A LOWER CARBONIFEROUS AÏSTOPOD AMPHIBIAN FROM SCOTLAND

by CARL F. WELLSTEAD

ABSTRACT. '*Ophiderpeton*', a mid-Viséan aïstopod from the Wardie Shales near Edinburgh is described. Although '*Ophiderpeton*' possesses many of the attributes characteristic of aïstopods and seems generally more closely comparable to ophiderpetontids than to phlegethontiids, details of cranial anatomy such as possession of a relatively short skull, short parietals, and the absence of a tabular-parietal contact, as well as the presence of spinal-nerve foramina in only a portion of the vertebral column and the absence of tetra-radiate ribs, postcranially, distinguishes '*Ophiderpeton*' from both of the currently recognized aïstopod families. On the basis of these differences, '*Ophiderpeton*' is renamed, *Lethiscus stocki*, and a new family, Lethiscidae, is erected to hold the new species.

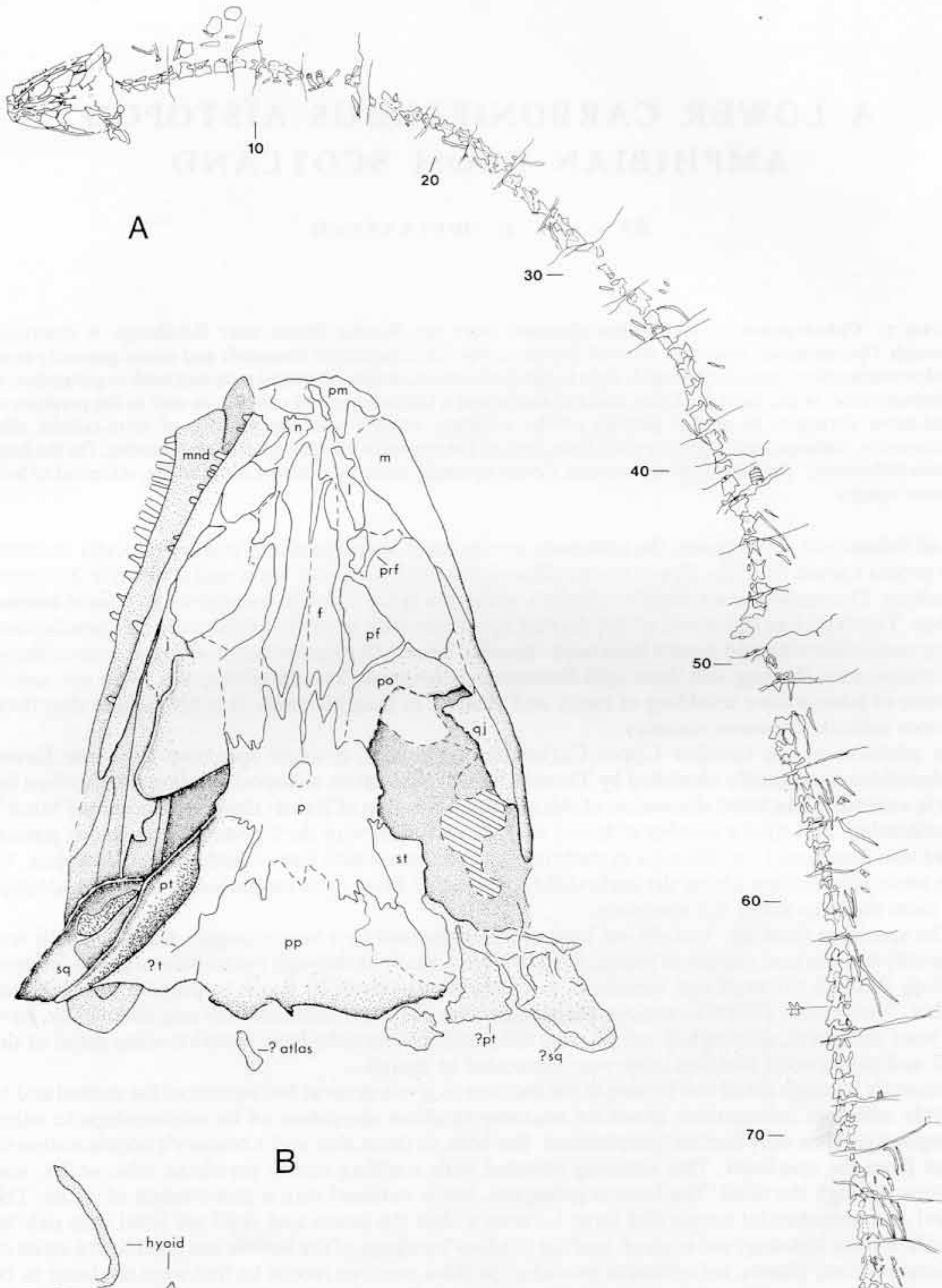
OF all Palaeozoic amphibians, the aïstopods are the most specialized and phylogenetically isolated. The genera known from the Upper Carboniferous are totally without limbs and have up to 230 trunk vertebrae. The vertebrae are simple cylinders, without a trace of trunk intercentra or caudal haemal arches. The skull has lost much of the dermal cover common to labyrinthodonts and rhipidistians. These snake-like aïstopod genera have been classified among the lepospondyls along with nectrideans and microsaurs, sharing with them such features as holospondylous vertebrae, lack of an otic notch, absence of labyrinthine infolding of teeth, and absence of palatine teeth. It is not certain that these features indicate common ancestry.

In addition to the familiar Upper Carboniferous genera, a single specimen from the Lower Carboniferous, originally identified by Thomas Stock (1882) as an aïstopod, has lain undescribed for nearly a century. The latest discussion of this specimen was that of Baird (1964), who accepted Stock's identification, and cited a number of broad similarities it held with the Upper Carboniferous genera. Baird also mentioned the difficulty in studying the specimen which had contributed to its neglect. To gain more information about the early differentiation of Palaeozoic amphibians, a further attempt has been made to study the specimen.

The specimen (text-fig. 1) is 49 cm long and is preserved in a very elongate nodule, which was originally broken into dozens of pieces, each of which was split through the middle to give a series of sections through the skull and vertebrae. No attempt was made by Stock to prepare the specimen further. Preliminary efforts to remove the matrix from the bone, mechanically and chemically, have not been successful, although X-ray photography and tomography have revealed some detail of the skull and postcranial skeleton otherwise concealed in matrix.

Presently, enough detail can be seen in the sections to give a general description of the animal and to provide sufficient information about its anatomy to allow discussion of its relationships to other lepospondyls. The only further 'preparation' has been to clean glue and a century's accumulation of grime from the specimen. This cleaning revealed with startling clarity vertebrae, ribs, scales, and sections through the skull. The bone is preserved, but is outlined with a thin coating of pyrite. The neural and notochordal canals and large lacunae within the bones and skull are filled with calcite. Details of bone histology are evident, and the random breakage of the nodule has produced a series of sections in many planes. Information provided by these sections would be lost were the bone to be removed for production of latex casts following Baird's technique (Baird 1955); therefore, this otherwise very effective method of preparing specimens was not attempted. Normal external views of the bone are rarely evident, but those available reveal sufficient detail along the column to allow

[Palaeontology, Vol. 25, Part 1, 1982, pp. 193–208.]



TEXT-FIG. 1. *Lethiscus stocki*, MCZ 2185. A, whole specimen, × ½. B, skull, × 3.

description of some regional differentiation. Revealed in the cleaned specimen were several characteristics which ally it with the Aïstopoda, but also others which distinguish it from aïstopod families Phlegethontiidae and Ophiderpetontidae.

MATERIALS AND METHODS

A standard medical X-ray machine and the Stratomatic tomography X-ray machine with tri-spiral movement and 0·6 focal spot were used to produce the X-ray photographs critical to the description of this specimen. The film used was Ilford X-ray film.

Text-fig. 3 is an X-ray of the half-nodule containing the skull less the posterior skull roof. X-rays of the half-nodule bearing the posterior skull roof revealed no more than can be seen with the naked eye. The matrix of the nodule is too dense for successful application of X-rays to the assembled skull-bearing nodule halves.

