A PROTOROTHYRIDID CAPTORHINOMORPH (REPTILIA) FROM THE UPPER CARBONIFEROUS OF NEWSHAM, NORTHUMBERLAND

by M. J. BOYD

ABSTRACT. A description is presented of the skull table of a protorothyridid captorhinomorph reptile from the lower Westphalian B (Upper Carboniferous) of Newsham, Northumberland. The specimen, which is not named, represents the first reptile to be recorded from the Carboniferous of the British Isles and from the north-west European paralic Coal Measures. It is closely contemporaneous with the earliest undisputed reptiles to have previously been described, from the lower Westphalian B of Joggins, Nova Scotia, and is the oldest fossil reptile yet reported from anywhere outside North America.

The specimen forms part of a large assemblage of (mostly aquatic) vertebrates preserved in the bottom sediments of a large coal-swamp lake, and is presumed to represent an erratic derived from a terrestrial/marginal environment.

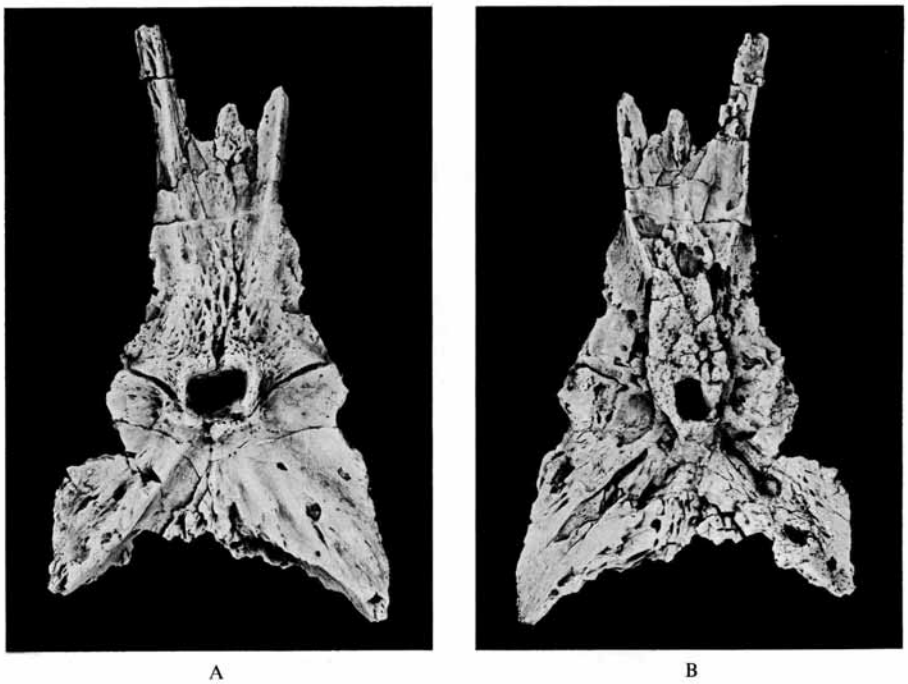
THE captorhinomorph reptile family Protorothyrididae includes the earliest and most primitive reptiles currently known. The family is represented in the Lower Permian of North America by two named species of *Protorothyris* and by at least two further, un-named, protorothyridid species (Clark and Carroll 1973; Reisz 1980). However, seven genera of protorothyridids, all but one of them monotypic, have so far been described and named from the Upper Carboniferous of Europe and North America. Of the seven genera, five are Westphalian D in age. These comprise *Brouffia* and *Coelostegus* from Nýřany in Czechoslovakia (Carroll and Baird 1972), *Palaeothyris* from Florence, Nova Scotia (Carroll 1969), *Anthracodromeus* from Linton, Ohio (e.g. Carroll and Baird 1972), and *Cephalerpeton*, which is known from both Mazon Creek, Illinois (e.g. Carroll and Baird 1972) and Linton (Reisz and Baird 1983), although apparently represented by a different species at each site. The two remaining described protorothyridid genera, *Hylonomus* and *Archerpeton*, are both from the lower Westphalian B of Joggins, Nova Scotia (Carroll 1964). They, together with the pelycosaur *Protoclepsydrops*, which occurs in the same deposits, constitute the earliest undisputed reptiles known. Although Baird and Carroll (1967) have described *Romeriscus periallus* from the Westphalian A of Cape Breton Island, Nova Scotia, as a limnoscelid reptile, both the limnoscelid status of *Romeriscus* and the reptilian status of limnoscelids are open to doubt (Panchen 1972; Heaton 1980).

