

A NEW ANTHRACOSAUR AMPHIBIAN FROM THE CARBONIFEROUS OF SCOTLAND

by T. R. SMITHSON

ABSTRACT. The anthracosaur amphibian *Proterogyrinus pancheni*, sp. nov., from localities in the Namurian of the Scottish Carboniferous, is the earliest known member of the Embolomeri to be described from Europe. It closely resembles the North American form *P. scheelei*, but is distinguished by differences in morphology of the dentition and vertebrae. Functional explanations for the presence of the large Meckelian fenestrae in the embolomere mandible are reconsidered, but it is suggested that they had no specific function and represent incomplete ossification of the mesial surface of the lower jaw. Recent discussions of anthracosaur systematics are reviewed. The newly proposed schemes are supported by very few synapomorphies and it is concluded that a solution to the problem of anthracosaur phylogeny will be found only within the framework of a larger study of the interrelationships of early tetrapods.

IN 1980 I published a preliminary account of the tetrapod fauna in a richly fossiliferous bone bed from the Dora opencast site, near Cowdenbeath, Fife, Scotland (Smithson 1980a). Since then, much of this material has been fully described (Smithson 1980b, 1985a; Panchen 1985), but still awaiting description are the specimens I placed in the anthracosaur assemblages 3 and 4 (Smithson 1980a, p. 420). The two assemblages include bones from different parts of the skeleton, and in 1980 I was uncertain whether they represented separate species or were partial skeletons of the same species. Each assemblage was found to share a number of derived features with a North American anthracosaur *Proterogyrinus scheelei* Romer, but at the time, only preliminary descriptions of *Proterogyrinus* had been published (Romer 1970; Hotton 1970) and the significance of these similarities could not be assessed.

P. scheelei was found in the Upper Mississippian Bickett Shale at Greer, West Virginia (Romer 1970). The Bickett Shale forms part of the Bluefield Formation which is equivalent in age to the uppermost Viséan (Lower Carboniferous) and the lowermost Namurian (Upper Carboniferous) of Europe (see Panchen 1970, table 3). The fossiliferous deposits at Greer are therefore roughly contemporaneous with those at the two principal Scottish Namurian tetrapod localities, Dora and Loanhead (Smithson 1985b). Following the recent complete description of *P. scheelei* (Holmes 1984), it is now clear that all the material in assemblages 3 and 4 from Dora belongs to the same species. It is described here as a new species of *Proterogyrinus* and it represents the earliest known member of the Embolomeri to be found in the Carboniferous of Europe.

MATERIALS AND METHODS

The specimens used in the description of *P. pancheni* sp. nov. are listed below. The following abbreviations are used for institutions housing the material: BM(NH), Department of Palaeontology, British Museum (Natural History), London; NUZ, Department of Zoology, University of Newcastle upon Tyne; RSM, Department of Geology, Royal Scottish Museum, Edinburgh. The grid reference (GR) given for specimens from Dora refers to the site map published elsewhere (Smithson 1985a, text-fig. 2).

Dora Bone Bed, Dora opencast site, near Cowdenbeath, Fife Region.

BM(NH) R9940	GR 88	Incomplete interclavicle.
NUZ 75.11.2	GR X12	Skull table and interorbital region.

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NUZ 77.1.6	GR W10	Left lacrimal.
NUZ 77.3.8	GR X10	Right intertemporal.
NUZ 76.10.17	GR D51	Incomplete intercentrum.
NUZ 77.2.17	GR W10	Cervical neural arch.
NUZ 78.3.33	GR C32	Caudal neural arch.
NUZ 77.2.19	GR X11	Incomplete left clavicle.
NUZ 77.2.20	GR U10	Incomplete right humerus.
RSM GY 1977.46.33	GR 89	Right mandible, trunk vertebra, and incomplete rib.
RSM GY 1975.48.49	GR —	Trunk vertebra.
RSM GY 1977.46.35	GR D30	Trunk vertebra.
RSM GY 1978.4.21	GR —	Trunk vertebra.
RSM GY 1983.9.1	GR L66/67	Incomplete trunk vertebra.
RSM GY 1976.19.48	GR K20	?Sacral vertebra.
RSM GY 1977.46.34	GR D30	Pleurocentrum.
RSM GY 1976.19.49	GR —	Intercentrum.
RSM GY 1983.9.2	GR H39	Haemal arch.

Burghlee Ironstone (Rumbles Ironstone, see Smithson 1985*b*), Burghlee colliery, Loanhead, Lothian Region.

BM(NH) R3960 Incomplete maxilla.

BM(NH) R4085 Right femur.

Shale overlying South Parrot Coal, Niddrie colliery, Niddrie, Lothian Region.

RSM GY 1893.135.84 Pleurocentrum.

Dora specimens from grid squares U, W, X were included in assemblage 3 (Smithson 1980*a*), the remaining material formed assemblage 4.

The Dora Bone Bed was prepared initially by the hot water technique developed by Mr Stanley Wood and the author (see Boyd and Turner 1980, p. 20). Further preparation of specimens was by mounted needles and an industrial airbrasive machine using sodium bicarbonate powder. Most specimen drawings were prepared using a camera lucida, but the illustrations of the skull table and lower jaw were based on photographs.

SYSTEMATIC DESCRIPTION

Order ANTHRACOSAURIA

Suborder ANTHRACOSAUROIDEAE

Infraorder EMBOLOMERI

Family PROTEROGRINIDAE Romer, 1970

Diagnosis. As for *Proterogyrinus*.

Genus PROTEROGRINUS Romer, 1970

Type species. *P. scheelei* Romer, 1970

Diagnosis. (Based on information in Holmes 1984 and author's studies.) Primitive embolomeres probably growing to about 1.5 m in length. Skull structure similar to that of *Palaeoherpeton* and *Pholiderpeton* but with a relatively shorter antorbital region. Median suture posterior to the pineal on a ridge flanked on either side by a depression. Kinetic junction extends the length of the skull table as in *Eoherpeton*. Biramous tabular horn. Jugal exposed on ventral skull margin. Maxilla makes no sutural contact with premaxilla. Laterosphenoid region of braincase unossified. Thirty-two presacral vertebrae. Atlas pleurocentrum incompletely ossified ventrally as well as dorsally. More posterior vertebrae gastrocentrous with disc-shaped pleurocentra and crescentic intercentra. Tall neural spines with areas of origin and insertion of median dorsal axial musculature well defined. Appendicular skeleton similar to that of *Archeria*, but with two foramina piercing the puboischiadic plate, instead of the single obturator foramen, and a poorly developed iliac blade. Four centralia in tarsus, the most proximal (fourth) being partly fused to tibiale.

Proterogyrinus pancheni sp. nov.

Diagnosis. As for genus, plus: parietal–postparietal suture on a ridge. Dentary with spaces for at least thirty-two sharply pointed, incurved, and strongly hooked teeth. Coronoid series covered entirely with denticles. Pleurocentra in trunk region well ossified and fused dorsally, small notochordal foramen.

Holotype. RSM GY 1977.46.33. Incomplete right ramus of lower jaw, trunk neural arch with articulated pleurocentrum, and incomplete rib.

Referred material. See Materials and Methods.

Type Horizon and Locality. Dora Bone Bed. Localized seatrock, beneath a coal seam below the Lochgelly Blackband Ironstone, upper part of the Limestone Coal Group (Namurian A, Upper Carboniferous), Dora opencast site, Cowdenbeath, Fife Region, Scotland.

Distribution. Lothian and Fife Regions, Scotland.

Range. Limestone Coal Group (Dora Bone Bed) to Upper Limestone Group (South Parrot Coal Shale). E₁ zone of Namurian A (Upper Carboniferous).

Derivation of specific name. After Dr Alec Panchen in recognition of his considerable work on Carboniferous anthracosaurs.

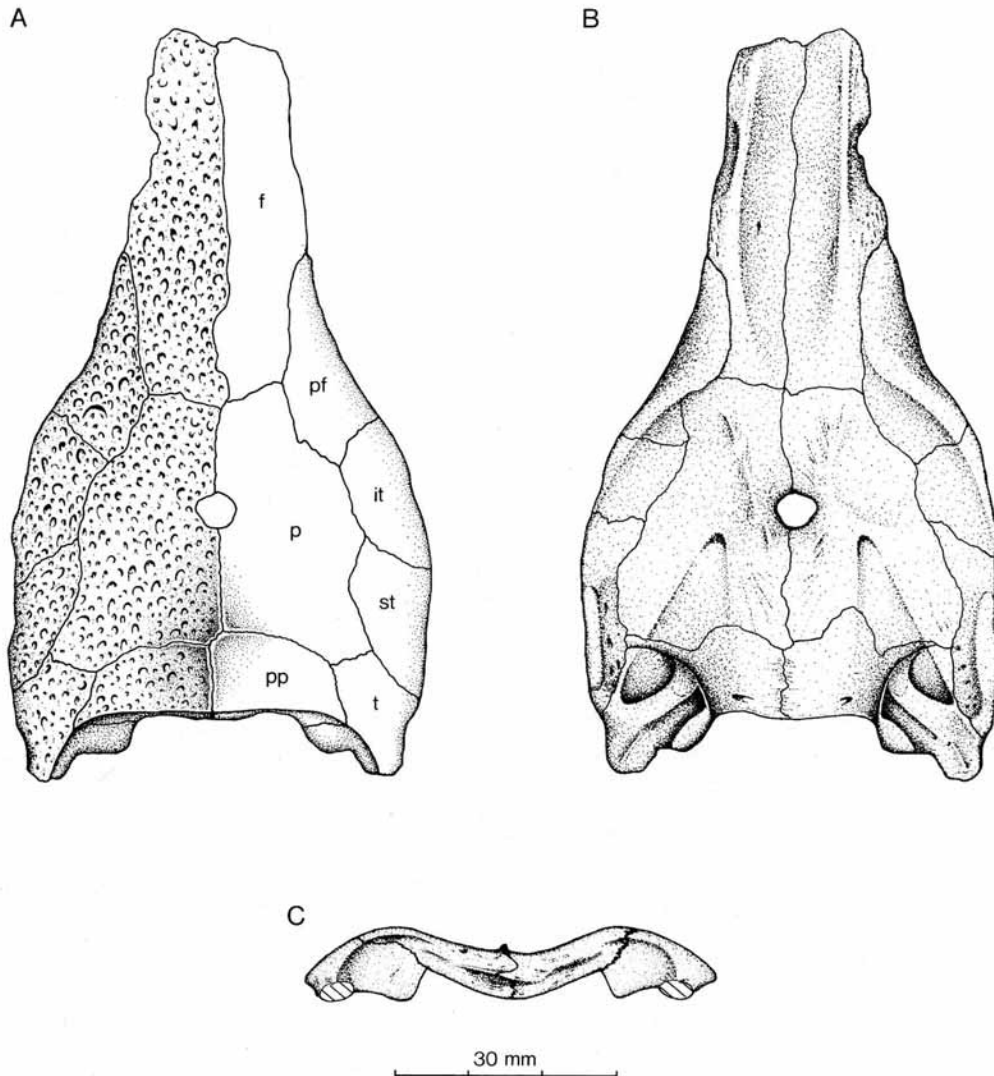
Description. The skull of *P. pancheni* is represented by the skull table and interorbital region NUZ 75.11.2, illustrated by Andrews *et al.* (1977, text-fig. 4), a displaced right intertemporal NUZ 77.3.8, a left lacrimal NUZ 77.1.6, and an incomplete right ramus of the lower jaw RSM GY 1977.46.33.

