

A NEW FAMILY OF CARBONIFEROUS AMPHIBIANS

by ROBERT L. CARROLL

ABSTRACT. The morphology of a new Carboniferous amphibian, *Acherontiscus caledoniae*, combines cranial characteristics typical of lepospondyls with a vertebral structure resembling that of embolomeres. The skull is relatively small and the trunk region quite long. Limbs are apparently poorly developed. This form cannot be placed in any of the recognized amphibian orders, but presumably represents an isolated lineage which originated prior to the establishment of the definitive characteristics which differentiate all known lepospondyls and labyrinthodonts. *Acherontiscus* is designated the type of a new family, Acherontiscidae. This genus is based on a single specimen from the Royal Scottish Museum which had no horizon or locality data. The matrix contains spores which indicate a horizon from the upper part of the Viséan to about the middle of the Namurian.

SINCE the publication of Zittel's *Handbuch der Paläontologie* (1890), it has been generally accepted that two major groups of Palaeozoic amphibians could be recognized: labyrinthodonts and lepospondyls. The groups included by him in the Lepospondyli—microsaurs, nectrideans, and aistopods—had been recognized by the Miall commission somewhat earlier, but at that time (1875) they were only vaguely defined and not really distinguished from labyrinthodonts. Zittel's grouping was based primarily on the structure of the vertebrae. Labyrinthodonts (or, to use Romer's (1933) term applying to the vertebrae, apsidospondyls) have distinct 'arch' centra: posteriorly the pleurocentrum, frequently paired, and anteriorly the intercentrum. These clearly correspond to the vertebral components in amniotes. Lepospondyls have typically been described as having holospondylous or husk vertebrae—a single central ossification for each segment. The gross similarity between the structure in lepospondyls and that in adult salamanders has led to the assumption that embryological development followed a similar pattern in both groups, with direct ossification from the perichordal sheath. The presumed distinction in the pattern of embryological development in the two groups of Palaeozoic amphibians makes it difficult, if not impossible, to homologize their components, although it has been suggested that the lepospondyl centrum was comparable with either the pleurocentrum (Parsons and Williams 1963) or the intercentrum (Thomson 1967, Carroll 1967) of labyrinthodonts.

In addition to the vertebral pattern, a series of cranial features also distinguish labyrinthodonts and lepospondyls. Labyrinthodonts (discussed at length by Romer in 1947, 1963, and 1964) typically have labyrinthine infolding of the enamel, large fangs on the ectopterygoids, palatines, and frequently the vomers, and typically parasymphyseal tusks. They generally possess an otic notch dorsal to the quadrate, and the stapes is directed laterally or dorso-laterally. Lepospondyls (reviewed by Baird 1965), in contrast, lack labyrinthine infolding of the enamel and distinct fangs on the palatal bones. They all appear to lack an otic notch. The stapes is directed ventro-laterally toward the quadrate. Lepospondyls (as most clearly shown in microsaurs, Carroll and Baird 1968) have a very well-developed articulation between the occipital condyle and atlas-axis complex in which the atlas fits into a large strap-shaped recess formed by the exoccipitals and

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basioccipital. Although the articulation is not as well defined in labyrinthodonts, the occipital condyle is typically a knob-shaped structure which fits into a ring formed by the atlas intercentrum, pleurocentrum, and paired arches. The latter pattern becomes better defined in early reptiles.

In addition to these fairly clearly defined anatomical differences, lepospondyls can also be characterized by their tendency to be small, aquatic forms, many of which have feeble limbs. In contrast to labyrinthodonts, lepospondyls are not known to have a distinct larval stage exhibiting external gills.

It has been possible to fit all adequately known Palaeozoic amphibians into one or other of these major taxonomic categories. The distinctions appear complete even in early Mississippian lepospondyls (notably the aistopods, Baird 1964) and the Upper Devonian ichthyostegids (Jarvik 1952). Despite the obvious distinctions between labyrinthodonts and lepospondyls, however, it is considered that they have a common ancestry, for, to quote Baird (1965, p. 293): 'a duplicate origin of the tetrapod appendicular skeleton is simply incredible.'