In the present paper, an account is given of a hitherto undescribed Upper Carboniferous protorothyridid specimen, the existence of which (as a 'romeriid') was briefly noted by Boyd (1984, p. 392). The specimen does not appear to be referable to any previously described protorothyridid species, but it is too incomplete for any satisfactory diagnosis. It is not, therefore, named. However, Carboniferous protorothyridid fossils are of rare occurrence, and the specimen under discussion merits description by reason of its stratigraphic and palaeobiogeographical importance.

MATERIALS AND METHODS

The specimen, which is registered in the collections of the Hancock Museum, Newcastle upon Tyne, as G24.84, consists of an incomplete skull table. It was collected at some time between 1860 and 1880 by the accomplished amateur palaeontologist Thomas Atthey, and is from the black shale immediately overlying the Northumberland Low Main Seam at Hannah Pit, Newsham Colliery, near Blyth in Northumberland. This horizon lies within the upper *Modiolaris* zone of the Middle Coal Measures (Land 1974) and is thus lower Westphalian B in age.

[Palaeontology, Vol. 28, Part 2, 1985, pp. 393–399.]



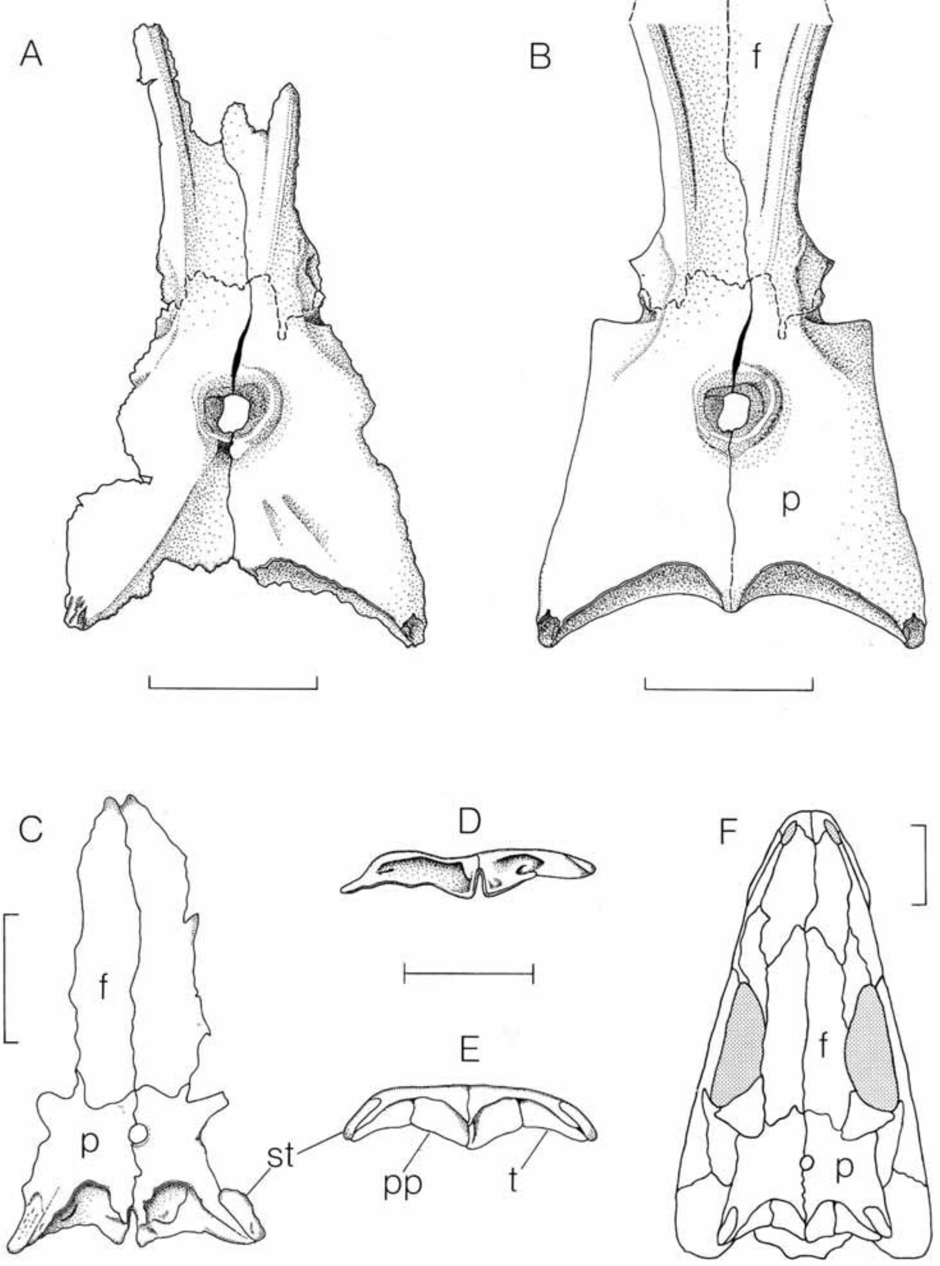
TEXT-FIG. 1. Skull table of protorothyridid reptile, Hancock Museum specimen G24.84, as preserved. A, dorsal view. B, ventral view. Both × 2·5.

