THE TEMNOSPONDYL AMPHIBIAN *DENDRERPETON* FROM THE UPPER CARBONIFEROUS OF IRELAND

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ABSTRACT. The temnospondyl amphibians *Erpetocephalus rugosus* Huxley and *Ichthyerpeton hibernicum* Lydekker from the Jarrow Coal (Westphalian A) of the Leinster coalfield in Eire represent a single species referable to the genus *Dendrerpeton*, namely *D. rugosum* (Huxley) comb. nov. *D. rugosum* is very similar to the slightly later *D. acadianum* from Nova Scotia, the palate and pectoral girdle of which are reinterpreted. The genotype species of *Ichthyerpeton*, *I. bradleyae* Wright and Huxley, also from the Jarrow Coal, is considered to be based on an indeterminate, though probably temnospondyl specimen, and the binomen is hence a *nomen dubium*.

The genera *Dendrerpeton*, *Eugyrinus*, and *Caerorhachis* share only primitive or unassessable temnospondyl character-states with each other and with the 'long-snouted' edopoids. The Dendrerpetontidae is therefore removed from the Edopoidea, and *Eugyrinus* and *Caerorhachis* are excluded from the Dendrerpetontidae which is thus restricted to *Dendrerpeton*. On the evidence available, *Eugyrinus* is an early offshoot of the Trimerorhachoidea, while *Caerorhachis* and the Dendrerpetontidae are primitive temnospondyls of uncertain relationships.

UPPER Carboniferous amphibians and fishes were discovered at Jarrow Colliery in the Leinster coalfield in Eire in 1864 by W. B. Brownrigg (Brownrigg 1866). The amphibian assemblage collected at Jarrow is of historical significance in that it was the first assemblage of small coal-swamp amphibians to be described. The amphibian material from the previously discovered but similar assemblage from Linton, Ohio, was not interpreted as such until Huxley's (1867) description of the Jarrow animals made comparison possible. Many of the subsequently discovered small amphibians from the Upper Carboniferous of Newsham, Northumberland and Nýřany, Czechoslovakia were initially described with reference to the Jarrow material. However, since the initial descriptions of the Jarrow amphibians by Wright and Huxley (1866), Huxley (1867), Baily (1876, 1879, 1884), and Woodward (1897), very little first-hand study of this material has been undertaken. Most of the specimens have never been described because, although usually consisting of articulated skeletons, they are very poorly preserved. The substrate in which the animals were initially buried appears to have been of such a low pH as to mobilize most but not all of the skeletal calcium phosphate after burial (Rayner 1971, p. 452). Most specimens are little more than vague outlines on cleavage planes in the coal but some are preserved with visible detail indicating that the degree of bone solution varied from individual to individual.

The significance of the Jarrow fauna has increased with the identification of the Jarrow Coal as Westphalian A in age (Eagar 1961, 1964). The amphibian assemblage is thus distinctly older than the comparable assemblages from Mazon Creek, Illinois; Linton, Ohio, and Nýřany, Czechoslovakia, all of which are Westphalian D in age.

Most of the determinate amphibian specimens in the Jarrow assemblage are nectrideans and aïstopods, few temnospondyl specimens having been identified. A natural cast of a loxommatid skull was first described as *Anthracosaurus edgei* by Baily (1884) but has recently been shown by Beaumont (1977) to be referable to *Megalocephalus pachycephalus*. A small temnospondyl was described as *Erpetocephalus rugosus* by Huxley (1867) and, from another specimen, as *Ichthyerpeton*

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hibernicum by Lydekker (1891). It has been referred to the Dendrerpetontidae by Romer (1945, 1966) and is redescribed in this work as a species of *Dendrerpeton*. The genotype of *Ichthyerpeton* is *I. bradleyae* Wright and Huxley, 1866, also from Jarrow, and the identity of this specimen is discussed here. Other undescribed temnospondyls from Jarrow are currently being studied by the author and will be described in due course.

Specimen numbers preceded by the following abbreviations refer to material in the respectively listed collections: AMNH: American Museum of Natural History, New York; BM(NH): Department of Palaeontology, British Museum (Natural History), London; DMSW: D. M. S. Watson collection, Cambridge University Museum of Zoology; MCZ: Museum of Comparative Zoology, Harvard; MM: Manchester Museum; NMI: National Museum of Ireland, Dublin; RM: Redpath Museum, McGill University, Montreal; SM: Sedgwick Museum, Cambridge.

SYSTEMATIC DESCRIPTION

Class AMPHIBIA
Order TEMNOSPONDYLI
Family DENDRERPETONTIDAE Frič, 1885

Diagnosis. As for *Dendrerpeton*; see remarks under generic diagnosis.

Genus DENDRERPETON Owen, 1853

Type species. *Dendrerpeton acadianum* Owen, 1853.

Diagnosis. (Based on information in Carroll 1967 and authors' studies.) Primitive temnospondyls probably growing to about a metre in length. Dermal bones of skull with ornamentation of pitting, not striated. Lateral-line sulci absent from dermal roofing bones. Snout short. Otic notches large, deep, and ovoid. Septomaxillae present as separate ossifications within the external nares. Lachrymals extend from borders of external nares to orbit margins. Centres of ossification of jugals behind level of posterior edge of orbits but jugals extend forwards to suture narrowly with lachrymals. Intertemporals present. Maxilla extends back to contact quadratojugal. Postero-lateral tabular process and dorso-medial quadrate process border otic notch. Palatine rami of pterygoids extend anteriorly to approach or contact anterior end of cultriform process of parasphenoid. Interpterygoid vacuities rounded anteriorly and occupying about $\frac{3}{5}$ of skull width. Internal carotid foramina on parasphenoid. Vertebral centra poorly ossified, pleurocentra small paired elements. Interclavicle slightly antero-posteriorly elongate with fimbriated anterior edge. Humerus with entepicondylar foramen. Ilium with postero-dorsal extension.

Remarks on classification. The family Dendrerpetontidae was most recently diagnosed by Romer (1947) as a monotypic family based solely on *Dendrerpeton* Owen, 1853. Romer later (1966) expanded the family to include *Erpetocephalus* Huxley, 1867 and *Eugyrinus* Watson, 1921. *Caerorhachis* Holmes and Carroll, 1977 is doubtfully referred to this family by its authors. In the present study the Dendrerpetontidae is treated as a monotypic family comprising only *Dendrerpeton* (including *Erpetocephalus*). Neither *Eugyrinus* nor *Caerorhachis* appears to be immediately related to *Dendrerpeton* in that there are no derived characters uniquely shared with that genus. Both genera are hence excluded from the Dendrerpetontidae so as to preclude the implication of close relationship to *Dendrerpeton* (see Discussion, p. 135).

Dendrerpeton rugosum (Huxley) comb. nov.

