THE TEMNOSPONDYL AMPHIBIAN
DENDRERPETON FROM THE
UPPER CARBONIFEROUS OF IRELAND

by ANDREW R. MILNER

ABSTRACT. The temnospondyl amphibians *Erpetocephalus rugosus* Huxley and *Ichthyorpeton 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. acutum* from Nova Scotia, the palate and pectoral girdle of which are reinterpreted. The genotype species of *Ichthyorpeton*, *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 *Caenorhachis* share only primitive or unassessable temnospondyl character-states with each other and with the ‘long-snouted’ edopoidea. The *Dendrerpetontidae* is therefore removed from the Edopoidea, and *Eugyrinus* and *Caenorhachis* are excluded from the *Dendrerpetontidae* which is thus restricted to *Dendrerpeton*. On the evidence available, *Eugyrinus* is an early offshoot of the *Trimerorhachioidea*, while *Caenorhachis* 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 Nyfany, 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 Nyfany, Czechoslovakia, all of which are Westphalian D in age.

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

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 Ichthyoperptum 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.


**SYSTEMATIC DESCRIPTION**

**Class Amphibia**

**Order Temnospondyli**

**Family Dendrerpetontidae** Frö, 1885

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

**Genus Dendrerpeton** Owen, 1853

**Type species.** *Dendrerpeton acadum*um 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 scale 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 parapetid. Interpterygoid vacuities rounded anteriorly and occupying about 1/3 of skull width. Internal carotid foramina on parapetidophid. Vertebrae 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 *Erpetochochloras* Huxley, 1867 and *Eugyrinus* Watson, 1921. *Caurotchlocus* 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 *Erpetochochloras*). Neither *Eugyrinus* nor *Caurotchlocus* 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. 1-3a, b

1867 *Erpetochochloras rugosus* Huxley, p. 368, pl. 23, fig. 2.

1890 *Ichthyoperptum bradleyae* Wright and Huxley; Lydekker, p. 169, non Wright and Huxley, 1866, Huxley, 1867—*Ichthyoperptum*.

1891 *Ichthyoperptum hibernicum* Lydekker, p. 343, figs. 1, 2.

1947 *Erpetochochloras rugosus* Huxley; Romer, p. 117.

1961 *Erpetochochloras 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. Tymanic 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 *Epicoelopus 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* (Harl.) 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**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>ANG</td>
<td>Angular</td>
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<tr>
<td>ART</td>
<td>Articular</td>
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<tr>
<td>CLA</td>
<td>Clavicle</td>
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<td>DEN</td>
<td>Dentary</td>
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<tr>
<td>ECT</td>
<td>Ectopterygoid</td>
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<tr>
<td>EPT</td>
<td>Ridge formed by Epitygoid</td>
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<tr>
<td>EXOC</td>
<td>Ridge formed by Exocipital</td>
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<tr>
<td>F</td>
<td>Frontal</td>
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<tr>
<td>ICL</td>
<td>Intercleivle</td>
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<td>IT</td>
<td>Intertemporal</td>
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<td>J</td>
<td>Jugal</td>
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<td>L</td>
<td>Lachrymal</td>
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<td>MX</td>
<td>Maxilla</td>
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<td>N</td>
<td>Nasal</td>
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<td>PA</td>
<td>Parietal</td>
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<td>PAL</td>
<td>Palatine</td>
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<td>Postfrontal</td>
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<td>PMX</td>
<td>Premaxilla</td>
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<td>Postorbital</td>
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<td>PP</td>
<td>Postparietal</td>
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<td>PR</td>
<td>Prefrontal</td>
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<td>PSP</td>
<td>ParaspHENOID</td>
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<td>PT</td>
<td>Pterygoid</td>
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<tr>
<td>Q</td>
<td>Quadrane</td>
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<tr>
<td>QJ</td>
<td>Quadratojugal</td>
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<td>SMX</td>
<td>Septomaxilla</td>
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<td>SPH</td>
<td>Ridge formed by Sphenethmoid</td>
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<td>Squamosal</td>
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<td>Supratemporal</td>
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<tr>
<td>T</td>
<td>Tabular</td>
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<tr>
<td>VOM</td>
<td>Vomer</td>
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TEXT-FIG. 2. *Dendrerpeton rugosum* (Huxley) comb. nov. a, dorsal aspect of NMI G3.1970, previously the holotype of *Ichthyopetum 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 *Ichthyopetum 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. 2a, 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. 2c).