Abbreviations used in figures

bo—basioccipital; bs—basisphenoid; c—coronoid; cap—capitulum; ect—ectopterygoid; ep—epipterygoid; f—frontal; it—intertemporal; j—jugal; l—lacrimal; m—maxilla; mnd—mandible; n—nasal; ot—otic capsules; p—parietal; pf—postfrontal; pm—premaxilla; po—postorbital; poz—postzygapophysis; pp—postparietal; prf—prefrontal; prz—prezygapophysis; ps—parasphenoid; pt—pterygoid; q—quadrate; qj—quadratojugal; sq—squamosal; st—supratemporal; t—tabular; tub—tuberculum; v—vomer.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA
Sub-class LEPOSPONDYLI
Order AÏSTOPODA
Family LETHISCIDAE fam. nov.

Diagnosis. Same as for the only known genus.

Lethiscus gen. nov.

Type species: *Lethiscus stocki* sp. nov.

Diagnosis. A small elongate amphibian with holospondylous vertebrae and short-snouted skull bearing lateral temporal fenestrae. Orbits placed in the anterior third of the skull and separated from the temporal fenestrae by the postorbital bones. The bones of the prefrontal-postfrontal-postorbital series increase in size posteriorly. Intertemporal absent. Parietals roughly equivalent in length to the frontals and surrounding a large parietal opening. Tabulars do not contact the parietal bones. Postparietals relatively large. Mandibles deep and long, approximating the length of the skull.

The trunk is very long. Differentiation along the vertebral column is expressed by the presence in the posterior portion of the column of spinal-nerve foramina, serrated neural spines and transverse processes rising, in part, from the centra. Anteriorly, transverse processes arise solely from the neural arches and spinal-nerve foramina are absent. Ribs are bicipital and robust.

Etymology. The generic name extends Cope's practice of naming serpentiform 'lepospondyls' for rivers in Hades. In this case, *Lethe* is a stream named for the Greek god of forgetfulness.

Lethiscus stocki sp. nov.

Diagnosis. The same as for genus. Specific name honours the discoverer of the specimen.

Holotype. MCZ 2185. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. Skull and postcranial skeleton. This is the only known specimen.

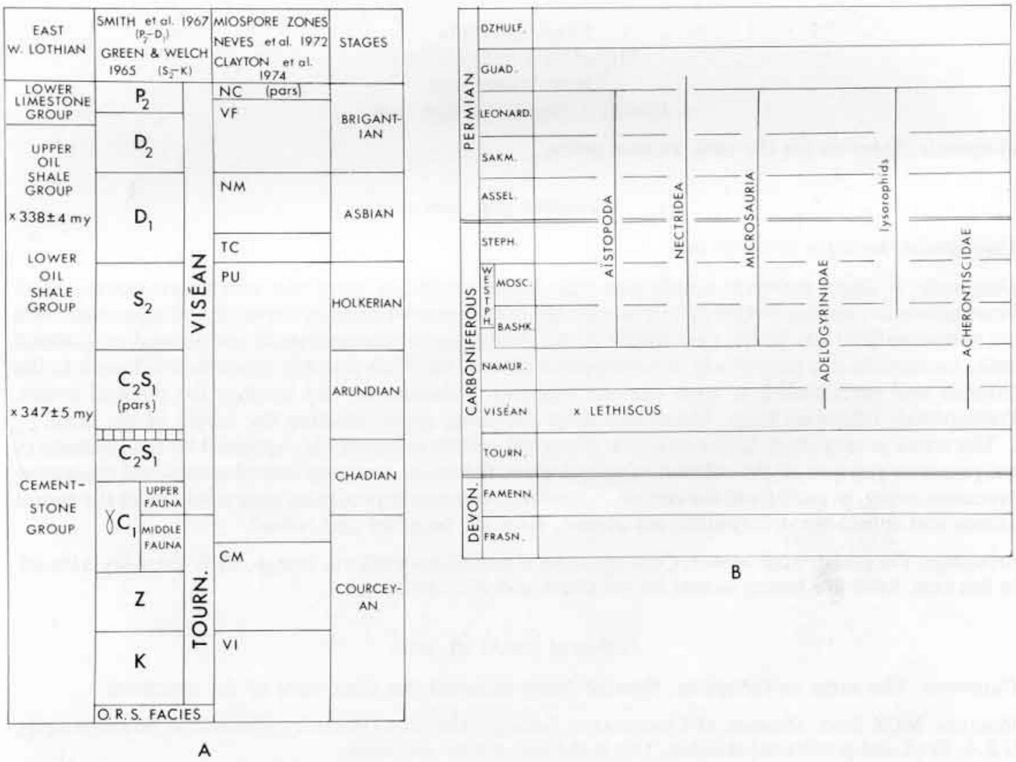
Locality and horizon. Stock (1882) discovered the specimen in the shales of the Wardie shore, north of Edinburgh, Scotland (Wood 1977, gives further locality data). These beds, the Wardie Shales, lie in the middle of the Lower Oil Shale Group (Mitchell and Mykura 1962) and have a mid-Viséan age (text-fig. 2*a*). The base of the Arthur's Seat Volcanic Beds defines the base of the group in the Edinburgh vicinity, though they cannot be traced regionally. Fitch, Miller, and Williams (1970) report a potassium-argon date of 347 ± 5 my B.P. from these volcanics. George, Johnson, Mitchell, Prentice, Ramsbottom, Sevastopulos, and Wilson (1976) place volcanic rocks dated at 338 ± 4 my B.P. (Fitch *et al.* 1970) in the lower portion of the Upper Oil Shale Group. The Wardie Shales can, therefore, be estimated as approximately 340 million to 345 million years old. George *et al.* (1976) correlate the mid-Viséan with the Middle Mississippian (Meramec) of North America.

DESCRIPTION

Skull

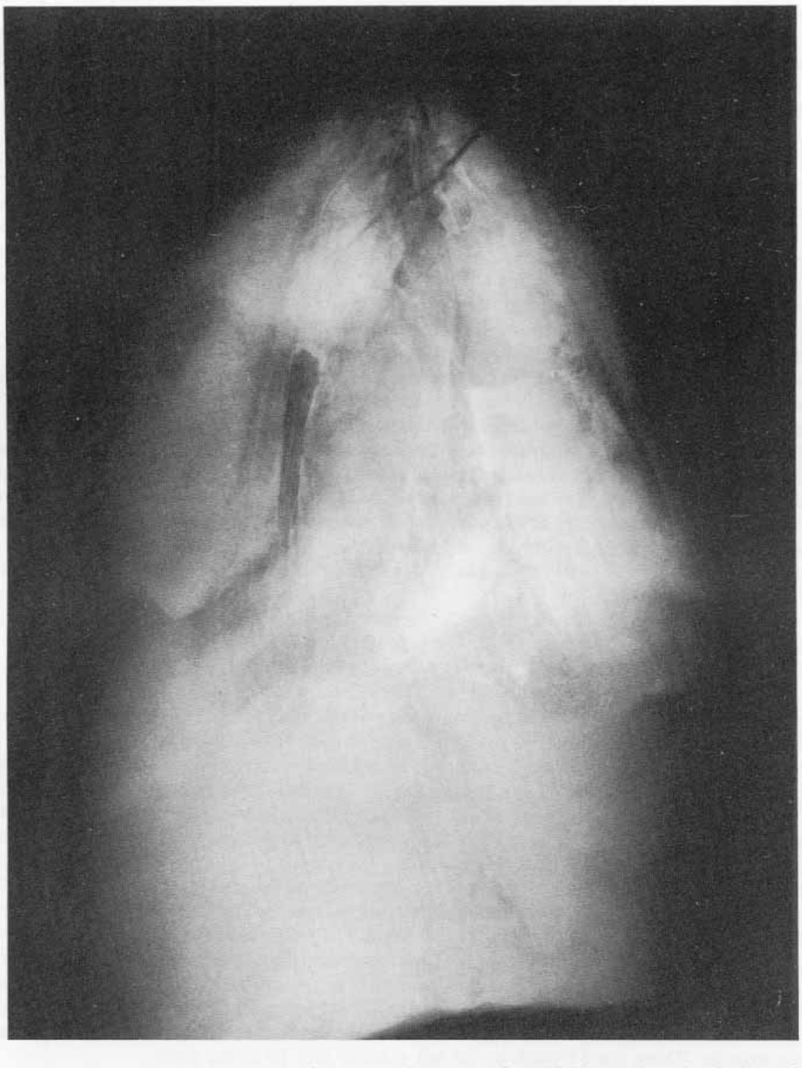
The skull (text-fig. 1) is exposed in an irregular para-frontal fracture which in one half-nodule yields an unobscured view of a portion of the left suspensorium and of the ventral surface of the skull table posterior to the fronto-parietal suture. In the other half-nodule only extremely irregular sections of the remainder of the skull can be seen. A second fracture yields an oblique section of the left lateral aspect of the skull. The circum-orbital bones have been interpreted through study of the specimen, an X-ray of the second half-nodule (text-fig. 3) and tomographs. The remainder of the skull, including the snout, lateral and ventral margins, portions of the palate and mandibles have been interpreted almost entirely from this X-ray and from the tomographs.