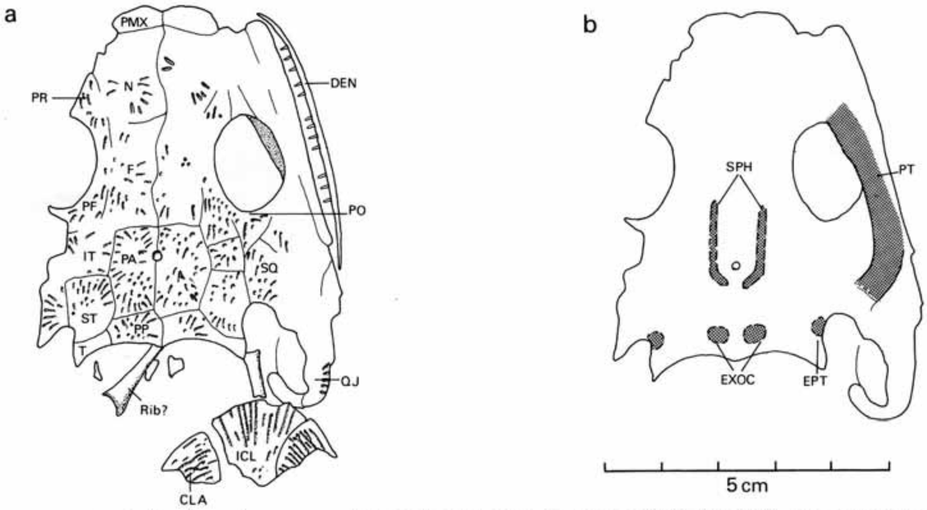
Text-figs. 1–3*a*, *b*

1867 *Erpetocephalus rugosus* Huxley, p. 368, pl. 23, fig. 2.
1890 *Ichthyerpetum bradleyae* Wright and Huxley; Lydekker, p. 169, *non* Wright and Huxley, 1866, Huxley, 1867—*Ichthyerpeton*.
1891 *Ichthyerpetum hibernicum* Lydekker, p. 343, figs. 1, 2.
1947 *Erpetocephalus rugosus* Huxley; Romer, p. 117.
1961 *Erpetocephalus rugosus* Huxley; Panchen and Walker, p. 326.

Diagnosis. As for genus, plus: jugal-lachrymal suture level with anterior margin of orbit. Snout very short, nasals as wide as, or wider than, own length. Tympanic notch large and nearly circular, almost as large as orbit.

Locality and horizon. All Jarrow Coal vertebrates were collected from the Jarrow Colliery about 7 km north-east of Castlecomer, Co. Kilkenny, Eire. The Jarrow Coal belongs to the lower *communis* zone, which is equated with the Westphalian A of the Upper Carboniferous (Eagar 1961, 1964).

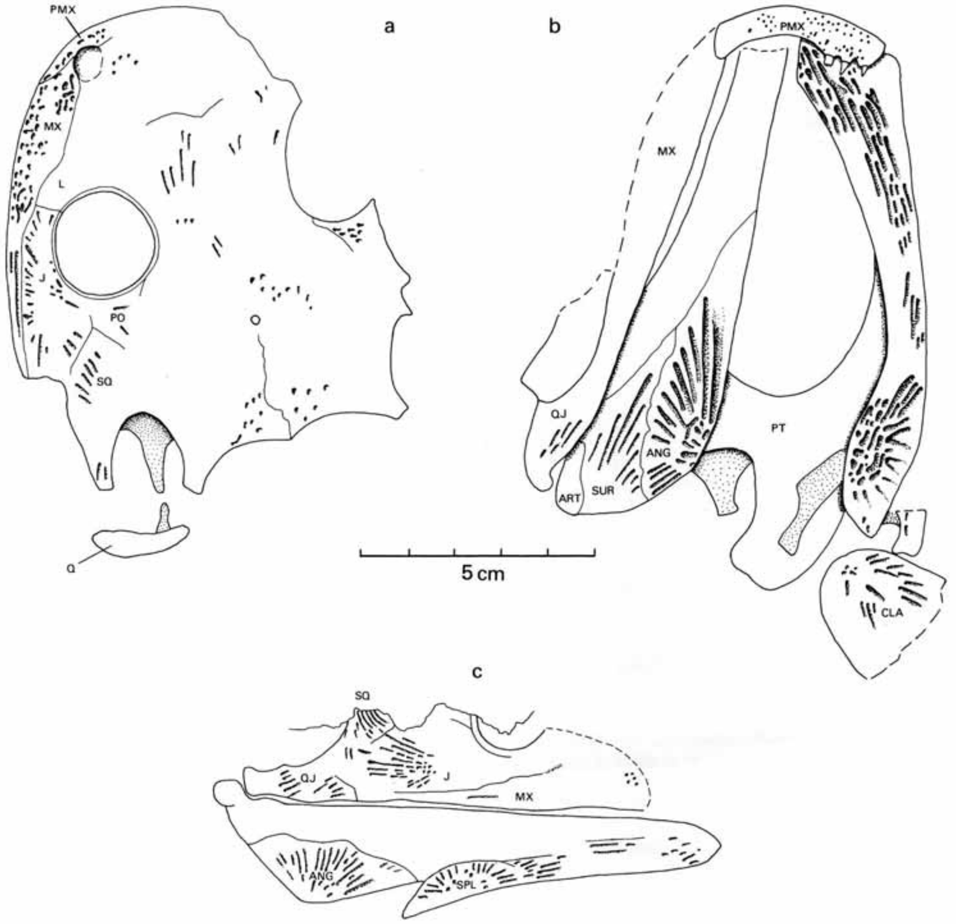
Holotype. NMI G39.1959, the holotype of *Erpetocephalus rugosus* consisting of a skull about 60 mm long, preserved in dorsal aspect with fragments of the pectoral girdle and ribs (text-fig. 1).



TEXT-FIG. 1. *Dendrerpeton rugosum* (Huxley) comb. nov., holotype, NMI G39.1959. *a*, specimen as preserved; *b*, diagram of skull roof showing pattern of ridges produced by underlying structures.

ABBREVIATIONS USED IN TEXT-FIGURES

ANG	Angular
ART	Articular
CLA	Clavicle
DEN	Dentary
ECT	Ectopterygoid
EPT	Ridge formed by Epipterygoid
EXOC	Ridge formed by Exoccipital
F	Frontal
ICL	Interclavicle
IT	Intertemporal
J	Jugal
L	Lachrymal
MX	Maxilla
N	Nasal
PA	Parietal
PAL	Palatine
PF	Postfrontal
PMX	Premaxilla
PO	Postorbital
PP	Postparietal
PR	Prefrontal
PSP	Parasphenoid
PT	Pterygoid
Q	Quadrate
QJ	Quadratojugal
SMX	Septomaxilla
SPH	Ridge formed by Sphenethmoid
SPL	Postsplenial
SQ	Squamosal
ST	Supratemporal
SUR	Surangular
T	Tabular
VOM	Vomer



TEXT-FIG. 2. *Dendrerpeton rugosum* (Huxley) comb. nov. *a*, dorsal aspect of NMI G3.1970, previously the holotype of '*Ichthyerpetum hibernicum*' Lydekker; *b*, ventral aspect of the same specimen; *c*, SM E19571, right cheek and mandible as preserved.

Referred material. NMI G3.1970, the holotype of *Ichthyerpetum hibernicum* consisting of a skull about 95 mm long exposed in both dorsal and ventro-lateral aspect as a result of preparation. A fragment of clavicle is present (text-fig. 2*a*, *b*). SM E19571, an undescribed specimen consisting of a skull mainly visible in palatal aspects but with the right cheek folded over and superimposed on the palate (text-fig. 2*c*).

Description

None of the specimens is well preserved although some surface detail can be seen on all of them. The proportions vary with size, and the description of the skull shape refers to the largest skull, presumed to be adult or most nearly so.

Skull. The skull is very short-snouted and the orbits are in the anterior half, their posterior margins being about half-way along the medial length of the skull. The orbits are circular but preservation is too poor to permit determination of the presence of a sclerotic ring. A pineal foramen is present in the anterior half of the suture between the parietals. The jaw suspensorium extends well behind the posterior edge of the skull table, and the otic notches are very large and deeply concave indicating the presence of large circular tympanic membranes. The tabular and quadrate extensions could have served to support the margin of a large tympanum. Typical temnospondyl-type pitting covers the dermal roofing bones, and no lateral-line pits or grooves are present.