The reason for reviewing the established classification of Palaeozoic amphibians is the discovery of a single specimen from the collections of the Royal Scottish Museum which appears to combine the characteristics of both labyrinthodonts and lepospondyls. This specimen, R.S.M. no. 1967/13/1, was discovered in a search for lepospondyls and early reptiles made in 1964. The specimen appeared to resemble the pattern of typical microsaurs such as *Microbrachis* and *Hylopleuron* in having a small head and an elongate body, with little or no evidence of limbs. The skull grossly resembled that of gymnarhids in having the orbits far forward and in possessing a small number of blunt cheek teeth. As originally preserved, the post-cranial skeleton showed very few details. The importance of the specimen was not recognized until a cast was made which revealed a series of vertebrae preserved as impressions. Instead of a series of single, elongate centra, as in microsaurs, the vertebrae were clearly formed on the pattern of embolomeres, with two rather similar, spool-shaped centra per segment. The specimen obviously belongs not only to a new genus, but also to an entirely new lineage, otherwise unreported in the fossil record of the Carboniferous.

The purpose of this paper is to describe this particular specimen, and to discuss the current concept of the classification of the lepospondyls in light of its anatomy.

Class AMPHIBIA
Subclass and Order Undesignated
ACHERONTISCIDAE nov.

Diagnosis. Small stegocephalian amphibia with both pleurocentra and intercentra well-developed cylinders. Skull with lateral line canals, orbits far forward, no otic notch, teeth without labyrinthine infolding of enamel. Dermal pectoral girdle well developed. Long trunk region.

ACHERONTISCUS gen. nov.

Type species. *Acherontiscus caledoniae* gen. et sp. nov.

Diagnosis. Same as for family. The generic name follows Cope's practice of naming serpentiform lepospondyls for tributaries of the Styx: *Cocytinus*, *Phlegethontia*, etc.

Acherontiscus caledoniae gen. et sp. nov.

Holotype. 1967/13/1 in the Royal Scottish Museum, Edinburgh. Skull and associated postcranial skeleton. This is the only known specimen.

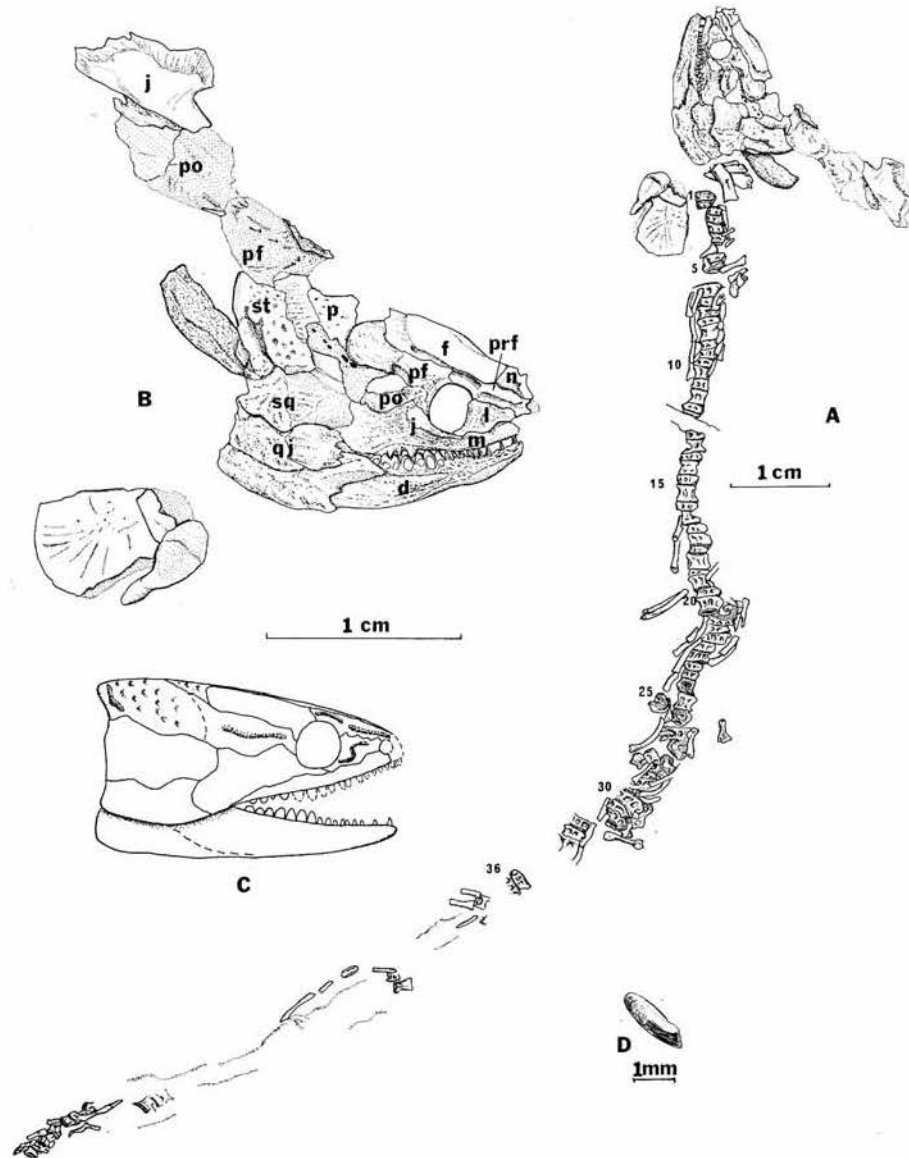
Locality and horizon. The specimen bears no data as to horizon, locality or collector. The matrix is a fine-grained coal shale which resembles that of amphibians from the Loanhead No. 2 Ironstone of the Limestone Coal Group at Burghlee, Midlothian, which is lower Upper Carboniferous in British terms and equivalent to the Continental Namurian A and the American Upper Mississippian. Ostracods preserved with the specimen have been variously identified. According to Dr. Robinson, University College, University of London, all are assignable to *Carbonita* (*Carbonia*) *fabulina*, which inhabits coal shale facies from the Viséan to the Coal Measures. Dr. Pollard, at Manchester, identifies most as *Carbonita humilis*, and others dubiously as *Carbonita inflata*. He suggests that these specimens may indicate Coal Measures, most likely Westphalian A or B.

