A LYSOROPHID AMPHIBIAN FROM THE COAL MEASURES OF NORTHERN ENGLAND

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ABSTRACT. A description is given of the presacral vertebrae and ribs of a lysorophid amphibian from the Middle Coal Measures (Westphalian B) of Northumberland. The specimen is the earliest lysorophid yet described and is the first certainly identifiable member of the group to be recorded from any horizon outside North America. An isolated presacral vertebra from an unknown Coal Measures horizon at Low Moor, West Yorkshire, may represent additional evidence of lysorophids in the British Carboniferous. Lysorophids appear to have been present in both lacustrine and coal swamp pool environments in the Upper Carboniferous as well as surviving in 'red bed' environments in the Lower Permian in North America.

THE Lysorophidae is a family of small 'lepospondyl' (*sensu* Romer 1966) amphibians hitherto known with certainty only from Upper Carboniferous and Lower Permian freshwater deposits in North America. The lysorophids have in the past been assigned to a number of different amphibian taxa, including the Orders Apoda (Moodie 1909) and Urodela (Sollas 1920; von Huene 1956). Romer (1966) regarded the lysorophids as constituting a family of aberrant microsaurs; in a recent discussion of lysorophid structure and relationships, however, Carroll and Gaskill (1978, p. 186) have suggested that the members of the group are sufficiently distinct from typical microsaurs to warrant exclusion from the Order Microsauria.

The type genus of lysorophid, *Lysorophus*, was first described by Cope (1877) on the basis of three isolated vertebrae from the Upper Pennsylvanian of Danville, Illinois. Unfortunately the absence of more diagnostic material makes it impossible to distinguish *Lysorophus* from other Carboniferous lysorophids (Carroll and Gaskill 1978). One of the most fully known of described Carboniferous lysorophids is *Cocytinus* Cope 1871, from the Westphalian D horizon of Linton in Ohio. An articulated specimen of *Cocytinus* from Linton has recently been figured by Carroll and Gaskill (1978, fig. 132B). A lysorophid referable to *Cocytinus* has also been reported by Baird (1964) from the lower Westphalian D of Mazon Creek, Illinois. Relatively abundant lysorophid material, usually referred to the genus *Lysorophus*, is known from the Lower Permian of Texas. Many of these last specimens are preserved in a matrix which renders preparation difficult, but serial-sectioning techniques enabled Sollas (1920) to give a detailed account of the skull and the anterior postcranial skeleton of one specimen. Further Lower Permian lysorophid material has, more recently, been described by Olson (1971) from the Hennessey Formation of Oklahoma.

No description has hitherto been published of a lysorophid from any locality outside North America. Although lysorophids have been reported from the Westphalian A ox-bow lake site of Jarrow in Co. Kilkenny, Eire (Thomson and Bossy 1970), the very poor state of preservation of most of the specimens from this locality (Rayner 1971) makes definite identification difficult. A small amphibian from the late Stephanian or early Autunian of Nièvre in France, tentatively identified as an aïstopod by Thevenin (1910), may also possibly be a lysorophid (Baird 1964) but, as at Jarrow, preservation is very poor and certain identification is not possible.

MATERIALS

The following description is of a previously undescribed lysorophid specimen which was collected, probably during the latter half of the nineteenth century, from the Coal Measures of Northumberland. The specimen, registered in the collections of the Hancock Museum, Newcastle upon Tyne, as

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G91.15, is from the black shale immediately overlying the Low Main Seam at the colliery of Newsham near Blyth. This horizon lies within the Upper Modiolaris zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age. Because the specimen lacks a skull, it is impossible to diagnose it at generic or specific level, and the specimen is therefore not named. However, it merits description as the first certainly identifiable lysorophid to be recorded from outside North America.

A single presacral vertebra, until recently housed in the Geology Museum of the Wigan College of Technology in Wigan, Lancashire, but now registered as G152.04 in the Hancock Museum collections, may represent additional evidence of the presence of lysorophids in the British Upper Carboniferous and is also described below. The vertebra was collected between 1880 and 1920 from the Coal Measures of Low Moor, near Bradford in west Yorkshire. Unfortunately, its precise horizon is not recorded. However, the holotype specimen of the large eogyrinid embolomere *Pholiderpeton scutigerum* Huxley 1869, which is also from the Low Moor area, was collected from the shale overlying the Black Bed Coal at Toftshaw and this horizon lies in the Lower Communis zone of the Lower Coal Measures (Westphalian A) (Panchen 1970). It is possible that vertebra G152.04 was collected from the same horizon.