Skull table. The overall shape and pattern of the skull roofing bones of *P. pancheni* (text-fig. 1A, B) is very similar to that of *P. scheelei* (Holmes 1984), and only brief notes on the general arrangement are given. The dorsal surface of the bones is ornamented with an irregular series of shallow pits and grooves which undercut the bone surface. This ornamentation is more strongly developed than in the contemporaneous form *Eoherpeton* (Smithson 1985b), and most closely resembles that in the Coal Measure embolomeres *Palaeoherpeton* (Panchen 1964) and *Pholiderpeton* (Panchen 1972). (I have accepted Dr Jennifer Clack's (*née* Agnew) conclusion, following her review of British Coal Measure embolomeres, that *Eogyrinus* is the junior synonym of *Pholiderpeton* (Agnew 1984).) All the material from the Westphalian B previously attributed by Panchen (1972) to *Eogyrinus attheyi* is here referred to as *P. attheyi*. Lateral line sulci are absent.

As preserved the skull table and interorbital region is 95 mm long from the anterior edge of the frontals to the posterior edge of the postparietals, and 57 mm wide in the region of the supratemporals. The bones have been displaced following post-mortem compression and collecting disturbance. The right intertemporal bone is missing from the skull table but was recovered from the bone bed approximately 0.5 m to the left of it. The ventral surface of NUZ.75.11.2 is exposed and permits detailed comparison with the ventral surface of the skull table and interorbital region of *Palaeoherpeton* (Panchen 1964, text-fig. 3).

The most notable features of the dorsal surface of NUZ 75.11.2 are the ridged midline sutures of the parietals (behind the pineal foramen) and postparietals, and the ridged transverse sutures between the parietals and postparietals. Ridged midline sutures are also present in *Proterogyrinus scheelei*, an undescribed specimen from Point Edward, Nova Scotia and *Pteroplax* (Holmes, 1984), but ridged transverse sutures are absent. Ridged sutures have not been observed in other anthracosaurs and are here regarded as an autapomorphy (uniquely derived feature) of the Proterogyrinidae. In *Proterogyrinus scheelei* and the Point Edward specimen the dorsal margin of the pineal foramen also bears a raised rim, but this is absent in *P. pancheni*.

In Carboniferous anthracosaurs the tabular bone exhibits two diagnostic features of the skull roof: a connection with the parietal bone and a tabular horn. In NUZ 75.11.2 the dorsal surface of the tabular is overlapped by the parietals anteriorly and the postparietals mesially. The postparietals are themselves overlapped by the parietals and this arrangement influences the relationship of the tabular and parietal on the ventral surface of the skull table. The characteristic tabular–parietal suture is



TEXT-FIG. 1. *Proterogyrinus pancheni* sp. nov., skull table and interorbital region restored. A, dorsal view. B, ventral view. C, posterior view. Natural size. Broken bone hatched. Abbreviations: f, frontal; it, intertemporal; p, parietal; pf, postfrontal; pp, postparietal; st, supratemporal; t, tabular.

evident only on the left side (ventral right) where the anterolateral corner of the tabular meets the parietal. On the right a narrow process of the postparietal extends laterally between the tabular and parietal to contact the supratemporal (text-fig. 1B). This difference in the pattern of bones on the dorsal and ventral surfaces of the skull table has not been observed previously in anthracosaurs.

The tabular horns are incomplete on both sides of the skull table, but on the left only the lateral edge of the horn is damaged. It appears that a blade-like posterior process of the type present in

Palaeoherpeton (Panchen 1964) and *Pteroplax* (Panchen 1970) was not developed in *Proterogyrinus pancheni*. In *P. scheelei* the tabular horn is biramous with a short accessory process projecting from the ventrolateral edge of the tabular (Holmes 1984). Because this region is damaged in NUZ 75.11.2 it is not possible to determine whether the horn was similarly biramous in *P. pancheni*.

The morphology of the ventral surface of the tabulars in NUZ 75.11.2 is very similar to that in *Palaeoherpeton* (Panchen 1964, text-fig. 3). A deep flange projects from the ventromesial edge of the tabular and forms a flat unornamented surface, which is oriented both posteroventrally and ventrolaterally. Its mesial edge is unfinished and forms part of a surface of attachment for the otic capsules which extend around the entire anteroventral edge of the tabular. In addition, a stout process projects from the centre of the bone which is unfinished anteromesially and forms a second area of attachment for the otic capsules. Between the flange and the process is a deep groove which Panchen (1964, p. 602) suggested carried a vena capitis lateralis, but which Holmes (1984, p. 457) has argued carried the vena capitis dorsalis.

In front of the tabulars the ventral surface of the parietals bears a pair of shallow V-shaped depressions, one on either side of the convex median portion of the skull table. Each recess extends forward to a point level with the posterior edge of the pineal foramen and they appear to mark the area of attachment of the otic capsules. A similar impression is present on the ventral surface of *Palaeoherpeton* (Panchen 1964, text-fig. 3) and also *Loxomma acutirhinus* (Beaumont 1977, text-fig. 2), although in neither does it extend forward to the pineal foramen. The ventral surface of each postparietal is excavated to form a short narrow transverse furrow medial to the postparietal–tabular suture. These furrows are absent in *Palaeoherpeton* and their function is unknown.

Behind and lateral to the pineal foramen a pair of short, ill-defined ridges run forward on either side of the pineal towards the anterior edge of the parietal. The ridge on the right is more strongly developed than that on the left. After a break in the ridge system between the orbit margins it continues forward on the lateral edge of the frontal bones. Here the ridge pair is strongly developed and forms the boundaries of a shallow trough on the undersurface of the frontals (text-fig. 1b). This ridge system almost certainly delimits the area of attachment between the sphenethmoid region of the braincase and skull roof. These ridges are absent in *Palaeoherpeton* but in *Proterogyrinus scheelei*, *Seymouria*, and primitive reptiles, for example, *Eocaptorhinus* (Heaton 1979), they support the thin walls of a Y-shaped sphenethmoid.

A short distance behind the anterior end of the frontals the lateral edges of the bones are excavated to form a pair of shallow concavities bounded mesially by the ridges for the sphenethmoid. The anterior end of each concavity is pierced by a small foramen. Their function is unknown.

At the lateral edge of the skull table the ventral surface of the supratemporal is excavated to form a shallow groove which extends along most of the length of the bone. In the complete skull it would have been occupied by the dorsal edge of the squamosal to form the characteristic 'kinetic' joint between the skull table and cheek. The groove is incised with a number of deep pits, not seen in *P. scheelei*, which probably served as areas of attachment for connective tissue which stabilised the joint (Panchen 1964). A shallow concavity on the lateral edge of the squamosal may also have formed part of this joint. Further posteriorly, the lateral edge of the skull table is strongly concave. This region is traditionally taken to represent the anterodorsal margin of an otic notch. However, a number of authors (e.g. Smithson 1982, 1985a; Clack 1983; Holmes 1984) have suggested recently that Carboniferous anthracosaurs lacked a tympanum, and this region may be a vestige of the spiracular cleft (Smithson 1982; Panchen 1985).

Lacrimal. An incomplete bone NUZ 77.1.6 recovered a short distance behind the skull table closely resembles the lacrimal of *Pholiderpeton* (Panchen 1972, text-fig. 6). It resembles no other bone in the anthracosaur skull or mandible. Its external surface is gently convex and exhibits the characteristic pitted ornament of anthracosaur dermal roofing bones. The thickened ventral edge of the bone is deeply incised with grooves which probably represent the area of contact with the maxilla. The posteroventral portion of the bone is missing but the external surface of the posterodorsal region is excavated to form a V-shaped area, exhibiting numerous ridges and grooves, which probably formed

an area of sutural overlap with the prefrontal or jugal. The dorsal margin of the bone is incomplete and I could not determine whether the lacrimal was included or excluded from the anterior border of the orbit. Similarly, I was unable to judge whether the anterior end of the bone formed part of the border of the external naris.

The internal surface of the lacrimal is divided by a braided longitudinal ridge which extends forward from the posterior end of the bone. Above the ridge the bone surface is mostly smooth although at the posterior end a small area of sutural overlap is developed. Below the ridge the surface is traversed by a second oblique deeply pitted ridge which probably had a sutural connection with either the maxilla or a lateral palatal bone.

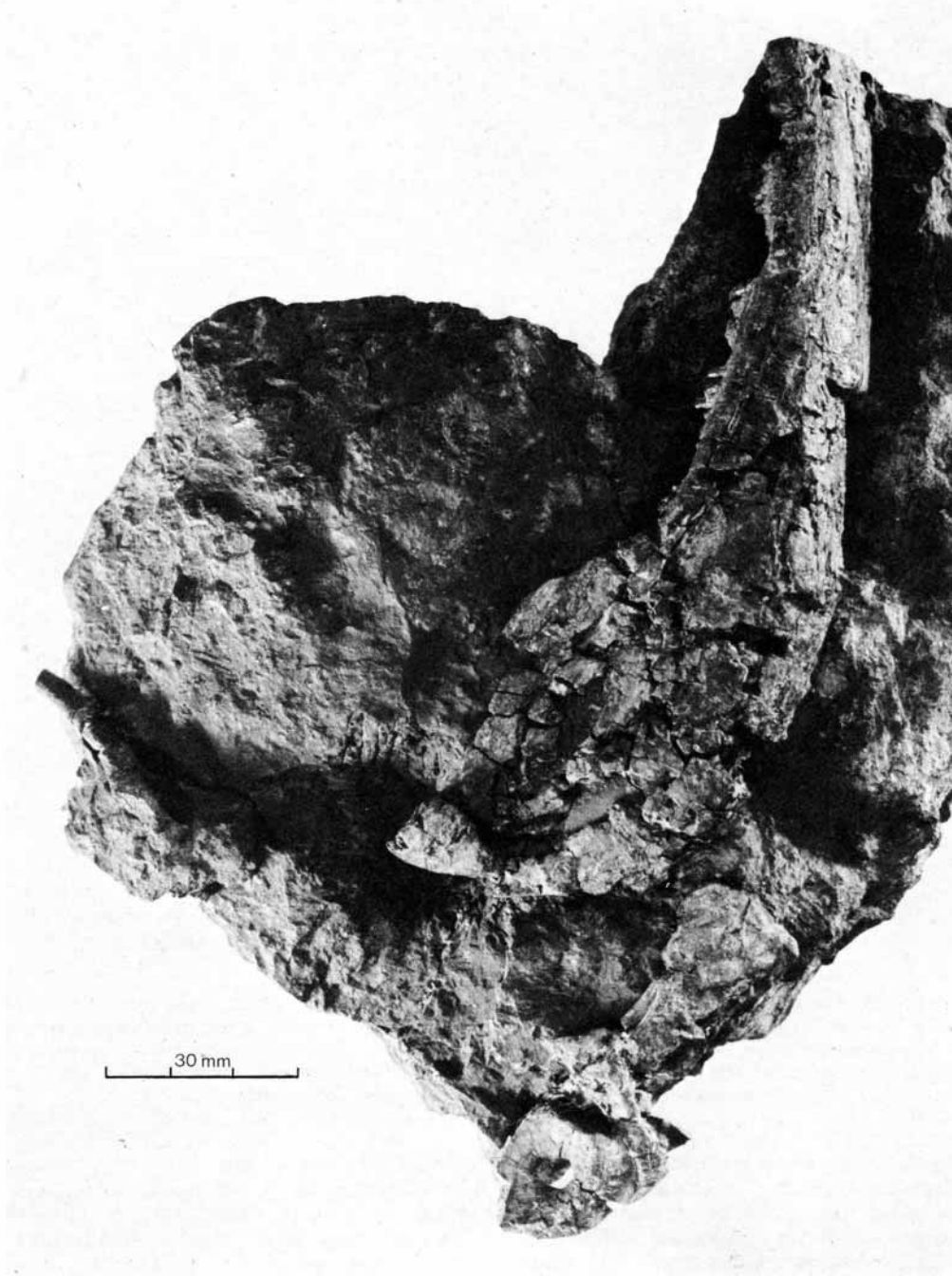
Lower jaw. The lower jaw of *Proterogyrinus pancheni* is represented by the type specimen. It is incomplete anteriorly and the external surface is badly fractured and incomplete in the region overlying the adductor fossa. The surface of the bone has been removed during preparation and very little detail of the ornamentation or the possible course of the mandibular lateral line canal can be distinguished. The internal surface of the anterior two thirds of the jaw was exposed by the author. The mesial wall of the jaw behind the anterior border of the anterior Meckelian fenestra has collapsed into the Meckelian space and has also been pushed forward, in part, between the presplenial and dentary. In addition the whole ramus has been laterally compressed forcing the coronoid series over the mesial shelf of the dentary. With one exception all the teeth in the dentary are incomplete.