Dr. A. H. V. Smith of the National Coal Board examined a piece of the matrix and reported that it: 'contained an assemblage of spores rich in species including such forms as *Cingulizonates cf capistratus*, *Rotaspora knoxi* and *Tripartites trilinguis*. By considering the stratigraphic ranges of all the species recovered from the sample, it is possible to assign the miospore flora to a horizon within Assemblage III of Smith and Butterworth 1967. In Scotland this Assemblage ranges from the upper part of the Lower Limestone Group, through the Limestone Coal Group to upper part of the Upper Limestone Group. In terms of the Heerlen classification, these lithological divisions range from Upper part of Viséan to about the middle of the Namurian. . . . The horizon is definitely not Coal Measures.' Although there is some question as to the exact age of this specimen, it is of sufficient anatomical significance to warrant description.

Description. The skull is exposed primarily from the right side. It is flattened, with much of the original bone surface badly damaged. In order to determine the position of the sutures more accurately, an attempt was made to etch away the bone so as to expose the impression of the ventral surface. The skull roof and lower jaws were crushed so closely together that what matrix there may have been between them was lost in the etching of the bone. This led to the etching of all three bone layers. It was hence felt better to save the poorly exposed dorsal surface, rather than to attempt further preparation.

To judge from the apparently complete right lower jaw, almost the entire length of the skull is preserved. The premaxillae are missing, however, and possibly small areas of the nasal and lacrimal bones. These bones appear to extend almost to the external naris, but the posterior margin of this opening is not clearly defined. As preserved, the skull is 16.5 mm. in length. In contrast to typical labyrinthodonts, the orbit is very small (approximately 2.4 mm. in diameter) and is located far anteriorly (its posterior margin is 10.5 mm. from the rear margin of the skull). Where the original surface of the bone is preserved, the posterior roofing bones are sculptured with shallow, irregular pits, somewhat as in the microsaure *Tuditatus*. The more anterior bones, particularly the frontal, are essentially smooth. Lateral line canals are evident on the supra-temporal, post-orbital, prefrontal, and lacrimal. What is preserved of this system suggests an arrangement typical of that of aquatic labyrinthodonts. As in the microsaure *Microbrachis*, the posterior portion of the skull is very wide.

The crushing and loss of much of the original surface makes it difficult to substantiate the pattern of the dermal bones. Three bones may, nevertheless, be fairly clearly distinguished across the back of the skull. These may be designated as supra-temporal, squamosal, and quadratojugal. One important point that can be safely established is the large size of the supra-temporal, since much of the surface of this bone is preserved. Such a large bone in this position follows the pattern of microsaurs and is distinct from that of labyrinthodonts. Although poorly preserved, the posterior margin of the cheek



TEXT-FIG. 1. *Acherontiscus caledoniae*. A. Skeleton, skull and dermal shoulder girdle drawn as a mirror image; postcranial skeleton drawn from rubber mould. Numbers indicate vertebral count. $\times 1\frac{1}{2}$. B. Skull and dermal shoulder girdle. $\times 3$. C. Restoration of skull. $\times 3$. D. Single ventral scale in medial view. $\times 12$.