Cranial dimensions (*in mm*)

	NMI G39.1959	SM E19571	NMI G3.1970
Skull tip to back of skull midline	61	–	95
Snout tip to quadrate	74	98	110
Tabular tip to tip width	30	–	43
Interorbital width	21	–	28
Orbit width	12·5	18	21
Extraorbital width	7	12	12

Dendrerpeton rugosum possesses all the dermal roofing bones typically found in primitive temnospondyls. The premaxilla is an antero-posteriorly narrow bone with no posterior extension against or near the medial edge of the external naris. The maxilla is deep anteriorly, but narrows sharply at the level of the anterior edge of the orbit and extends back as a narrowing ossification to suture with the quadratojugal at the level of the pineal foramen. The precise shape of the lachrymal is uncertain but it appears to extend from the external naris to the margin of the orbit. The jugal extends narrowly around the outer margin of the orbit to suture with the lachrymal just anterior to the level of the anterior margin of the orbit. Where it borders the orbit, the jugal is less than half the width of the orbit itself. The broad interorbital region is comprised of wide frontals and broadly suturing prefrontals and postfrontals. The postorbital is approximately equilaterally triangular in shape and not antero-posteriorly elongate. A rhomboidal intertemporal is present. The skull table is of typical temnospondyl configuration, the parietal and tabular being separated by a supratemporal–postparietal suture. The postparietals do not bear any superficial posterior extensions, often called postparietal lappets, such as occur in *D. acadianum* as small unornamented structures and in *Cochleosaurus bohemicus* as large ornamented structures. The tabulars extend outwards and backwards beyond the level of the postparietals, these extensions being square-ended in larger specimens (NMI G3.1970). The outer face of the squamosal is large and crescent-shaped bordering a deep, rounded otic notch. The quadratojugal extends from a narrow contact with the maxilla to the back of the jaw suspensorium. At its posterior end it apparently bears an extension behind the squamosal, although the poor preservation makes the relationships of the bones in this part of the skull difficult to ascertain. There is, however, a raised process which extends mesially or dorsomesially over the presumed position of the quadrate and forms a partial posterior border to the otic notch (text-fig. 2*a*). Comparison with similar structures in many temnospondyls of the superfamily Dissorophoidea suggests that this is a dorsomesial process of the quadrate (Bolt 1969). The tabular extension and the quadrate process both appear to be supports for the posterior margin of a large tympanum, and it is possible that the gap between the tabular and the quadrate process was bridged by an annular cartilage as in frogs.

The anterior part of the palate and parasphenoid are unknown. The interpterygoid vacuities are large, being comparable to those in the later Carboniferous and Permian temnospondyl family Dissorophidae, for example *Tersomius* and *Broiliellus* as figured by Carroll (1964, figs. 4, 10). The palatine ramus of the pterygoid is relatively narrow while the basipterygoid ramus is relatively broad.

The braincase is not visible, but indirect evidence of its general proportions is present in the holotype (text-fig. 1*b*). Post-burial flattening of the skull has compressed the skull table on to the underlying braincase and associated structures, producing a series of broken ridges where the dermal bones have been crushed upwards by underlying structures. Comparison with the skull of *Edops* (from Romer and Witter 1942) and *Amphibamus* (from Carroll 1964) suggests the following interpretation. The parallel ridges superimposed on the frontals and parietals and converging posterior to the pineal foramen appear to be the dorsal edges of the sphenethmoid, forming the sides of the braincase and converging, but not meeting, at about the level of the basipterygoid processes. The two raised structures posterior to these appear to have been produced by the paired exoccipitals. The two lateral raised structures appear from their position to have been produced by the ascending processes of the epipterygoids. None of the specimens shows preserved stapes, although the large tympanic notches indicate that these must have been present.

The lower jaw bears pronounced ornamentation on the angular, surangular, and splenials (text-fig. 2*c*) as in all primitive temnospondyls. The inner face is not visible on any specimen. The teeth are simple and conical but no quantitative assessment of the dentition is possible.

Pectoral girdle. The interclavicle has a complex anterior margin with a fimbriated anterior edge as in *D. acadianum*, *Eugyrinus wildi* (pers. obs.), and *Acroplous vorax* (Hotton 1959). This occurs frequently in small Palaeozoic amphibians. The interclavicle is substantially overlapped by the ovoid blades of the clavicles.

Remarks

D. rugosum is very similar to the type species of *Dendrerpeton* namely *D. acadianum* Owen from the Westphalian B tree-stump assemblages from Joggins, Nova Scotia. This material was reviewed by Carroll (1967), and the following comments are intended to supplement Carroll's description and to qualify the diagnoses given to distinguish the two species of *Dendrerpeton* in this study. The diagnostic characters are all that the material permits, *D. rugosum* consisting of three poorly preserved specimens while *D. acadianum* consists of many fragmentary and disarticulated specimens, not all of which are of certain attribution.

One distinguishing feature for the two species is the position of the lachrymal–jugal common suture. In *D. rugosum* this is level with the anterior edge of the orbit (text-fig. 2*a*, *c*), in *D. acadianum* it is level with the middle of the orbit and is little more than a point-contact (text-fig. 3*c*). The tendency to posterior withdrawal of the jugal and narrowing of its anterior process occurs in several other tetrapod groups and, as a trend, culminates in complete separation of the lachrymal and jugal, often with a dorsal process of the palatine occupying some of the intervening space (Bolt 1974). As noted by Bolt, this occurs independently in dissorophoids, saurerpetontids, and seymouriamorphs and is not, by itself, an indication of relationships between groups.

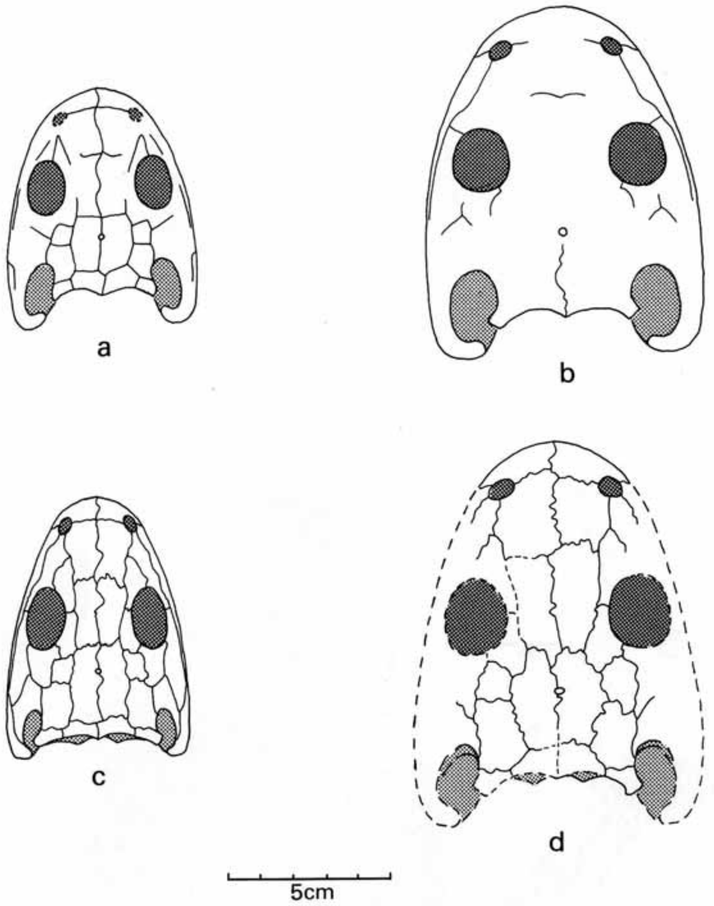
The other distinguishing features concern over-all proportions of the snout and the otic notch (text-fig. 3). Independent of absolute size, the snout of *D. rugosum* is shorter and the otic notches larger, than in *D. acadianum*. The skull of *D. rugosum* tends towards an *Amphibamus*-like shape.