In its general morphology the lower jaw is similar to those of the *P. scheelei* (Holmes 1984), *Pholiderpeton* (Panchen 1970, 1972; Agnew 1984), *Eobaphetes* (Panchen 1977), and *Neopteroplax* (Romer 1963). It exhibits the characteristic surangular crest and has a pair of moderately large Meckelian fenestrae on the mesial surface of the jaw. As preserved it is 144 mm long, reaches a maximum depth of 45 mm beneath the surangular crest and tapers to a depth of 15 mm at its incomplete anterior end. In front of the adductor fossa the jaw is approximately parallel sided in dorsal view. There is no apparent curvature in this region and it is reasonable to assume that when articulated with its antimeres and two rami described a V as in *Pholiderpeton* (Panchen 1972, text-fig. 12).

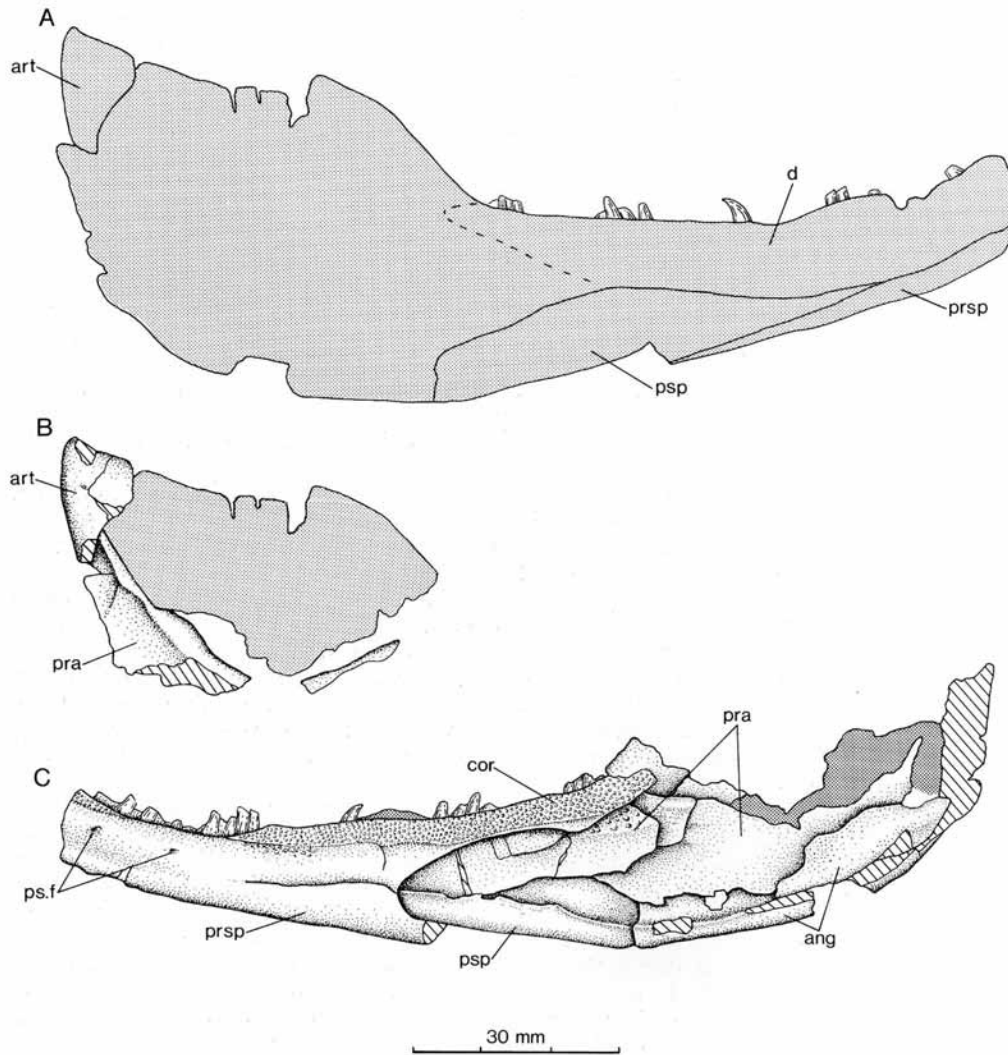
An outline drawing of the external surface of RSM GY 1977.46.33, as preserved, is given (text-fig. 3A) showing the course of discernable sutures. The extent of surface damage is shown in text-fig. 2. The exposed mesial surface of the jaw is fully illustrated (text-fig. 3C). The restorations (text-fig. 4A, B) of the internal and external views of the jaw have been modified from those published elsewhere (Smithson 1980a, text-fig. 7), in particular with respect to the course of the sutures on the posterior half of mesial surface and the size of the Meckelian fenestrae.

The dentary accounts for more than half of the total length of the dorsal margin of the jaw, as preserved. Its convex lateral surface has broad overlapping sutures with the infradentary bones (presplenial, postsplenial, angular, and surangular) and it reaches its maximum depth above the postsplenial. Projecting from the mesial surface of the dentary, a short distance below its dorsal edge, is a horizontal tooth bearing shelf. It appears to maintain an almost constant width along its length although the posterior region is concealed by intractable matrix. The shelf is slightly broader than the bases of the teeth it supports. Further mesially it is excavated to form a shallow recess which is normally occupied by the ventrolateral portion of the coronoid series. This recess is visible in the anterior portion of the jaw where the coronoids have been displaced by lateral compression post-mortem. Details of the dentition are discussed separately.

The coronoid series forms an almost horizontal roof to the Meckelian space but the sutures between individual coronoid bones could not be traced. The floor of the Meckelian space comprises two splenials and the angular. They wrap around the ventral edge of the jaw forming a distinct angle between the gently convex external surface and the almost vertical internal surface. The presplenial forms a considerable portion of the anteromesial surface of the jaw. It contacts the coronoid series dorsally and forms the anterior border of the anterior Meckelian fenestra posteriorly. Unfortunately, I cannot determine if it contacted the prearticular. In the jaw of primitive tetrapods, for example *Ichthyostega* (Jarvik, 1980), *Metaxygnathus* (Campbell and Bell 1977), and *Doragnathus* (Smithson 1980b), the prearticular has a broad contact with the presplenial. In the jaw of embolomeres,



TEXT-FIG. 2. *Proterogyrinus pancheni* sp. nov. Right mandible, trunk vertebra, and rib, RSM GY 1977.46.33, lateral view. Natural size.



TEXT-FIG. 3. *Proterogyrinus pancheni* sp. nov., right mandible, RSM GY 1977.46.33. A, lateral view. B, lateral (internal) view showing dorsal edge of adductor fossa. C, mesial view. Natural size. Broken bone hatched, eroded external surface of mandible light mechanical stipple, matrix heavy mechanical stipple. Abbreviations: ang, angular; art, articular; cor, coronoid; d, dentary; Meck. fen, Meckelian fenestra; pra, prearticular; ps.f, postsymphysial foramen; prsp, postsplenial; sp, splenial.

however, for example *Pholiderpeton* (Panchen 1970, 1972), *Eobaphetes*, and *Anthracosaurus* (Panchen 1977), the prearticular is prevented from contacting the presplenial by the anterior coronoid. Among the anthracosaurs this feature appears to be unique to embolomeres, although Agnew (1984) has described *Pholiderpeton* as having an arrangement similar to that found in primitive tetrapods with a short suture between the prearticular and presplenial.

Anteriorly the internal surface of the presplenial is gently concave and pierced by two postsymphysial foramina. The posterior end of the bone is strongly concave and in my earlier restoration of the mesial surface of the lower jaw of *Proterogyrinus pancheni* (Smithson 1980a) I interpreted the whole of this concave region as representing the anterior border of the anterior Meckelian fenestra. I now think this is incorrect. The dorsal rim of this concavity appears on closer examination to be a broken surface originally attached to bone pushed between the dentary and presplenial, rather than the border of a fenestra. As a result the restored height of the anterior Meckelian fenestra has been reduced. However, the ventral margin of the fenestra is preserved and its length in the two restorations remains unchanged.

The postsplenial forms the posteroventral and anteroventral borders of the anterior and posterior Meckelian fenestrae respectively. The two fenestrae were presumably divided by a projection of the prearticular which contacted the postsplenial a short distance above the ventral margin of the jaw. This region is not preserved in RSM GY 1977.46.33 although the sutural surface on the postsplenial is visible (text-fig. 3c).

The angular forms the posteroventral border of the posterior Meckelian fenestra. The bone has cracked along the ventral margin of the jaw and in my previous restoration I took this crack to represent the angular prearticular suture. This is incorrect and the true line of contact is more dorsally placed (text-fig. 4b).

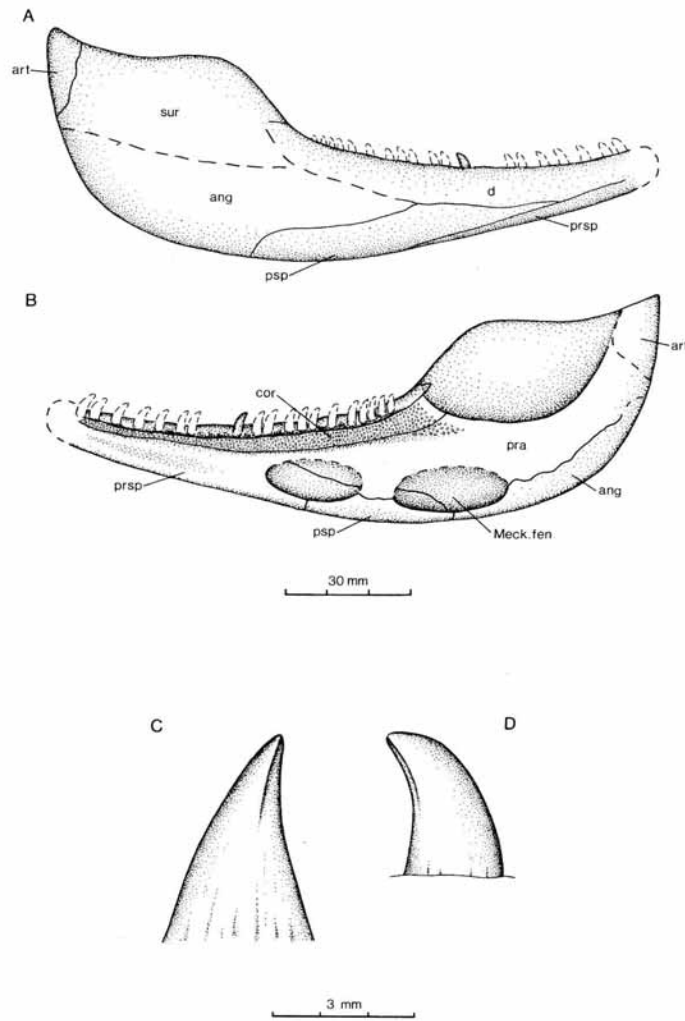
Fracturing of the bones overlying the adductor fossa has obliterated the angular-surangular suture. However, I have assumed that parts of both bones are present in RSM GY 1977.46.33, and that the suture between them extends across the external surface of the jaw approximately midway between its dorsal and ventral edges (text-fig. 4A).