The skull is preserved in three dimensions with some distortion and fracturing of the snout, ventral skull margins, and tabular-suspensorium regions. As is the case with the post-cranial portion of the specimen, the



TEXT-FIG. 2. A, correlation chart of Lower Carboniferous stratigraphy in the Scottish Midland Valley (after George *et al.* 1976). B, range chart of the 'lepospondyls' (Carroll 1977; Olson 1972; Thomson and Bossy 1970).

bone is well preserved, but much softer than the enclosing matrix, rendering mechanical preparation hazardous. Bones are coated with pyrite, which accentuates sutures as well as cracks, but adheres closely to the bone. This coating obscures any ornamentation and evidence of lateral line canals which might exist. The skull is triangular in shape, widest at its posterior extreme and is approximately twice as wide as it is high. Openings are present in the skull roof for external nares, orbits, the parietal opening, and temporal fenestrae. The orbits are in the anterior third of the skull.



TEXT-FIG. 3. X-ray photograph of skull, *Lethiscus stocki*, MCZ 2185, less the skull roof posterior to fronto-parietal suture. × 3.

The relationships of the bones in the skull table can be viewed directly and are, therefore, more confidently interpreted than are those seen in X-ray. The bones surrounding the parietal opening are assumed to be the parietals and further homologies within the skull table follow the discussion of the skull bones in *Ophiderpeton* by Thomson and Bossy (1970, p. 24).

The parietals bear dentate sutures with surrounding bones and are fused to one another posterior to the parietal opening. The postparietals are also fused and together with the parietals comprise two-thirds of the skull table area. The postparietals are broader posteriorly than at the parietal border and extend to the rear margin of the skull.

The postparietals are excluded from the temporal fenestrae by the supratemporal and tabular bones. Intertemporal bones are absent. The supratemporals are rectangular bones approximately three times as long as they are wide. Their medial sutures with the postparietals and parietals are smoothly sinuous while their anterior margins have dentate sutures with the parietal bones. The posterior margins are poorly defined. Ventrally, the supratemporals appear to bear sutures with the pterygoids, although the contact is obscured by sediment and breakage along the parafrontal fracture.

A suture-like lineation, seen in the specimen intersecting the posterior margin of the left postparietal, taken in conjunction with the posterolateral borders of the skull table and the posterior regions of the supratemporals, provides the evidence for the tabular bones. An element between the right supratemporal and the fused postparietals appearing to bear a contact with the parietals may be a medial process of the right tabular. However, the mate of this 'tabular' process is not found on the left side of the skull table, suggesting that the feature is more probably an irregular fracture within the postparietals and that the tabulars have no contact with the parietals. The ventral margins of the tabulars are obscured by sediment and breakage, but would seem to have had a short suture with the squamosal posterior to the squamosal-pterygoid contact.

The relationships of the frontals, parietals, and the right orbital series can be observed directly. The frontals are paired, narrow, and equal in length to the parietal and postparietal. They share an interdigitating suture with the parietals, but have a sinuous suture with pre- and postfrontals and postorbitals.

The fragment anterolateral to the left frontal is taken questionably as the small left nasal.

The postfrontal and postorbital separate the orbit from the temporal fenestrae. The prefrontals are small elements of indistinct shape. The postfrontals are approximately twice as long as the prefrontals and are wedge-shaped. While the posterior portion of the right postorbital is missing, the left one seems to be complete and is large, approximately 2·5 times the size of the postfrontal. The exact nature of the relationship of postorbital to the lateral edge of the parietal is obscured by sediment.

The lacrimals are elongate bones which seem to form the anterior portions of the orbital margin and extend to the external nares.

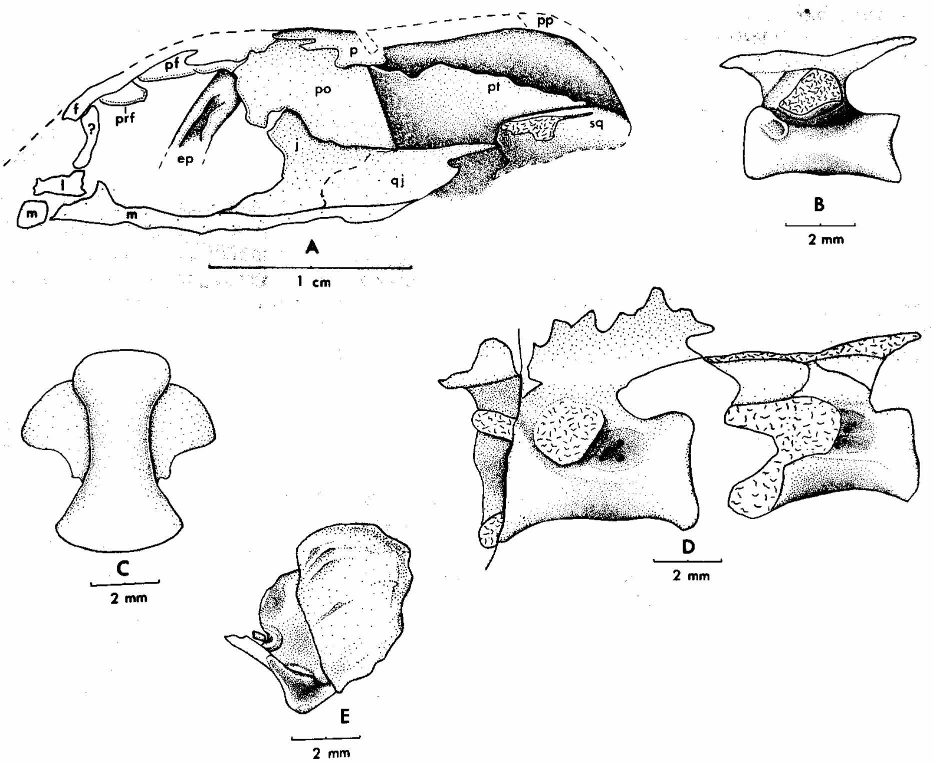
The left and right jugals can be seen directly in the specimen, although the left jugal is the better exposed along the oblique lateral fracture surface (text-fig. 4A). The indefinite suture indicated between jugal and quadratojugal represents a conspicuous separation between two bony elements in the specimen, but which cannot be interpreted confidently as either a suture or fracture. The dorsal surfaces of these two bony elements appear in text-fig. 3 as one distinct dark element. The orbital margin of the jugal is visible in X-ray as well. This portion of the orbital margin is completed dorsally by a large anterodorsal process of the jugal.