region appears to have been nearly vertical, without an otic notch. The anterior extent of the supra-temporal, squamosal, and quadratojugal is difficult to ascertain, but they may be reconstructed as meeting the jugal and post-orbital in the manner of *Microbrachis* (Steen 1938). The mid-dorsal region of the skull is not well preserved posteriorly; there may have been small postparietals as in *Microbrachis*. The parietal appears to extend a lappet laterally between the supra-temporal and post-frontal; the area of the pineal foramen is missing. The left post-frontal, post-orbital, and jugal are disarticulated and lie behind the remainder of the skull. The post-frontal is shown as an impression of its ventral surface, the post-orbital as an impression of the lateral surface, and the jugal is exposed medially. The latter shows very large areas of overlap with the post-orbital, squamosal, and quadratojugal. The portion of these bones entering the margin of the orbit seems to be somewhat different from those of the corresponding bones preserved on the right side, but this is not surprising considering the extent of overlap shown by the jugal. The frontal appears much longer than the nasal, but the former bone was probably overlapped quite extensively by the parietal. Where the surface is preserved, the maxilla appears smooth. The upper dentition is obscured by that of the lower jaw. Neither the palate nor the braincase is exposed, nor can these structures be readily prepared without danger to the skull roof.

The right jaw, which is displaced slightly posteriorly, reaches just beyond the posterior margin of the cheek. The anterior end narrows, suggesting that only a very short portion has been lost. Like the other bones, those of the lower jaw have lost most of their surface. It remains only on the antero-ventral margin of the dentary, which shows no sculpturing. No lateral line canal grooves are preserved on the lower jaw. Including the impressions of the anterior teeth, 16 are present in the lower jaw, with room for at least 2 more. The posterior 7 teeth are bluntly-rounded cones, while those more anterior are slim and sharply pointed. The posterior teeth were 'sectioned' by some earlier preparator, showing that the pulp cavity is very large and that the enamel is definitely not infolded. The tips of the posterior teeth are not well exposed in the right jaw, but those of the left can be seen protruding through the skull roof in the area of the post-orbital. They are laterally compressed and marked by vertical ridges, much as the teeth of *Cardiocephalus* (Gregory, Peabody, and Price 1956, p. 18). They show little, if any, wear. There is no evidence for more than a single row of marginal teeth. The posterior portion of the lower jaw is very deeply worn, making it impossible to establish sutures between the dentary, angular, and surangular. The medial surface of the left jaw is exposed behind the skull. It is very poorly preserved. The articular surface appears to be at the level of the posterior end of the jaw, with no retro-articular process.

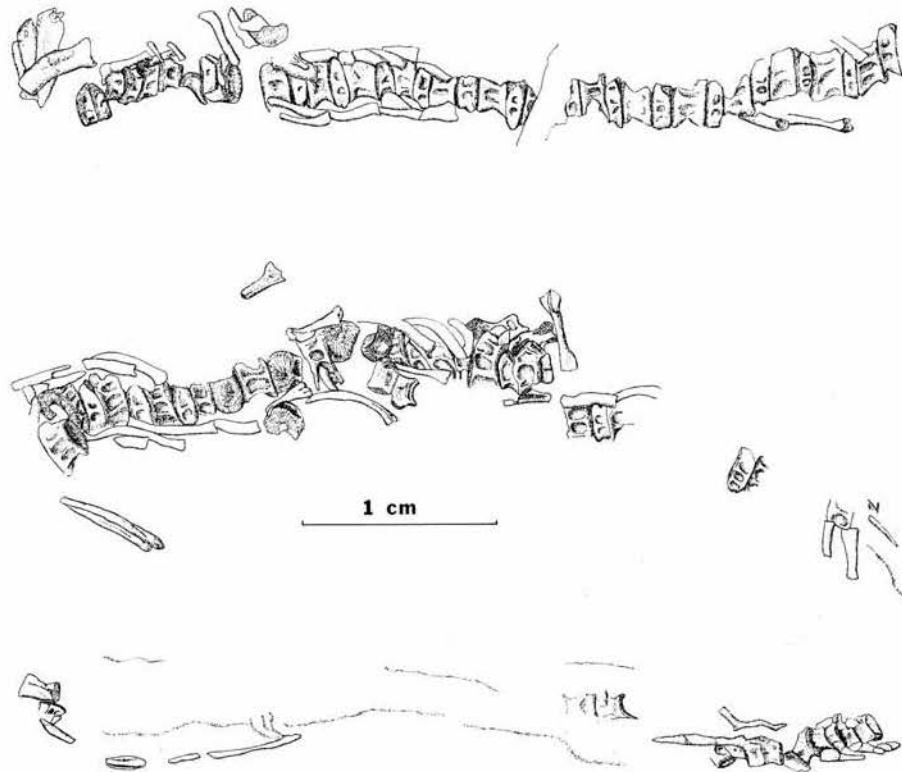
Immediately behind the skull are a number of bones which presumably are remains of the visceral arch apparatus. They resemble in general the bones described by Sollas (1920, p. 513, fig. 39) in *Lysorophus*, but their disarticulation in *Acherontiscus* precludes homologizing the individual elements.