Behind the tooth row the dorsal margin of the surangular rises steeply to form a strongly convex surangular crest similar to that of *Pholiderpeton* (Panchen 1972, text-fig. 11; Agnew 1984). This region is obscured in most specimens of *Proterogyrinus scheelei* by the overlying bones of the cheek. The base of the crest immediately behind the tooth row is thickened and excavated to form a short shallow groove. The edge of the crest is chamfered and forms a sharp dorsal margin of the jaw. It was not possible to determine whether the bone was thickened below the dorsal margin as in *Pholiderpeton* (Panchen 1972, p. 306) or whether the surangular wrapped around the posterior edge of the jaw to contact the prearticular.

The prearticular is very poorly preserved. It occupied a position on the mesial surface of the jaw between the infradentary series and the coronoid bones and formed a part of, or possibly all, the dorsal border of the Meckelian fenestrae. In addition it formed the concave mesial edge of the adductor fossa which remained attached to the matrix when the anterior portion of the jaw was removed (text-fig. 3b). The bone in this region is considerably thickened and probably acted as an area of insertion for the adductor muscles as in *Eoherpeton* (Smithson 1980a, 1985a).

The articular is embraced on its lateral surface by the surangular and overlaps the prearticular mesially. In dorsal view the articular surface forms a strongly concave arc with the internal corner of the articulation projecting in front of its external corner. It is not saddle-shaped as in *Pholiderpeton* (Panchen 1972, p. 308) and presumably formed a simple hinge joint with the quadrate. The precondyloid process is incomplete but the postcondyloid process is well defined and forms the posterior edge of the jaw; no retroarticular process is developed and the prominent boss present on the articular of *Proterogyrinus scheelei* is absent.

Dentition. With the exception of a single tooth, all the marginal teeth in the type specimen of *P. pancheni* are damaged. Judging from the incomplete portions preserved they appear to have been of a uniform size along most of the tooth row becoming smaller towards its posterior end. The bases of the teeth are oval in outline with their long axes oriented at right angles to the jaw margin. In lateral view the complete tooth is strongly hooked back (text-fig. 4d) and in anterior view gently incurved (text-fig. 4c). A clearly defined sharp ridge runs up the apical half of the anterior surface of the tooth and passes over the apex to run down on to the posterior surface. This type of tooth is unlike that of any other described anthracosaur and represents the most diagnostic feature of the type specimen.



TEXT-FIG. 4. *Proterogyrinus pancheni* sp. nov. A, B, right mandible restored. A, lateral view. B, mesial view. Approx. $\times \frac{2}{3}$. C, D, marginal tooth. C, anterior view. D, lateral view. $\times 7$. Abbreviations: see text-fig. 3.

There are spaces for thirty-two teeth in the preserved portion of the dentary and labyrinthine infolding of the enamel is restricted to the region below the dorsal alveolar margin of the jaw.

The coronoid bones are covered with a shagreen of very small denticles. A small patch of denticles is also present on the dorsal rim of the presplenial between the posterior postsymphysial foramen and the anterior margin of the anterior Meckelian fenestra, and on the prearticular immediately in front of the adductor fossa. The expanse of denticles on the coronoid series suggests a similarly extensive cover on the pterygoids of *P. pancheni*. In most amphibia the area of denticle covering on the coronoid bones is coincident with that present on the pterygoids for example *Pholiderpeton* (Panchen

1972, cf. text-figs. 7 and 12) and *Greererpeton* (Smithson 1982, cf. text-figs. 11 and 19). A similar situation is present in osteolepiform fishes, although here it is the prearticular rather than the coronoids which exhibit denticle covering, for example *Eusthenopteron* (Jarvik 1980, cf. text-figs. 124 and 125). Somewhat unusually, the lower jaw referred to *Anthracosaurus* by Panchen (1977) exhibits denticles on the three coronoids while the palatal bones of the two skulls are bare.

Remarks. One of the characteristics of the lower jaw of embolomeres anthracosaurs is the pair of large Meckelian fenestrae on the mesial surface of each ramus. *A. russelli* exhibits a slight variation of this pattern in that the two fenestrae have coalesced to form a single, large oval opening (Panchen 1981). Large Meckelian fenestrae are also present in two other groups of early tetrapods, colosteid temnospondyls (Smithson 1982) and the Diadectomorpha (*sensu* Heaton 1980). In the latter two groups the fenestra is similar to that found in *Anthracosaurus* and represents a considerable opening on the mesial surface of the jaw.

The arrangement of bones around the Meckelian fenestrae differ in the three groups. Embolomeres and colosteids retain both splenial bones while the diadectomorphs retain only one. The colosteids and diadectomorphs maintain the plesiomorphic connection between the prearticular and presplenial (cf. *Doragnathus*, Smithson 1980b and *Ichthyostega*, Jarvik 1980) while in some embolomeres the anterior coronoid extends posteroventrally between the presplenial and prearticular precluding a connection (see above). These differences in the pattern of bones surrounding the enlarged Meckelian fenestrae in colosteids, diadectomorphs, and embolomeres suggests that the fenestrae developed convergently in the three groups.

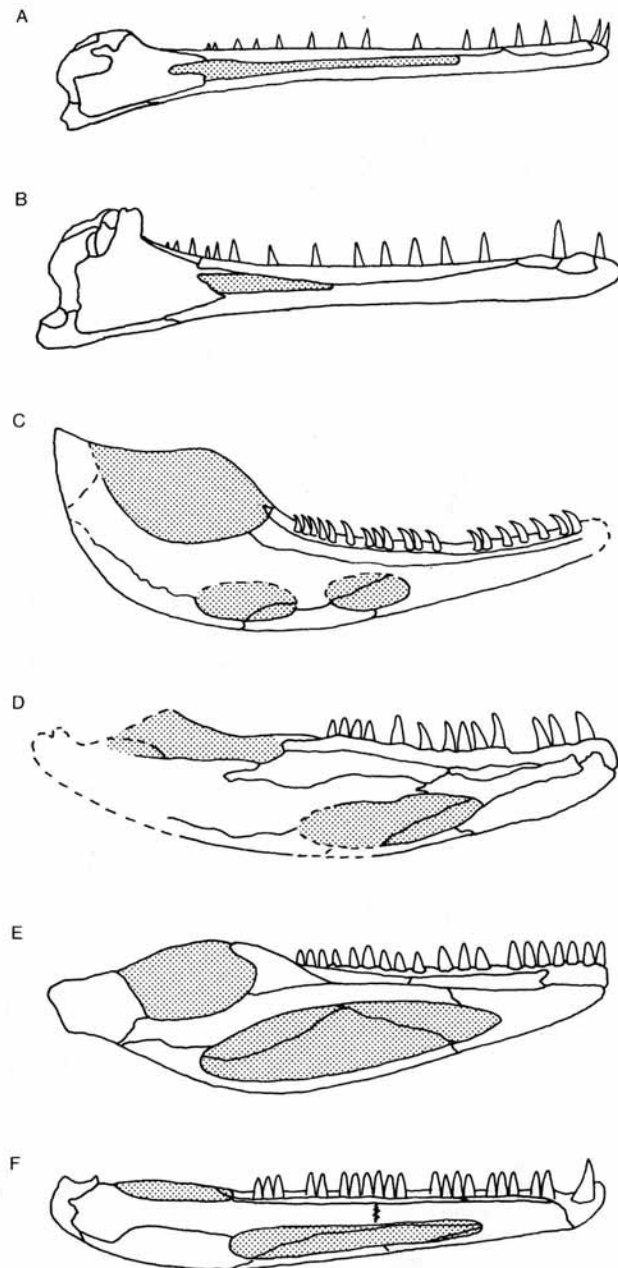
The function of the fenestrae has been discussed by Panchen (1972) for anthracosaurs and by Heaton (1980) for diadectomorphs. Both agree that they developed, in part, in association with the intermandibular musculature. This proposal was based partially on the assumption that the presence of a retroarticular process in 'more advanced labyrinthodonts' is a derived condition, and its absence in embolomeres is primitive (Panchen 1972, p. 309). However, recent descriptions of the mandibles of *Metaxygnathus* (Campbell and Bell 1977), *Doragnathus* (Smithson 1980b), and *Ichthyostega* (Jarvik 1980) have demonstrated that a retroarticular process is present in the earliest amphibia, and its absence in embolomeres need not necessarily be primitive. In addition, colosteids (Smithson 1982) and diadectomorphs (Heaton 1980) retain the retroarticular process suggesting that enlarged intermandibular muscles are not directly related to its absence.

Heaton (1980) suggested that the large fenestrae in diadectomorphs were also correlated with enlarged intermandibular muscles. He suggested that the vacuity was a space which accommodated contracting muscles and proposed that its function was analogous with that of the external mandibular foramen of crocodiles.

In fishes, for example *Amia* (Allis 1897), and many tetrapods (Romer and Parsons 1977) the intermandibular muscles form a thin sheet of tissue between the jaws. If these muscles were enlarged in diadectomorphs, as suggested by Heaton, contraction would almost certainly result in an increase in muscle volume between the jaws rather than in the immediate vicinity of their origins. It therefore seems unlikely that Meckelian fenestrae developed to accommodate contracting muscles.

A further explanation which may account for the presence of enlarged Meckelian fenestrae in colosteids, diadectomorphs, and embolomeres is afforded by reference to the jaws of lepisosteid fishes (text-fig. 5). In *Lepisosteus platyrhinus* (Nelson 1973) a large area of Meckel's cartilage is exposed on the mesial surface of the jaw as a result of incomplete ossification of the surrounding dermal bones. In a related form *Atractosteus spatula* (Wiley 1976) Meckel's cartilage is also exposed to a lesser degree. Removal of Meckel's cartilage from the jaws of both fishes would leave fenestrae analogous to those in the jaws of embolomeres, diadectomorphs, and colosteids and it is possible that rather than having a specific function the enlarged Meckelian fenestrae in some early tetrapods represent persistent incomplete ossification of the mesial surface.