Carroll's reconstruction of *D. acadianum* differs from *D. rugosum* in several other respects, but my examination of the *D. acadianum* material housed in the British Museum (Natural History), suggests that some of the characters of Carroll's *D. acadianum* reconstructions require qualification, as follows.

Postparietal lappets. These are not visible in *D. rugosum* specimens but can be seen in a minority of *D. acadianum* specimens and are depicted in the reconstruction by Carroll (1967, text-fig. 3B). As Carroll notes, the lappets are unsculptured and slope ventro-posteriorly from the lower posterior edge of the postparietal to support the exoccipitals. In this orientation the lappets can be seen only in specimens in which the occipital region is at least partly exposed (BM(NH) R.439 and R.4167). The non-visibility of such structures in the two Jarrow specimens with skull tables cannot be taken as proof of absence.

Postero-lateral development of the tabulars. These processes are pronounced in both species, and Steen (1934, text-fig. 11) depicts them on most skull tables, although Carroll (1967, text-fig. 3B) barely suggests their presence. Specimens such as BM(NH) R.436 (text-fig. 4*a*) show a very pronounced process and it is clear that both species of *Dendrerpeton* possess these processes. Another feature of the skull table of both species which Carroll does not depict in his reconstruction is the biconcave undulation of the back of the skull table. In all specimens where the skull table is well preserved, there is a shallow but distinct concavity in each half of the posterior edge above the postparietal lappets.

Palatal vacuities and pterygoid configuration. Carroll (1967, text-fig. 3C) depicts *D. acadianum* with interpterygoid vacuities which are antero-posteriorly elongate, almost parallel-sided, and bordered anteriorly by the undulating posterior edge of the vomers. However, BM(NH) R.4167 (text-fig. 4*b*) and DMSW B.45 (Watson 1956, fig. 30) show the palatine rami of the pterygoids to be markedly curved. Each interpterygoid vacuity must have been almost semicircular in outline and slightly broader and shorter than depicted by Carroll. In the palate of BM(NH) R.4167 (text-fig. 4*b*), an

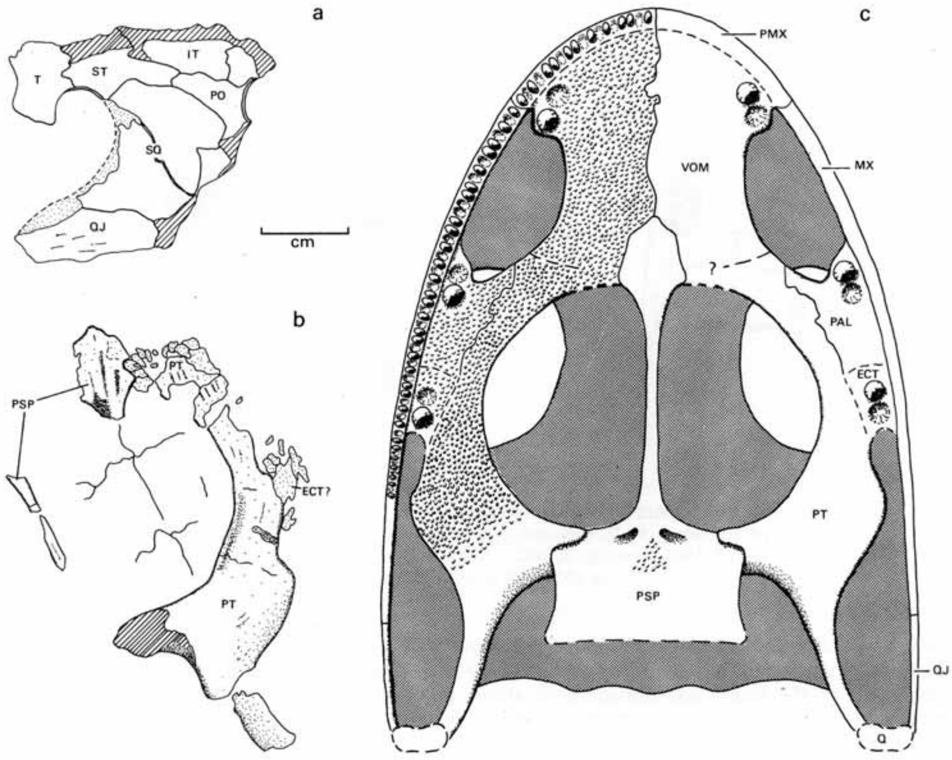


TEXT-FIG. 3. Reconstructions of *Dendrerpeton* skulls in dorsal aspect. *a*, *D. rugosum*, holotype specimen; *b*, *D. rugosum*, NMI G3.1970; *c*, *D. acadianum*, composite after Carroll 1967, text-fig. 3, with modifications; *d*, *D. acadianum*, BM(NH) R.4554. All to the same scale.

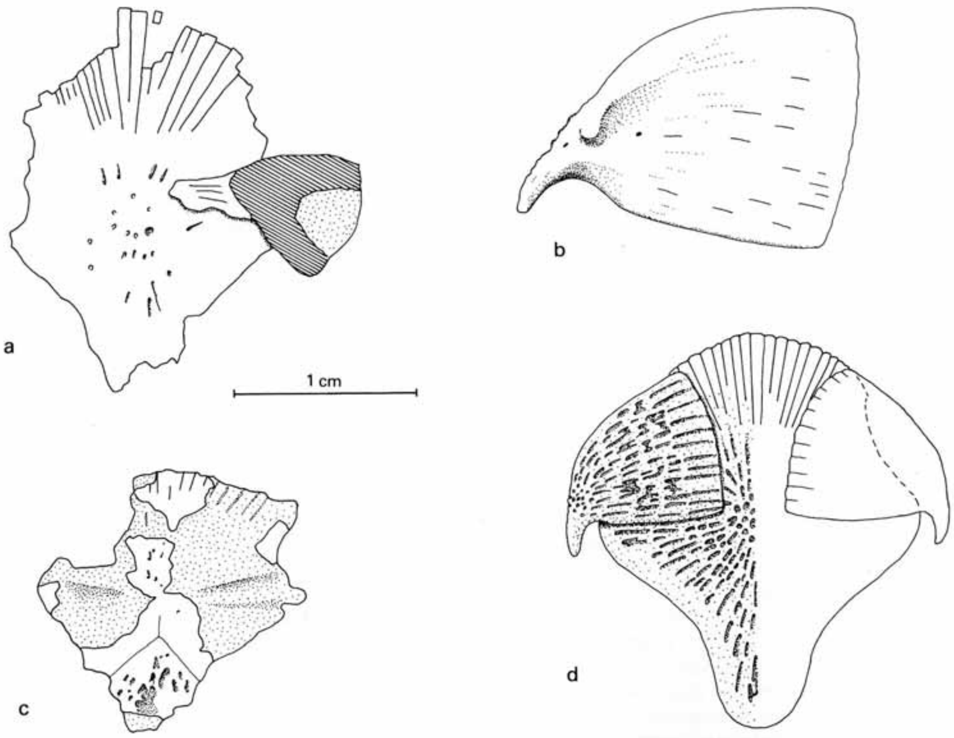
anterior median rhomboidal structure can be seen which I interpret, following Steen (1934), as an anterior expansion of the cultriform process of the parasphenoid. Although some crushing and displacement of the bones has occurred, striations on the lateral palatal series suggests that the pterygoid extends around the front of the interpterygoid vacuity and either approaches closely, or reaches, the cultriform process. A revised reconstruction of the palate of *D. acadianum*, modified from that of Carroll, is given in text-fig. 4*c*. The palatine is based on that in the lectotype skull BM(NH) R.4158 (Carroll 1967, text-fig. 2c). The general conclusion is that both species of *Dendrerpeton* possessed rounded interpterygoid vacuities only slightly smaller than those of primitive dissorophids such as *Amphibamus*, but with a more extensive anterior pterygoid border.

