AN ADELOGYRINID LEPOSPONDYL AMPHIBIAN
FROM THE UPPER CARBONIFEROUS

ROBERT L. CARROLL

Redpath Museum, McGill University, Montreal, Qué.

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A new genus of the Paleozoic amphibian subclass Lepospondyli is described. It is a member of the family Adelogyrinidae, orginally based on three specimens from the Lower Carboniferous of Scotland. Further information provided by this genus forms the basis for consideration of the relationships of the adelogyrinids to other lepospondyls. Adelogyrinids might be considered aberrant members of the Microsauria or Nectridea, but may better be thought of as a separate group. They show little evidence of affinity with the lysorophids. Evidence is presented suggesting that lepospondyl centra may be homologous with the intercentra of labyrinthodonts.

Introduction

The most common and best known of the Paleozoic amphibians are the labyrinthodonts: such forms as *Eryops*, *Trimerorhachis*, and *Archeria*, of relatively large size, with labyrinthine infolding of the enamel, and characteristically possessing vertebral centra which consist of more than a single unit. There is also a considerable variety of smaller forms, the lepospondyls, in which the vertebral centra always consist of a single unit and the teeth lack labyrinthodont infolding. The lepospondyls are comparatively rare forms which are generally poorly known. The entire group has recently been discussed by Baird (1965). The lepospondyls are usually grouped in three orders, Nectridea, Aïstopoda, and Microsauria (after Miall 1875). The aïstopods, which are all closely related, limbless, snakelike forms, have recently been surveyed by Baird (1964). The nectrideans are apparently all aquatic forms, with relatively small limbs. They can be recognized by the peculiarity of the caudal vertebrae in which the neural and haemal arches are very similar. This group has never been thoroughly treated as a whole. The most recent discussion is that of Beerbower (1963).

While both the aïstopods and nectrideans are compact groups of closely related forms, the Microsauria is a much more heterogeneous assemblage. Since they have frequently been considered possible ancestors of either reptiles or one or more groups of living amphibians, microsaurs have always aroused considerable interest. Unfortunately, details of their anatomy have been poorly known, and the specific content of the order ill defined. It has long been recognized that at least three quite separate groups are included (Romer

1950). Most of the genera conform to a single morphological pattern, with fully roofed skulls and relatively short trunk regions. The anatomy of these forms, for which no appropriate overall name is available, will be discussed in a forthcoming paper (Carroll and Baird, in press). In addition, there are two groups which have a reduced component of skull bones, the adelogyrinids and lysorophids. The lysorophids are extremely elongate forms, but limbs are retained in all genera. *Molgophis* and *Cocytinus* are known from the Middle Pennsylvanian of Linton, Ohio (Romer 1930; Steen 1931); a larger form, *Megamolgophis*, has recently been described from the Lower Permian of West Virginia and Pennsylvania (Romer 1952). Most of our knowledge of this group comes from the genus *Lysorophus*, known primarily from the Lower Permian of Texas. It was described in 1920 by Sollas through the use of serial sections. A further genus, which may belong to this group, is being described by the Broughs in Cardiff. It is from the Lower Carboniferous.

The adelogyrinids are known from three specimens, all from the Lower Carboniferous of Scotland, described by Watson in 1930. These are currently being restudied by the Broughs. On the basis of vertebral similarities, Watson united these with the lysorophids as the order Adelospondyli. More recent authors (Romer 1950; Baird 1965) have placed these forms in the Microsauria. According to Watson's illustrations, however, the adelogyrinids differ considerably from typical microsaurs in the number and configuration of the skull bones.

Fortunately a further specimen belonging to this group has been discovered which permits a much more complete description of the cranial anatomy and enables further comparison with other lepospondyl groups. This specimen, 1885.57.51, in the Royal Scottish Museum, is from the Black Band Ironstone, and so is Upper Carboniferous in age—Yorkian, or Westphalian B equivalent (Panchen and Walker 1960). It is hence considerably younger than those specimens described by Watson, but is similar to them in most features of the anatomy.

Adelospondylus, new genus
TYPE SPECIES *Adelospondylus watsoni*

Diagnosis: Adelogyrinid lepospondyl in which the postorbital is separated from the postfrontal by an extension of the jugal. The generic name is from the ordinal name proposed by Watson.

Adelospondylus watsoni, new species
Figs. 1–9

Diagnosis: Same as for genus. Specific name in honor of Professor Watson.
Type: Number 1885.57.51 in the Royal Scottish Museum, Edinburgh. Skull and lower jaws with associated vertebrae, ribs, pectoral girdle, limb bones, and scales. This is the only known specimen.
Locality: Loanhead No. 2 mine, near Edinburgh, Midlothian, Scotland.
Horizon: Blackband ironstone. Yorkian, Upper Carboniferous.

The entire specimen was enclosed in a single small block of matrix from which the palate and lower jaws protruded. Unlike most specimens from the British Carboniferous, the matrix is neither a coal shale nor an ironstone, but
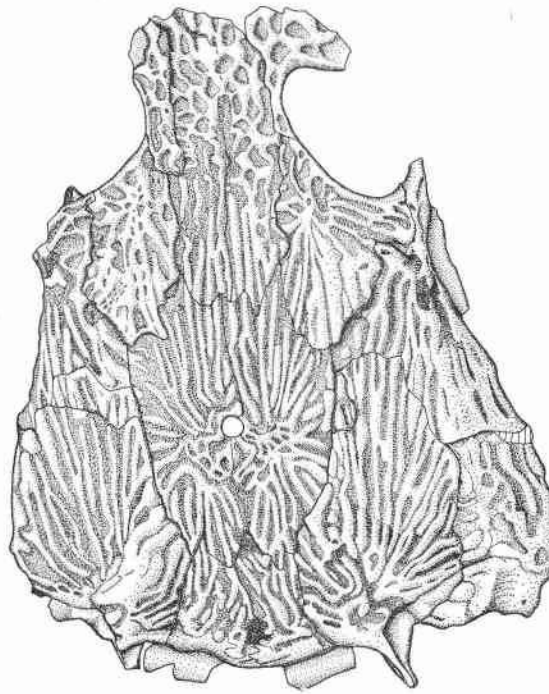
FIG. 1. *Adelospondylus watsoni.* Skull roof. ×2.

a fine-grained sandstone, composed almost entirely of angular quartz grains, with conspicuous flakes of muscovite, bonded by a weak argillaceous cement. The nature of the matrix, as well as the rarity of this group, suggests that the adelogyrinids may have lived in a different environment from that of the more common embolomeres and loxommatids.

