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THE FIRST ARTICULATED SKELETON OF *DENDRERPETON ACADIANUM*  
(TEMNOSPONDYLI, DENDRERPETONTIDAE) FROM THE LOWER  
PENNSYLVANIAN LOCALITY OF JOGGINS,  
NOVA SCOTIA, AND A REVIEW OF ITS RELATIONSHIPS

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**ABSTRACT**—The discovery of the first articulated, well-preserved specimen of *Dendrerpeton acadianum* makes it possible to describe this taxon completely for the first time, and reassess its phylogenetic relationships. Large, laterally facing orbits, large, rounded squamosal embayments, absence of lateral line sulci, a short presacral column of only 24 vertebrae that is less than twice the length of the skull, and large stout limbs all suggest a terrestrial lifestyle distinct from the aquatic and semiaquatic adaptations of most contemporary Carboniferous amphibians. Although *Dendrerpeton* bears a general resemblance to the highly terrestrial dissorophoid temnospondyls and even shares with them a large squamosal embayment supported ventrally by the quadratojugal and a quadrate process, phylogenetic analysis does not support a sister-group relationship. Rather, *Dendrerpeton* is best considered the primitive sistergroup of a clade of temnospondyls including trimerorhachoids, “eryopoids” (*Eryops*, *Parioxys*, and *Sclerocephalus*), zatracheids, and dissorophoids.

## INTRODUCTION

The fauna preserved in the erect stumps of fossil lycopoid trees at Coal Mine Point, Joggins, Nova Scotia, has long been recognized as an important source of information on the early evolution of terrestrial tetrapods (Dawson, 1878; Steen, 1934; Carroll, 1967). These deposits, of the Cumberland Group, have recently been determined to be equivalent in age to the Westphalian A (=Langsettian, ratified by the Carboniferous Congress in 1987) of the European system (Calder, 1994) rather than Westphalian B (=Duckmantian) as previously thought (e.g., Carroll et al., 1972), making them roughly 5 million years older than previously assumed, or between approximately 309 and 316 million years before present. This locality predates the classic North American Carboniferous localities of Linton, Ohio (Westphalian D), and with the exception of a few other Westphalian A localities (Milner and Sequeira, 1994), most of the “Coal Measures” localities of Europe. Although a few older localities, most notably in East Greenland (Jarvik, 1952), Greer, West Virginia (Romer, 1969), Goreville, Illinois (Schultze and Bolt, 1996), Delta, Iowa (Lombard and Bolt, 1995), two Scottish localities of Cowdenbeath and the East Kirkton (Milner et al., 1986), and the mid-Viséan locality in Queensland, Australia (Thulborn et al., 1996) have recently produced significant quantities of tetrapod material, none has yielded such an abundance of small animals, including several microsaur and the oldest amniote (Carroll et al., 1972). The unusual mode of accumulation, in which animals are believed to have become trapped in the hollow centers of the dead, rotted out stumps of the lycopoid genus *Sigillaria*, has, in contrast to all other Carboniferous localities except Florence, Nova Scotia (Reisz, 1972), preferentially preserved a terrestrial fauna (Carroll et al., 1972). An unfortunate consequence of this mode of preservation is that scavenging by subsequent captives has scattered most skeletons. Thus, descriptions of most taxa are necessarily based on disarticulated, often disassociated elements.

Most of the vertebrate material from Joggins was collected between 1851 and 1879 from stumps in one horizon at Coal Mine Point. Additional productive stumps were subsequently collected from several other horizons by McNaughton in 1893 and Bell in 1911. However, more or less regular visits to the

locality since that time yielded little additional material until the late 1970's, when a nodule (NSM 978 GF 53.1) containing a complete but badly eroded skull of the temnospondyl amphibian *Dendrerpeton acadianum* was collected (Godfrey et al., 1987).