DESCRIPTION

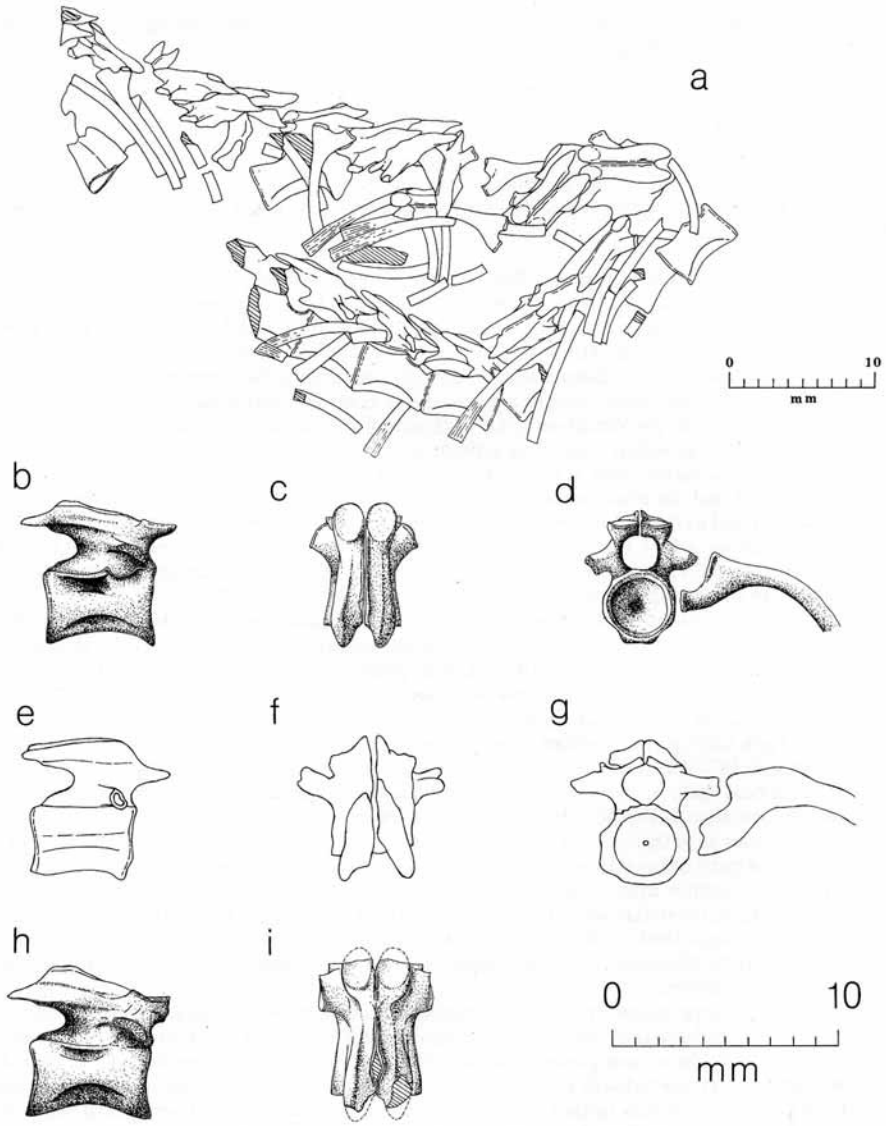
As preserved, specimen G91.15 (text-fig. 1*a*) consists of a small slab of shale bearing an articulated series of eighteen well-preserved presacral vertebrae, in addition to the fragmentary and incomplete neural arches of the three preceding vertebrae. Most of the neural arches present have become detached from their respective centra but the component parts of almost all vertebrae still lie closely adjacent to one another and exhibit few traces of distortion or crushing. Trunk ribs are associated with the majority of the twenty-one vertebrae represented in G91.15. There is no obvious variation in the structure of either vertebrae or ribs within the preserved series. This uniformity of structure would seem to suggest that the complete animal possessed an, at least moderately, elongated presacral vertebral column, and it is of interest to note that *Cocytinus* is known to possess approximately seventy-two presacral vertebrae (Carroll and Gaskill 1978).