The skull table, originally preserved on a small slab of shale, has been completely cleared of matrix by the use of mounted needles and of an S.S. White Industrial Airbrasive Unit (Stucker 1961), employing sodium bicarbonate as the abrasive powder. After preparation the specimen was strengthened by a coat of 'Perspex' applied as a dilute solution in ethyl acetate.

DESCRIPTION

As preserved, specimen G24.84 (text-figs. 1A–B, 2A) consists only of the paired frontal and parietal elements of the skull table. The frontals are truncated anteriorly by a fracture and their original extent in this direction can no longer be determined. The posterolateral 'corners' of both frontals are also absent, as is much of the anterior part of the lateral margin of the left parietal. The left parietal, which

TEXT-FIG. 2. Protorothyridid reptile skulls. A–B, Hancock Museum specimen G24.84 in dorsal view: A, as preserved. Ornament and cracks omitted for sake of clarity; B, suggested restoration. Ornament omitted. C–F, *Protorothyris archeri*: C, holotype skull table in dorsal view, as preserved. Cracks and ornament omitted; D, holotype skull table in posterior view, as preserved; E, skull table in posterior view, restored; F, skull in dorsal view, restored (C–F modified from Clark and Carroll 1973, figs. 2–3). All scale bars represent one centimetre. Abbreviations: f—frontal; p—parietal; st—supratemporal; pp—postparietal; t—tabular.