Pectoral girdle. The unconventional orientation of the clavicles on the interclavicle of *D. acadianum* reconstructed by Carroll (1967, text-fig. 13) is based on a misinterpretation of the pectoral girdle in BM(NH) R.436 (Carroll 1967, text-fig. 10; this paper, text-fig. 5*c*). In this specimen, the 'right clavicle' of Carroll is the fimbriated leading edge of the interclavicle and his 'left clavicle' is a symmetrical crack on the posterior process of the interclavicle, which is thus orientated at 90° to Carroll's interpretation and actually has no associated clavicles. The clavicles (text-fig. 5*a*, *b*) are broader-bladed than depicted by Carroll (1967, text-fig. 12c), and a suggested reconstruction of the interclavicle and clavicles is given in text-fig. 5*d*. This also corresponds with such of the pectoral girdle as is visible in the holotype of *D. rugosum* (text-fig. 1*a*).

In conclusion, first-hand study of the two assemblages of *Dendrerpeton* suggest that they are extremely similar and distinguishable only in the over-all shape of the skull and otic notch and the position of the lachrymal-jugal suture. Thus specific separation seems the most that can be justified, and the Jarrow material is maintained as a separate species. The two species of *Dendrerpeton* are not widely separated in time (mid Westphalian A for *D. rugosum* and early Westphalian B for



TEXT-FIG. 4. *Dendrerpeton acadianum* Owen, cranial anatomy. *a*, BM(NH) R.436, left temporal region in internal aspect, showing postero-lateral process of tabular; *b*, BM(NH) R.4167, incomplete parasphenoid and right pterygoid in dorsal aspect; *c*, reconstruction of skull in palatal aspect based on BM(NH) R.4158, R.4167, and RM2.1125.



TEXT-FIG. 5. *Dendrerpeton acadianum* Owen, clavicles and interclavicle. *a*, BM(NH) R.4553, interclavicle and fragmentary clavicle; *b*, reconstructed left clavicle in dorsal aspect based on both clavicles in BM(NH) R.4165 and R.4167 (counterparts); *c*, BM(NH) R.436, interclavicle, misinterpreted as interclavicle with overlapping clavicle blades by Carroll 1967, text-fig. 10; *d*, reconstruction of interclavicle and clavicles in ventral aspect, based on several specimens associated with *D. acadianum* skulls.

D. acadianum) and, during the early Westphalian, the localities in Ireland and Nova Scotia would have been about 1500 km apart in the pre-Atlantic Euramerica as depicted by Smith *et al.* (1973). It is thus a further example of a Carboniferous tetrapod genus showing a Euramerican distribution.

Expression of characters and growth in Dendrerpeton

Because of the small size of much of the *Dendrerpeton* material, it has been suggested that it could be juvenile material of a much larger amphibian (Romer 1947, p. 111). Carroll (1967, p. 119) reports several growth-linked changes in the genus, including elongation of the antorbital region, relative reduction in orbit size, and lowering of the skull table. With the identification of the Jarrow amphibians as *Dendrerpeton*, it is possible to make further observations on some of the growth-linked changes in the genus.

The holotype of *D. rugosum* and the lectotype of *D. acadianum* are both skulls of about 60–70 mm midline length, and Carroll's composite reconstruction of a *D. acadianum* skull depicts one of about this size. However, individual specimens of both species possess skulls of about 100 mm midline length, which presumably belonged to animals which were adult or more nearly so. The largest *D. acadianum* skull is BM(NH) R.4554, which has a midline length of 102 mm but lacks the cheeks (text-fig. 3*d*). The 95 mm long skull of NMI G3.1970 from Jarrow (reconstructed in text-fig. 3*b*) is comparable. A comparison of these larger skulls with the smaller type skulls (text-figs. 3*a*, *c*) reveals that in each species there is an over-all growth pattern, comprising reduction in relative orbit size and an increase in relative width of the skull but no increase in antorbital skull length. There is no tendency to elongation of the nasals, prefrontals, and lachrymals such as occurs in the ontogeny of long-snouted temnospondyls, but there is relative widening of the nasals, the posterior region of the postfrontals, and the midline region of the parietals, so that in the larger individuals the anterior skull is broader in outline. The large, deep otic notch remains relatively large with size increase and the tympanum apparently required increased skeletal support in large individuals. As a result of these extensions, the tabular processes thicken and become 'square'-ended and the back of the skull table becomes concave. The jaw suspensorium continues to support the ventral edge of an enlarged tympanum by means of a dorsal process of the quadrate. As noted by Romer (1947) this is a similar situation to that in the dissorophids; in both cases this is the consequence of the possession of a large circular tympanic membrane.

Although the size range of *Dendrerpeton* skulls depicted in text-fig. 3 is limited, it demonstrates that no allometric snout elongation or skull table elongation occurs with growth. Hence, if *Dendrerpeton* did grow to a much larger size, it would not have come to resemble the 'long-snouted' edopoids but would have possessed a rounded short-snouted skull, like that of the largest known specimens but with relatively smaller orbits. The possession of a large tympanum which appears to have remained relatively large with over-all size increase suggests that the genus probably did not attain a much greater size than that recorded, otherwise the tympanum would have become too large a structure to be useful. Those amphibian lineages (e.g. the dissorophids and trematopids) which possess a relatively large tympanum do not attain a skull length much greater than 150 mm. I suggest, therefore, that the largest known *Dendrerpeton* skulls represent, or approach, the adult shape and size for the genus.

This emphasis on the configuration of the skull of the presumed adult of *Dendrerpeton* is particularly relevant to consideration of the phylogenetic position and relationships of the genus. The larvae and subadults of many temnospondyls are relatively similar to one another, as evidenced by the confusion engendered by 'branchiosaurs' over the last century. Lacking many of the adult specializations and fully expressed characters produced by local allometric growth, the larvae can be difficult to distinguish from one another, and it is possible to 'derive' a wide range of adults from a given juvenile either ontogenetically or phylogenetically if a time lag is involved. Carroll's reconstruction of *Dendrerpeton* (1967, text-fig. 3), being based on subadult material, shows little evidence of local allometric growth or specialization of the otic notch region and is a plausible 'ancestral form' for many temnospondyls. The similarity of subadult temnospondyls is evidenced by the fact that Frič (1885) referred several juvenile *Cochleosaurus* specimens to *Dendrerpeton* as *D. pyriticum* and *D. ?deprivatum*. Even Steen's reconstruction of the skull of *Cochleosaurus* (1938, text-fig. 30) is similar to *Dendrerpeton*, being based on 70-mm-long skulls, although *Cochleosaurus* grew to three times that skull length and acquired a considerably more elongate snout than depicted in Steen's reconstruction. The nearly ovoid skull of the adult *Dendrerpeton* and the superficially crocodile-like skull of the adult *Cochleosaurus* are far more distinct than the widely figured reconstructions of subadults would suggest. The significance of this in the determination of relationships of *Dendrerpeton* with other temnospondyls is that the adult material, though imperfect, may be more suitable for determination of relationships than the more completely available and more usually figured subadult material.