DESCRIPTION

The skull (Figs. 1 and 2) has a low profile, accentuated by postmortem crushing. It is complete except for a portion anterior to the orbits. The extent of this area may be estimated from the length of the lower jaws. Like the other adelogyrinids, the eyes are far forward. The proportions of the antorbital region are similar to those in other Paleozoic amphibians, however, and the apparent shortness is a result of the great elongation of the region behind the orbits. The pineal foramen is located about midway between the orbits and the back of the skull. It is round, as in other Paleozoic forms. The pineal foramen in *Adelogyrinus* is drawn by Watson as being keyhole-shaped. This configuration is a result of the fact that in the only known specimen of that genus, the skull roof is known from a mold of the *inner* surface of the bones. In other Paleozoic amphibians, the ventral surface of the parietals is often recessed anterior to the pineal, yet the dorsal surface of the opening is round. The dorsal opening of the pineal foramen was probably round in *Adelogyrinus* as well.
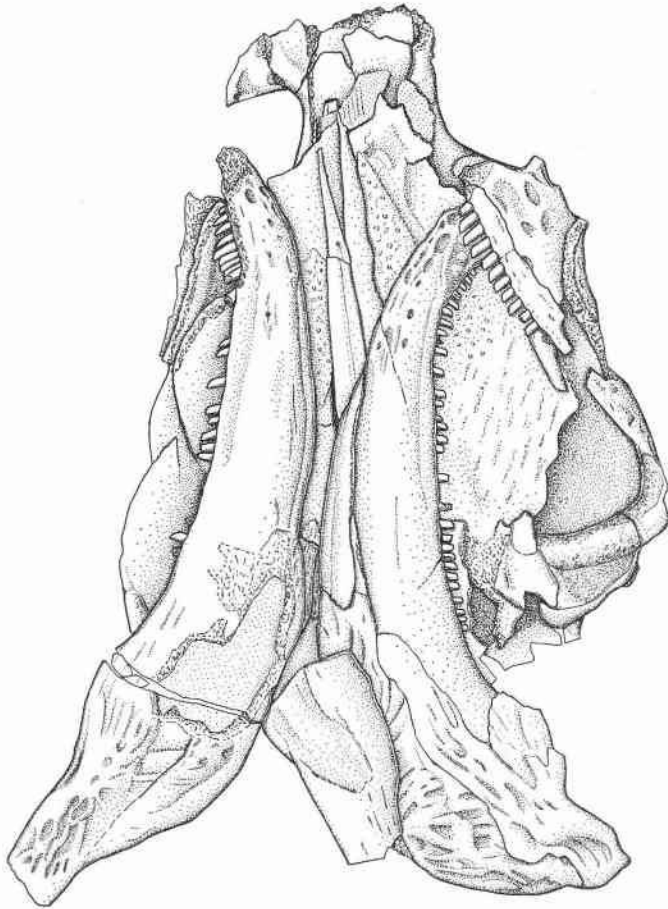
FIG. 2. *Adelospondylus watsoni.* Palate and lower jaws. ×2.

As restored, the skull is more than twice as long as it is wide, and the height equal to about one-third the width. The surface is deeply sculptured in a pattern of pits and grooves. All of the bones behind the orbits show what Bystrow (1935) referred to as areas of secondary growth, indicating that the anterior position of the orbits is not primitive, as suggested by Romer (1950), but a secondary feature. The deep sculpturing, although it makes preparation more difficult, assists in substantiating the number of centers of ossification, and determining the extent of the individual bones. No lateral line canal grooves are evident in this skull. On the jugal and postparietal are small areas on which the sculpturing is particularly deep which may represent remnants of such a system. A groove on the postorbital of the type of *Dolichopareias* was noted by Watson, as well as on the supratemporal and postparietals of the fragment from Pitcorthie associated with that genus. Much of the skull of *Adelogyrinus* is preserved as a mold of the inner surface, so the presence or absence of grooves can not be determined.
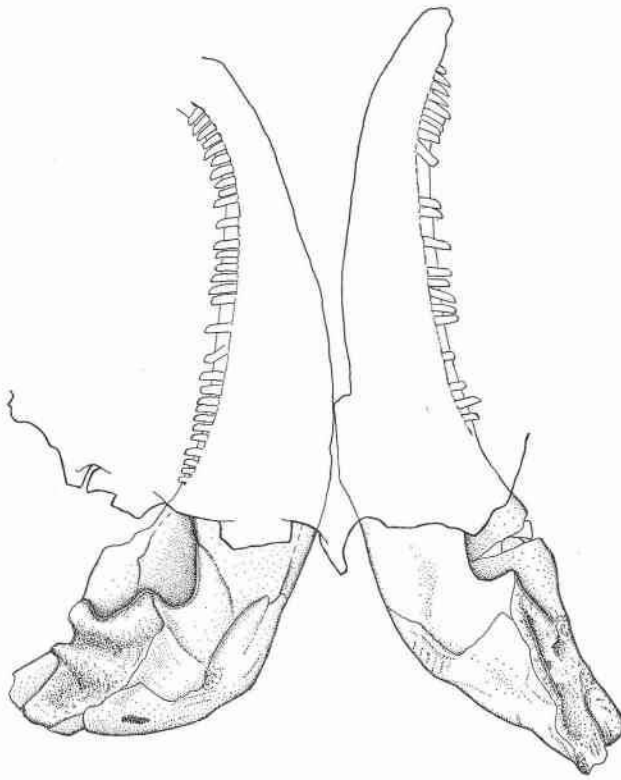
FIG. 3. *Adelospondylus watsoni*. Medial view of lower jaws. Unshaded portion restored from lateral view. ×2.