A
B
f
p
C
f
p
st
D
E
pp
t
F
f
p

also lacks most of its posterior edge, has suffered severe distortion during preservation, resulting in a mesial shift in position of the parietal 'horn'. That it is the left, and not the right, parietal which is distorted is confirmed by the contrast between the 'crazed' ventral surface of the former and the smooth, well-preserved ventral surface of the latter (text-fig. 1B). A large crack crosses the specimen at the level of the parapineal foramen and many smaller cracks are present. The mid-line suture of the skull-table is, none the less, clearly distinguishable in both dorsal and ventral views. That passing transversely between the frontals and parietals is, however, apparent in its entirety only in ventral view. The course of the latter suture is, therefore, depicted as a broken line in the illustrations of the skull table in dorsal view (text-fig. 2A–B), since dermal skull roofing bones often have sloping suture faces which are not perpendicular to their outer surfaces (Milner 1978, p. 673). In G24.84 the parietals appear slightly to overlap the dorsal surfaces of the frontals.

The lateral margins of both frontals are thickened for most of their preserved lengths, suggesting a rather more extensive orbital exposure than is the case in any of the described Westphalian D protorothyridids (Carroll and Baird 1972). However, the frontals of *Hylonomus*, which is closely contemporaneous with G24.84, also enter more largely into the mesial margins of the orbits than those of later protorothyridids, having orbital exposures for approximately half their total lengths (Carroll 1964, fig. 2). In G24.84 as preserved, the thickened lateral rims of the frontals are more apparent dorsally than ventrally; it is possible, however, that this is an artefact produced by downward crushing of the thinner mesial part of each element during preservation. The frontals bear little ornament except posteriorly, where they exhibit shallow elongate pits mesially and a much more subdued ornament of tiny pits near their lateral edges (text-fig. 1A).

Any description of the parietals must of necessity be based largely upon the right element. This is a large bone, thickening towards its posterior margin and drawn out posterolaterally into a tapering 'horn'. The lateral margin of the right parietal is well-preserved in its posterior half. The bone becomes progressively thinner as the margin is approached and this fact, together with the simple contour presented by the line of the edge itself, would seem to indicate the absence (in the complete skull) of any skull table elements lateral to the parietals in this region. As in all described protorothyridids, the parietals of G24.84 appear to have formed the posterior edge of the horizontal dorsal surface of the skull, the postparietals, tabulars, and supratemporals having been relegated in part to the upper occipital region. The right parietal is embayed posteriorly, bearing a shallow transverse depression in the dorsal part of its posterior edge, below which a thin shelf of bone (damaged in the specimen) extends backwards. The surface of the depression and the dorsal surface of the shelf are slightly roughened. A similar situation exists in all protorothyridids in which this region of the skull has been described, where the posterior recesses in the parietals (text-fig. 2C–D) house the postparietals and tabulars (text-fig. 2E–F). Both parietals of G24.84 exhibit a shallow notch in the dorsal surface of the tip of the parietal 'horn'. Similar notches are present in this position in the known protorothyridids and serve to receive the anterior extremities of the supratemporal bones. The parapineal foramen is large and is surrounded dorsally by a slightly raised rim. Ventrally the foramen is also surrounded by a raised area of bone; this, however, extends forward to the level of the fronto-parietal sutures and presumably represents an area of contact between neurocranium and dermal skull roof. The ornament of the parietals is largely restricted to the region anterior to the parapineal foramen, where deep anteroposteriorly elongate pits, becoming shallower and less elongate laterally, are present (text-fig. 1A). The nature and distribution of the parietal ornament, and that of the frontal elements, appear to be typical of Carboniferous protorothyridids (e.g. Carroll 1969; Carroll and Baird 1972).

DISCUSSION

Despite the very incomplete nature of specimen G24.84 there can be little doubt that it pertains to a protorothyridid reptile. It cannot be referred to any known group of Palaeozoic fish (see e.g. Moy-Thomas and Miles 1971). In addition, the following features of the specimen together preclude reference to any known group of Palaeozoic Amphibia and indicate its reptilian status:

1. The absence of any dermal bones in the skull table lateral to (at least the posterior halves of) the parietals.
2. The formation of the posterior edge of the horizontal skull table by the parietals.
3. The embayment and recessing of the posterior margins of the parietals (presumably for the reception of the postparietals and tabulars).
4. The dorsal notches on the tips of the parietal 'horns' (presumably for the reception of the anterior extremities of the supratemporals).