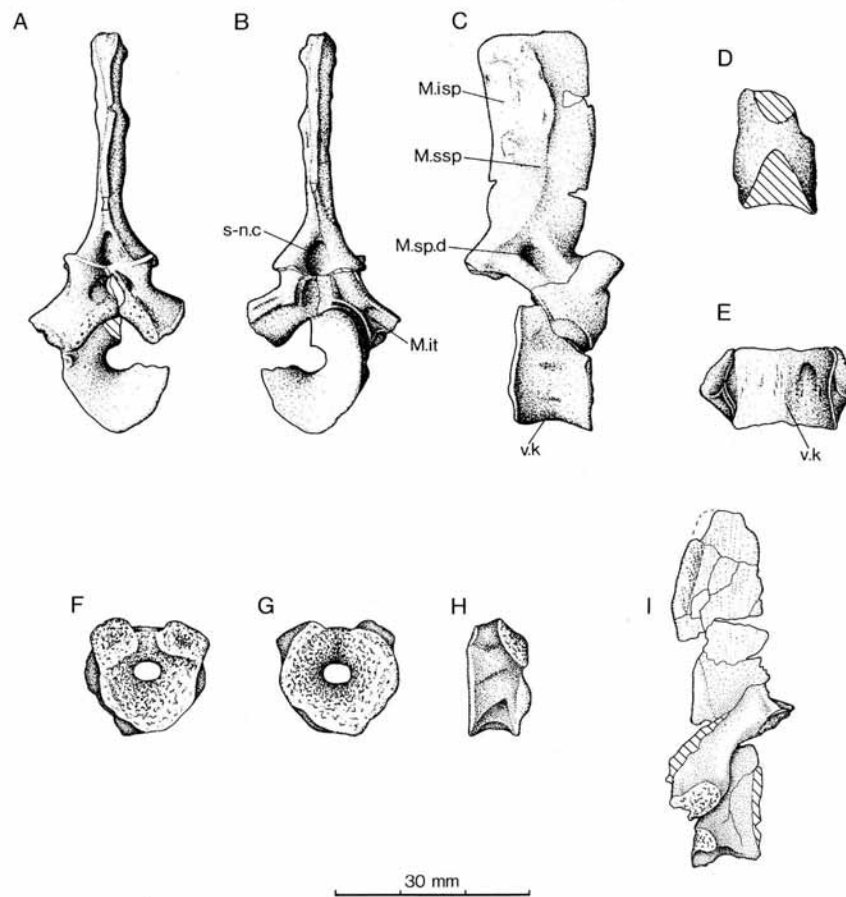
Axial skeleton. Twelve vertebral elements and one incomplete rib from the Dora Bone Bed are referred to *Proterogyrinus pancheni*, together with an isolated pleurocentrum from Niddrie. Six pleurocentra and associated neural arches were recovered but successive vertebrae were never found



TEXT-FIG. 5. Mandibles of lepisosteid fishes and Palaeozoic tetrapods. A, *Lepisosteus platyrhinus* (after Nelson 1973). B, *Atractosteus spatula* (after Wiley 1976). C, *Proterogyrinus pancheni* sp. nov. D, *Anthracosaurus russelli* (after Panchen 1977). E, *Tseajaia campi* (after Moss 1972). F, *Greererpeton burkemorani* (after Smithson 1982).

in articulation. The vertebrae are very similar to those of *P. scheelei*. They are gastrocentrous with short intercentra and well-ossified pleurocentra. All parts of the vertebral column are represented by the material from Dora.

Pleurocentrum. The description of the pleurocentrum is based on an isolated specimen from Cowdenbeath RSM GY 1977.46.34 (text-fig. 6F-H). In most respects it is very similar to the pleurocentra of the embolomeres *Pholiderpeton* (Panchen 1966; Agnew 1984) and *Pteroplax* (Boyd 1980). It is subcircular in anterior view, deeply amphicoelous, and perforated by a small notochordal



TEXT-FIG. 6. *Proterogyrinus pancheni* sp. nov., vertebrae. A-E, trunk vertebra, RSM GY 1975.48.49. A, anterior view. B, posterior view. C, right lateral view. D, sagittal section through pleurocentrum. E, ventral view. F-H, pleurocentrum, RSM GY 1977.46.34. F, anterior view. G, posterior view. H, right lateral view. I, sacral/postsacral vertebra, RSM GY 1976.19.48, left lateral view. Natural size. Broken bone hatched. Abbreviations: M, area of attachment of axial musculature; M.isp, interspinalis muscle; M.it, intertransversarii muscle; M.ob.cap.mag, obliquus capitis magnus muscle; M.rect.cap.p, rectus capitis posterior muscle; M.sp.c, spinalis capitis muscle; M.sp.d, spinalis dorsi muscle; M.ssp, semispinalis muscle; M.ssp.c, semispinalis capitis muscle; s-n.c, supra-neural canal; v.k, ventral keel.

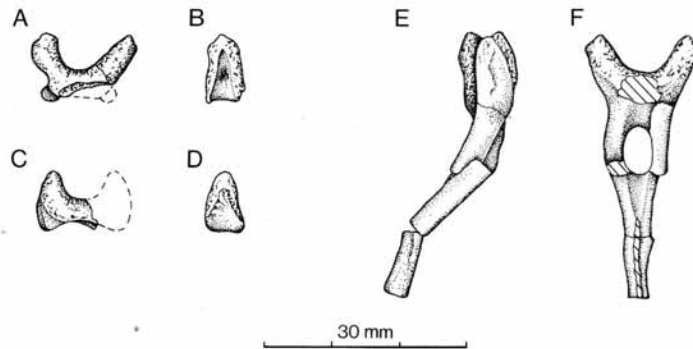
foramen. A periosteal bone covering is restricted to the ventrolateral portion of the centrum which is excavated over most of its length to form a concave rim to the bone. The ventromedial region is not excavated and forms a pronounced ventral keel which is most clearly seen on RSM GY 1975.48.49 (text-fig. 6c). A pair of steeply inclined, concave facets, which articulated with the neural arch, form the dorsolateral corners of the anterior face of the centrum. They bound the gently convex floor of the neural canal which is fully ossified, as in *Pholiderpeton* and *Pteroplax*, and lacks the suture present in *Proterogyrinus scheelei* (Holmes 1984). The centrum is more deeply amphicoelous posteriorly and is pierced by the notochordal canal slightly above its centre. In RSM GY 1977.46.34 the diameter of the anterior surface is somewhat smaller than the posterior surface suggesting that in a fully articulated skeleton it occupied a position immediately in front of the larger trunk vertebrae.

The centra with attached neural arches and the larger, isolated specimen from Niddrie differ from RSM GY 1977.46.34 in a number of respects. They are oval rather than circular in outline and most taper ventrally (text-fig. 6A, B). In addition the most complete vertebra RSM GY 1975.48.49 (text-fig. 6A-E) is relatively much longer than any other attributed to *P. pancheni*.

The pleurocentrum of RSM GY 1976.19.48 (text-fig. 6i) is similar in most details to RSM GY 1977.46.34 but directly below the neural arch facets it bears a pair of concave facets for the capitulum of the ribs. In *P. scheelei* the last presacral, the sacral, and the first three postsacral pleurocentra exhibit rib facets. It is reasonable to assume that RSM GY 1976.19.48 occupied a similar position in the skeleton of *P. pancheni*.

Intercentrum. Two trunk intercentra and one haemal arch from Dora are referred to *P. pancheni* (text-fig. 7). They are smaller than the intercentra referred to *Eoherpeton* (Smithson 1985a), not so strongly horseshoe shaped and lack the concave facets which cup the anterior surface of the pedicel of the neural arch. The trunk intercentrum is crescent shaped in anterior view and when articulated with a pleurocentrum of similar diameter it extends dorsally to the ventral edge of the neural arch facets. In lateral view it narrows dorsally to form a bony wedge. A periosteal covering is restricted to the ventral surface of the intercentrum and a narrow groove on the lateral edge. A facet for the capitulum of the rib is not developed on the ossified portion of the bone. Projecting from the ventrolateral corner of RSM GY 1976.19.49 is a small tubercle, restricted to one face of the centrum where it forms a continuation of the articulating surface (text-fig. 7A). In NUZ 76.10.17 this tubercle forms a well-defined ridge along the length of the ventral surface (text-fig. 7c) and presumably formed the lateral margin of a groove for the dorsal aorta.

The haemal arch RSM GY 1983.9.2 (text-fig. 7E, F) is almost complete and lacks only the ventral tip



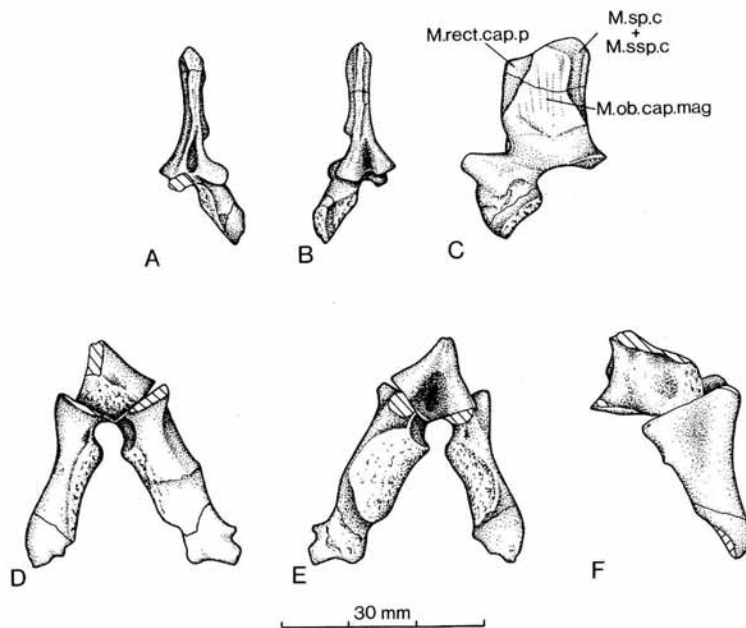
TEXT-FIG. 7. *Proterogyrinus pancheni* sp. nov., vertebrae. A, B, intercentrum, RSM GY 1976.19.49. A, ?anterior view. B, lateral view. C, D, intercentrum, NUZ 76.10.17. C, ?anterior view. D, lateral view. E, F, haemal arch, RSM GY 1983.9.2. E, lateral view. F, anterior view. Natural size. Broken bone hatched.

and the thin anterior and posterior edges of the haemal spine. It has been crushed slightly but the overall form of the bone is readily determined. The dorsal articulating surface corresponds very closely with the trunk intercentrum RSM GY 1976.19.46 and fused to it is a chevron-shaped arch which surrounded the haemal canal. The canal is oval in anterior view, its long axis oriented vertically. The arch tapers ventrally to form a narrow spine which is inclined posteriorly at an angle of 35° to the vertical. This is similar to that of the anterior haemal arches of *P. scheelei* (Holmes 1984, text-fig. 22).

Cervical neural arch. A neural arch NUZ 77.2.17 (text-fig. 8A-C) is considered to be from the cervical region of *P. pancheni* on the basis of scars which are here interpreted as areas of origin and insertion of occipital muscles. It differs markedly from the atlas and axis neural arches of *P. scheelei* (Holmes 1984, text-fig. 21) and it therefore probably formed the first undifferentiated cervical vertebra, the most posterior of the three vertebrae from which occipital muscles originated (see Olson 1936). Unfortunately the third and fourth neural arches of *P. scheelei* have not been described and it is not possible to confirm the interpretation of NUZ 77.2.17 by direct comparison.

The neural arch is reasonably well preserved but the right pedicel and prezygapophysis are missing. It is 21 mm long between the zygapophyses and the neural spine has a maximum height of 18 mm. This compares with an average length of 23 mm and height of 37 mm in the trunk vertebrae attributed to *P. pancheni*. The angle of inclination of the prezygapophysis is 25° which compares with 25° in the trunk vertebrae and *c.* 50° in the caudal vertebra attributed to *P. pancheni*.

The pedicel accounts for less than half the total length of the neural arch. Its internal and anterior surfaces form a continuous surface of unfinished bone which articulated with the pleurocentrum



TEXT-FIG. 8. *Proterogyrinus pancheni* sp. nov., vertebrae. A-C, cervical neural arch, NUZ 77.2.17. A, anterior view. B, posterior view. C, left lateral view. D-F, caudal neural arch, NUZ 78.3.33. D, anterior view. E, posterior view. F, right lateral view. Natural size. Broken bone hatched. Abbreviations: see text-fig. 6.

posteromesially and the intercentrum anteriorly. The ventrolateral edge of the pedicel is also unfinished and forms the articulation for the tubercular rib head. In lateral view this articulating surface is oriented at an angle of 38° to the horizontal.

The neural spine is straight sided in lateral view, gently inclined posteriorly, and with a forward sloping dorsal edge. Between the zygapophyses the base of the spine is pierced by a supraneural canal. The muscle scars are clearly differentiated and their arrangement differs markedly from that found on the posterior trunk vertebrae (see below). The interpretation of the scars follows Olson's (1936) analysis of the dorsal axial musculature in early tetrapods.