The sutures are clearly evident, except dorsally between the frontals and nasals. Fortunately this area is visible ventrally. In general, the position and configuration of the bones compare very closely with those determined by Watson in the Mississippian genera. The most important feature is that there are only three pairs of bones at the back of the skull roof, as in Watson's drawings, but unlike the restoration by Romer (1950). In this specimen there is no question of the identity of the lateral bone as the quadratojugal since the quadrate is in place on both sides. Medially there are small postparietals. There is a single bone between the postparietal and quadratojugal, termed here the supratemporal, but labeled squamosal by Watson. It may have a compound origin, but there is no evidence of this in this specimen. In labyrinthodonts this area is occupied by the tabular, squamosal, supratemporal, and sometimes intertemporal; in typical microsaurs by the supratemporal and squamosal. In the adelogyrinids it may incorporate some of the area originally occupied by the postorbital as well. The use here of the term supratemporal is arbitrary. This bone, as in Watson's genera, extends posteriorly as a "horn" beyond the back of the skull. The horn is recessed both medially and laterally. Medially it may have accommodated an anterior extension
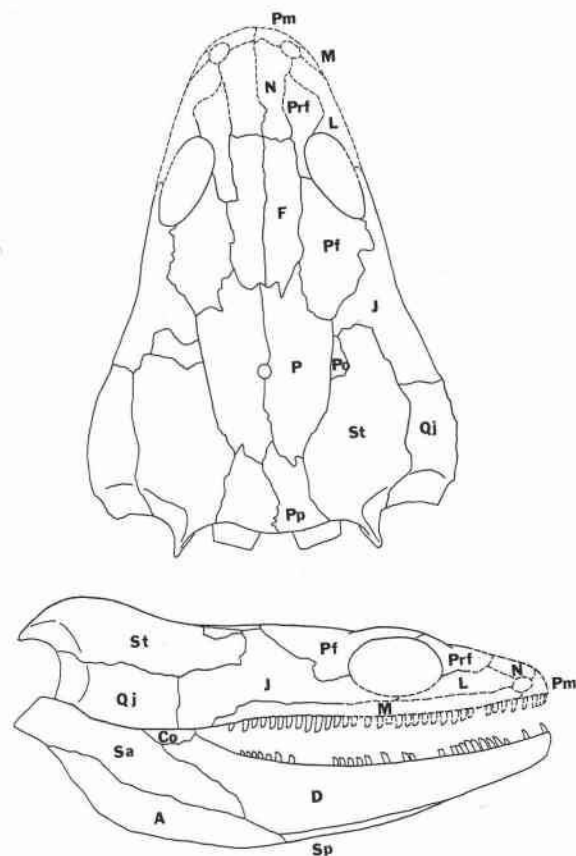
FIG. 4. *Adelospondylus watsoni.* Reconstruction of skull in dorsal and lateral views. Broken lines are restored. ✕1⅓. A, angular; Co, coronoid; D, dentary; F, frontal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; Pf, postfrontal; Pm, premaxilla; Po, postorbital; Pp, postparietal; Prf, prefrontal; Qj, quadratojugal; Sa, surangular; Sp, splenial; St, supratemporal.

from the dermal shoulder girdle, or provided an area for insertion of epaxial musculature. Watson termed the lateral area an otic notch. If this is an otic notch (in the sense of a structure to support a tympanum), this is the only group among the lepospondyls to have such a feature. This notch has the same relationship to the supratemporal as does the otic notch in anurans to the squamosal. With only a single bone in the temporal region, it is difficult to compare this notch with that which is present in the labyrinthodont amphibians. Unfortunately the back of the braincase is not preserved so the relationship of the notch to the auditory region cannot be determined. The stapes is not preserved. As will be mentioned below with description of the lower jaw, this recess could have accommodated muscles to open the mouth. The posterior portion of the supratemporal is further distinguished in being extended dorsally above the level of the parietals and postparietals.
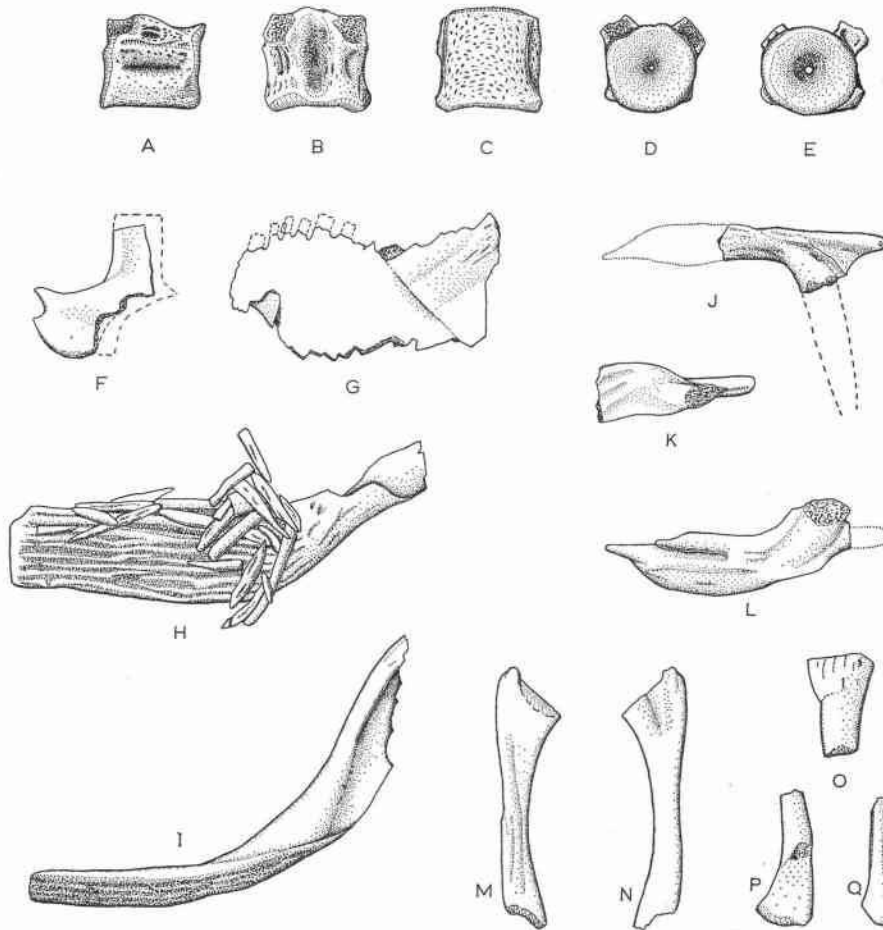
FIG. 5. *Adelospondylus watsoni*. Vertebrae, dermal shoulder girdle, and forelimb. A–E, centrum of a single vertebra in lateral, dorsal, ventral, anterior, and posterior views; F, isolated neural arch in lateral view (broken lines restored); G, interclavicle in dorsal view (broken lines restored); H and I, right clavicle in ventral and posterior views; J, ?left cleithrum in medial view (dotted line restored from ?right cleithrum, broken line reconstruction of stem); K, ?left cleithrum in ventral view; L, ?right cleithrum in ventral view (dotted line restored from ?left cleithrum); M and N, right ulna in dorsal and ventral views; O, proximal end of left radius in dorsal view; P and Q, distal extremity of right radius in dorsal and medial views. All ×2.