Although the oldest known species of synapsid reptile, *Protoclepsydrops haplous* Carroll, 1964, occurs at Joggins and demonstrates that the Pelycosauria were in existence by (at least) lower Westphalian B times, it does not seem that G24.84 can be regarded as pertaining to a pelycosaur. Non-pelycosaurian features of G24.84, which are, however, compatible with protorothyridid status, include:

1. The form of the frontal elements. The frontal elements are not known for *Protoclepsydrops* but those of the oldest known pelycosaur in which these bones have been described, *Archaeothyris* from the Westphalian D of Linton, Nýřany and Florence, Nova Scotia (Reisz 1972; 1975), differ in at least three ways from those of G24.84. They are, relatively, somewhat wider structures, and they have much more restricted exposures in the orbital margins. Most importantly, that part of each frontal which is exposed in the rim of the orbit is a distinct lateral process of the element (Reisz 1972; Kemp 1980, fig. 1b). The presence of this lateral process is the usual pelycosaurian condition (Langston and Reisz 1981, p. 76), although absent in the family Varanopidae. Varanopids, however, are known only from the Permian. The frontals of G24.84 lack any lateral processes of pelycosaurian type.
2. The proportions of the parietals. Those of both *Protoclepsydrops* (Carroll 1964, fig. 13A) and *Archaeothyris* (Reisz 1972; Kemp 1980) appear to be significantly wider relative to their length than those of G24.84.

Excepting the extent to which the frontals enter into the orbital margins, there do not seem to be any structural features of G24.84 which would positively preclude its being the skull table of a captorhinid, rather than a protorothyridid, reptile. However, the proportions of the specimen are certainly more suggestive of the high, narrow skulls characteristic of protorothyridids than of the lower and wider skulls which characterize known captorhinids (Reisz 1980). Moreover, G24.84 is considerably older than the earliest known captorhinids (Heaton 1979), which are thought to have evolved from protorothyridid ancestors (Clark and Carroll 1973).

The tentative restoration of specimen G24.84 (text-fig. 2B) is based upon the assumption of bilateral symmetry. It has also been assumed that the complete frontals were, like those of *Hylonomus*, approximately the same length as the parietals, and that the posterior recessing of the parietals, to accommodate the postparietals and tabulars, was (as in other Carboniferous protorothyridids) rather less extensive than in *Protorothyris* itself. The asymmetry of the ventral opening of the parapineal foramen and the dorsal depression between the thickened lateral margins of the frontals have been retained in the attempt at reconstruction, it being uncertain whether or not these two features are artefacts resulting from *post-mortem* distortion of the specimen.

Specimen G24.84 represents the first reptile to be recorded from the Carboniferous of the British Isles and from the north-west European paralic Coal Measures as a whole. It is also the oldest fossil reptile yet described from anywhere outside North America, and is closely contemporaneous with the earliest undisputed reptiles previously described (the protorothyridids *Hylonomus* and *Archerpeton* and the pelycosaur *Protoclepsydrops* from Joggins).