THE STATUS OF '*ICHTHYERPETON BRADLEYAE*' WRIGHT AND HUXLEY

1866 *Ichthyerpeton* Etheridge, p. 4, *genus coelebs*.
1866 *Ichthyerpeton bradleyae* Wright and Huxley, p. 168.
1867 *Ichthyerpeton bradleyae* Wright and Huxley, p. 367, pl. 23, fig. 1.
1890 *Ichthyerpetum bradleyae* Wright and Huxley; Lydekker, p. 168 (*Ichthyerpeton* emend.).
1947 *Ichthyerpeton bradleyae* Wright and Huxley; Romer, p. 266.
1970 *Ichthyerpeton bradleyae* Wright and Huxley; Panchen, p. 63, as *nomen vanum*.

Holotype. NMI G42.1959.

Referred material. Huxley (1867) refers NMI G.43.1959 here. Lydekker (1890) refers BM(NH) R.8453–8455 and R.8458–8459 here (see Panchen 1970, p. 63 for details). Because of the indeterminate nature of the holotype, all assignations of material are undemonstrable.

Locality and horizon. Jarrow Colliery, Castlecomer, Co. Kilkenny, Eire; *communis* zone, Westphalian A, Upper Carboniferous.

Remarks. In 1890 Lydekker suggested that *Erpetocephalus rugosus* was a junior synonym of *Ichthyerpeton bradleyae*. No subsequent author has accepted this synonymy but it is, perhaps, appropriate at this point to discuss the identity of the holotype of *I. bradleyae*.

The holotype specimen, which I have examined, consists of a poorly preserved articulated trunk and tail with pelvic girdle and hind limb present but no skull or anterior appendicular skeleton. There is about 105 mm of trunk present bearing twenty-eight presacral vertebrae, and 120 mm of tail which is incomplete. The trunk bears distinct chevrons of ventral dermal scales. As noted by Panchen (1970) the structure of the vertebrae cannot be determined, but they do not appear to be embolomerous. The holotype bears a general resemblance to undescribed colosteid material from this locality, and the presence of a long presacral column (twenty-eight presacral vertebrae posterior to the pectoral girdle) supports this possibility. However, the specimen could possibly belong to one of the other temnospondyl taxa which occur in the same assemblage and which are not known from articulated postcranial material. Most of Lydekker's referred specimens are equally indeterminate except for BM(NH) R.8453, an undescribed *Gaudrya*-like form and BM(NH) R.8455, a colosteid. Thus, the combination of poor preservation and the absence of associated cranial material renders the holotype of *I. bradleyae* indeterminate, and the binomen is a *nomen dubium* restricted to the holotype specimen.

DISCUSSION

Relationships of Dendrerpeton

Dendrerpeton *and the Edopoidea*. The superfamily Edopoidea, as used by Langston (1953), Carroll (1967), and Holmes and Carroll (1977), comprises a group of Carboniferous and Lower Permian temnospondyls which Langston places in four families: the Edopidae, Cochleosauridae, Chenoprosopidae, and Dendrerpetontidae. The former three families are comprised of 'long-snouted' forms while *Dendrerpeton* is a 'short-snouted' form. Romer's (1966) doubtful inclusion of the Colosteidae in the Edopoidea has not been endorsed by subsequent workers, and Romer later (1969) described the relationships of colosteids as problematical.

Most of the characters used to define the Edopoidea and to assign *Dendrerpeton* to this superfamily are primitive temnospondyl or even primitive tetrapod characters. Among these may be noted the presence of intertemporals, a movable basipterygoid–basisphenoid articulation, small–medium size interpterygoid vacuities, and a single occipital condyle. The association of *Dendrerpeton* with the 'long-snouted' edopoids is based substantially on an over-all primitive similarity rather than on derived characters. Likewise, the superfamily Edopoidea defined on the above characters would be a primitive grade rather than a clade. The 'long-snouted' families do, in fact, share a further suite of derived characters which support the contention that they are more closely related to each other than any is to *Dendrerpeton*. These will be discussed in a separate publication but include an ornamented septomaxilla incorporated into the skull roof, a prefrontal–jugal suture excluding the lachrymal from the orbit margin, and the postero-distal region of the jugal separating the maxilla from the quadratojugal. *Dendrerpeton* shares none of these characters and, if it is an edopoid, is the most primitive offshoot of the superfamily. This is not a new observation; Romer (1947), Langston (1953), and Carroll (1967) all observe that *Dendrerpeton* is not only one of the earliest 'conventional' temnospondyls (i.e. excluding the colosteids and the loxommatids), but is also a plausible 'near-ancestor' both for the 'long-snouted' edopoids and for the dissorophoid–eryopoid complex.

The only possibly derived character-state attributed to *Dendrerpeton* and the 'long-snouted' edopoids which might indicate relationship is the absence of lateral-line sulci in the dermal bones of the skull (Carroll 1967; Holmes and Carroll 1977). However, although no specimen of *Dendrerpeton* possesses lateral-line sulci, these structures are present in at least some edopoids. Langston (1953, p. 365 and fig. 5) describes lateral-line sulci and foramina in pit-bottoms in *Chenoprosopus*. I have examined a cast of the acid-etched specimen (AMNH 6954 from Linton, Ohio) depicted as '*Leptophractus obsoletus*' by Romer (1930, fig. 23 *right*), and this shows a clear series of lateral-line pits. They do not form a continuous sulcus but are present as unusually deep ornament pits, each with a basal foramen, and are visible on the right postfrontal, postorbital, intertemporal, and supratemporal. Thus, at least some edopoids possessed a buried lateral-line system in the skull, which is presumably a retention of the primitive tetrapod condition as seen in ichthyostegids. The absence of a lateral-line system in *Dendrerpeton* may simply be attributed to terrestriality as in the dissorophids rather than being indicative of close relationship to the 'long-snouted' edopoids.

Suggestions of an immediate relationship between *Dendrerpeton* and later 'advanced' temnospondyls have been based on the interpretation of the palate of *D. acadianum* as possessing large interpterygoid vacuities, pterygoids which do not extend to meet anteriorly, and a parasphenoid cultriform process which sutures with the vomers (Romer 1947; Langston 1953). As Carroll (1967) observes and as I have indicated in text-fig. 4*c*, the anterior part of the palate is not sufficiently preserved to permit its structure to be reconstructed with confidence in the area immediately anterior to the palatal vacuities. However, the interpterygoid vacuities in small specimens of *Cochleosaurus* are relatively smaller than in similar size specimens of *Dendrerpeton*, so that the large size of the interpterygoid vacuities does appear to be a size-independent character indicative of relationship to later dissorophoid and eryopoid temnospondyls. Further characters shared with the Dissorophoidea *sensu* Bolt, 1969 but not the Eryopoidea *sensu* Milner, 1978 are the anterior reduction of the jugal, particularly in *D. acadianum*, the large tympanic notch, and the apparent presence of a dorsal process on the quadrate.