The postparietals are relatively small and are partially overlapped by the supratemporals. Unsculptured portions of the postparietals extend ventrally and posteriorly to the exoccipitals. The quadratojugal wraps around the back of the quadrate; this area is unsculptured and essentially a continuation of the recess in the supratemporal. The posteroventral surface of the quadratojugal is modified to form an extension of the articular surface of the quadrate. The jugal is greatly elongated, and extends dorsally to the parietal. Behind
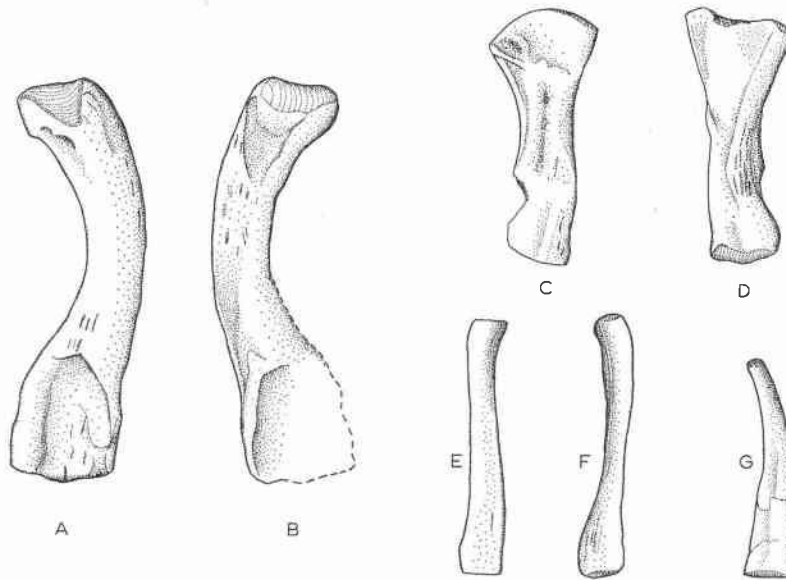
FIG. 6. *Adelospondylus watsoni*. Rear limb. A and B, right femur in dorsal and ventral views; C and D, right tibia in dorsal and ventral views; E and F, ?left fibula in dorsal and ventral views; G, ?right fibula in ventral view. All ×2.

this dorsal extension, between the parietal and supratemporal is a bone corresponding in position to one which Watson termed the supratemporal in *Adelogyrinus* and *Dolichopareias* (Fig. 7). From a comparison of the three successive species of adelogyrinids, it is apparent that this bone is becoming smaller and more posterior in position. Since the posterior orbital margin is made up of only two bones, the jugal and postfrontal, it seems very likely, as suggested by Romer, that this bone is the postorbital. The bone is much larger on the left side in this specimen than it is on the right. Its margins are difficult to trace, but the pattern of sculpturing is interrupted on all sides. This area of ossification is gradually being taken over by the jugal and supratemporal. A similar exclusion of the postorbital from the orbital margin has occurred in both *Diploceraspis* and *Diplocaulus* among the nectrideans, which also have very large postorbital areas.

The bones surrounding the orbit dorsally may best be termed the prefrontal and postfrontal. Ventrally a suture may be seen between the right prefrontal and the lacrimal, which makes up the remainder of the anterior margin. The prefrontals, lacrimals, and nasals are all incomplete anteriorly. It is not possible to determine definitely whether the jugal and lacrimal meet beneath the orbit, although this is suggested by the extent of the jugal beneath the posterior portion of the orbit. Neither the premaxillae nor the area of the external nares are preserved.

