls 5-6.
- SCHULTZE, H. P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid-zu Rundschuppen). *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **126** : 232-314, pls 49-53.
- SIMPSON, G. G. 1961. *Principles of animal taxonomy*. xii+247 pp. 30 figs. Columbia.
- SMITH, I. C. 1956. The structure of the skin and dermal scales in the tail of '*Acipenser ruthenus*' L. *Trans. R. Soc. Edinb.*, **63** : 1-14, 3 pls.
- STENSIÖ, E. A. 1921. *Triassic fishes from Spitzbergen*. Pt. I. xxviii+307 pp., 34 pls. Vienna.
- 1925. Triassic fishes from Spitzbergen. Pt. II. *K. svenska VetenskAkad. Handl.*, Stockholm, (3), **2** : 261 pp., 34 pls.
- 1932. Triassic fishes from East Greenland collected by the Danish Expeditions in 1929-1931. *Meddr Grønland*, Kjøbenhavn, **83**, 3 : 305 pp., 39 pls.
- STOLLEY, E. 1920. Beiträge zur Kenntnis der Ganoiden des deutschen Muschelkalks. *Palaeontographica*, Stuttgart, **63** : 25-96, pls 10-14.
- SWINNERTON, H. H. 1925. A new Catopterid fish from the Keuper of Nottingham. *Q. Jl geol. Soc. Lond.*, **81** : 87-99, 2 pls.
- 1928. On a new species of *Semionotus* from the Keuper of Nottingham. *Geol. Mag.*, London, **65** : 406-409, 1 fig.
- THOMSON, K. S. & HAHN, K. V. 1968. Growth and form in fossil rhipidistian fishes (Crossopterygii). *J. Zool.*, London, **156**, 2 : 199-223, 4 pls.
- TRAQUAIR, R. H. 1879. On the structure and affinities of the Platysomidae. *Trans. R. Soc. Edinb.*, **29** : 343-391, pls 3-6.
- WADE, R. T. 1931. The fossil fishes of the Australian Mesozoic Rocks. *J. Proc. R. Soc. N.S.W.*, Sydney, **64** : 115-147, 1 fig.
- 1932. Preliminary note on *Macroaethes brookvalei*, representing a new family of Chondrosteian fishes, the Pholidopleuridae. *Ann. Mag. nat. Hist.*, London, (10), **9** : 473-475, 1 pl.
- 1933. On a new Triassic Catopterid fish from New South Wales. *Ann. Mag. nat. Hist.*, London, (10), **12** : 121-125, 3 figs.
- 1935. *The Triassic fishes of Brookvale, New South Wales*. xiv+110 pp., 10 pls. Brit. Mus. (Nat. Hist.), London.
- 1940. The Triassic fishes of Gosford, New South Wales. *J. Proc. R. Soc. N.S.W.*, Sydney, **73** : 206-217, 1 pl.
- 1941a. The Jurassic fishes of New South Wales. *J. Proc. R. Soc. N.S.W.*, Sydney, **74** : 71-84, 2 pls.
- 1941b. Australian Triassic fishes. I. The Triassic fishes of St. Peter's, Sydney, New South Wales. II. The Relationships of the Australian Triassic fishes to each other and to other bony fishes. *J. Proc. R. Soc. N.S.W.*, Sydney, **74** : 377-396, 1 pl.
- 1942. The Triassic fishes of New South Wales. *J. Proc. R. Soc. N.S.W.*, Sydney, **75** : 144-147, 1 pl.
- 1953a. Note on a Triassic fish fossil from Leigh Creek, South Australia. *Trans. R. Soc. S. Aust.*, Adelaide, **76** : 80-81, 1 fig.
- 1953b. Jurassic fishes of New South Wales (Macrosemiidae) with a note on the Triassic genus *Promecosomina*. *J. Proc. R. Soc. N.S.W.*, Sydney, **87** : 63-72, pls 8-9.
- WATSON, D. M. S. 1925. The structure of certain Palaeoniscids and the relationships of that group with other bony fish. *Proc. zool. Soc. Lond.*, **1925** : 815-870, 2 pls.