In 1987, Lin Kegang and Wu Xiao-chun, members of a field party from the Redpath Museum, discovered an articulated, nearly complete skeleton of *Dendrerpeton* (NSM 987 GF 99.1) contained in a loose boulder on the beach. No *Sigillaria* “bark” is preserved. The hard, silty sandstone bears no resemblance to the carbonaceous sediments most commonly found in productive stumps, and the undisturbed nature of the skeleton is in marked contrast to the badly disarticulated condition typical of tree stump specimens. These features suggest that this boulder is not a weathered section of a large stump, but rather that the specimen was buried outside the stumps during an episode of rapid deposition.

Although *Dendrerpeton* is known from hundreds of partial, disarticulated specimens and dissociated elements (Carroll, 1967), this excellently preserved, well-ossified, three-dimensional specimen permits a detailed description of virtually the entire skeleton, establishing the basic body proportions such as skull/trunk ratios, presacral vertebral count, and limb/skull ratios for the first time (Fig. 1). It is much better preserved and/or more nearly complete than other primitive Carboniferous temnospondyls (e.g., *Balanerpeton*, Milner and Sequeira, 1994; *Cochleosaurus*, Godfrey and Holmes, 1995; *Caerorhachis*, Holmes and Carroll, 1977), and provides not only additional insight into the life habits of early tetrapods, but also badly needed morphological data for reevaluation of the taxonomy and phylogenetic relationships of *Dendrerpeton* in particular and early temnospondyls in general.

## GEOLOGY

The boulder containing this specimen was found on the beach near the town of Joggins, about one km north of Coal Mine Point. This places the specimen in proximity to beds considerably lower in the section than those from which previous fossil finds have been collected, and certainly below the intersection of the Forty Brine coal seam with the beach. However,

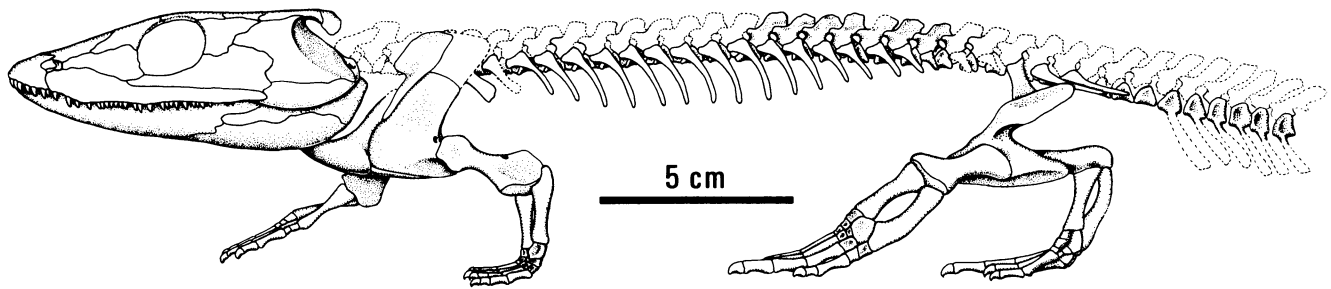


FIGURE 1. *Dendrerpeton acadianum*. Skeletal reconstruction based primarily on NSM 987 GF 99.1.

the smoothly rounded edges of the boulder indicate that it has been exposed for a considerable period to wave and tide action, providing ample opportunity for lateral transport along the beach. The matrix, a very hard, gray, sandy siltstone, is oxidized and extremely variable in hardness next to the bone.

### DESCRIPTION

The specimen, lacking only the metapodials, phalanges, and posterior portion of the tail, was preserved in natural articulation and initially exposed in ventral view (Fig. 2). It is about 35 cm in length to the end of the tail as preserved. Milner (1980), on the basis of cranial material and assuming a typical temnospondyl head to trunk to tail ratio, estimated a maximum length of one meter for *Dendrerpeton*. However, since the skull of this specimen is only about 10 percent shorter than the largest known (RM 2.1185, Carroll, 1967), this estimate seems rather high unless a very long tail is assumed. Since there is insufficient data to estimate the length of the tail, maximum size will here be expressed as snout-vent length, which probably did not exceed 35 cm.