The posterior portion of the left maxilla is preserved, and with it 12 teeth. The portion preserved is very narrow. Unless there is considerable regional variation in size, the upper jaw would have held 42–45 teeth. Those preserved
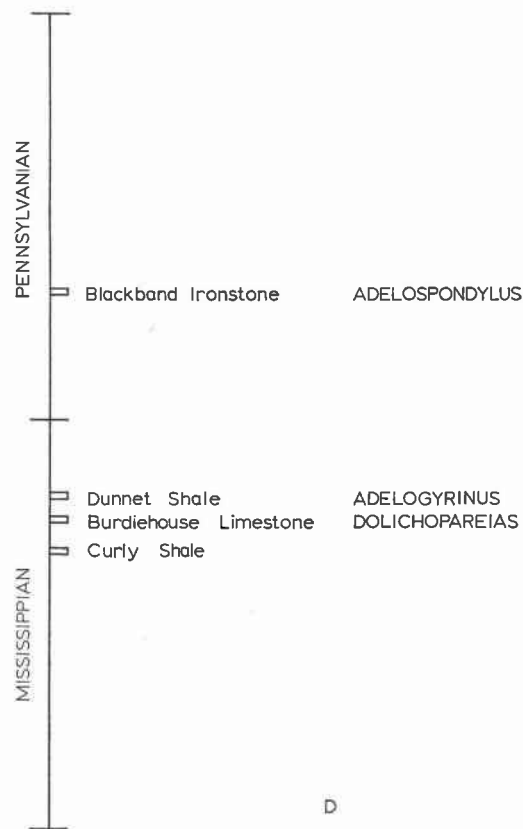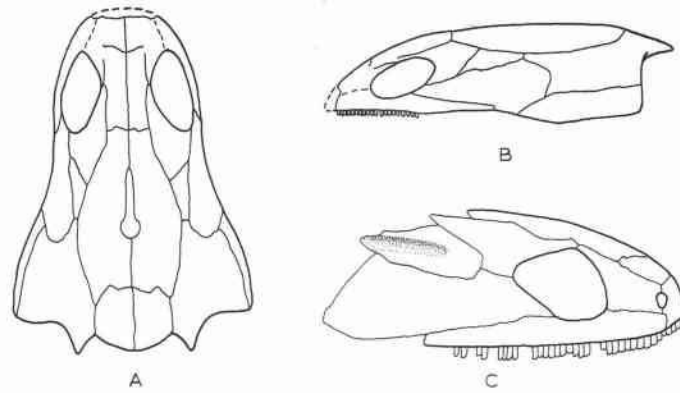
FIG. 7. A and B, *Adelogyrinus*: skull roof in dorsal and lateral views (after Watson, 1930, ×1); C, *Dolichopareias*: skull roof in lateral view (after Watson, 1930, ×1); D, chart showing relative stratigraphic position of the adelogyrinids and the Curly shale from which the earliest lysorophid is known.

are cylindrical pegs, with a distinctive chisel-shaped tip. They lack labyrinthine infolding. They are identical with the teeth in other adelogyrinids.

The quadrate is visible only ventrally. Anteriorly it forms a convex condyle which is continuous with an apparent articulating surface of the quadratojugal. There is a large recessed posterior extension, widening medially.

Most of the palate is preserved (Fig. 2), but much is obscured by the lower jaws. The region anterior to the middle of the orbits is missing, so no information is available on the vomers or the internal nares. Most of the area of the palate appears to be made up of very extensive pterygoids, partially covered with small denticles. The palate is closed, with the pterygoids abutting against the parasphenoid. The margins of the palate are partially obscured by other bones, and partially missing, so that neither the ectopterygoid nor palatine is evident. No palatine fangs are visible. Except for questionable fragments of the posterior plate protruding from beneath the jaws, all that is visible of the parasphenoid is a long, narrow cultriform process. It extends to the middle of the orbits before tapering to a point. A ventral ridge runs most of the length of the bone. An area of bone showing between the parasphenoid and the left pterygoid is apparently the sphenethmoid. This is the only portion of the braincase which is visible.

The lower jaws are plastered against the ventral surface of the palate (Figs. 2 and 3). Their lateral surface is visible throughout, and the posterior portion of the medial surface is visible where it extends beyond the back of the skull. Almost the entire length of both jaws is preserved. Each would have accommodated about 45 teeth. These teeth generally resemble those in the maxilla, except for the shorter length that is exposed laterally. They are evidently set in a groove on the medial margin of the dentary. The depth of this groove may be estimated from an area at the anterior end of the right jaw where the lateral margin is missing. The posterior teeth are chisel-shaped like those in the posterior portion of the maxilla, but those near the anterior end appear to be tapered from near the base. The anterior end of the dentary is sculptured by a number of deep pits; more posteriorly the surface is smooth, except for a groove running longitudinally near the dorsal margin. Running beneath the dentary for much of its length is a splenial. It is not certain whether this is a single bone, or divisible into anterior and posterior portions. The back of the jaw is made up of a large, strongly sculptured angular, surangular, and coronoid.

The medial surface of both lower jaws is visible almost to the level of the beginning of the tooth row. The masseteric fossa is surprisingly short. Beneath it the prearticular extends anteriorly from the medial portion of the angular. The articular is very large. A transverse groove accommodates the condyle of the quadrate. Posterior to this is a ridge which fits into the posterior groove in the quadrate. The articular continues posteriorly as a considerable retroarticular process. This is sheathed medially and laterally by the surangular. This process lies immediately beneath the notch in the quadratojugal and supratemporal. A strong retroarticular process may be developed to accommodate muscles to force open the lower jaw in forms which have large masseteric muscles, as in animals with a specialized crushing dentition. Neither *Adelospondylus* nor the other adelogyrinids have a crushing dentition, and the
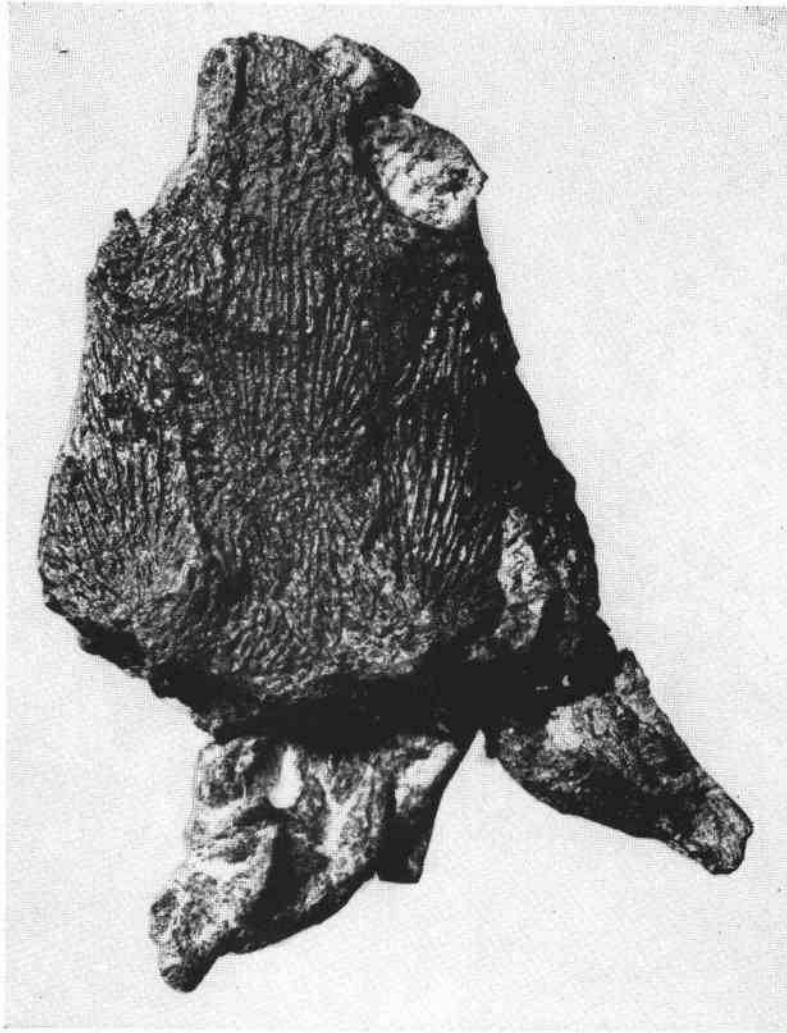
PLATE I