The quadratojugal is an elongate bone which bears a long suture with the maxilla and a comparatively brief one with the postorbital. The posterior portion of the left quadratojugal appears to have been lost through breakage. However, some indication of this portion of the right quadratojugal is supplied by the lateral margin of the subtemporal fossa (text-figs. 3 and 5B), which is interpreted as quadratojugal. The manner of attachment of the quadratojugal to the suspensorium is uncertain.

An element appearing in the X-ray at the anterior extremity of the specimen to the right of the midline is interpreted as the right premaxilla. The element has one process directed laterally toward the right maxilla and a second directed posteriorly toward the right frontal bone. No teeth can be distinguished, however.

Both left and right maxillae appear in X-ray. They are long slim bones which extend well posterior to the orbits and form a portion of the narial margin. The right maxilla is essentially in place and is cracked along its orbital margin. It is expanded anteriorly into a broad process. The indentification of this process is uncertain, for depending upon the amount of distortion in this region of the skull, it may be either a nasal process or palatal process of the maxilla. There are 11 teeth in the left maxilla and 18 in the right.

A limited portion of the left squamosal (text-figs. 1 and 4A) is exposed. It is a rounded, rectangular bone and is somewhat displaced to exhibit a portion of its sutural contact with the quadrate ramus of the pterygoid.



TEXT-FIG. 4. *Lethiscus stocki*, MCZ 2185. A, lateral view of skull. Composite of information from left and right sides of skull, × 3. B, left lateral view of vertebra seven. Composite, × 5. C, ventral view of vertebra fifteen, × 5. D, left lateral views of vertebrae 57 and 58, × 5. E, notched sarcopterygian scale and associated elongate element, × 5.

Temporal fenestrae

The temporal fenestrae (text-figs. 4A and 6A) are bounded dorsally by the parietal, supratemporal, and tabular bones, anteriorly by the postorbital, laterally by the quadratojugal, and medially by the squamosal and by the ascending flange of the quadrate ramus of the pterygoid. The fenestrae continue to the posterior margin of the skull.

Palate

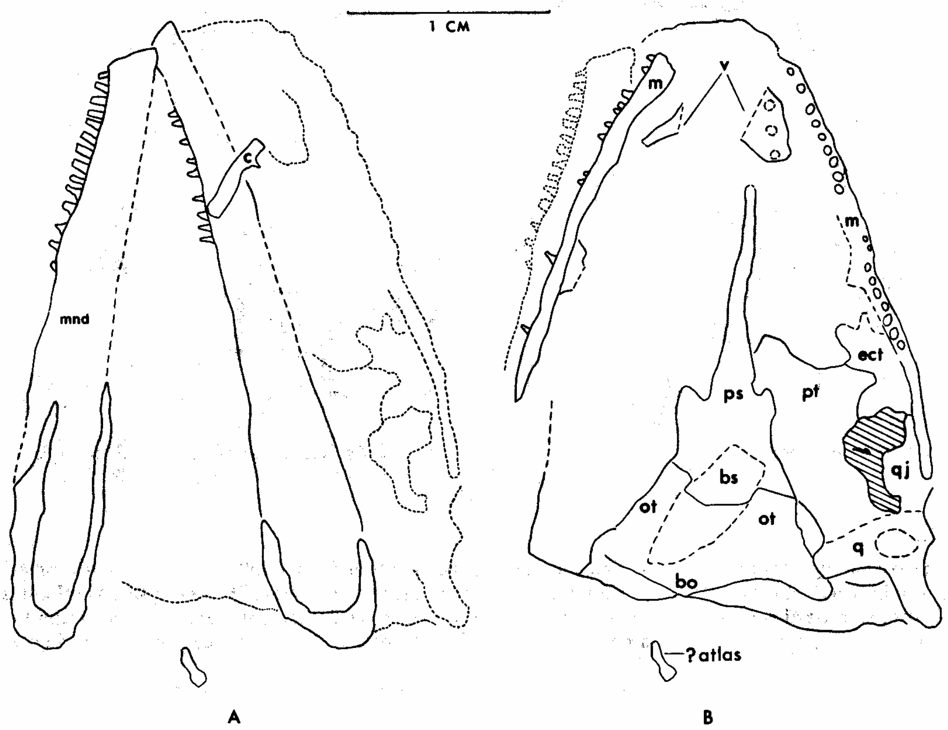
Elements of the palate (text-fig. 5B) are interpreted entirely from the X-rays.

Two elements, which appear in tomographs of ventral portions of the skull, may be vomers judging from their relatively anterior position. Their relationships to each other and to surrounding bones are not known. The right vomer appears to bear three teeth comparable in cross-sectional area to maxillary teeth. Nothing of the palatine bones can be distinguished in the X-rays.

Portions of the right pterygoid and ectopterygoid are seen in text-fig. 5. The pterygoid bears a high dorsal flange (text-fig. 4A) which extends from the quadrate ramus toward the supratemporal and posteriorly contacts the squamosal. The portion of the right pterygoid identified in text-fig. 1B is probably a fragment of this flange. The anterior portions of the pterygoids cannot be discerned in the X-ray and may be missing. Sutural contact between the pterygoid and supratemporal is obscured by matrix and bone loss along the fracture surface of the nodule.

The subtemporal fossa is defined by the pterygoid, ectopterygoid and quadratojugal. The fossa is small and is constricted by a blunt portion of the quadratojugal. Its small size and irregular lateral margin suggest that this region has been distorted.

The parasphenoid appears clearly in X-ray. It is displaced to the right, partially overlying the medial edge of the right pterygoid. The cultriform process is long and has a narrow base. The basicranial processes can be confidently interpreted on either side of the base of the cultriform process of the parasphenoid. The posterior portions of the parasphenoid cannot be distinguished from the basisphenoid.



TEXT-FIG. 5. *Lethiscus stocki*, MCZ 2185. A, mandibles interpreted from X-ray and viewed dorsally, ×3. B, portions of palate and braincase interpreted from X-ray and viewed dorsally, ×3.

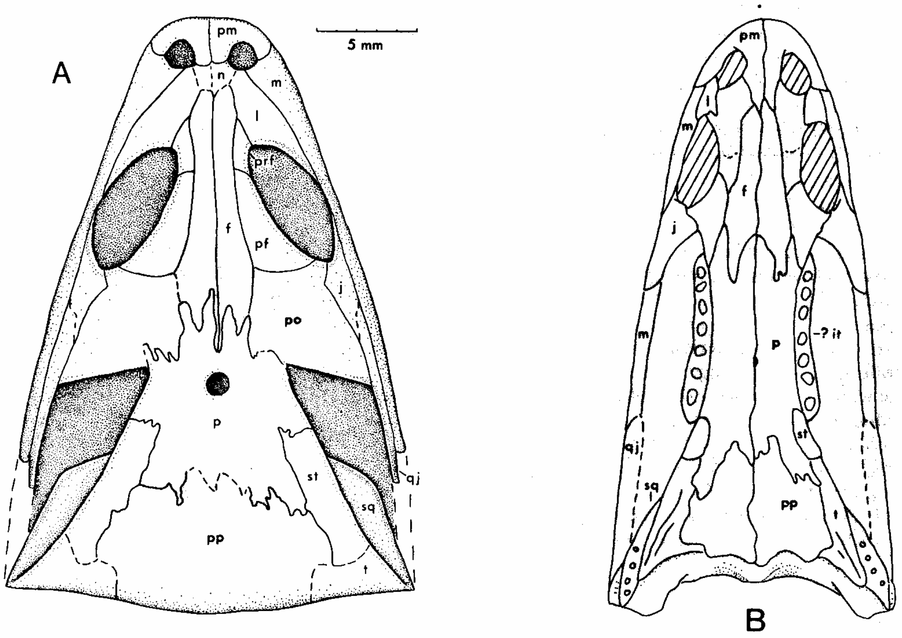
Braincase

There is no evidence of braincase contact with the dermal roofing bones, suggesting that the dorsal portions of the braincase were not ossified.

The oblong, X-ray opaque structure (text-fig. 3) centrally placed in the braincase is taken to be the matrix-filled brain cavity. It is distorted to the right as is the entire braincase-parasphenoid unit.