*Dendrerpeton* resembles dissorophoid temnospondyls (Carroll, 1964a; Williston, 1910) in having a large, broad skull and short trunk, and well-developed limbs (Table 1).

### Skull

The skull and mandible have been prepared in ventral and left lateral views (Fig. 3). The lower margin of the right side of the skull and mandible has also been exposed. Although the left half of its dorsal aspect has been cleared of matrix, the specimen is too fragile and the matrix too hard to allow preparation of the occiput or the right half of the skull roof.

As exposed, it is complete and undisturbed except for dorsoventral compression that has fractured and dislocated some of the bone on its dorsal surface. Nevertheless, nearly all sutures, including those on the displaced sections, are visible and it is possible to produce a detailed reconstruction (Fig. 4). With a total length (premaxilla to quadrate) of 94 mm and a midline length (tip of premaxilla–back of postparietal) of 84 mm, it is slightly smaller than the largest reasonably complete specimen (RM 2.1185), which has a midline length of 104 mm (Carroll, 1967).

This specimen confirms many of the significant features described previously on the basis of fragmentary material, including: absence of lateral line canals, presence of coarse pit and ridge sculpturing, a large intertemporal, a lacrimal that borders both the naris and orbit, a small septomaxilla that does not form any of the external skull surface, a small tabular that does not contact the parietal, and a deep skull with large, laterally facing orbits.

The posterior margin of the skull table is gently “biconcave” in dorsal view as noted by Milner (1980). The dorsally convex

temporal regions are separated by a shallow median trough that runs from the postparietals forward between the orbits, where it fans out and dissipates over the posterior parts of the nasals. Shallow depressions also occur on the lacrimal anterior to the orbit, the jugal posteroventral to the orbit, the posteroventral part of the postorbital, and the ventral part of the squamosal. The “pit and ridge” ornamentation is distinctly muted on the depressions of the lacrimal and squamosal, although not to the same extent as in the edopoid *Cochleosaurus* (Godfrey and Holmes, 1995).

**Skull Roof**—The premaxilla has room for about 10 teeth, some of which are as large as the largest maxillary teeth, although there is no premaxillary “canine” as is the case in colosteids (Hook, 1983; Smithson, 1982) or trematopids (Dilkes, 1990). The presence of unusually large gaps between the teeth that are easily misidentified as empty alveoli resulted in a much higher original count of 20 premaxillary teeth (Carroll, 1967). The premaxillae have considerable dorsal exposure, although not quite as much as restored in Carroll (1967). A small, irregular-shaped rostral fontanel, possibly indicating the position of a lost median rostral bone, interrupts the median premaxillary suture. Posterodorsally, the premaxilla is drawn out into an alary process that overlaps the nasal. The large, oval, dorsolaterally-facing naris is located a considerable distance from the ventral skull margin. The alary process and morphology of the naris, not previously observed in less well-preserved material, are unlike those seen in edopoids, but are shared by more derived temnospondyls.

A well-preserved, concave septomaxilla forms the ventral, posterior, and part of the medial walls of the exposed left nasal vestibule. Its curved, lateral edge bears scattered small, rounded pits, but lacks the coarse ridging characteristic of the dermatocranium. It appears to be only loosely attached to the anteromedial edge of the lacrimal, from which it is separated by a deep furrow. In contrast to edopoids, it lacks a triangular, ornamented lamina that wedges between the maxilla and lacrimal. A “free” septomaxilla is thought to be a synapomorphy of the eryopoid-dissorophoid-lissamphibian clade (Sequeira and Milner, 1993).

The maxilla has room for between 40 and 42 teeth. Its broad dorsal lamina forms much of the lateral surface of the snout. Posteriorly, it contacts the quadratojugal, excluding the jugal from the ventral margin of the skull.