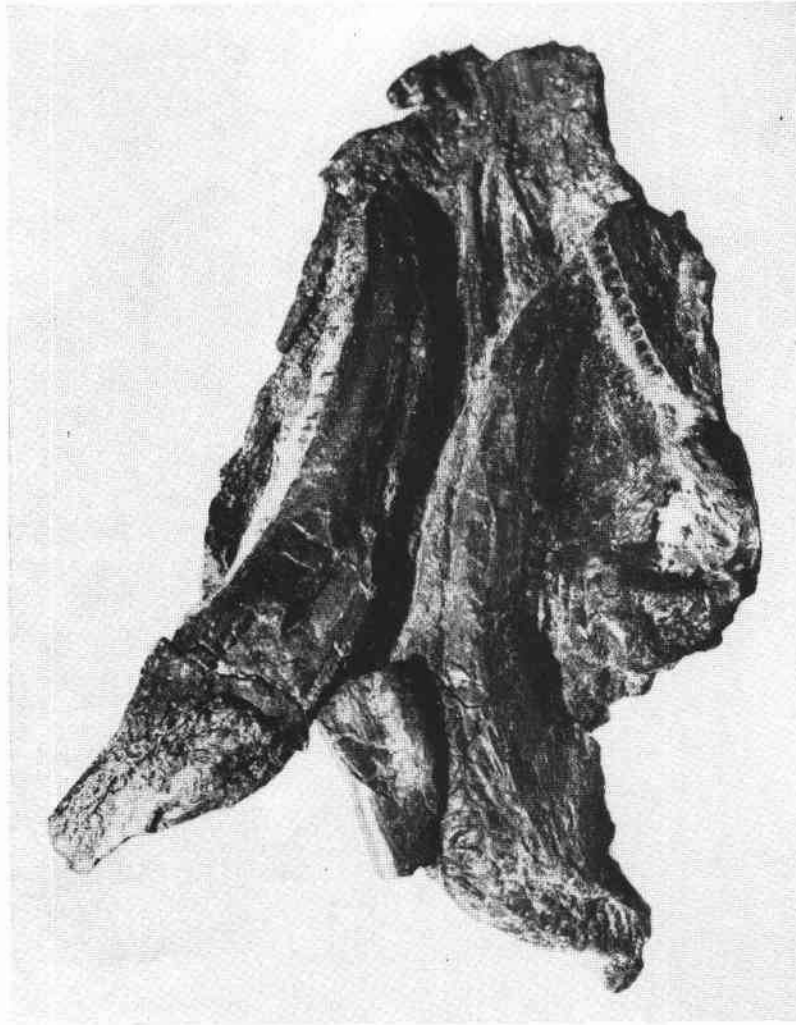FIG. 8. *Adelospondylus watsoni.* Skull roof. ×2.

Carroll—Can. J. Zool.

PLATE II

FIG. 9. *Adelospondylus watsoni.* Palate and lower jaws. ×2.

small size of the masseteric fossa suggests that the musculature for closing the jaw was little developed. Massive muscles to open the mouth may have another function, however. Particularly in forms with very flat skulls (sometimes associated with bottom living animals, e.g. metoposaurs), the lower jaws may remain at rest while the skull is moved relative to them. *Adelospondylus* may have opened its mouth in this way as well. This would explain the presence of a retroarticular process, and possibly the so-called otic notch. It should be noted, however, that the earlier adelogyrinids have a higher profile, and yet possess a notch.

In the same block with the skull are a number of postcranial fragments. Although they are not articulated, it is evident that they all belong with the skull on the basis of their proximity, relative size, and absence of any definitely allochthonous elements. Among these bones are the centra of three vertebrae, the most complete illustrated in Fig. 5, A–E, together with an isolated neural arch (Fig. 5, F). The centra are typically lepospondylous, composed of a single spool-shaped ossification recessed at both ends, with a central opening for the notochord. The lateral and ventral surfaces are marked by pits and grooves very much as in the lysorophids (see Romer 1952, Fig. 7). The posterior margin is expanded laterally near the ventral edge for reception of the capitulum of the ribs. Dorsally the centrum is deeply recessed in the midline. The neural arches were only suturally attached and are missing from all three centra. They were attached to short pedicels on the anterior one-third of the centra. Only the left side of a single arch is sufficiently preserved for description. The right side is too badly crushed to determine whether the two halves were normally co-ossified, or separate elements, as in some lysorophids. According to Watson, the two halves of the neural arch are completely fused in the Mississippian adelogyrinids. The arch, which is not swollen, has a tall spine, incompletely preserved. The transverse process is large, extending anteriorly and laterally from the arch. The pedicels of the arch are not visible. The prezygapophyses and postzygapophyses are like those of typical microsaurs, with no evidence of the accessory articulating surfaces typical of nectrideans.