What is visible of the structure of the skull resembles in general that of lepospondyls such as the 'typical' microsaur *Microbrachis* and *Cardiocephalus*. It shows none of the characteristics expected in labyrinthodonts, such as infolding of the enamel, multiple bones in the temporal region, or an otic notch.

Aside from the dermal shoulder girdle, the post-cranial skeleton of this animal was prepared by etching away the bone with hydrochloric acid and casting the resulting

impressions with silicone rubber. This results in the post-cranial skeleton being viewed from the opposite side from the skull, and explains the necessarily composite nature of text-fig. 1. This method of preparation was necessary since the bone surface as exposed was so damaged and weathered that very little structure could be determined.

The vertebral column is visible primarily in ventral view, with the neural arches only occasionally exposed. The centra, in contrast, are readily seen for much of the length of



TEXT-FIG. 2. *Acherontiscus caledoniae*. Postcranial skeleton drawn in three sections. $\times 3$.

the column. It is immediately apparent from their configuration and from the arrangement of the few neural arches present, that each vertebra consists of two centra, typically complete cylinders, which may be compared with the intercentra and pleurocentra of embolomeres and other labyrinthodonts. There is absolutely no question of the association of the skull and these vertebrae, which demonstrates a combination of lepospondyl cranial features and apsidospondylous vertebral structure in a single form.

The first segment has only a single centrum. Posterior to this, some 32 central pairs are exposed in sequence. More posteriorly, the column is intermittently visible, with

much of it represented only by a depression in the matrix. A few vertebrae are more clearly exposed at the extremity of the column. The entire trunk region and most, if not all, of the tail were apparently in place, with the elements quite well articulated, when the animal was buried. By extrapolation from the well-preserved sections, a total of approximately 64 vertebrae were present. The posterior 3 or 4 show haemal arches and so are definitely caudals. More caudal vertebrae may originally have been present, but the series ends without reaching the margin of the block. Bones which may represent elements from the pelvic girdle and rear limb are present in the area from the 26th through the 31st vertebra. This suggests approximately 27 presacra, although this is only very tentatively established. At least as far back as the 36th vertebra the intercentra are not modified to support haemal arches, although poorly preserved structures which might be so identified are present in the area of approximately the 40th vertebra.

There is some regional variation in the centra. There was apparently only one element in the 1st segment, a narrow crescentic pleurocentrum. It would be very interesting to know the manner of articulation between the anterior cervicals and the brain-case, but it is impossible to determine this on the basis of this skeleton as it is preserved. The 2nd segment consists of a crescentic intercentrum, which bears facets for the articulation of the capitulum of the first cervical ribs, and a rather short pleurocentrum. Apparently the first 4 pleurocentra are crescentic rather than cylindrical, judging from the 4th which is disarticulated. The 5th and those more posterior are complete cylinders, but retain a large passage for the notochord. All (except the two most anterior) are considerably longer than the intercentra. The 6th intercentrum is displaced and evidently crescentic. The 25th, 26th, and 27th intercentra are visible end-on and are cylindrical, with most, if not all, of the notochordal canal closed. With the centra oriented as they are, it is not possible to judge where, between the 6th and 25th segments, they become cylindrical. In addition to their short length, the intercentra are characterized by the presence of facets for the articulation of the capitulum of the ribs. Dorsal to the area for rib articulation, the surface of the intercentra is of unfinished bone, presumably marking the area for articulation with the neural arch.

Both pleurocentra and intercentra are marked laterally and ventrally by a regular pattern of deep pits, giving them a marked resemblance to those of embolomeres. The posterior caudal vertebrae differ from those in the trunk region in being less deeply and regularly pitted, and seem to have rather thin walls. The intercentra more closely approach the length of the pleurocentra in this region. The pleurocentra, and apparently the intercentra as well, are complete cylinders as far posteriorly as the tail is preserved. The haemal arches appear to articulate with rather than being solidly attached to the intercentra.

Poorly preserved neural arches are present on the 26th, 30th, and 31st vertebra. The most posterior is visible ventrally, showing both posterior zygapophyses. The two halves of the arch are completely fused. The neural spines appear to be short and located far posteriorly. The pedicle of the arch and the transverse process are never well exposed. Where visible, the arches are disarticulated from the centra. It is probable from the structure of the centra that, as in embolomeres, they were never solidly attached.