The frontoparietal suture can only be traced for part of its length, but the frontal was clearly at least 25 mm, and more probably 28 mm long, and is largely responsible for the formation of a preorbital region that is relatively longer than that of the considerably smaller NSM 987 GF 53.1 (Godfrey et al., 1987:fig. 1). The prefrontals, postfrontals, and frontals all contribute to a very broad interorbital plate that comprises more than 50 percent of the total skull width. As a result, the large orbits (having a diameter equivalent to about 20 percent of the



FIGURE 2. *Dendrerpeton acadianum*. NSM 987 GF 99.1 in ventral view.

snout–postparietal length) face almost directly laterally. Dorsoventral compression has disrupted the circumorbital bones, and broken off a large ventrally directed tongue-like process of the prefrontal that passed medial to the lacrimal (to which it appears to have been only weakly attached) to form most of the anterior wall of the orbit. Its ventral extremity could not be exposed, making it impossible to determine whether it made contact with the palatine as in dissorophoids.

Correlated with the large orbits is the narrow suborbital ra-

TABLE 1. Selected measurements (mm) and ratios of *Dendrerpeton acadianum* (NSM 987 GF 99.1).

Skull length	94
Presacral column	175
Vertebral length	7
Femoral length	37
Humerus length	31
Ulna length	16
Radius length	15
Fibula length	21
Tibia length	20
Rib length (max.)	20
Head/trunk ratio	0.54
Femur/presacral column	0.21
Humerus/presacral column	0.18
Epipodial/humerus	0.50
Epipodial/propodial	0.55
Femur/skull	0.39
Humerus/skull	0.33

mus of the jugal, which forms a short, almost horizontal suture with the lacrimal at the level of the anterior rim of the orbit. Milner suggested (1980) that *Dendrerpeton acadianum* could be distinguished from *D. rugosum* by a reduction in both length and breadth of the suborbital ramus of the jugal, resulting in a much shorter jugal-lacrimal suture that is located below the center of the orbit (Carroll, 1967:fig. 3). *Dendrerpeton rugosum* shows the more conventional temnospondyl configuration in which a broad contact is located more anteriorly, at the level of the anterior edge of the orbit. Although the jugal-lacrimal suture is short and the suborbital ramus narrow in NSM 987 GF 99.1 in comparison to *D. rugosum* and other temnospondyls, the anterior position of the suture suggests that the proportions of bones and position of sutures in this region are variable in *Dendrerpeton*, and of no taxonomic significance.

Five overlapping sclerotic plates are preserved in position in the lower half of the partially exposed right orbit.

The nearly vertical cheek meets the skull table at an abrupt, approximately right angle, contributing to the box-like appearance of the skull. The large quadratojugal sweeps ventrally in a broad arc, giving the cheek a distinctly convex ventral margin posterior to the tooth row. Posteriorly, it turns medially to sheath part of the squamosal and a small portion of the quadrate from behind. A similar posteromedial process of the quadratojugal has been hypothesized as a synapomorphy of dissorophoids (Bolt, 1969), although this configuration also occurs in brachyopid temnospondyls (Watson, 1956). No quadratojugal foramen is evident.

The ornamentation on the external surface of the squamosal radiates anteriorly and ventrally from its posterodorsal center of ossification. Midway between its dorsal and ventral edges, this pattern is interrupted by a horizontal “step”, below which the pits become distinctly broader and shallower. Posteriorly, the ornamented lateral surface of the squamosal is set off from a smooth posterolaterally facing lamina by a curved ridge that forms the boundary of the squamosal embayment. Posteroventrally, the ridge appears to be supported by the dorsal edge of the quadratojugal for a short distance before it turns medially onto the posterior surface of the quadrate just dorsal to the mandibular condyle. At the medial termination of this ridge, the quadrate bears a modest swelling that may be homologous to the dorsal process of dissorophoids. A similar process has been reported in *D. rugosum* (Milner, 1980). A small oval pit (better developed on the left quadrate, but present on both sides) occupies its lateral surface. Dorsally, the ridge turns posteriorly onto the dorsal edge of the embayment, then curves ventrally as it runs off the posterior end of the large supratemporal. The