A few rib fragments are scattered in the block. They appear to have simple cylindrical shafts. From the configuration of the vertebrae, the ribs must have been double-headed.

The endochondral shoulder girdle is not preserved, unless some small featureless scraps are fragments of this bone. The dermal elements are present, however (Fig. 5). The right clavicle is complete, except for the very end of the stem. The ventral portion is an extensive, elongated plate, deeply sculptured ventrally by grooves and ridges. It curves gently to join the shaft. The shaft is deeply grooved posteriorly for reception of the stem of the cleithrum. Portions of both cleithra are present; neither, however, shows much of the shaft. The area of dorsal expansion is very large and massive: not sculptured in the manner of other dermal elements, but deeply grooved ventrally. It extends anteriorly as a narrow rod; it is possible that this process fits into the recess medial to the horn of the supratemporal. The stem of the cleithrum, judging by the configuration of the recess for its reception in the stem of the clavicle, would have been a long cylindrical rod. A triradiate cleithrum of this

general configuration is known in several nectrideans (e.g. *Scincosaurus*, Steen 1938, Fig. 8). A portion of the interclavicle is preserved showing the anterior margin which, as in many Paleozoic tetrapods, is extended in a series of narrow processes, like the teeth of a comb. The overall configuration of this bone is not evident. The ventral surface is covered with a number of bony scales, obscuring most of the bone. It does not appear to be deeply sculptured.

The humerus is not preserved.

Both ulnae are preserved, although the left could not be prepared without damage to the cleithra. The right is complete except for the very end of the area of distal expansion (Fig. 5). The olecranon is well ossified, with a distinct, although shallow, sigmoid notch. A prominent ridge runs along the dorsal (extensor) surface. Two fragments of the radii have been identified: the proximal end of what appears to be the left radius, and the distal end of the right. The radius appears to be more lightly built than the ulna.

The pelvis is not preserved. The right femur (Fig. 6, A and B) is preserved with the ventral surface of the distal extremity crushed against the lower jaws. The bone has a long shaft which is curved so that the posterior margin is markedly concave and the anterior convex. There is no internal trochanter nor an adductor ridge. The intertrochanteric fossa is in the form of a shallow depression in the shaft, just distal to the head. The right tibia (Fig. 6, C and D) is somewhat crushed on the dorsal surface; the cnemial crest is not apparent. The ventral surface is well preserved, showing a large raised area of rugosity just below the middle of the shaft. On the lateral margin of the bone is a ridge which runs along the shaft, to terminate abruptly about one-third of the way from the end of the bone. Two bones have tentatively been identified as fibulae (Fig. 6, E–G). The ?left is complete, and very close to the length of the tibia. It is, however, much more lightly built and the shaft is almost straight. The area of distal expansion is very small compared with that of other Paleozoic tetrapods. It is twisted relative to a stouter proximal expansion. The area for articulation with the tarsals is at right angles to the shaft.

No foot bones have been recognized.

A number of scales are preserved, some scattered within the block and others adhering closely to the ventral surface of the dermal shoulder girdle. The scales vary somewhat in shape and size, but most are heavy, sculptured rods, tapering at both ends. Some appear to be forked, more flattened bones. The scales of this genus and other adelogyrinids are distinct from those of other Paleozoic vertebrates, but with some resemblance to those of such nectrideans as *Ptyonius*. No scales of the typical microsaurian pattern were observed, although it is possible that they would not be preserved in such a coarse matrix.

Affinities of *Adelospondylus*

A detailed comparison of this genus with other adelogyrinids awaits the work of the Broughs. It may certainly be included in the same family, as a late member carrying on the trends evident in the Mississippian genera. The skull appears to be considerably lower, while the postorbitals have become progressively smaller and more posterior in position.

A more important consideration is the position of the adelogyrinids among the lepospondyls. Except for Watson's initial separation of the Adelospondyli as an order, most authors have placed them among the microsaurs. Watson's original distinction was based on the sutural attachment of the neural arch, which has been shown to be a variable feature among the Microsauria and of no taxonomic significance. Subsequent authors have interpreted Watson's reconstruction of the skull to conform to the pattern of other microsaurs, rather than accepting the peculiar arrangement of the cranial bones shown in Watson's illustrations. Study of *Adelospondylus* has shown that Watson's illustrations are basically correct, particularly in the important feature of the number of bones at the back of the skull. The presence of a single bone in the position of the supratemporal and squamosal in typical microsaurs indicates first that the adelogyrinids cannot possibly be ancestral to these forms, and secondly suggests that they may not be at all closely related. No typical microsaur has the supratemporal notch which characterizes these genera. The absence of typical microsaurian scales is a further point for separating these forms. The most important feature which has been used to distinguish microsaurs, the configuration of the occipital condyle and the atlas–axis complex (Carroll and Baird, in press), unfortunately cannot be considered, since these areas are not described in any adelogyrinid.

There are relatively few points of comparison with the lysorophids (see Sollas 1920). The skull is totally different. According to Baird (1965), *Lysorophus* has both the supratemporal and squamosal, while losing most of the cheek region. While the skull pattern of *Lysorophus* and that of the adelogyrinids may have been modified from the same ancestral condition, this would have been so distant that it included the ancestry of all lepospondyls. The centra are similar in the two groups, but this alone is a poor basis of comparison. Until more is known of both lysorophids and adelogyrinids, it seems premature to consider them closely related. The earliest lysorophid, apparently already showing most of the peculiarities of the group, is being described by the Broughs. It is from the Curly shale of the Lower Carboniferous, which is slightly older than the horizons from which the adelogyrinids are known. This indicates that both the adelogyrinids and the lysorophids are very ancient groups, which long preceded the known members of the central microsaur stock.