Fragments of ribs are visible throughout the column; none are well preserved, and the articulating surfaces appear incompletely ossified. Since there are well-ossified facets for the articulation of the capitulum on the intercentrum, it is probable that the ribs were

double headed in the manner of embolomeres and most early reptiles and typical microsaurs. Their length can be nowhere adequately established, but there does not appear to be any marked modification in length in the suggested area of the pelvic girdle, except for the 'sacral ribs' themselves. Structures which appear to be quite long ribs extend nearly to the end of the vertebral column.

The dermal shoulder girdle is represented by the interclavicle, in the form of a large oval plate, and the clavicles. The left clavicle is complete, with a narrow, unsculptured blade, and a short, thick stem. The interclavicle is marked ventrally by a very low median ridge, and fine radiating grooves. It is complete posteriorly and definitely has no stem. The anterior margin is covered by the clavicles, preventing determination of the presence of a fimbriated margin. Neither the cleithra nor the endochondral shoulder girdle is visible.

No elements identifiable as belonging to the fore limb are visible. Considering the size of the bones of the dermal shoulder girdle, it would be most surprising if this animal lacked forelimbs. They may, however, have been small and/or poorly ossified, or lost prior to burial.

Nothing can be very confidently identified as representing the pelvic girdle and rear limb. There are a few elements in the area of the 26th through 31st vertebrae which are definitely not normal ribs or vertebral elements. Two, apparently paired, blocks are adjacent to the 28th vertebra. They might represent remnants of the pelvic girdle, but they do not compare with any bones described from other Paleozoic tetrapods. They are quite thick and well ossified, except for margins which appear to be surfaces of articulation. They might conceivably be sacral ribs. A pair of bones reasonably identifiable as limb elements is found adjacent to the 26th and 31st vertebra. Each is approximately the length of a single segment. They resemble in a vague way the tibia of other Palaeozoic tetrapods, but, in the absence of other evidence, they could as well be the femora of this animal. Some of the bones in this region, otherwise accepted as ribs, may be part of the appendicular skeleton. It is unfortunate, in the light of the very interesting evidence of the axial skeleton, that so little of the appendicular skeleton is preserved in this animal.

Numerous fragmentary scales are associated with *Acherontiscus*. Most are poorly preserved, represented by roughly oval patches of fine parallel rods, resembling in a general way the dorsal scales of microsaurs. One scale, shown in text-fig. 1D, is almost complete and resembles closely the ventral scales of microsaurs, as viewed medially (Carroll and Baird 1968, fig. 20). Although more closely resembling those of microsaurs, the scales of *Acherontiscus* also resemble in a general way those of such labyrinthodonts as *Trimerorhachis* (Colbert 1955).

The presence of lateral line canals indicates that *Acherontiscus* was primarily aquatic. This habit would explain the small size and incomplete ossification of the elements of the pelvic girdle and rear limb (assuming that they have been correctly identified). Such poor ossification might also be attributed to immaturity. Judging from the solid attachment of the bones of the skull and the degree of ossification of the vertebrae, this animal appears to be essentially mature. In lepospondyls in general, however, there is very little difference in the anatomy of individuals of different size within a given taxon.

The fairly long trunk region, as well as the small size of the skull, suggests a snake-like habitus. As has been suggested by Panchen (1966) and Parrington (1967, p. 277), the

development of an embolomeric or lepospondylic vertebral structure are both methods of lengthening the segments so as to assist a sinuous type of locomotion, usually associated with an aquatic habit and anguilliform swimming.

Taxonomic position. The significance of this specimen is its combination of cranial features accepted as typifying lepospondyls with a vertebral structure closely resembling that of embolomeric labyrinthodonts. This combination makes classification of this particular genus difficult, but contributes to our understanding of vertebral homologies among other Palaeozoic amphibians.

The great range in vertebral structure among the labyrinthodonts indicates that this feature alone is not a sufficient basis for classification within that group. Within both the temnospondyls and anthracosaurs the pleurocentrum varies from being a major structural element to being little more than an accessory. The relative importance of the intercentrum likewise differs greatly within each group. Although such a range in vertebral structure has not been recognized among the lepospondyls, the presence of haemal arches in *Pantylus* and *Lysorophus* (Carroll 1968) indicates that multipartite vertebral centra do occur within that group.

The pattern of the bones of the skull roof appears a much more valid basis for classifying both labyrinthodonts and lepospondyls. Ichthyostegids, anthracosaurs, and temnospondyls can all be defined on the basis of the relative position of the bones in the temporal series (Romer 1947). No labyrinthodonts are known which have a pattern which could be confused with that of any described lepospondyl. The patterns within each of the lepospondyl groups seem similarly stereotyped. All typical microsaurians have a particular pattern (Carroll and Baird 1968) as do the better-known lysorophids and adelogyrinids (Carroll 1967).