A suture distinguishes the basisphenoid region of the braincase from the basioccipital. The structures lateral to the brain cavity are assumed to be the otic capsules, although pro- and opisthotic bones cannot be individually distinguished nor are the otic regions clearly delimited from the occipital elements.

A tubular bone is exposed in the calcite filling of the inter-orbital space (text-fig. 4A). It tilts posteriorly as it rises toward the skull roof and is broken at its ventral extremity. From its structure the bone appears to be the left epipterygoid, although displaced anteriorly from its normal position dorsal to the basicranial articulation.



TEXT-FIG. 6. Comparison of skulls. A, reconstruction of *Lethiscus stocki*, MCZ 2185, ×3. B, *Ophiderpeton* (Thomson and Bossy 1970), drawn to length of *Lethiscus* skull.

Mandibles

With the exception of tooth alveoli revealed in a fracture section of the left mandible, the lower jaws are visible only as outlines in X-ray. The left mandible lies with its medial surface turned dorsally. The right mandible has its lateral surface upward. In the posterior margin of each mandible, U-shaped structures corresponding to the positions of surangular, articular, and angular can be differentiated, but no sutures can be discerned between these elements.

An elongate, rectangular element lies across the right mandible approximately one-third of its length from the symphysis. It bears a pointed process and is tentatively identified as a coronoid, probably of the right mandible.

Fourteen teeth are apparent in the left mandible. Nine can be counted in the right. The teeth of the mandibles seem to be short and peg-like as are those of the maxillae, though the nature of their crowns is not certain.

Hyoid elements

Two elongate elements revealed in the X-ray (text-fig. 3; also 1B) are hyoid elements, perhaps epibranchials. Fragments lateral to vertebrae 4 and 5 (text-fig. 7A) may be additional hyoid elements or possibly ribs, but no positive identification can be made. There is no evidence of gill rakers, internal or external gills, nor of the sickle-shaped hyoid noted in other aïstopods (Baird 1964).

Vertebrae

Seventy-eight vertebrae are visible in sequence (text-figs. 7, 8, 9). An additional vertebra can be distinguished in X-rays dorsal to vertebra 65. Vertebrae 1 through 5, 9 through 12, 15 through 28, and 42 through 46 are viewed ventrally. Alternating with these series are vertebrae exposed in lateral view and vertebrae 49, 50, and 51 which are seen end-on.

The vertebrae are clearly holospondylous. Bony elements seen between centra of the sixth, seventh, and eighth vertebrae are found nowhere else in the column and may be mineralized intercentral cartilages similar to those described in salamanders (Wake 1970; Wake and Lawson 1973) or merely displaced fragments of the adjacent centra.

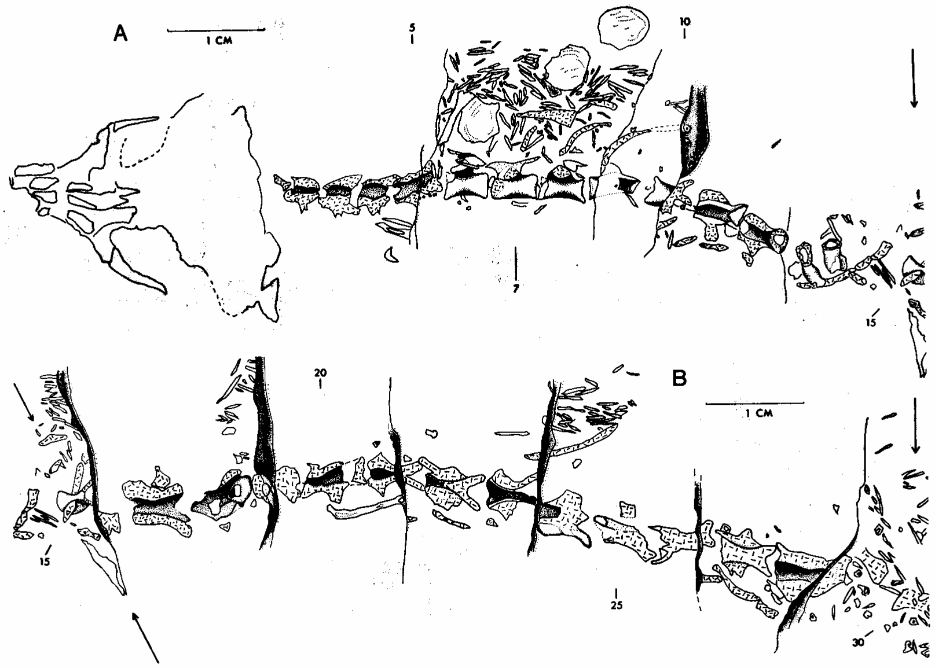
The centra are hour-glass-shaped and deeply amphicoelous. Sections along the column show the notochord to be severely constricted and possibly discontinuous at midcentrum. The lateral and ventral surfaces of the centra are smooth except for slightly concave, round facets near the anterior rim which are the articular surfaces for the rib capitulum (text-fig. 4B). The centra bear no pits, grooves, or accessory processes.

Vertebral length increases antero-posteriorly along most of the column. The average length for vertebrae 6, 7, and 8 is 4·5 mm. Vertebrae 34, 35, and 37 average 5·2 mm in length, while vertebrae 52 through 78 average approximately 6 mm in length. The untapered nature of these vertebrae, as well as the presence of ribs along the column, suggests that this portion of the skeleton represents the trunk of *Lethiscus*. The isolated vertebra is only 4 mm long and, by virtue of its small size, is the only indication of a tail in the specimen.

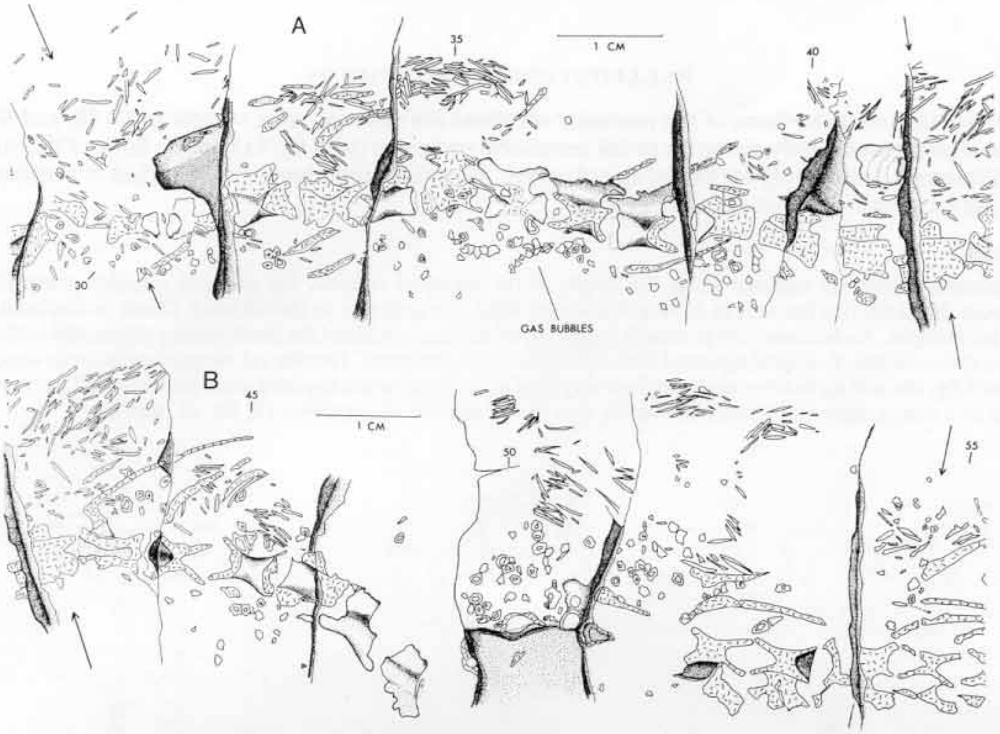
Neural arches of the vertebrae are swollen, unpaired, and are fused to their centra with no trace of suture The pedicel length is approximately two-thirds that of the centrum. The neural spines anterior to vertebra 37 are not well exposed. However, a transverse section of vertebra 9 (text-fig. 10A) shows the spine to be relatively high. More posteriorly, the neural arches can be seen to extend the length of the neural arch and to be tall, rising antero-posteriorly (text-fig. 9A and B). The spines bear jagged edges and have faint grooves between the teeth of the serrations, suggesting a crinkled appearance. It is not clear whether the jagged appearance is natural or due to poor ossification or breakage. Transverse sections through the vertebral column show that the neural spines bifurcate at their posterior extremities and bear a deep medial groove (text-fig. 10 C and D).