The Newsham protorothyridid specimen forms part of a large and diverse assemblage of tetrapods from the site. In a recent palaeoecological review (Boyd 1984), the present writer divided the (then) eight known Newsham tetrapod species, which were certainly determinate at least to family level, into three ecological associations, derived from different environments. The criteria employed were the relative frequency of the various taxa present, the size distribution and degree of articulation of the specimens, the functional morphology of the animals themselves, and the environmental and faunal contexts in which the taxa present occurred elsewhere. The environment of preservation of the Newsham tetrapods appears to have been a large and deep freshwater lake, occupying a stretch of abandoned river channel in which peat had previously accumulated (Boyd 1984), and there can be little doubt that G24.84 represents an erratic from a terrestrial/marginal tetrapod community, probably (judging by the nature of the specimen) transported into the lake *post-mortem*. It is the only protorothyridid specimen recorded from the site and although, as pointed out by Romer (1974), the known Carboniferous protorothyridids were probably 'persistent coal-swamp dwellers', they show no evidence of aquatic adaptation. On the contrary, their well-developed limbs and well-ossified skeletons suggest that (by coal-swamp standards at least) they were active terrestrial animals (Carroll 1969; Carroll and Baird 1972). The essentially terrestrial nature of Carboniferous protorothyridids is also indicated by the fact that, of the five large, compact Westphalian tetrapod assemblages currently known (those from Jarrow in Co. Kilkenny (Ireland), Newsham, Joggins, Nýřany, and Linton), only that from Joggins includes members of this family as other than very rare components. Whereas the tetrapods at the other four sites are preserved in sediments deposited in bodies of standing water (e.g. Rayner 1971; Boyd 1984; Milner 1980), those from Joggins are preserved in sediments laid down originally in the upright, hollow stumps of large lycopods, which functioned as pit-fall traps for small terrestrial animals (Carroll 1967). Significantly, protorothyridids, very rare at Nýřany (Milner 1980), Linton (Reisz and Baird 1983), and Newsham and not reported from Jarrow, are represented at Joggins by at least eighteen specimens of *Hylonomus* and sixteen of *Archerpeton* (Carroll *et al.* 1972).

The description of protorothyridid specimen G24.84 increases the number of tetrapod species (certainly determinate at least to family level) whose presence at Newsham has been established, from the eight listed by Boyd (1984, p. 372) to nine. An updated 'faunal' list of the tetrapods so far reported from the site is given below, with the taxa present grouped into the three ecological associations represented in the assemblage:

1. *Terrestrial/marginal association.* Two species—the anthracosaurid embolomere *Anthracosaurus russelli* Huxley and an un-named protorothyridid captorhinomorph reptile.
2. *Shallow-water/swamp-lake association.* Four species—the ophiderpetontid aïstopod *Ophiderpeton nanum* Hancock and Atthey, a urocordylid nectridean, a lysorophid (the latter two not determinate below family level) and, less certainly, the eogyrinid embolomere *Pteroplax cornutus* Hancock and Atthey.
3. *Open-water/lacustrine association.* Three species—the loxommatid *Megalocephalus pachycephalus* Barkas, the keraterpetontid nectridean *Batrachiderpeton reticulatum* (Hancock and Atthey), and the eogyrinid embolomere *Eogyrinus attheyi* Watson.

Acknowledgements. My thanks are, naturally, due first to Mr. A. M. Tynan, Curator of the Hancock Museum, for his permission to study the important specimen which forms the subject of the present paper. I also thank Professor M. R. House (Department of Geology, University of Hull), who very kindly provided facilities for preparation of the specimen, Dr. D. J. Siveter of the same department and institution, who took the photographs, and Mr. G. R. Edwards (Kingston upon Hull Museum) who developed and printed them. I am indebted, too, to Dr. J. A. Clack (University Museum of Zoology, Cambridge), Dr. P. L. Forey (British Museum (Natural History)), Dr. A. R. Milner (Birkbeck College, University of London), and Drs. A. L. Panchen and T. R. Smithson (Department of Zoology, University of Newcastle upon Tyne) for helpful information, comment, and discussion.

REFERENCES

BAIRD, D. and CARROLL, R. L. 1967. *Romeriscus*, the oldest known reptile. *Science, N.Y.* **157,** 56–59.

BOYD, M. J. 1984. The Upper Carboniferous tetrapod assemblage from Newsham, Northumberland. *Palaeontology*, **27,** 367–392.

CARROLL, R. L. 1964. The earliest reptiles. *J. Linn. Soc.* (*Zool.*), **45,** 61–83.

—— 1967. Labyrinthodonts from the Joggins Formation. *J. Paleont.* **41,** 111–142.