The pattern of the skull roof of *Acherontiscus* resembles most closely that of the microsauros *Microbrachis*. The absence of an otic notch and labyrinthine infolding of the enamel support association with lepospondyls, as do the general body proportions. This genus differs from all labyrinthodonts in these features. The presence of multipartite centra indicates closer association with microsaurians and lysorophids than with aïstopods or nectrideans, but no more specific assignment of this genus among the lepospondyls is possible. The dentition is similar to that of the gymnarthrid microsaurians, but this probably does not indicate any particularly close relationship. The fact that *Acherontiscus* is as old or older than any of the known microsaurians makes it a possible ancestor to some or all members of that group, but there is no very convincing evidence for this while the well-developed embolomeric vertebral pattern suggests that it diverged from the lineage leading toward microsaurians at a stage when neither had yet developed its definitive vertebral pattern.

On the basis of our present knowledge of the one described genus, the family Acherontiscidae should be recognized as representing an isolated lineage, of equivalent rank with nectrideans, aïstopods, lysorophids, adelogyrinids, and typical microsaurians.

DISCUSSION

Acceptance of *Acherontiscus* as a lepospondyl raises several problems in regard to our concept of that group. This genus provides the first conclusive evidence of the presence of multiple central elements in the trunk region. There seems no reason to argue against

the obvious identification of these structures as intercentra and pleurocentra, or to reject their general homology with their counterparts in labyrinthodonts. The presence of haemal arches in *Pantylus* (Carroll 1968) and '*Hylonomus*' *fritschia* (Credner 1885) supports identification of the major central elements as pleurocentra in microsaurs as well, although trunk intercentra have never been conclusively demonstrated in this group. Haemal arches, but not trunk intercentra, are also present in the lysorophids *Lysorophus* (Carroll 1968) and *Molgophis*. It seems plausible to assume that primitive microsaurs and lysorophids derived their vertebral structure from an apsidospondylous pattern. Unfortunately no members of either group are known prior to the Lower Pennsylvanian, by which time all genera had lost all trace of trunk intercentra and most typical microsaurs had eliminated the haemal arches as well. *Acherontiscus*, from the earlier Carboniferous, appears to have retained a more primitive configuration.

If the central elements in typical microsaurs, lysorophids and acherontiscids can be homologized with those of labyrinthodonts, can these forms be considered as lepospondyls? The term lepospondyl may be used in a descriptive manner, as does Romer in 1966: '... the centrum forms as a single, spool-shaped bony cylinder around the notochord ...' (p. 96), or to imply a particular mode of embryonic development '... in which arch-centra preformed in cartilage do not occur; instead, the centrum forms directly as a bony cylinder around the notochord' (Romer 1945, pp. 157-8). In terms of adult structure, there is no evidence for more than a single vertebral element in either the trunk or tail of any nectridean or aistopod, although the vertebral anatomy is well known. In both groups, outgrowths from the major central elements in the tail act as haemal arches, precluding the presence of a separate element with this function. Whatever their homology, the vertebrae in these forms are structurally lepospondylous.

At present we have no way of knowing whether the intercentra and pleurocentra of *Acherontiscus* are preformed in cartilage, or ossify directly as bony sheaths around the notochord. It is possible that the retention of multipartite central elements indicates retention of the primitive developmental pattern, but there is no proof of this.

Unless one assumes that the developmental pattern in nectrideans, and presumably aistopods, implies a separate origin for the vertebrae from that described for labyrinthodonts and other lepospondyls, the centra in all amphibian groups must be generally homologous. This implies a suppression of the normal cartilaginous precursors of the centra in nectrideans, if not in other forms which are structurally lepospondylous. It seems probable that the small size of the vertebrae and their simple structure in the adult made such abbreviated development possible.

If the vertebral structure and developmental pattern in nectrideans was initially derived from the rhipidistian or labyrinthodont condition, then the adult configuration in *Acherontiscus*, lysorophids, and microsaurs can be accepted as representing slightly more primitive stages in the same general pattern. In all but *Acherontiscus*, there is a strong tendency to develop a single central element. On this basis, all of these forms may be retained within the Lepospondyli, whatever the pattern of embryonic development.