Neural-arch processes bearing zygapophyses project at approximately 30° from the sagittal plane, but extend little laterally beyond the centrum (text-fig. 10C and D). Zygapophyses are oblique to the sagittal plane.

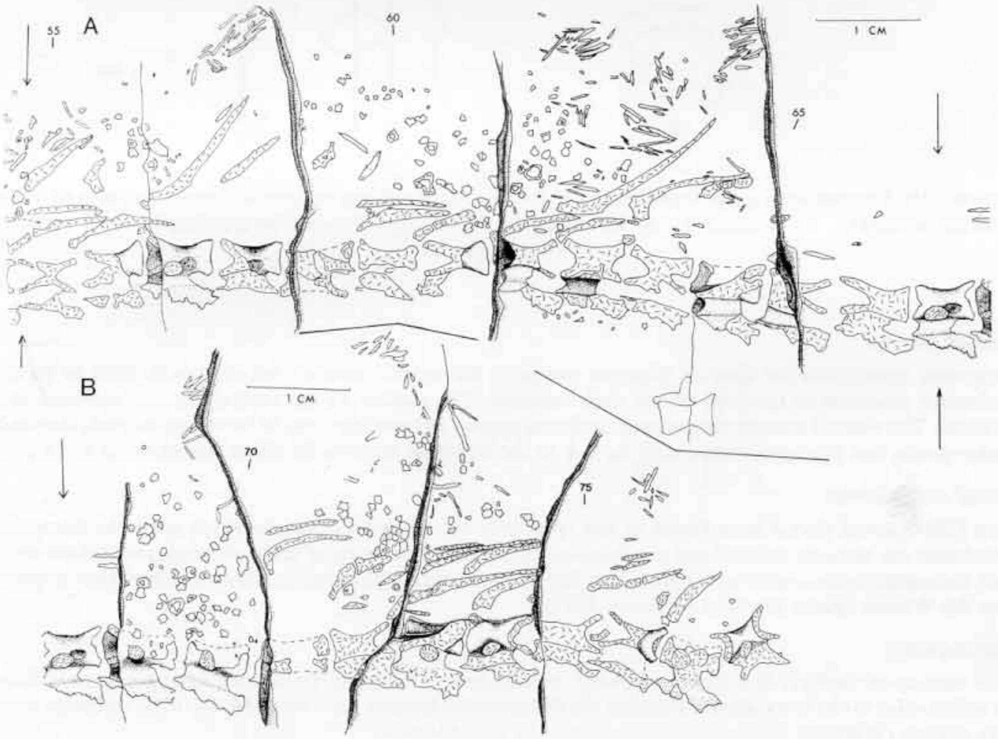
All post-atlantal vertebrae bear stout transverse processes which, in the more anterior vertebrae, are located on the neural arches (text-figs. 7A and 10A), rather than on the centra as in other aïstopods. The processes project laterally, but breakage obscures the surface of rib articulation. In contrast to the transverse processes of the anterior vertebrae, the transverse processes of vertebrae 44, 57, and 68 through 78 can be seen to arise, in part, from the centra (text-figs. 9 and 10B).



TEXT-FIG. 7. *Lethiscus stocki*, MCZ 2185, postcranial skeleton, × 1·4. A, vertebrae 1 through 15. B, vertebrae 15 through 30.



TEXT-FIG. 8. *Lethiscus stocki*, MCZ 2185, postcranial skeleton, × 1·4. A, vertebrae 28 through 43. B, vertebrae 42 through 56.

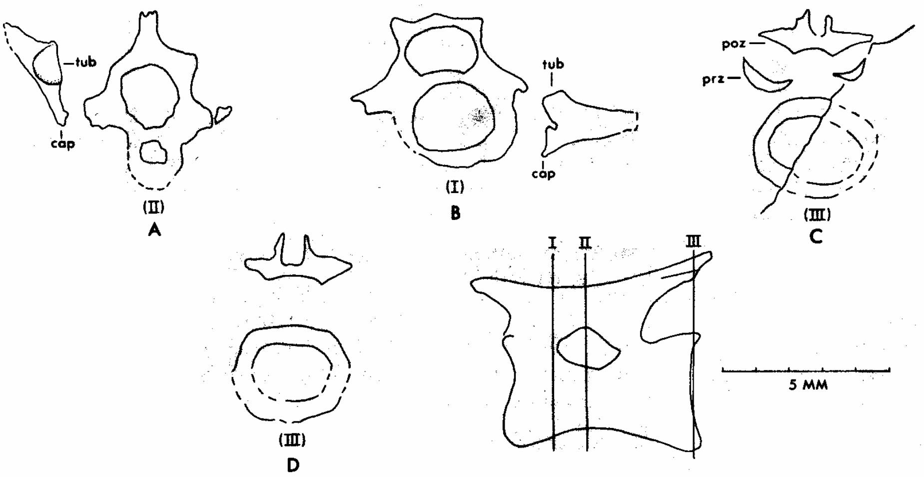


TEXT-FIG. 9. *Lethiscus stocki*, MCZ 2185, postcranial, × 1·4. A, vertebrae 55 through 68 and isolated vertebra. B, vertebrae 68 through 78.

Where the lateral surfaces of the posterior vertebrae are exposed, as in vertebrae 57, 58, and 68, a fossa is seen immediately posterior to the transverse processes (text-fig. 9A). In the floor of this fossa are foramina, presumably for exit of spinal nerves. Such foramina cannot be identified in vertebra 7, the only anterior vertebra suitably exposed.

Ribs

Fragments of ribs are exposed along the length of the vertebral column, but are best revealed posterior to vertebra 36. Here, ribs are seen to have a dog-legged bend just posterior to the rib head. Distal to this bend the ribs are straight. An accessory rib process is suggested by the sharp angle of the bend, but no substantial evidence of the characteristic K-shaped aïstopod rib is exhibited in the specimen. The ribs are bicipital anterior to vertebra 44 (text-fig. 10A and B), but the nature of their vertebral articulation is not exposed more posteriorly. The rib head is set at a sharp angle to its body as can be seen in the vicinity of vertebrae 19, 20, 43, and 60.



TEXT-FIG. 10. Selected sections of vertebrae, × 5. Roman numerals indicate approximate position of section in reference vertebra. A, vertebra 9. B, vertebra 44. C, vertebra 15 and prezygapophyses of vertebra 16. D, vertebra 23.

Ventral armour

Numerous, spindle-shaped dermal elements comprise the ventral armour, which would seem to have been continuous posterior to the level of the sixth vertebra. The pattern of the ventral armour has been severely disrupted. The ventral armour elements in *Lethiscus* appear to be stouter and to have blunter ends than those in *Ophiderpeton*, but this appearance may be due to the irregular sections in which the elements are exposed.

Dorsal osteoderms

Baird (1964) noted dorsal osteoderms in this specimen, but the only elements which might be interpreted as osteoderms are actually mineralized gas bubbles (text-fig. 8A). Sections of these elements show them not to be bone, but calcite cores coated with pyrite. Gas bubbles preserved in this manner have been reported in specimens from the Wardie Shales previously (Wood 1977).

Enterospira

In the vicinity of the forty-first vertebra is what appears to be a coprolite. Its segmented appearance is likely due to a spiral valve in the intestine of *Lethiscus*. As the coprolite has not been excreted, the term *enterospira* may be more correct (Williams 1972).