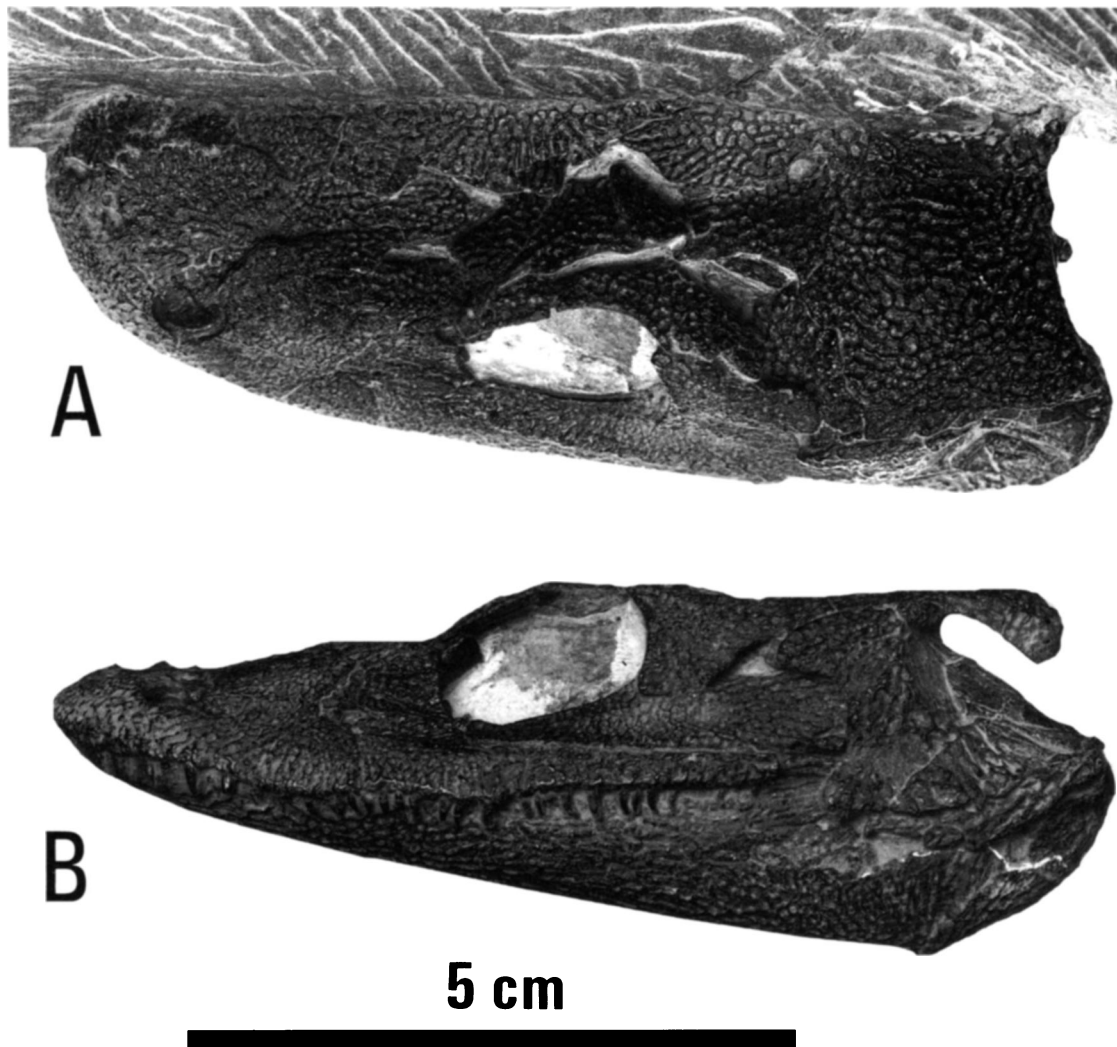


FIGURE 3. *Dendrerpeton acadianum*. Skull of NSM 987 GF 99.1 in **A**, dorsal; **B**, ventral; and **C**, lateral views.

morphology of the ridge suggests that a frog-like tympanic ring may have been present.