In a typical anterior presacral vertebra the centrum is holospondylous, spool-shaped and deeply amphicoelous. It is probable that, as in *Lysorophus* (Sollas 1920), the centrum is perforated for passage of the notochord. There is no evidence of the presence of distinct intercentra in G91.15. The external surface of the centrum is excavated ventro-laterally to form a pair of longitudinally elongate depressions which extend almost the full length of the element. A pair of similar depressions is present dorso-laterally but these are restricted to the posterior half of the centrum. In the anterior one-third of the centrum is situated a pair of dorsally directed depressed facets for articulation with the neural arch pedicels. The articulation between neural arch and centrum is clearly sutural in all the vertebrae present in G91.15. The most notable feature of the neural arch is its ossification in two separate halves, with the line of separation running along the length of the neural spine. The presence of a longitudinally divided neural arch and spine in the trunk vertebrae was clearly demonstrated in *Lysorophus* by Sollas (1920). Although occurring in very immature microsaurs (Carroll and Gaskill 1978) and the adults of some 'labyrinthodont' amphibians, this phenomenon is not known in adult 'lepospondyls' except in the lysorophids. The neural spine is very much reduced and consists of a scarcely perceptible ridge running the length of the dorsal surface of the neural arch. Both pre- and postzygapophyses possess horizontally orientated articular surfaces. In the anterior one-third of the neural arch, at the level of the neurocentral articulation, is situated a pair of elongate, antero-laterally directed diapophyses. A similar orientation of the diapophyses is present in the anterior dorsal vertebrae of *Lysorophus* described by Sollas (1920, fig. 42).

The ribs of G91.15 (text-fig. 1*a*, *d*) are dichocephalous and possess long, curved shafts which are compressed antero-posteriorly. None of the vertebrae show any evidence of a facet to receive the rib capitulum. The probable original relationships of neural arch, centrum and rib are shown in text-fig. 1*d*.

DISCUSSION

The vertebrae of G91.15 are typically lysorophid in structure and very closely resemble those of *Lysorophus* as described by Sollas (1920). A series of Sollas's restorations of the dorsal vertebrae of *Lysorophus*, based upon serial sections, is figured (text-fig. 1*e–g*) for comparison with those of



TEXT-FIG. 1. Presacral vertebrae of lysorophids. *a*, semi-diagrammatic representation of Hancock Museum specimen G91.15 as preserved; *b–d*, restoration of an anterior trunk vertebra of specimen G91.15 in *b*, right lateral view; *c*, dorsal view and *d*, anterior view articulated with proximal part of trunk rib; *e–g*, anterior trunk vertebra of *Lysorophus* in *e*, right lateral view; *f*, dorsal view and *g*, anterior view articulated with proximal part of trunk rib (*e–g* after Sollas); *h–i*, Hancock Museum specimen G152.04 in *h*, right lateral view as preserved and *i*, dorsal view with probable original extent of zygapophyses restored. Cross-hatching indicates broken bone surface.

G91.15. Among the more significant resemblances between described lysorophids and specimen G91.15 may be cited the following:

1. Dorsal vertebrae with a neural arch ossified in separate lateral halves.
2. A sutural, rather than fused, neurocentral articulation.
3. A neural spine reduced to a low ridge on the neural arch.
4. Prominent zygapophyses with horizontally orientated articular surfaces.
5. A holospondylous and deeply amphicoelous centrum.
6. The possession of elongate, dichocephalous trunk ribs, the tuberculum of which articulates with a diapophysis.

Whilst characters 2–6 are all parallelled in other 'lepospondyl' taxa and 3–5 are present simultaneously in aïstopods (e.g. Baird 1964), character 1 and hence the combination of all six listed characters is apparently unique, amongst described 'lepospondyl' amphibians, to the Lysorophidae.