Sarcopterygian scales and possible pectoral girdle

Dorsal to vertebrae 6, 7, and 8 are many bony elements. Most of these are the spindle-shaped armour seen elsewhere in the specimen. Four others are probably slim fragments of rib. Most interesting are the three largest elongate bones and three irregularly round elements near them.

The round elements bear faint concentric rings and compare favourably with scales of sarcopterygian fishes. It should be noted, however, that concentric growth structures similar to these rings occur in endochondral limb and girdle elements of tetrapods as well (*Mesosaurus*, de Ricqlès 1974). The middle 'scale' has a notch in its rim which is similar to a glenoid fossa (text-fig. 4E). In the notch is a tiny fragment of bone, but whether the fragment has actually come to rest in a notch-like glenoid or whether compressional forces merely created the notch by forcing the fragment into the rim is uncertain.

The three large elongate elements could be posteriorly displaced hyoid elements or possibly remnants of the dermal pectoral girdle.

Although these six bones occur where a pectoral girdle would be expected, their lamentably poor exposure allows no confident identification. There is no other evidence of girdles or limbs in the specimen.

COMPARISONS

Skull

The skulls of both *Lethiscus* and *Ophiderpeton* (text-fig. 6) are relatively high-sided and possess temporal fenestrae bordered by identical elements of the skull roof. The orbits are anterior in position. Maxillae are elongate, slim, and extend far posterior to the orbit. The frontal bones have a similar proportional length relationship with the orbits. In *Lethiscus*, *Ophiderpeton*, and nectrideans (Thomson and Bossy 1970) the skull table is comprised primarily by the parietal and postparietal bones. *Lethiscus*, however, appears to represent a more primitive pattern in that its parietal-postparietal suture is anterior to the supratemporal-tabular suture (Panchen 1970). As a result, *Lethiscus* lacks the tabular-parietal contact, the presence of which has been suggested as linking aïstopods and nectrideans (Thomson and Bossy 1970). The later establishment of the tabular parietal contact in *Ophiderpeton* may then have come as the result of the posterior movement of the parietal-postparietal suture as suggested in anthracosaurs (Panchen 1970). Concomitant with the movement of this suture may have been the proportional increase in length of the parietal bones seen in *Ophiderpeton*.

In contrast to *Ophiderpeton* the supratemporals of *Lethiscus* are large and the skull table is much shorter. There is no indication of the intertemporal in *Lethiscus*. This bone may have been incorporated into the large postorbital. However, elongate pustulated bones have been identified as intertemporals in *Ophiderpeton* (Thomson and Bossy 1970).

In contrast to *Ophiderpeton* the jugal and quadratojugal in *Lethiscus* contact one another. The quadratojugal in *Lethiscus* also bears contacts with the postorbital and maxilla, perhaps strengthening the connection of the lateral skull margin with the skull table in response to bone loss resulting from fenestration of the skull roof. In *Lethiscus* the maxilla contacts the narial margin, but is excluded from it by the lacrimal in *Ophiderpeton* as reconstructed by Thomson and Bossy.

Other possible differences, such as the presence of nasals and the extent of the lacrimals and prefrontals cannot be determined unequivocally. The mandibles in *Lethiscus* and the palate and braincase in both *Lethiscus* and *Ophiderpeton* are also too poorly known to allow useful comparison.

Vertebrae

The vertebrae of *Lethiscus* differ from those of other aïstopods in lacking basipophyseal accessory articulations and median ventral ridges (as seen in *Ophiderpeton nanum*, Steen 1931) and in possessing high neural spines. Absence of incontestable limb girdles makes distinction of trunk and caudal regions difficult. *Lethiscus* does, however, exhibit antero-posterior differentiation of the vertebral column in the position of transverse processes and by the possession of spinal-nerve foramina only in the posterior portion of the column. Similar differentiation has not been found in *Ophiderpeton*, although McGinnis (1967) reported that the two anterior-most vertebrae in *Phlegethontia* do lack spinal-nerve foramina.

The anterior vertebrae of *Lethiscus* are remarkable in their similarity to those of some microsaurs, as well as to those of early reptiles. These in each case have smooth, unpitted surfaces, and are hour-glass-shaped. The neural-arch pedicels also bear the transverse processes. In contrast, neuro-central sutures are present consistently within the microbrachiomorph microsaurs and variably within the tuditanomorphs, but are absent in *Lethiscus*. *Lethiscus* also lacks trunk intercentra, which occur in several microsaur genera.

The vertebrae of adelogyrinids and 'lysorophids' (including both the Molgophidae and Lysorophidae) differ from those of *Lethiscus* in the consistent presence of neuro-central sutures, but are similar in lacking accessory articulations and in bearing the transverse processes on neural arches. The lysorophids further differ in the paired nature of their neural arches. The paired status of neural arches in the adelogyrinids is equivocal (Carrol 1967; Brough and Brough 1967; Watson 1921-1923).

The trunk vertebrae of nectrideans are similar to those of *Lethiscus* in lacking intercentral elements and in ossifying as single units. However, the only described nectridean in which intravertebral spinal nerve foramina can actually be seen is the urocordylid *Crossotelos*; keraterpetontids do not possess such spinal nerve foramina (Milner, A. C., pers. comm.). Furthermore, nectridean neural spines are specialized in their possession of accessory articulations, and rugose ornamentation (as in *Diploceraspis* and *Diplocaulus*), or in being flat-topped, fan-shaped structures with crenulated edges (as in *Sauropleura* and *Keraterpeton*, Baird, 1965; Steen 1938). Some faint suggestion of neural-spine crenulation is present in *Lethiscus*, but, as noted, the neural spines are otherwise serrated and inclined antero-posteriorly to the frontal plane.

The high number of trunk vertebrae found in *Lethiscus* is seen elsewhere only in aïstopods and in the tiny-limbed *Lysorophus* (Olson 1971) among the 'lepospondyl' amphibians. Nectrideans, in contrast, characteristically have short trunks (and long tails).

Limbs and girdles

Baird (1964) wrote that there is nothing interpretable as pectoral or pelvic girdle in any aïstopod. Although there is no contradictory evidence in *Lethiscus*, a recent study (see Boyd, M. J. F., this volume) has discovered an interclavicle in *Ophiderpeton nanum*.

Ventral armour

Spindle-shaped ventral armour like that in *Lethiscus* is seen in other aïstopods and nectrideans (Fritsch 1879; Huxley 1867) and with sculptured surfaces in the adelogyrinid *Adelospondylus* (Carroll 1967). Ventral armour in the microsaurs is variable (Carroll and Gaskill 1978), but never consists of spindle-shaped elements. Such dermal armour is unknown in the lysorophids.

DISCUSSION

Lethiscus possesses nearly all the aïstopod characteristics compiled by Baird (1964). Aïstopod character states which can not be confidently identified in *Lethiscus* (e.g. hypapophyseal flanges of caudal vertebrae, K-shaped ribs, and sickle-shaped hyoid) are those in portions of the specimen not preserved or which are poorly exposed.

While *Lethiscus* is more closely comparable to *Ophiderpeton* than to *Phlegethontia* in the relatively primitive nature of its skull, robust ribs, and heavy ventral armour, it is distinct in further details of its skull and post-cranial anatomy. Its short skull and the absence of a tabular-parietal contact indicate a less derived state than that of *Ophiderpeton*, while the absence of accessory vertebral processes and K-shaped ribs and the presence of tall neural spines indicate that *Lethiscus* possessed a differently specialized post-cranial skeleton and trunk musculature than either the Ophiderpetontidae or the Phlegethontiidae.

The presence of spinal-nerve foramina in a portion of the vertebral column of *Lethiscus* is especially interesting, for such foramina are known to occur only in urodelan lissamphibians, the Aïstopoda, and the nectridean *Crossotelos*. The presence of these foramina is considered to be a derived state in salamanders (Edwards 1976; Hecht and Edwards 1977) and would appear to be so in aïstopods and *Crossotelos*. Particularly significant is the observation that the spinal-nerve foramina of salamanders are expressed in patterns characteristic of the various families (Edwards 1976). Although the pattern of spinal-nerve foramina is not well known in the vertebral column of *Ophiderpeton*, the contrast in patterns between *Phlegethontia* and *Lethiscus* suggests that the spinal-nerve foramina pattern may allow distinction of aïstopod families also.