The posterior region of the lateral surface of the neural spine, above the level of the supraneural canal, is excavated to form a shallow rugose recess which is separated from the more anterior portion of the spine by a strongly defined ridge. The morphology of this region is very similar to the posterodorsal corner of the axis neural spine in *Eryops* illustrated by Olson (1936, text-fig. 8G). It represents the area of insertion of *M. spinalis cervicus* and *M. semispinalis cervicus*.

A similar, but less extensive, recessed area is present on the anterior region of the left lateral surface of NUZ 77.2.17. In *Eryops* this represents the area of origin of *M. rectus capitis posterior*. Between the recessed areas on the anterior and posterior edges of the spine the median region is heavily striated. It is not developed into the characteristic median ridge for *M. semispinalis* present on the trunk vertebrae. This region in *Eryops* represents the area of insertion of *M. obliquus capitis magnus*.

The occipital muscles *M. rectus capitis posterior* and *M. obliquus capitis magnus* are restricted to the first three cervical vertebrae (Olson 1936, p. 299) where they form with *M. obliquus capitis superior* and *M. obliquus capitis inferior* a series of short muscles passing forward to insert on the occipital region of the skull.

Trunk neural arch. Eight trunk neural arches from Dora are attributed to *P. pancheni*. The most complete specimen RSM GY 1975.48.49 (text-fig. 6A-C) forms the basis of the description. It closely resembles the trunk neural arches of *P. scheelei* (Holmes 1984, text-fig. 22), with neural spines considerably taller than those of *Pholiderpeton* and *Pteroplax*, and clearly defined areas of attachment of the median dorsal axial musculature.

The pedicels account for only half the total length of the neural arch. They bear two pairs of articulating surfaces: a large pair on the posterolateral surface which articulate with the pleurocentrum and a smaller pair on the anterior surface, directly beneath the prezygapophyses, which presumably articulated with a cartilaginous extension of the intercentrum. In RSM GY 1975.48.49 the transverse processes are very short and only the posterior portion projects laterally beyond the neural arch facets. Its dorsal edge is steeply inclined ventrolaterally and its lateral margin lies well below the dorsal edge of the prezygapophyses. The articulation for the tuberculum of the rib is a strap of unfinished bone oriented anteroventrally, at an angle of approximately 45° to the horizontal, and also slightly anteromesially. The posterior surface of the transverse process/pedicel is excavated to form a well-defined recess which probably marks the origin of *M. intertransversarii*. In the less well-preserved specimen RSM GY 1977.46.35 the transverse process is more pronounced and forms a distinct lateral projection from the body of the pedicel. The facet for the tuberculum is less steeply inclined anteroventrally than that of RSM GY 1975.48.49 and appears to project wholly laterally.

Extending posterodorsally from the posterior edge of the pedicel is a strong ridge which buttresses the postzygapophysis. A similar ridge extends anteroventrally from the base of the neural spine to buttress the prezygapophysis. Between them a deep fossa probably marks the origin of *M. spinalis dorsi*. A distinct origin of *M. spinalis dorsi* has not been described on the vertebrae of Coal Measure embolomeres but it is present in *Proterogyrinus scheelei* and is a characteristic of the vertebrae of *Diadectes*, pelycosaurs, and other amniotes (Olson 1936).

The prezygapophyses are closely spaced, project slightly in front of the facets for the intercentrum, and are inclined ventromesially and slightly posteroventrally. The postzygapophyses are correspondingly inclined dorsolaterally and very slightly anterodorsally, allowing a certain degree of rotation and dorso-ventral bending. Between the zygapophyses the base of the neural spine is pierced by a

small supraneural canal for the dorsal ligament. The spine is approximately one and a half times the length of the neural arch with a gently convex anterior margin and concave posterior margin. The lateral surfaces are roughly divided into two equal halves by a median ridge. On the right side of the spine of RSM GY 1975.45.49 the posterior half is the largest while on the left the anterior half is the largest. The median ridge marks the origin and insertion of *M. semispinalis* and the areas on either side of it mark the origin (anterior) and insertion (posterior) of *M. interspinalis* (Olson 1936). Such a clear differentiation of areas of muscle attachment have not been observed on the vertebrae of Coal Measure embolomeres but they are well defined on the vertebrae of *P. scheelei* (Holmes 1984, text-fig. 22).

Specimen RSM GY 1977.46.33, preserved on the same block as the lower jaw of *P. pancheni*, is very similar to RSM GY 1975.48.49. The neural arch of the sacral or immediately post-sacral vertebrae RSM GY 1976.19.48 is also similar but the median ridge on the neural spine and the fossa for *M. spinalis dorsalis* are less well defined. In RSM GY 1983.9.1 the supraneural canal is slightly more extensive dorsally and the base of the spine somewhat narrower.

Caudal neural arch. A neural arch NUZ 78.3.33 (text-fig. 8D-F) is thought to be from the tail of *P. pancheni* on the basis of steeply inclined zygapophyses and the absence of rib facets. Although the specimen has been crushed and the neural spine is missing, it is clearly different from the trunk neural arch RSM GY 1975.48.49. The angle of inclination of the postzygapophyses, *c.* 50°, is more than twice that measured from the trunk neural arches. In *P. scheelei* there appears to be a progressive increase in the angle of inclination along the tail. The zygapophyses of caudal vertebrae 5 and 11 are inclined at 26° and 45° respectively (Holmes 1984, p. 477). If a similar trend occurred in *P. pancheni* NUZ 78.3.33 would have occupied a position between caudal vertebra 13 and 20.

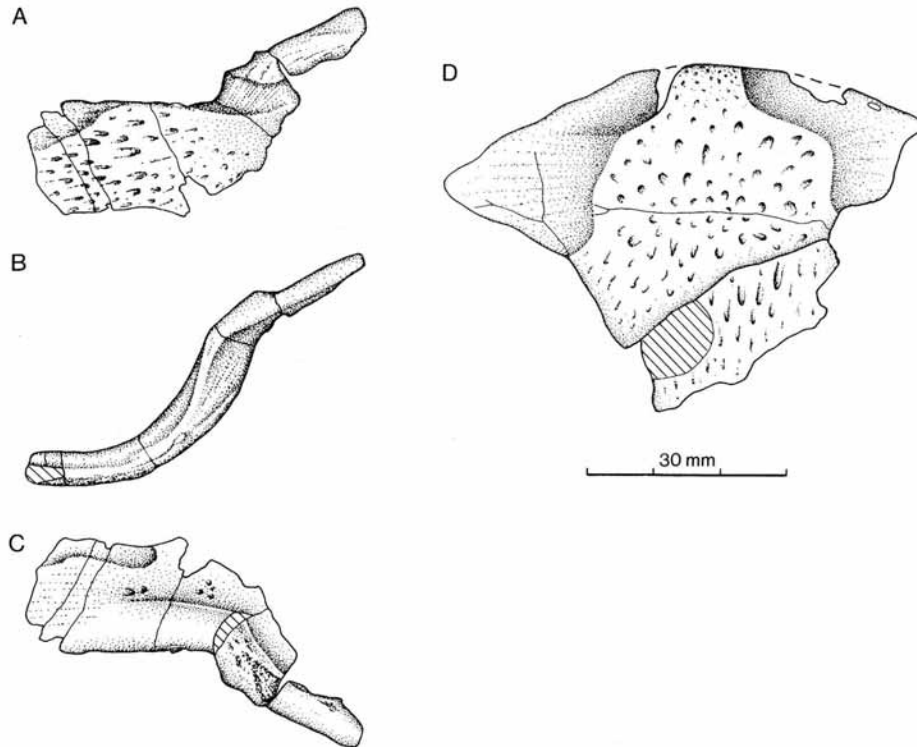
The pedicels lack the normal transverse processes with articulating surfaces for the ribs, but projecting anteroventrally from their bases are a pair of flanges. Unfortunately they are incomplete on both sides, that of the left being most fully preserved. They are very thin with delicate lateral processes and completely covered in periosteal bone. Their form is mostly clearly appreciated from text-fig. 8D-F.

Ribs. The incomplete rib preserved with the lower jaw of *P. pancheni* is the only specimen from Dora referred to this species with confidence. It is 43 mm long and considerably smaller than the ribs from Dora attributed to *Eoherpeton* (Smithson 1985a). The tubercular rib head is preserved but the capitulum is missing. The estimated span of the rib head is approximately half that of the ribs of *Eoherpeton*.

Appendicular skeleton. Clavicle. An incomplete left clavicle NUZ 77.2.19 (text-fig. 9A-C) was recovered from the grid square immediately adjacent to the skull table NUZ 75.11.2. The external surface of the ventral plate of the clavicle is ornamented with the undercutting pits and grooves which characterizes anthracosaur dermal skull roofing bones. It differs from all other clavicles recovered from the Dora Bone Bed which exhibit the characteristic pit and ridge ornament of temnospondyls.

The clavicle of *P. pancheni* resembles closely those of *Archeria* (Romer 1957) and *P. scheelei* (Holmes 1980, 1984). It is divided into two regions; a ventral plate which overlaps the interclavicle mesially, and a dorsally directed shaft which overlaps the cleithrum dorsomesially and the scapulocoracoid ventromesially. The ventral plate is incomplete and its outline could not be determined. The shaft is almost entire but has been slightly crushed.

The ventral plate is relatively thick anteriorly and tapers to a thin lamina posteriorly. Its sharp anterior edge extends dorsally on to the shaft where it divides to form two ridges. One ridge forms the leading edge of the clavicular shaft while the other, more posterior ridge, extends across the dorsolateral region of the ventral plate and separates the ornamented external surface from a highly striated area which Holmes (1980) suggested may mark an area of origin of the ventral throat musculature. At the ventral end of this area is a small tubercle. Running down the internal surface of the clavicular shaft is a broad ridge which fades out anteromesially as it meets the ventral plate.



TEXT-FIG. 9. *Proterogyrinus pancheni* sp. nov. A–C, left clavicle, NUZ 77.2.19. A, ventral view. B, anterior view. C, dorsal view. D, interclavicle, BM(NH) R9940, ventral view. Natural size. Broken bone hatched.

Behind the ridge a deep recess is scarred with pits which probably mark areas of ligamentous attachment. The recess was probably occupied by the anteroventral edge of the scapulocoracoid.