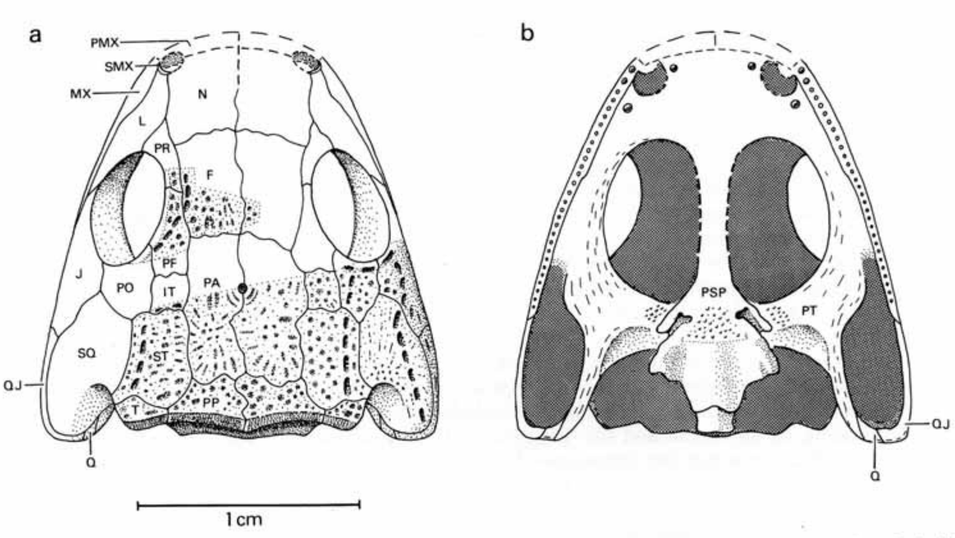
In conclusion, *Dendrerpeton* appears to share no derived character-states with the Edopoidea, and the presence of an undescribed *Gaudrya*-like edopoid in the Westphalian A of Jarrow indicates that *Dendrerpeton* is too late to be an ancestor to the 'long-snouted' Edopoidea. *Dendrerpeton* shares one derived character with the later 'advanced' temnospondyls such as the Dissorophoidea and Eryopoidea, and further characters with the Dissorophoidea alone. Neither the Dissorophoidea nor the Eryopoidea have been reported earlier than the Westphalian D. On the basis of this evidence I suggest that *Dendrerpeton*, with the family Dendrerpetontidae, be removed from the Edopoidea and be regarded as Temnospondyli *incertae sedis*, possibly as an early side-branch of the lineage leading to the dissorophoids.

Dendrerpeton, Caerorhachis, *and* Eugyrinus. Two other Carboniferous temnospondyls have an over-all similarity to *Dendrerpeton* and have been included in the Dendrerpetontidae. *Caerorhachis bairdi* Holmes and Carroll 1977 is doubtfully referred to the Dendrerpetontidae by its authors, and *Eugyrinus wildi* (Woodward) has been variously placed in the monotypic family Eugyrinidae by Watson (1940), in the synthetic family Peliontidae by Romer (1947), and in the Dendrerpetontidae, also by Romer (1966). Both monotypic genera are based on single, small, incomplete specimens and consequently both are imperfectly known and their relationships correspondingly difficult to assess. The following observations are based on Holmes and Carroll's description of *Caerorhachis* and on my own examination of *Eugyrinus*.

C. bairdi, probably from the Namurian A of Scotland, was first described by Holmes and Carroll (1977). It has an over-all primitive similarity to *Dendrerpeton* but differs from it in several fundamental respects. *Caerorhachis* appears to lack an otic notch, a prominent structure in *Dendrerpeton*, and the interpterygoid vacuities are much smaller, with the broad anterior rami of the pterygoids meeting extensively anteriorly. If the absence of the otic notch is the primitive condition as seen in colosteids (Panchen 1975, p. 611; 1977, p. 314), then *Caerorhachis* may be more primitive than any other non-colosteid temnospondyl. The broad anterior rami of the pterygoids and the small interpterygoid vacuities in such a small skull represents a more primitive palatal condition than occurs in *Dendrerpeton*, *Eugyrinus*, or the edopoids. Only in *Edops* is there a short anterior contact of pterygoids with broad anterior rami, and in that genus this condition can be attributed to the very large absolute size and the broad pre-orbital region of the snout. The vertebrae of *Caerorhachis* are unusual for a temnospondyl in that the pleurocentrum is large and 'horseshoe-shaped' and the over-all construction is not rhachitomous but resembles that in the primitive batrachosaurs *Gephyrostegus* and *Proterogyrinus*. As Holmes and Carroll (1977) and Panchen (1977) observe, this vertebral construction could be interpreted as a primitive condition for temnospondyls or as a derived condition, functionally convergent with that of the primitive batrachosaurs. If the vertebral construction is primitive, it indicates that *Caerorhachis* is substantially more primitive than all the rhachitomous forms including *Dendrerpeton* and the 'long-snouted' edopoids. If the vertebral construction is a derived specialization within the Temnospondyli, it is unique within that group and gives no indication as to the relationships of *Caerorhachis*. The morphology of *Caerorhachis* admits of at least two interpretations of its phylogenetic position. One is that it is an extremely primitive small temnospondyl, the absence of an otic notch and the presence of gastrocentrous vertebrae indicating an offshoot of the temnospondyl line which is not only pre-*Dendrerpeton* and pre-edopoid but quite possibly pre-loxommatoid as well. If this interpretation is correct, it cannot reasonably be included in the Dendrerpetontidae or the Edopoidea unless these taxa are to be used as 'dustbin' taxa for generalized small early temnospondyls. An alternative interpretation is that *Caerorhachis* represents the juvenile of a large *Edops*-like form. The configuration of the pterygoids, the medio-dorsally angled articulating surface of the articular bone, and the suggestion of 'canine peaking' in *Caerorhachis* are consistent with this interpretation. Small skulls of *Cochleosaurus* from Nýřany possess relatively short snouts compared to the largest skulls (Steen 1938), so the short snout of *Caerorhachis* need not preclude such an interpretation. Because of the incomplete nature of the only skull, the apparent absence of an otic notch is not so obvious as to preclude this interpretation either. The vertebral construction remains a character of uncertain significance. On this interpretation, *Caerorhachis* could either be a juvenile 'long-snouted' edopoid such as *Edops* or a juvenile of a more primitive edopoid-like temnospondyl. It does not appear to share any derived characters with *Dendrerpeton* and there is no basis for placing it in the same family. It seems preferable to refer *Caerorhachis* to Order Temnospondyli *incertae sedis* at a primitive, possibly pre-loxommatid level, rather than to assign it to any of the presently established families or superfamilies of temnospondyls and to imply relationships which cannot be demonstrated.

Our knowledge of *Eugyrinus wildi* derives from the single specimen MM.W1222 from the Westphalian A of Colne, Lancashire, although there is also an undescribed '*Eugyrinus*-like' skull from the Westphalian A of Parrsboro, Nova Scotia (Carroll *et al.* 1972, p. 63). *E. wildi* has been successively described by Woodward (1891) and Watson (1921, 1940) and, being primitive and either juvenile or neotenous, it has been assigned to several higher taxa as an ancestral or near-ancestral form. Watson (1940) identified it as an early representative of a 'phyllospondyl'-anuran group, Romer variously referred to it as an early juvenile edopoid (1947, p. 116), an early juvenile trimerorhachoid (1947, p. 312), and later as a dendrerpetontid (1966). Chase referred to it as an early edopoid and not a trimerorhachoid (1965, p. 215), but later noted that it is an edopoid which is an ideal trimerorhachoid ancestor in most respects (1965, p. 220). Evidently both Romer and Chase considered the Edopoidea to be a primitive grade from which the Trimerorhachoidea emerged, with *Eugyrinus* somewhere in the continuum between the two.