The occurrence of an aïstopod in mid-Viséan rocks provides some limited confirmation of the estimated several million or tens of millions of years required to accomplish limb loss in tetrapods (Lande 1977). Although *Lethiscus* cannot be described with absolute certainty as lacking limbs or girdles, the rudiments of a possible pectoral girdle demonstrate the degenerate nature of any limbs it may have possessed. Assuming tetrapod monophyly, this limb reduction was achieved within a period of at least 30 million to 40 million years elapsing between Late Devonian tetrapod origins, represented by *Metaxygnathus* (Campbell and Bell 1977) and *Ichthyostega*, and the occurrence of *Lethiscus* in the mid-Viséan.

Lethiscus is the earliest known member of a group of small Palaeozoic amphibians known as 'lepospondyls', but unfortunately it reveals little about the evolution of any of these animals or of tetrapods in general because of the specializations of the skull and post-cranial anatomy already attained in the Lower Carboniferous. *Lethiscus* seems to confuse the issue somewhat, for, although Thomson and Bossy (1970) linked nectrideans and aïstopods through the shared possession of the tabular-parietal contact, the absence of such a contact in *Lethiscus* suggests that it was either achieved independently in the two orders or was lost in *Lethiscus* subsequent to a nectridean-aïstopod dichotomy. Similarly, the extremely limited occurrence of intravertebral spinal-nerve foramina in nectrideans suggests that these foramina were probably developed separately in nectrideans and aïstopods, arguing against consideration of the presence of the foramina as a shared derived-character state.

Acknowledgements. I am pleased to acknowledge Dr. Robert L. Carroll for giving me the opportunity to study this specimen. This report benefitted critically from comments received from Dr. Carroll, Dr. Donald Baird, Dr. A. R. Milner, Dr. A. C. Milner, Mr. Timothy Smithson, and Mr. Robert Holmes, to all of whom I am grateful.

X-ray photography has been indispensible to the description of portions of this specimen. I thank Dr. Robert Hanson and Sandra and Andre Hamelin of the Radiology Unit of the Royal Victoria Hospital, Montreal, for their kind and patient assistance.

REFERENCES

BAIRD, D. 1955. Latex micro-molding and latex-plaster molding mixture. *Science*, **122**, 202.

—— 1964. The aïstopod amphibians surveyed. *Breviora*, No. 206, 1-17.

—— 1965. Paleozoic lepospondyl amphibians. *Am. Zool.* **5**, 287-294.

BROUGH, M. C. and BROUGH, J. 1967. Studies of early tetrapods. I. The Lower Carboniferous microsaurs. II. *Microbrachis*, the type microsaur. III. The genus *Gephyrostegus*. *Phil. Trans. R. Soc.* **252**, 107-165.

CAMPBELL, K. S. W. and BELL, M. W. 1977. A primitive amphibian from the late Devonian of New South Wales. *Alcheringa*, **1**, 369-381.

CARROLL, R. L. 1967. An adelogyrinid lepospondyl amphibian from the Upper Carboniferous. *Can. J. Zool.* **45**, 1-16.

—— 1977. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. *In* HALLAM, A. (ed.). *Patterns of evolution as illustrated by the fossil record.* Elsevier Sci. Publ. Co., Amsterdam. 591 pp.

—— and GASKILL, P. 1978. The order Microsauria. *Mem. Am. Phil. Soc.* **126**, 211 pp.

EDWARDS, J. L. 1976. Spinal nerves and their bearing on salamander phylogeny. *J. Morph.* **148**, 305-328.

FITCH, F. J., MILLER, J. A. and WILLIAMS, S. C. 1970. Isotopic ages of British Carboniferous rocks. *In Sixieme Congress International de Stratigraphie et de Geologie du Carbonifere*, Sheffield, 1967. **2**, 771-789.

FRITSCH, A. 1879. *Fauna der Gaskohle und der Kalksteine der Permformation Bohmens.* 1. Prague. 182 pp., 48 pls.

GEORGE, T. N., JOHNSON, G. A. L., MITCHELL, M., PRENTICE, J. E., RAMSBOTTOM, W. H. C., SEVASTOPULO, G. D., WILSON, R. B. 1976. A correlation of Dinantion rocks in the British Isles. *Spec. Rept. 7, Geol. Soc. Lond.* 87 pp.

HECHT, M. K. and EDWARDS, J. L. 1977. The methodology of phylogenetic inference above the species level. *In* HECHT, M. K., GOODY, P. C. and HECHT, B. M. (eds.). *Major patterns in vertebrate evolution.* Plenum, New York. pp. 3-51.

HUXLEY, T. H. 1867. Description of vertebrate remains from Jarrow colliery. Pt. 1. *Trans. R. Ir. Acad.* **24** (*Science*), 353-369.

LANDE, R. 1977. Evolutionary mechanisms of limb loss in tetrapods. *Evolution*, **32,** 73-92.

MCGINNIS, H. J. 1967. The osteology of *Phlegethontia*, a Carboniferous and Permian aïstopod amphibian. *Univ. Calif. Publs. geol. Sci.* **71,** 1-46.

MITCHELL, F. H. and MYKURA, W. 1962. The geology of the neighbourhood of Edinburgh. *Mem. geol. Surv. U.K.*, 3rd edn., 159 pp.

OLSON, E. C. 1971. A skeleton of *Lysorophus tricarinatus* (Amphibia: Lepospondyli) from the Hennessey Formation (Permian) of Oklahoma. *J. Paleont.* **45,** 443-449.

—— 1972. *Diplocaulus parvus* n.sp. (Amphibia: Nectridea) from the Chikasha formation (Permian: Guadalupian) of Oklahoma. Ibid. **46,** 656-659.

PANCHEN, A. L. 1970. Batrachosauria: Anthracosauria. *Handb. Paläoherp.* **5/A,** 84 pp.

RICQLÈS, A. J. DE 1974. Recherches paléohistologiques sur les os longs des tétrapodes. 5. Cotylosaurs et Mésosaures. *Annls. Paléont. Vertébrés*, **60,** 13-48, 7 pls.

STEEN, M. C. 1931. The British Museum collection of Amphibia from the Middle Coal Measures of Linton, Ohio. *Proc. zool. Soc. Lond.* **(1930),** 849-891.

—— 1938. On the fossil Amphibia from the Gas Coal of Nyrany and other deposits in Czechoslovakia. Ibid. B, **108,** 205-283.

STOCK, T. 1882. Notice of some discoveries recently made in Carboniferous vertebrate paleontology. *Nature*, **27,** 22.

THOMSON, K. S. and BOSSY, K. H. 1970. Adaptive trends and relationships in early Amphibia. *Forma et Functio*, **3,** 7-31.

WAKE, D. B. 1970. Aspects of vertebral evolution in the modern Amphibia. Ibid. 33-60.

—— and LAWSON, R. 1973. Development and adult morphology of the vertebral column in the plethodontid salamander *Euryces bislineata*, with comments on vertebral evolution in the Amphibia. *J. Morph.* **139,** 251-300.

WATSON, D. M. S. 1921-23. The Carboniferous Amphibia of Scotland. *Palaeont. hung.* **1,** 221-251.

WILLIAMS, M. E. 1972. The origin of spiral coprolites. *Paleont. Contr. Univ. Kans.* **59,** 1-19.

WOOD, S. P. 1977. Recent discoveries of Carboniferous fishes in Edinburgh. *Scott. J. Geol.* **2,** 251-258.

CARL F. WELLSTEAD
Redpath Museum
McGill University
859 Sherbrook Street West
Montreal, P.Q., Canada H3A 2K6

Typescript received 8 July 1980
Revised typescript received 24 October 1980