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 pinal 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 concealed 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)**

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<tr>
<td>Skull tip to back of skull midline</td>
<td>61</td>
<td>–</td>
<td>95</td>
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<tr>
<td>Snout tip to quadrate</td>
<td>74</td>
<td>98</td>
<td>110</td>
</tr>
<tr>
<td>Tabular tip to up width</td>
<td>30</td>
<td>–</td>
<td>43</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>21</td>
<td>18</td>
<td>28</td>
</tr>
<tr>
<td>Orbital width</td>
<td>12.5</td>
<td>18</td>
<td>21</td>
</tr>
<tr>
<td>Extraorbital width</td>
<td>7</td>
<td>12</td>
<td>12</td>
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*Dendrerpeton rogusum* 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 pinal 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 sutured 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. acutum* 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 medially or dorsomedially over the presumed position of the quadrate and forms a partial posterior border to the otic notch (text-fig. 3a). Comparison with similar structures in many temnospondyls of the superfamly Dissorophoidea suggests that this is a dorsomesial process of the quadrates (Bole 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 paraphyseal are unknown. The interpterygoid vacuities are large, being comparable to those in the later Carboniferous and Permian temnospondyl family Dissorophidae, for example *Tetronius* and *Broilaius* 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. 1b). 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 *Amphibianthus* (from Carroll 1964) suggests the following interpretation. The parallel ridges superimposed on the frontals and parietals and converging posterior to the pinal foramen appear to be the dorsal edges of the plectronomod, 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. 2c) 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. acadium*, *Enygenus wildi* (pers. obs.), and *Acroplosus 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. acadium* Owen from the Westphalian B tree-stamp 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. acadium* 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 lacrymal-jugal common suture. In *D. rugosum* this is level with the anterior edge of the orbit (text-fig. 2a, c), in *D. acadium* it is level with the middle of the orbit and is little more than a point-contact (text-fig. 3c). 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 lacrymal and jugal, often with a dorsal process of the palate occupying some of the intervening space (Bolt 1974). As noted by Bolt, this occurs independently in dissorophoids, saurapetontids, and symmoriomorphs 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. acadium*. The skull of *D. rugosum* tends towards an *Amphibamus*-like shape.

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

**Postparietal lappets.** These are not visible in *D. rugosum* specimens but can be seen in a minority of *D. acadium* specimens and are depicted in the reconstruction by Carroll (1967, text-fig. 3a). 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. 4d) 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 biconvex 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. acadium* with interpterygoid vacuities which are antero-posteriorly elongated, almost parallel-sided, and bordered anteriorly by the undulating posterior edge of the vomers. However, BM(NH) R.4167 (text-fig. 4e) 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. 4b), an
anterior median rhomboidal structure can be seen which I interpret, following Steen (1954), 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. 4c. 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 dicynodonts 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. 5e). 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. 5a, 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. 5d. This also corresponds with such of the pectoral girdle as is visible in the holotype of *D. rugosum* (text-fig. 1a).

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

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. acadiculum skull is BM(NH) R.4554, which has a midline length of 102 mm but lacks the cheeks (text-fig. 3a). The 95 mm long skull of NMI G3.1970 from Jarrow (reconstructed in text-fig. 3b) is comparable. A comparison of these larger skulls with the smaller type skulls (text-figs. 3a, 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 diatremodonts; 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 diatremodonts and trematocephalians) 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 ‘branchiosaurids’ 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 Friè (1885) referred several juvenile Cochleosaurus specimens to Dendrerpeton as D. pyriticum and D. ’deprivatum. Even Steen’s reconstruction of the skull of Cochleosaurus (1928, 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 cœlebs.
1866 Ichthyerpeton bradleyae Wright and Huxley, p. 168.
1867 Ichthyerpeton bradleyae Wright and Huxley, p. 367, pl. 23, fig. 1.
1890 Ichthyerpeton bradleyae Wright and Huxley, Lydekker, p. 168 (Ichthyerpeton emend.).
1894 Ichthyerpeton bradleyae Wright and Huxley; Romer, p. 266.
1970 Ichthyerpeton bradleyae Wright and Huxley; Panchen, p. 63, as nomen vanum.

Holotype. NMI G.42.1959.