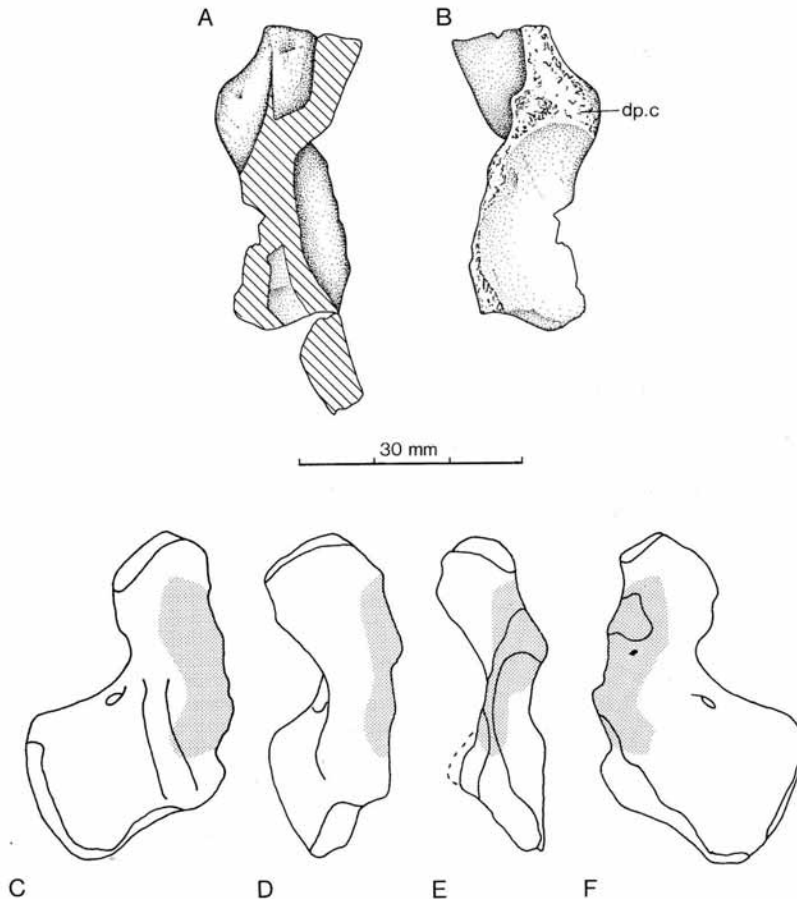
Interclavicle. An interclavicle, BM(NH) R9940 (text-fig. 9D) was recovered from the grid square adjacent that which yielded the lower jaw of *P. pancheni* and associated vertebra and rib. It is preserved in ventral (external) view on a small block of bone bed. The incomplete posterior portion of the interclavicle has been displaced anterolaterally and slightly overridden the ventral surface. Its anterior edge was damaged during preparation and the left lateral corner of the area of clavicular overlap is missing. As preserved the interclavicle is 53.0 mm long and has a maximum width of 72.5 mm; the estimated maximum width of the intact specimen was *c.* 88.0 mm.

BM(NH) R9940 is similar to the interclavicles of *P. scheelei* (Holmes 1980, text-fig. 3) and that attributed by Panchen (1972, text-fig. 13) to *Pholiderpeton* but which Agnew (1984) suggests might pertain to *Pteroplax*. The anterior edge is gently convex and lacks the anterior process of *Archeria* (Romer 1957, text-fig. 1). The concave lateral edges taper posteriorly and possibly continued to form a modest parasternal process. The areas of clavicular overlap are well developed on the dorsolateral margins of the interclavicle. They are separated from the ornamented median portion by a shallow step which accommodates the thickness of the clavicular plate and allows the external surfaces of the clavicles and interclavicle to form a plane surface when articulated. Anteriorly the step is excavated to form a deep groove which was probably occupied by a ridge on the anterior edge of the clavicle. In

BM(NH) R9940 the mesial edge of the overlap area is sinuous but is oriented principally anteromesially. Anteriorly the two sides are separated by a thickened rugosity 10 mm wide.

The median portion of the interclavicle is ornamented with small shallow pits which slightly undercut the bone surface. Towards the margins of the exposed surface the pits are drawn out into shallow furrows and the anterior end of the interclavicle is finely pitted. The areas of clavicular overlap are lightly striated.

Humerus. An incomplete right humerus, NUZ 77.2.20 (text-fig. 10A, B) was found at Dora in the same general area as the skull table NUZ 75.11.2. It was damaged during collection and unfortunately the



TEXT-FIG. 10. *Proterogyrinus pancheni* sp. nov. A, B, right humerus, NUZ 77.2.20. A, dorsal view. B, ventral view. Natural size. Broken bone hatched. C-F, *P. scheelei* right humerus (after Holmes 1980, text-fig. 6, reversed). Position occupied by preserved portion of the *P. pancheni* humerus represented by mechanical stipple. C, dorsal view in plane of distal dorsal surface. D, dorsal view in plane of proximal dorsal surface. E, anterior view. F, ventral view in plane of distal ventral surface. Not to scale. Abbreviation: dp.c, deltopectoral crest.

broken pieces were not recovered. The entepicondyle and ectepicondyle are missing and the proximal end of the bone is incomplete. However, despite this, the specimen is readily identified as a humerus and the preserved portion resembles that of *Proterogyrinus scheelei* (Holmes 1980, text-fig. 6).

The most diagnostic feature of NUZ 77.2.20 is a short deltopectoral crest (text-fig. 10B). Its gently convex unfinished surface faces anteroventrally and lacks the deep pit present on the humerus of *Eoherpeton* (Smithson 1985a, text-fig. 25). The crest continues distally as a narrow, sinuous, unfinished edge which forms the anterior margin of the humerus. This region is very similar to that in *P. scheelei* and lacks the small tubercle described as a supinator process on the humerus of *Eoherpeton*.

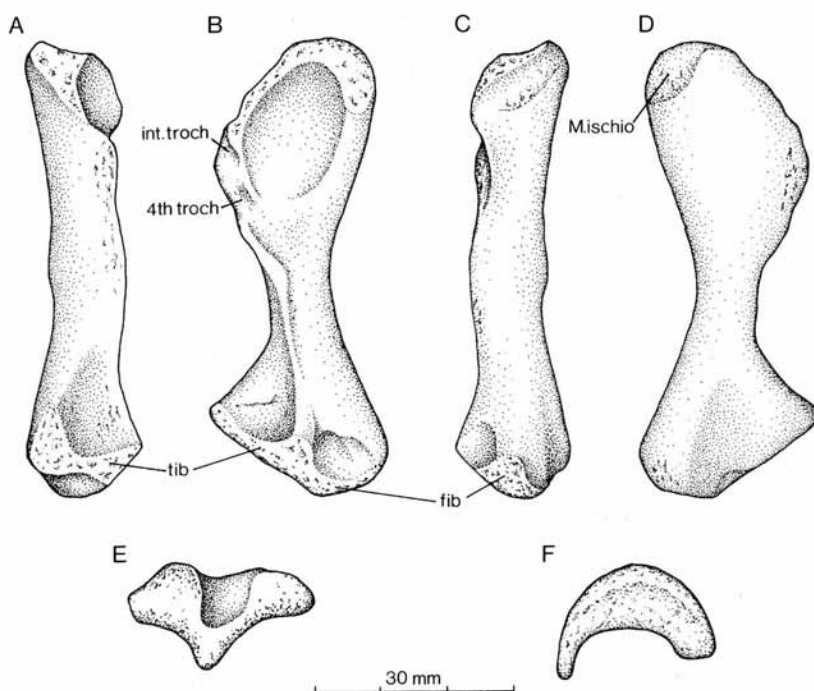
No other diagnostic feature of the anthracosaur humerus is preserved on NUZ 77.2.20. The position the preserved portion occupied in the intact bone is outlined on the illustration of the humerus of *P. scheelei* (text-fig. 10C-F).

Femur. In 1914 Watson described a right femur, BM(NH) R4085, which originally formed part of a collection of Scottish Lower Carboniferous lungfish made by Dr R. H. Traquair and later acquired by the British Museum of Natural History. No data accompanied the specimen, but on the basis of a small piece of matrix Watson (1914) attributed it to the Loanhead No 2 Ironstone. Unfortunately this cannot be verified. Until 1954 the entire Carboniferous Limestone Series in Scotland was included in the Lower Carboniferous (Currie 1954) and thus the pre-Coal Measures localities, for example, Burghlee, Burdiehouse, Gilmerton, Loanhead, and Niddrie, were regarded as Lower Carboniferous. The matrix associated with the femur is insufficient to allow a full appraisal of its lithology, and comparison with that from other 'Lower Carboniferous' localities neither corroborates nor refutes the view that the specimen was collected at Loanhead. However, as it may have been found in pre-Coal Measures rocks, possibly at Loanhead, and is well preserved and yields important data on the morphology of the femur of early tetrapods, it is here fully described for the first time.

Watson erected the name *Papposaurus traquairi* for the femur and in his description noted its likeness to those of early reptiles. Subsequently White (1939) remarked on its similarity with the femur of *Archeria* and recently Holmes (1984) emphasized its close resemblance with that of *Proterogyrinus scheelei*. It is possible, therefore, that the specimen collected by Traquair is a femur of the anthracosaur here named *P. pancheni*. If it could be demonstrated that the femora of *Papposaurus* and *Proterogyrinus scheelei* were sufficiently similar to indicate the two taxa were members of the same genus *Proterogyrinus* would become a junior synonym of *Papposaurus*. However, the absence of features shared uniquely by the femora of *Proterogyrinus scheelei* and *Papposaurus* prevents such a demonstration. This paucity of valid diagnostic features and the uncertainty surrounding the provenance of the *Papposaurus* femur, suggests that the name *P. traquairi* should be considered a *nomen vanum* (Simpson 1945) and refer to the type specimen only.

BM(NH) R4085 (text-fig. 11) is well preserved and the fully ossified proximal and distal condyles suggest it formed part of a mature adult. It is 69 mm long and less robust than the femora of *Archeria* (Romer 1957, text-fig. 8) and *Proterogyrinus scheelei* (Holmes 1984, text-fig. 33). The proximal end of the femur has a gently rounded parabolic outline in dorsal view. The articulating surface forms a dorsally convex strap of unfinished bone which extends along the anterior edge towards the internal trochanter. The medial portion of the articulation is deeper than the anterior and posterior margins and the whole surface is oriented ventrolaterally. Above the condyle the posterior edge of the dorsal surface bears a large, well-defined muscle scar, which probably marks the insertion of *M. ischio-trochantericus*.

The adductor fossa is a deep oval recess bounded, in part, by the unfinished proximal articulating surface. It reaches its maximum depth behind the anterior edge of the condyle forming a prominent ridge which bears the internal and fourth trochanters. The internal trochanter lies mid way between the proximal edge of the femur and the fourth trochanter. It is less well defined than that on the femora of *Archeria* and forms a continuous unfinished surface with the proximal condyle. Below it the fourth trochanter forms a modest rugosity which passes over the anterior edge of the femur and is visible in all aspects except distal view. Extending distally from the trochanter is a prominent, but



TEXT-FIG. 11. *Papposaurus traquairi* Watson, right femur, BM(NH) R4085. A, anterior view. B, ventral view. C, posterior view. D, dorsal view. E, distal view. F, proximal view. Natural size. Abbreviations: fib, fibial condyle; int.troch, internal trochanter; tib, tibial condyle; 4th troch, 4th trochanter; M.ischio, insertion of ischiotrochantericus muscle.

slightly eroded, adductor crest. At its proximal end the crest is oriented posterodistally but below the adductor fossa it curves forward and runs down toward the intercondylar ridge. It occupies a more anterior position than that in *Archeria*, but unlike *Ichthyostega* (Jarvik 1980, text-fig. 162) and *Eoherpeton* (Smithson 1985a, text-fig. 29) where the crest forms part of the anterior edge of the femur, it is not visible in dorsal view.

The distal articulating surface is divided into anterior and posterior condyles by a deep intercondylar groove dorsally and a prominent intercondylar ridge ventrally, which together give the distal end of the femur a distinctly V-shaped outline in lateral (distal) view. The posterior condyle is the smaller of the two articulations and forms a gently convex, triangular surface which articulated with the fibula. In front of the condyle, on the ventral surface of the femur is a deep, subcircular depression, similar to that in *Eoherpeton* and more pronounced than that in *Archeria*. It lacks the rugosities for joint ligaments and flexor muscles present in *Eoherpeton*. Above the fibular condyle the dorsal surface is slightly scarred and probably marks the origin of *M. extensordigitorum communis*.

There is no clear division on the articulating surface between the tibial and fibular condyles. As a proportion of the entire distal articulation the tibial condyle appears to be relatively smaller than that in *Archeria* or *Eoherpeton* suggesting a relatively smaller tibia in *Papposaurus*. The condyle lies, in part, beneath the intercondylar groove and is an anteriorly expanded strap which is wholly oriented ventromesially. In front of it, on the ventral surface of the femur, is a shallow recess, the popliteal space which is slightly less extensive than in *Archeria* but notably larger than in *Eoherpeton*.