Further consideration of the lysorophids is not possible at this time. The next question is whether, although the adelogyrinids are not typical microsaurs, they should be retained in that order, transferred to another lepospondyl group, or, as originally suggested by Watson, be placed in an order of their own.

There is no basis for inclusion of the adelogyrinids among the aïstopods, which were already highly specialized in the Lower Mississippian. There are several points of comparison with the nectrideans, however. Both *Keraterpeton* and *Diceratosaurus* have supratemporal horns of a similar nature, and *Scincosaurus* has a reduced number of bones at the back of the skull. There are also similarities between the cleithra of *Adelospondylus*, *Scincosaurus*, and *Diceratosaurus*. Caudal vertebrae have yet to be described among the adelogyrinids, but the dorsal vertebrae show no important similarities to those of

nectrideans. While the similarities between adelogyrinids and nectrideans may not be sufficient to indicate any close relationship, they are as numerous as those between adelogyrinids and typical microsaurs. One can equally well consider this family aberrant members of either of these orders, or alternately as a totally isolated group. The latter may be the safest course at the present time. With a group which is so limited in numbers and diversity, however, it seems best to consider it as a family, rather than giving it ordinal status. Like the rodents (Wood 1959), the lepospondyls may not be amenable to classification as an evenly ordered series of hierarchies.

Although separation of the Adelogyrinidae from the Microsauria complicates the classification of the Lepospondyli, the mixture of microsaurian and nectridean features in this family supports the idea of a common ancestry for the Lepospondyli.

Consideration of Lepospondyl Vertebrae

The origin and homology of the elements of the vertebral centra in labyrinthodonts are clearly shown from fossil evidence. The most primitive of the known labyrinthodonts, the ichthyostegids, have large, crescentic intercentra and small, paired pleurocentra (Jarvik 1952). These are directly comparable to the elements in the rhipidistian *Eusthenopteron*. The condition in *Eusthenopteron* and the ichthyostegids (termed proto-rhachitomous) forms a basis for the vertebrae in all labyrinthodonts and amniotes (Romer 1964).

Lepospondyl centra, in contrast, are of indefinite origin and homology. All lepospondyls have holospondylous centra, that is, a single spool-shaped ossification in each segment. These centra are usually considered either (1) formed from the direct ossification of the notochordal sheath (in analogy to the condition in living urodeles) without any relationship to the pleurocentra or intercentra of Paleozoic labyrinthodonts (Romer 1945); or (2) equivalent to the pleurocentra of labyrinthodonts and amniotes, with the complete loss of the intercentra (Williams 1959; Baird 1964). The latter suggestion would support derivation of the lepospondyls from the same rhipidistian stock as that which gave rise to the labyrinthodonts. This assumes, however, a very rapid growth of the pleurocentra and suppression of the intercentra, with a completely holospondylous condition resulting by the Lower Mississippian, if not earlier. In contrast, reptiles and their descendants the mammals, in which the vertebrae are definitely known to have evolved from the proto-rhachitomous condition, retain the intercentra even in living forms, at least in the caudal region and in the atlas–axis complex.

In *Adelospondylus*, as in other adelogyrinids, it is surprising that the neural arch has only a weak sutural attachment with the centrum, especially if one assumes that the centrum itself has evolved from a less well-ossified or multipartite structure, to give more strength to the vertebral column. The neural arch is also only suturally attached in the lysorophids, and in fact may remain a paired structure.

This weak attachment of the neural arch, together with the very early occurrence of holospondylous centra, suggests that the lepospondyl condition may not have evolved within the group, but rather that it was retained from their fish ancestry. Among the rhipidistians, not all genera have the proto-

rhachitomous pattern of *Eusthenopteron*. Even within the rhizodontoids, *Rhizodus* has vertebrae which are formed from a single ring-shaped ossification homologous to the intercentra of *Eusthenopteron*. This condition is also present in *Megalichthys* and *Ectosteorhachis* among the osteolepoids. The pleurocentra are not ossified at all in these genera (Thomson, personal communication). If amphibians had evolved from genera having such a vertebral pattern, they too would possess a single vertebral ossification. If lepospondyls evolved from such a stock, it would explain their lack of intervertebral ossification, since the definitive centra would be homologous to the intercentra of labyrinthodonts. This would also explain the peculiar position of the haemal arches in the nectrideans. If the caudal vertebrae are formed only from the intercentra, it is only natural that the haemal arches would be attached midway in their length.

The initial absence of the pleurocentra in the lepospondyls might also explain the configuration of the atlas–axis complex in microsaurs (Carroll and Baird, in press) and nectrideans (Beerbower 1963). The cervicals of aïstopods (Gregory 1948) may be interpreted in a similar fashion. In these groups there is essentially a single modified cervical, which functions in the same way as both the atlas and axis in the amniotes. The first cervical of lepospondyls resembles in general the atlas of metoposaurs (Sawin 1945) in which the centra are formed entirely from the intercentra.

If the centrum in lepospondyls was derived directly from rhipidistians with holospondylous centra, then labyrinthodonts and lepospondyls must have had a separate ancestry at the rhipidistian level. This idea is supported by the lack of any forms which can be considered intermediate between labyrinthodonts and lepospondyls, and by the high degree of specialization of the lepospondyls, especially the aïstopods (Baird 1964), even in the early Mississippian. Considering the variation in vertebral configuration among closely related rhipidistians, the ancestors of the labyrinthodonts and lepospondyls might belong within the same family or superfamily. As recently discussed by Schaeffer (1965), at least the early stages of the transition between rhipidistians and amphibians probably took place in a number of related lines. All would have had the same basic morphology, and even the same limb structure. Modification in limb and girdle configuration would necessarily have proceeded in similar patterns in all lines. Vertebral modification may, on the other hand, have occurred by elaboration of either the intercentra or the pleurocentra.

Acknowledgments

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