The tabular swells at its posterolateral corner, in lateral view suggesting the incipient closure of the squamosal embayment that characterizes most dissorophoids, but its lateral surface bears no part of the rim of the embayment. In contrast to some specimens of *Dendrerpeton acadianum* described by Milner (1980), the tabular projects only slightly laterally. Although the general form of the tabular resembles that of dissorophoids, there is no semilunar curvature, supratympanic flange, or supratympanic shelf believed to be diagnostic of that taxon (Bolt, 1974a).

The concave, unornamented occipital flange of each postparietal bears a ventrolaterally directed buttress, the postparietal lappet, to support the exoccipital.

**Palate**—The mandible, preserved in articulation with the skull, obscures the perimeter of the palate. Otherwise, the slightly disturbed palate is readily reconstructed (Fig. 4). All exposed elements are covered with small denticles. The indistinguishably fused vomers form a gently concave plate that comprises about 30 percent of the snout–postparietal length, only slightly shorter than that described by Carroll (1967). They form the broadly curved anterior margin of the interpterygoid vacuities and widely separate the anterior ends of the pterygoids. Each vomer bears a pair of small tusks immediately me-

dial to the choanal margin as in the specimen described by Godfrey et al. (1987), but are different from those in one specimen described by Carroll (1967:fig. 7), in which the tusks are larger, arranged parallel to the marginal dental arcade, and located anterior to the choana. This particular specimen probably pertains to a cochleosaurid rather than to *Dendrerpeton* (Milner, 1996). Each palatine extends far forward to form the posterior half of the thickened medial, parasagittal margin of the choana. Posteriorly, this margin sweeps laterally and then anteriorly in a tight arc producing a choana that is distinctly narrower posteriorly than described in Godfrey et al. (1987). About midway to its anterior end, the lateral margin curves abruptly laterally around the base of the anterior palatine tusk. The remainder of its margin is obscured by the mandible, but the choana was clearly wider anteriorly. Although these general proportions are also seen in NSM 978 GF 53.1 (Godfrey et al., 1987), the choana has a distinctly different shape, suggesting that this is a variable feature. The groove coinciding with the pterygoid–palatine suture figured in Godfrey et al. (1987:fig. 2) is not present, although a small foramen immediately posterior to the left vomerine tusk pair occupies a position equivalent to its anterior termination. Incomplete ossification of the common suture of the pterygoid and marginal palatal bones that permitted postmortem separation of these elements is the probable expla-