DISCUSSION

During the past eighteen months, three detailed reviews of anthracosaur systematics have been published (Holmes 1984; Panchen 1985; Smithson 1985a). Each followed a study of new material from sites in the Viséan and Namurian of Scotland and North America, and, with the exception of Panchen's review which included discussion of ideas presented by Smithson, each author wrote without detailed reference to his colleagues unpublished work.

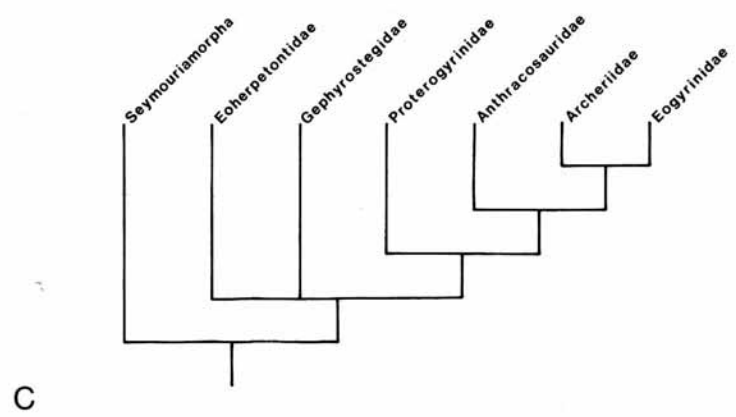
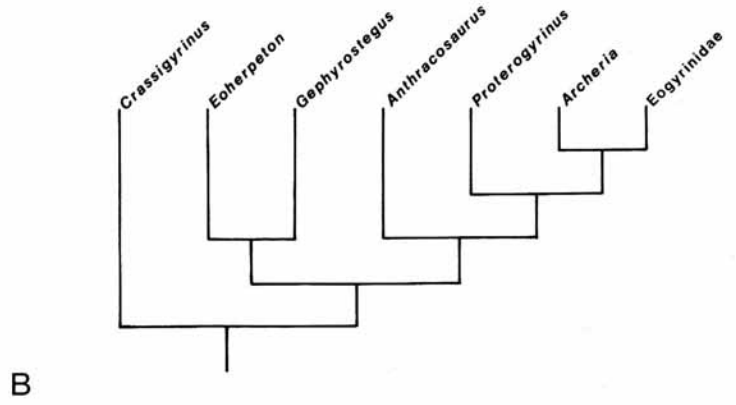
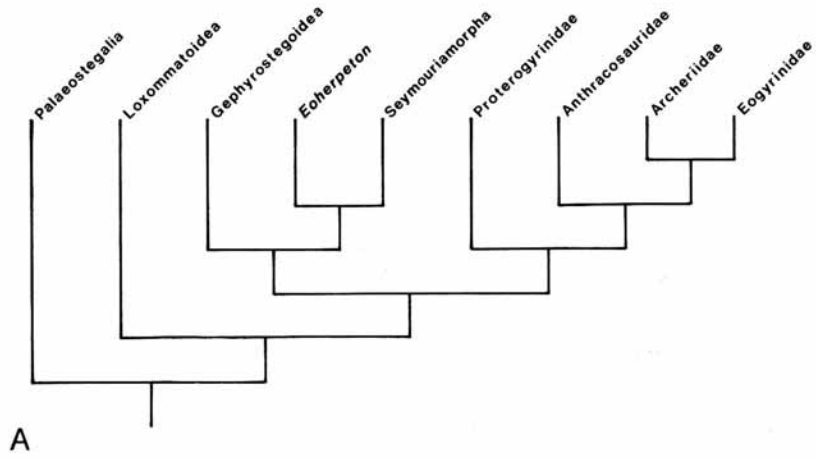
The three hypotheses of relationships proposed by Holmes, Panchen, and Smithson are illustrated in text-fig. 12. It is clear from the three cladograms that the authors accept the traditional view that the Carboniferous anthracosaur taxa, the Eoherpetontidae, Gephyrostegidae, and Embolomeri, are closely related, although differ as to how they are interrelated, but that they disagree on the closeness of relationships of the Palaeostegalia (*Crassigyrinus*) and the Seymouriamorpha to Carboniferous anthracosaurs.

Holmes's scheme (text-fig. 12A) is an extension of that proposed by Panchen in 1980 but which he has now rejected (Panchen 1985). The additional characters Holmes has used to support his scheme are nevertheless important and have a direct bearing on the validity of the hypotheses proposed by Panchen and Smithson. The principal difference between this scheme and those of Panchen and Smithson is the position of the Seymouriamorpha. A sister-group relationship between the Gephyrostegoidea (Gephyrostegidae and Eoherpetontidae) and Seymouriamorpha was proposed first by Panchen (1980). It was based on the view that *Eoherpeton* retained posttemporal fossae and had an incipient otic tube (Panchen 1975) and that among anthracosaurs these features were shared uniquely with the seymouriamorphs. However, on the basis of new material from Dora, I have shown (Smithson 1985a) that the braincase of *Eoherpeton* closely resembles that of embolomeres and lacks both the otic tube and posttemporal fossae. There appear to be no other derived characters which support a sister-group relationship between *Eoherpeton* and the seymouriamorphs and this part of Holmes's scheme must be rejected.

Panchen (text-fig. 12B) and I (text-fig. 12C) both agree that the Eoherpetontidae, Gephyrostegidae, and Embolomeri form a monophyletic group, which I named the Anthracosauroidae (Smithson 1985a). In addition I accepted the traditional view that the Anthracosauroidae and the Seymouriamorpha are sister-groups and together comprise the Anthracosauria. This relationship was based on the view that the tabular-parietal suture on a skull roof including all three bones of the temporal series, the tabular, supratemporal, and intertemporal, was a feature uniquely shared by the two groups (Smithson 1985a). (In a recent review of the systematic position of intasuchid temnospondyls, Gubin (1984) corrected Konzhukova's (1956) interpretation of the pattern of their skull roofing bones (see Heaton 1980). Konzhukova had shown a tabular-parietal suture like that of anthracosaurs in both species of intasuchid *Intasuchus silvicola* and *Syndyodosuchus tetricus*. However, this was in error. Intasuchids exhibit the supratemporal-postparietal suture present in all temnospondyls (Gubin 1984, text-figs. 1 and 2).) Holmes (1984) has suggested that the absence of posttemporal fossae and the presence of tabular horns may also be synapomorphies uniting taxa traditionally placed in the Anthracosauria, but this is disputed by Panchen (see below). Prior to Holmes's suggestion, I had assumed that the absence of posttemporal fossae was a synapomorphy of the Anthracosauroidae (Smithson 1985a) but I now accept Holmes's (1984) interpretation of the occiput of the seymouriamorphs *Karpinskiosaurus* and *Seymouria*, and agree with him that posttemporal fossae are probably absent in all seymouriamorphs.

Panchen's scheme (text-fig. 12B) breaks completely with tradition. He rejects the idea that the Anthracosauria is a monophyletic group, and suggests that 'the tabular-parietal contact uniting anthracosauroids and seymouriamorphs must be a case of parallelism or homoplasy' (Panchen 1985, p. 555). Instead, he proposes that the anthracosauroids are most closely related to *Crassigyrinus* and supports this relationship with four characters he considers to be uniquely shared by the two groups: *a*, the dermal ornament on the skull roof and dermal pectoral girdle; *b*, tabular horns; *c*, the lack of posttemporal fossae; *d*, the histology of the teeth.

Panchen contrasts the dermal ornament of loxomatids and temnospondyls which he defines as 'a



TEXT-FIG. 12. The phylogeny of the Anthracosauria. A, after Holmes (1984). B, after Panchen (1985). C, after Smithson (1985a).

raised honeycomb pattern which becomes extended in zones of intensive growth' with that of anthracosauroids and *Crassigyrinus*, which he defines as 'less regular than the temnospondyl type and . . . consists of rounded pits more widely separated by less sharp ridges' (Panchen 1985, p. 551). However, the polarity of this character has not been established and there is no reason to assume that the ornament of anthracosauroids and *Crassigyrinus* is derived with respect to that of loxommatids and temnospondyls. The ornament of *Ichthyostega* is different again being largely pustular, while that of sarcopterygian fishes is extremely variable but none has dermal ornament like that of early tetrapods. Thus, this character must be regarded as equivocal until polarity can be established and should not be used to support a relationship between anthracosauroids and *Crassigyrinus*.

Modified tabular horns have been described by Holmes (1984) in seymouriamorphs and he has also reported the absence of posttemporal fossae in this group. These two features are therefore not unique to anthracosauroids and *Crassigyrinus* but may define a group which also includes the seymouriamorphs (see below).

Crassigyrinus shares a unique tooth histology with two Coal Measure embolomeres *Anthracosaurus* and *Pholiderpeton* (Panchen 1985). In primitive tetrapods, for example *Ichthyostega*, the histology of the palatal tusks sectioned at or near the junction of the root and the crown, shows a characteristic zigzag folding of the dentine into the open pulp cavity, with most of the angles bearing short side branches. In temnospondyls, there is a progressive reduction in the number of side branches and the most derived condition is found in *Mastodonsaurus* where side branches are absent. This derived condition is also found in *Crassigyrinus*, *Anthracosaurus*, *Pholiderpeton*, and probably *Archeria* (Panchen 1985). In addition, the tusks of *Crassigyrinus*, *Anthracosaurus*, and *Pholiderpeton* show a second feature which has not been described in the teeth of other early tetrapods. Panchen (1985, p. 529) notes that 'between each successive pair of radial infoldings of primary dentine . . . there is a wedge-shaped zone of "dark dentine" with densely-packed tubules oriented radially'. This condition is unique to these three taxa and may, as Panchen suggests, be a shared derived character uniting *Crassigyrinus* and anthracosauroids. However, as noted by Panchen, its distribution among other anthracosauroids, particularly the smaller forms (*Crassigyrinus*, *Anthracosaurus*, and *Pholiderpeton*) are among the largest known Carboniferous tetrapods, with skull lengths greater than 30 cm) is not known. Consequently this synapomorphy must also be regarded as equivocal until its distribution within the Anthracosauroideae is established.

Thus in summary, it is clear that both the traditional view of the Anthracosauria, as a group embracing the Carboniferous taxa, Eoherpetontidae, Gephyrostegidae, and Embolomeri, and the Seymouriamorpha, and the new scheme proposed by Panchen, are supported by very few synapomorphies. The traditional view is supported by a single character which Panchen suggests may have developed independently in anthracosauroids and seymouriamorphs, while Panchen's new scheme is supported by two characters which are regarded here as equivocal either because the polarity of the character state has not been established or the extent of the character within the group is not known. Additional work is now necessary to demonstrate the validity of these characters. This should be done within the framework of a larger study of the interrelationships of early tetrapods. Currently, there is some measure of agreement between Holmes, Panchen, and Smithson that *Crassigyrinus*, anthracosauroids, and seymouriamorphs form part of a 'reptiliomorph' clade which also includes loxommatids, diadectomorphs, and amniotes. However, the intrinsic relationships of the members of this clade are disputed (see Holmes 1984; Smithson 1985a). It is hoped that new loxommatid material, including postcrania, from the Coal Measures of Lancashire being prepared by Dr Angela Milner at the British Museum (Natural History), and new anthracosauroid material from the Lower Carboniferous of West Lothian, Scotland (Wood *et al.* 1985), will provide new data on which to reappraise these relationships and test the competing hypotheses discussed here. Until then, we must accept that for Palaeozoic tetrapods, as for most other groups of fossil vertebrates, a generally agreed phylogeny and classification remains to be proposed.

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