Remarks. In 1890 Lydekker suggested that Eupetocephalus 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 embolomeres. 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 Guadrya-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 superfamilly 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 Edopiidae, 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 problematic.

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 superfamilly 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 coelostoids and the lackianatothids), 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 6734 from Linton, Ohio) depicted as 'Leptophractus obsoletus' by Romer (1950, 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. acadium* as possessing large interpterygoid vacuities, pterygoids which do not extend to meet anteriorly, and a paraphenoid cultriform process which sutures with the vomers (Romer 1947; Langston 1953). As Carroll (1967) observes and as I have indicated in text-fig. 4c, 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 *Coelophosaurus* 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 Eryopidea sensu Mäurer, 1978 are the anterior reduction of the jugal, particularly in *D. acadium*, the large tympanic notch, and the apparent presence of a dorsal process on the quadratojugal.

In conclusion, *Dendrerpeton* appears to share no derived character-states with the Edopidea, and the presence of an undescribed Gondwana-like edopoid in the Westphalian A of Jarrow indicates that *Dendrerpeton* is too late to be an ancestor to the 'long-snouted' Edopidea. *Dendrerpeton* shares one derived character with the later 'advanced' temnospondyls such as the Dissorophoidea and Eryopidea, and further characters with the Dissorophoidea alone. Neither the Dissorophoidea nor the Eryopidea 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 Edopidea 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 bairdii* 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 Eugyriniidae by Watson (1940), in the synthetic family Pelioticidae 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 intertemporal 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 osteoderms (Panchen 1975, p. 611; 1977, p. 314), then Caerorhachis may be more primitive than any other non-oosteodont temnospondyl. The broad anterior rami of the pterygoids and the small intertemporal 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 overall 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 gastrocentrum 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 angulated articulating surface of the articular bone, and the suggestion of 'canine peaking' in Caerorhachis are consistent with this interpretation. Small skulls of Cochleosaurus from Nyfany 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 Temnospondylia incertae sedis as 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 Parshboro, 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 neonous, 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 'phylospondyl'-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 Trimerorhachoida 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
previous descriptions, the jugal extends forwards narrowly to contact the lachrymal outside the orbit (text-fig. 6a). Thus the maxilla does not border the orbit margin and Eugyrinus does not share that condition with Branchiosauras 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 neotenic 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 Branchiostegal, Acrepolus, 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 trimorphanichthoids (Chase 1965; Coldiron 1978) and suggest that Eugyrinus is most immediately related to the superfamily Trimorphanichthoidea as suggested by Chase (1965, p. 220) and Carroll (1967, p. 132). Coldiron (1978) reports two further derived characters which Eugyrinus shares with the trimorphanichthoid-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 Euryprinus, Cacops, and the trimerorhachoids). Because Euryprinus 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 Trimerorhachoida as defined by Chase share further derived characters not possessed by Euryprinus such as the relatively short limbs (those of Euryprinus are fragmentary but not very reduced) and the secondary 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 Dinosauridae, 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 primitive notochordal labyrinthodonts with long, partly kinetic skull tables such as the Colosteidae. Some trimerorhachoids, 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 notches 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 notches and slender dorso-laterally orientated stapes evolved once and that the trimerorhachoids are secondary aquatic 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 Euryprinus, but the characters which Euryprinus does share with later trimerorhachoids indicates that it is an early offshoot of the trimerorhachoid-brachyopoid line. One unique feature possessed by Euryprinus 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 quadratojugal on the articulatory surface (text-fig. 6b). There is no dorsal extension of the quadrate associated with tympanicum support as there appears to be in D. rugosum. The unusual nature of the quadratojugal precludes Euryprinus from ancestry to any known trimerorhachoid.

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

**SYSTEMATIC CONCLUSIONS**

*Dendrerpeton, Caerorhachis, and Euryprinus* are the earliest relatively unspecialized temnospondyls, only the extremely specialized colostoids and boxommatids 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 Coeloleosauridae. Only Euryprinus and the monotypic family Euryrinidae can be assigned to another superfamily, namely the Trimerorhachoida. *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*, *Cuarorhachis bairdi*
Superfamily: Edopoida, Families Edopidae, Cochleosauridae
Superfamily: Trimerorhachoidea, Family: Eugyrinidae

*Eugyrinus waldi*

Superfamily: *incertae sedis*, Family: Dendrerpetontidae

*Dendrerpeton academum*

*Dendrerpeton rucusum*

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