- WATSON, D. M. S. 1928. On some points in the structure of Palaeoniscid and allied fish. *Proc. zool. Soc. Lond.*, **1928** : 49-70, 15 figs.
- 1931. Note on the occurrence of fossil fish at Bekker's Kraal, Dist. Rouxville, Orange Free State. *Proc. zool. Soc. Lond.*, **1931** : 235-236.
- WESTOLL, T. S. 1934. The Permian Palaeoniscid fishes of Northumberland and Durham. Ph.D. Thesis, Durham University.
- 1937a. On the cheek bones in Teleostome fishes. *J. Anat.*, London, **71** : 362-382, 8 figs.
- 1937b. On a remarkable fish from the Lower Permian of Autun, France. *Ann. Mag. nat. Hist.*, London, (10), **19** : 553-578, 7 figs.
- 1941. Latero-sensory canals and dermal bones. *Nature*, Lond., **148** : p. 168.
- 1944. The Haplolepididae, a new family of Late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Am. Mus. nat. Hist.*, New York, **83** : 1-122, 10 pls.
- WHITE, E. I. 1933. New Triassic palaeoniscids from Madagascar. *Ann. Mag. nat. Hist.*, London, (10), **11** : 118-128.
- 1939. A new type of palaeoniscid fish, with remarks on the evolution of the actinopterygian pectoral fins. *Proc. zool. Soc. Lond.*, B, **109** : 41-61, pl. 1.
- 1950. A fish from the Bunter near Kidderminster. *Trans. Worcs. Nat. Club*, Worcester, **10** : 185-189, 1 pl.
- WHITE, E. I. & MOY-THOMAS, J. A. 1941. Notes on the nomenclature of fossil fishes, Part III. Homonyms N-Z. *Ann. Mag. nat. Hist.*, London, (11), **7** : 395-400.
- WILSON, J. A. 1953. Permian vertebrates from Taylor County, Texas. *J. Paleont.*, Tulsa, **27** : 456-470, figs 1-15.
- WOODWARD, A. S. 1888. On two new Lepidotoid Ganoids from the early Mesozoic deposits of Orange Free State, South Africa. *Q. Jl geol. Soc. Lond.*, **44** : 138-143, 1 pl.
- 1890. The fossil fishes of the Hawkesbury Series at Gosford. *Mem. geol. Surv. N.S.W. Paleont.*, Sydney, **4** : 55 pp., 10 pls.
- 1895. *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, London, **3** : xliii + 544 pp. 18 pls. Brit. Mus. (Nat. Hist.), London.
- 1908. The fossil fishes of the Hawkesbury Series at St. Peter's. *Mem. geol. Surv. N.S.W. Paleont.*, Sydney, **10** : v + 30 pp. 4 pls.
- 1910. On *Dipteronotus cyphus*, Egerton. A Ganoid fish from the Lower Keuper of Bromsgrove, Worcestershire. *Proc. Geol. Ass.*, London, **21** : 322-323.

P. HUTCHINSON, Ph.D.,
 GOTHIC HOUSE,
 DRAYTON,
 BERKS.
 ENGLAND.



Hutchinson, Peter. 1973. "A REVISION OF THE REDFIELDIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKERS KRAAL SOUTH AFRICA AND BROOKVALE NEW-SOUTH-WALES." *Bulletin of the British Museum (Natural History) Geology* 22, 233–254.

View This Item Online: <https://www.biodiversitylibrary.org/item/113711>

Permalink: <https://www.biodiversitylibrary.org/partpdf/83424>

Holding Institution

Natural History Museum Library, London

Sponsored by

Natural History Museum Library, London

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder

Rights Holder: The Trustees of the Natural History Museum, London

License: <http://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <http://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.