CARROLL, R. L. 1969. A middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *J. Paleont.* **43,** 151–170.

—— and BAIRD, D. 1972. Carboniferous stem-reptiles of the family Romeriidae. *Bull. Mus. comp. Zool. Harv.* **143,** 321–363.

—— BELT, E. S., DINELEY, D. L., BAIRD, D. and MCGREGOR, D. C. 1972. *Excursion A59, Vertebrate palaeontology of eastern Canada.* Guidebook, 24th Int. Geol. Cong. 1–113.

CLARK, J. and CARROLL, R. L. 1973. Romeriid reptiles from the Lower Permian. *Bull. Mus. comp. Zool. Harv.* **144,** 353–407.

HEATON, M. J. 1979. Cranial anatomy of primitive captorhinid reptiles from the late Pennsylvanian and early Permian, Oklahoma and Texas. *Bull. Okla. geol. Surv.* **127,** 1–84.

—— 1980. The Cotylosauria: a reconsideration of a group of archaic tetrapods, 497–551. *In* PANCHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates,* xii + 633 pp. Systematics Association Special Volume No. 15. London: Academic Press.

KEMP, T. S. 1980. Origin of the mammal-like reptiles. *Nature, Lond.* **283,** 378–380.

LAND, D. H. 1974. Geology of the Tynemouth district. *Mem. geol. Surv. Gt Br.* **15.**

LANGSTON, W. and REISZ, R. R. 1981. *Aerosaurus wellesi,* new species, a varanopseid mammal-like reptile (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. *J. Vert. Paleont.* **1,** 73–96.

MILNER, A. R. 1978. A reappraisal of the early Permian amphibians *Memonomenos dyscriton* and *Cricotillus brachydens. Palaeontology,* **21,** 667–686.

—— 1980. The tetrapod assemblage from Nýřany, Czechoslovakia, 439–496. *In* PANCHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates,* xii + 633 pp. Systematics Association Special Volume No. 15. London: Academic Press.

MOY-THOMAS, J. A. and MILES, R. S. 1971. *Palaeozoic Fishes,* 2nd edn., xi + 259 pp. London: Chapman and Hall.

PANCHEN, A. L. 1972. The interrelationships of the earliest tetrapods, 65–87. *In* JOYSEY, K. A. and KEMP, T. S. (eds.). *Studies in vertebrate evolution—essays presented to Dr F. R. Parrington, F.R.S.,* 284 pp. Edinburgh: Oliver and Boyd.

RAYNER, D. H. 1971. Data on the environment and preservation of late Palaeozoic tetrapods. *Proc. Yorks. geol. Soc.* **38,** 437–495.

REISZ, R. R. 1972. Pelycosaurian reptiles from the Middle Pennsylvanian of North America. *Bull. Mus. comp. Zool. Harv.* **144,** 27–62.

—— 1975. Pennsylvanian pelycosaurs from Linton, Ohio, and Nýřany, Czechoslovakia. *J. Paleont.* **49,** 522–527.

—— 1980. A protorothyridid captorhinomorph reptile from the Lower Permian of Oklahoma. *Life Sci. contr. R. Ont. Mus.* **121,** 1–16.

—— and BAIRD, D. 1983. Captorhinomorph 'stem' reptiles from the Pennsylvanian coal-swamp deposit of Linton, Ohio. *Ann. Carneg. Mus.* **52,** 393–411.

ROMER, A. S. 1974. Aquatic adaptation in reptiles—primary or secondary? *Ann. S. Afr. Mus.* **64,** 221–230.

STUCKER, G. F. 1961. Salvaging fossils by jet. *Curator,* **4,** 332–340.

MICHAEL J. BOYD

Department of Natural History
Kingston upon Hull Museum
Queen Victoria Square, Kingston upon Hull
North Humberside

and

Department of Geology
University of Reading
Reading, Berkshire
RG6 2AB

Typescript received 25 July 1984