Hancock Museum specimen G152.04, from an unknown Coal Measures horizon at Low Moor (text-fig. 1*h–i*) is less certainly lysorophid. Although resembling the vertebrae of G91.15 in the possession of a holospondylous, deeply amphicoelous centrum, and a neural arch with a much-reduced neural spine and horizontally orientated zygapophyseal articular surfaces, G152.04 differs in two respects. The neural arch is ossified as a single structure and would appear to be firmly united, and possibly fused, to the centrum. It is possible, however, that both characters may be age-related or may represent regional variation within the vertebral column, and G152.04 is, therefore, here very tentatively attributed to the Lysorophidae. The relative shortness of the diapophyses compared with those of the vertebrae of G91.15 and their directly lateral, rather than antero-lateral, orientation may indicate that vertebra G152.04 derives from a more posterior region of the presacral vertebral column than is present in the former specimen.

In addition to representing the first certain record of lysorophid amphibians outside North America, specimen G91.15 is the earliest recognizable lysorophid yet described. The stratigraphic range of previously described members of the Lysorophidae extends from the Upper Freeport Coal of Linton, Ohio (Upper Allegheny or lower Westphalian D), where the group is represented by the genera *Cocytinus* Cope 1871 and *Molgophis* Cope 1868 (Steen 1931), to the Choza Formation of the Texas Clear Fork Group (Leonardian, Lower Permian) which has yielded specimens referable to *Lysorophus* Cope 1877 (Olson 1958). The presence of specimen G91.15 in the black shale overlying the Low Main coal seam at Newsham extends the known range of the lysorophids down into the Upper Modiolaris zone of the Middle Coal Measures (Westphalian B).

The uncertainties as to the horizon and relationships of the amphibian represented by the isolated vertebra G152.04 must debar it from consideration in any discussion of the stratigraphic range of the Lysorophidae. Of greater importance is the possibility of the presence of lysorophids in the small tetrapod assemblage from Jarrow in Co. Kilkenny. The Jarrow Seam lies in the lower part of the Communis zone (Eagar 1964) of the Lower Coal Measures (Westphalian A) and, should the reported material prove to be diagnostically lysorophid, this would considerably antedate the Newsham specimen described above.

The fact that the, approximately 200, amphibian specimens from Newsham in the collections of the Hancock Museum include only the single lysorophid described in this present study suggests that G91.15 may possibly be a transported specimen rather than a normal member of the Newsham fauna. Romer (1930) reported only four lysorophid specimens amongst approximately 170 tetrapod fossils from Linton, and it may be that lysorophids were atypical members of permanent water-body communities in the Carboniferous and possibly erratics from small ponds and streams of a more temporary nature. If, however, G91.15 is interpreted as a genuine member of the Newsham amphibian community (previously described members of which have been listed by Land 1974, p. 61) the nature of its environment in life is of some interest. The black shale at Newsham is usually considered to represent the sapropel deposited in a large and deep, possibly coastal or deltaic, lake (Panchen 1970) which was almost certainly the original environment of most of the larger fish and amphibians known from this site. Milner (1978) has noted that Coal Measures lake deposits such as

that at Newsham appear to be characterized by a rather limited assemblage of amphibians including eogyrinid embolomeres, loxommatids, the nectrideans *Keraterpeton* and *Batrachiderpeton*, and the aïstopod genus *Ophiderpeton*, all of which taxa are scarcely or not at all represented in the pond or small pool faunas such as those of Linton or Nýřany in Czechoslovakia. Pointing out that, unlike the small tetrapod assemblages of the latter sites, the member groups of the Coal Measures lacustrine fauna appear to have no representatives in the Permian, Milner (1978) suggested that the demise of this assemblage was due to reduction in number, and loss in continuity, of large lakes in Euramerica as a result of the late Carboniferous Armorican orogeny. In view of this hypothesis it is interesting to note the possibility that lysorophid amphibians inhabited both lacustrine (Newsham) and coal swamp pool (Linton) environments in the Coal Measures, and that the group also survived into the Lower Permian in North America. Olson (1958) has described lysorophid aestivating burrows from the Texas Clear Fork Group, and it seems not unlikely that the acquisition of the ability to aestivate under dry conditions may have been an important factor in the adaptation of the lysorophids to the conditions of life prevailing in the early Permian.

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