Despite the common tendency toward a holospondylous vertebral structure, small size, and aquatic habit, there is little convincing evidence that all of the groups accepted as lepospondyls share a single common ancestry separate from the labyrinthodonts (Parrington 1967). Whatever the developmental pattern, the adult structure of the vertebrae clearly separates aistopods and nectrideans from microsaurs, lysorophids, and

acherontiscids. The morphology of each group is stereotyped and distinctive throughout its known fossil record. They are united primarily by their common distinctiveness from labyrinthodonts. It is quite conceivable that all of the known lineages evolved separately from primitive labyrinthodonts or their ancestors among the rhipidistians.

While knowledge of *Acherontiscus* appears to confirm the homology of the major central elements in microsaur and lysorophids with the pleurocentra in labyrinthodonts it contributes little to our understanding of the vertebrae in neotrideans or aistopods and emphasizes the difficulties in classifying the lepospondyls in general.

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REFERENCES

- BAIRD, D. 1964. The aistopod amphibians surveyed. *Breviora*, **206**, 1-17.
 — 1965. Paleozoic lepospondyl amphibians. *Am. Zool.* **5**, 287-94.
 CARROLL, R. L. 1967. An adelogyrid lepospondyl amphibian from the Upper Carboniferous. *Can. J. Zool.* **45**, 1-16.
 — 1968. The postcranial skeleton of the Permian microsaure *Pantylus*. *Ibid.* **46**, 1175-92.
 — and BAIRD, D. 1968. The Carboniferous amphibian *Tuditanus* [*Eosauravus*] and the Distinction between Microsaurs and Reptiles. *Am. Mus. Novit.* **2337**, 1-50.
 COLBERT, E. H. 1955. Scales in the Permian amphibian *Trimerorachis*. *Ibid.* **1740**, 1-17.
 CREDNER, H. 1885. Die Stegocephalen aus dem Rothliegenden des Plauenschen Grundes bei Dresden. V Theil. *Z. dtsh. geol. Ges.* **37**, 694-736.
 GREGORY, J. T., PEABODY, F. E., and PRICE, L. I. 1956. Revision of the Gymnarthridae, American Permian microsaur. *Bull. Peabody Mus.* **10**, 1-77.
 JARVIK, E. 1952. On the fish-like tail in the ichthyostegid stegocephalians. With descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddr Grønland* **114**, 1-90, 21 pls.
 MIAL, L. C. 1875. Report of the Committee, consisting of Professor Huxley, Professor Harkness, F.R.S., Henry Woodward, F.R.S., James Thomson, John Brigg, and L. C. Miall, on the structure and classification of the Labyrinthodonts. Drawn up by L. C. Miall, Secretary to the Committee. *Rep. Br. Ass. Advmt. Sci.* 149-92, pls. IV-VII.
 PANCHEN, A. L. 1966. The axial skeleton of the labyrinthodont *Eogyrinus attheyi*. *J. zool. Lond.* **150**, 199-222.
 PARRINGTON, F. R. 1967. The vertebrae of early tetrapods. *Colloques internationaux du Centre National de la Recherche Scientifique*, No. 163, Problèmes actuels de paléontologie (évolution des vertébrés), 269-79.
 PARSONS, T. S. and WILLIAMS, E. E. 1963. The relationships of the modern Amphibia: A re-examination. *Q. Rev. Biol.* **38**, 26-53.
 ROMER, A. S. 1933. *Vertebrate paleontology*. 1st ed. Chicago.
 — 1945. *Ibid.* 2nd ed. Chicago.
 — 1947. Review of the Labyrinthodontia. *Bull. Mus. comp. Zool. Harv.* **99**, 3-352.
 — 1963. The larger embolomere amphibians of the American Carboniferous. *Ibid.* **128**, 415-54, pls. 1-2.
 — 1964. The skeleton of the Lower Carboniferous labyrinthodont *Pholidogaster pisciformis*. *Ibid.* **131**, 129-156, pl. 1.
 — 1966. *Vertebrate Paleontology*. 3rd ed. Chicago.

- SMITH, A. H. V. and BUTTERWORTH, M. A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Spec. Paper Palaeont.* **1**.
- SOLLAS, W. J. 1920. On the structure of *Lysorophus* as exposed by serial sections. *Phil. Trans. R. Soc. Ser. B*, **209**, 481–527.
- STEEN, M. 1938. On the fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. *Proc. zool. Soc. Lond.* **108**, 205–83.
- THOMSON, K. S. 1967. Notes on the relationships of the rhipidistian fishes and the ancestry of the tetrapods. *J. Paleont.* **41**, 660–674.
- ZITTEL, K. A. 1890. *Handbuch der Paläontologie. III Band. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. München und Leipzig.

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R. L. CARROLL
Redpath Museum
McGill University
Montreal 110, P.Q.