Re-examination of the specimen permits a few new observations to be made. Contrary to



TEXT-FIG. 6. *Eugyrinus wildi* (Woodward), holotype and only specimen MM W1222. *a*, reconstruction of skull roof, composite of outer (ornament depicted) and inner surfaces as preserved; *b*, reconstruction of palate.

previous descriptions, the jugal extends forwards narrowly to contact the lachrymal outside the orbit (text-fig. 6*a*). Thus the maxilla does not border the orbit margin and *Eugyrinus* does not share that condition with *Branchiosaurus* as described by Watson (1940). Also unmentioned in earlier accounts is the presence of an incomplete sclerotic ring in the left orbit and an interclavicle with a fimbriated leading edge, as in *Dendrerpeton*.

Most of the characteristics of *Eugyrinus* are primitive or juvenile character-states which do not assist in determination of its relationships to other Palaeozoic temnospondyls. The short snout, the mobile basipterygoid–basisphenoid articulation, the intertemporals, and the single occipital condyle are all primitive temnospondyl character-states. Other features relate to its juvenile or neotenous condition. The narrow lachrymal-jugal contact, the absence of most palatal denticles, the simple dorsal blade of the ilium, the unossified vertebral centre, and the fimbriated leading edge of the interclavicle, are all characters associated with juvenile or small aquatic temnospondyls. Small specimens of *Dendrerpeton* possess a simple dorsal blade to the ilium (Carroll 1967, text-fig. 16c), while most small larval temnospondyls have proportionately narrower lachrymal–jugal contacts than the adults and also possess unossified vertebral centra (Boy 1972). The fimbriated anterior edge to the interclavicle occurs in diverse small amphibians such as *Branchierpeton*, *Acroplous*, and *Microbrachis*.

Eugyrinus shares with *Dendrerpeton* and most later temnospondyls the presence of large rounded interpterygoid vacuities but it appears to share no derived characters uniquely with *Dendrerpeton*. Unlike *Dendrerpeton*, *Eugyrinus* possesses prominent superficial lateral-line sulci on the skull, shallow but distinct otic notches, a parasphenoid with a slightly elongate basal plate narrowing anteriorly and posteriorly and bearing a medial ridge (all depicted in text-fig. 6), and a coronoid process on the lower jaw (Watson 1940, fig. 15). These are all derived characters reported in some or all of the Upper Carboniferous and Lower Permian trimerorhachoids (Chase 1965; Coldiron 1978) and suggest that *Eugyrinus* is most immediately related to the superfamily Trimerorhachoidea as suggested by Chase (1965, p. 220) and Carroll (1967, p. 132). Coldiron (1978) reports two further derived characters which *Eugyrinus* shares with the trimerorhachoid–brachyopoid complex, namely a broad cultriform process of the parasphenoid (which is not found in *Dendrerpeton*) and a retroarticular process of moderate length (which occurs in few early temnospondyls other than *Eugyrinus*, *Cacops*, and the trimerorhachoids). Because *Eugyrinus* lacks the anterior region of both the snout and the mandibles, it is not possible to ascertain whether or not it possessed the trimerorhachoid character of anterior palatal fenestrae and symphysial tusks. The Trimerorhachoidea as defined by Chase share further derived characters not possessed by *Eugyrinus* such as the relatively short limbs (those of *Eugyrinus* are fragmentary but not very reduced) and the secondarily elongate skull table (even in tiny *Saurerpeton* from Linton, Ohio). The elongation of the posterior region of the skull and the reduction of the tympanic notch in the families Trimerorhachidae, Saurerpetontidae, and Dvinosauridae, are here interpreted as secondary developments within a temnospondyl clade characterized by the possession of akinetic skulls and tympanic notches, rather than as direct retentions from primitively notchless labyrinthodonts with long, partly kinetic skull tables such as the Colosteidae. Some trimerorhachids, such as the *Trimerorhachis* specimens figured by Case (1935, fig. 3 and pls. 2–7) and Watson (1956), have shallow tympanic notches and slender dorso-laterally orientated stapes. The typical temnospondyl otic notch and stapes appear to be part of an impedance matching system for airborne sound reception and could be expected in terrestrial and amphibious forms, but not in aquatic specialists. It seems more economical to assume that the akinetic temnospondyl skull with deep otic notch and slender dorso-laterally orientated stapes evolved once and that the trimerorhachoids are secondary aquatics with a degenerate tympanic system and secondarily elongate skull, rather than to assume that the aquatic trimerorhachoids have inherited their elongate skull tables from primitive colosteid-like aquatic labyrinthodonts and have acquired otic notches and akinetic skulls independently of other temnospondyls.

On the basis of the characters of skull table length and reduced limbs, the trimerorhachoids are more closely related to each other than any is to *Eugyrinus*, but the characters which *Eugyrinus* does share with later trimerorhachoids indicates that it is an early offshoot of the trimerorhachoid–brachyopoid line. One unique feature possessed by *Eugyrinus* is, as noted by previous authors, the quadratojugal incorporated into the jaw articulation. The quadratojugal extends mesially behind and under the squamosal and partly replaces the quadrate on the articulatory surface (text-fig. 6*b*). There is no dorsal extension of the quadrate associated with tympanum support as there appears to be in *D. rugosum*. The unusual nature of the quadratojugal precludes *Eugyrinus* from ancestry to any known trimerorhachoid.

In conclusion, such derived characters as *Eugyrinus* possesses do not support an immediate relationship to *Dendrerpeton* despite an over-all primitive similarity, but indicate that *Eugyrinus* is an early offshoot within the Trimerorhachoidea *sensu* Chase, 1965. It is suggested therefore that *Eugyrinus* in the monotypic family Eugyrinidae be transferred to the superfamily Trimerorhachoidea.

SYSTEMATIC CONCLUSIONS

Dendrerpeton, *Caerorhachis*, and *Eugyrinus* are the earliest relatively unspecialized temnospondyls, only the extremely specialized colosteids and loxommatids having characters indicative of a more primitive origin. These three genera represent the primitive grade of small unspecialized temnospondyls and have been previously classified together, with some doubt, in the family Dendrerpetontidae on the basis of shared primitive characters. Their association with the 'long-snouted' edopoids in the superfamily Edopoidea has been on the same basis. The three genera do not, however, appear to share any derived characters with one another or with the 'long-snouted' edopoids and hence there is no evidence for immediate relationship among them. All three genera are removed from the Edopoidea, which is restricted to the contents of the families Edopidae and Cochleosauridae. Only *Eugyrinus* and the monotypic family Eugyrinidae can be assigned to another superfamily, namely the Trimerorhachoidea. *Caerorhachis* and *Dendrerpeton* are of indeterminate affinities, both probably being individual side-branches off the temnospondyl stem-lineage with *Caerorhachis* being distinctly more primitive than *Dendrerpeton*. The resultant classification is less tidy but represents the uncertainty of the relationships of these forms.

Order: TEMNOSPONDYLI

Superfamily: *incertae sedis*, *Caerorhachis bairdi*
Superfamily: Edopoidea, Families Edopidae, Cochleosauridae
Superfamily: Trimerorhachoidea, Family: Eugyrinidae
Eugyrinus wildi
Superfamily: *incertae sedis*, Family: Dendrerpetontidae
Dendrerpeton acadianum
Dendrerpeton rugosum

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