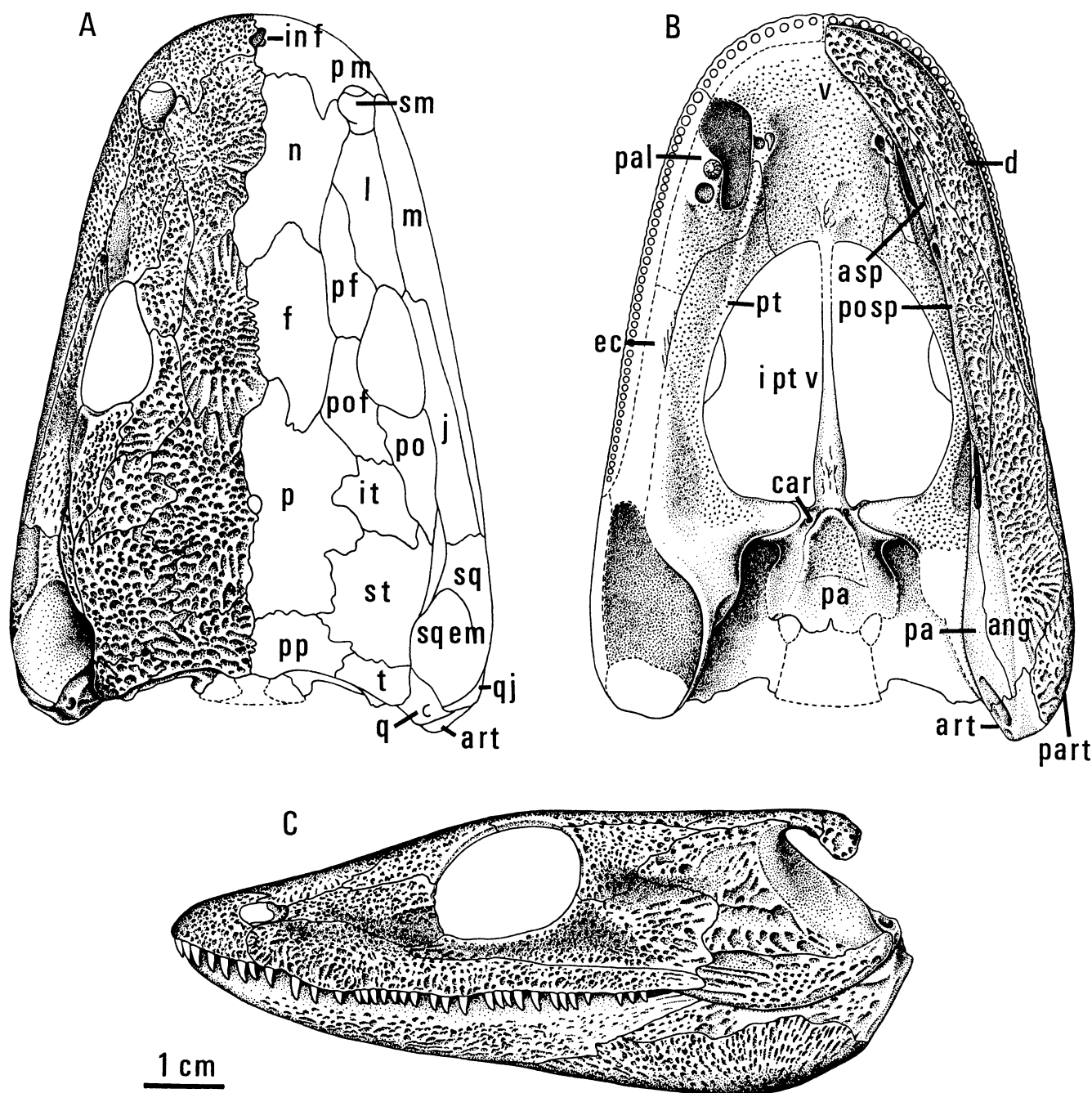


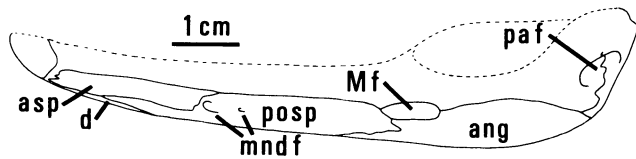
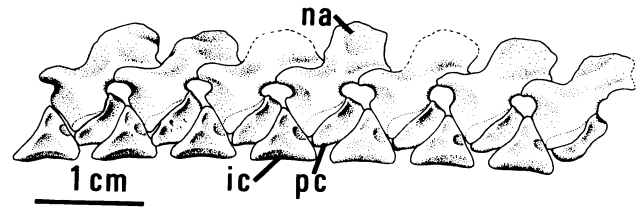
FIGURE 4. *Dendrerpeton acadianum*. Reconstruction of the skull based on NSM 987 GF 99.1 in **A**, dorsal; **B**, ventral; and **C**, lateral views. Dermal ornamentation of all elements to the left of the midline has been reproduced as accurately as possible. Suture patterns of unexposed sections on the right side of the midline have been restored assuming bilateral symmetry.

nation of this unusual feature in the smaller (and presumably less mature) NSM 978 GF 53.1. Delicate pterygoids form the lateral and posterior margins of the interpterygoid vacuities that are similar in shape to those described in Godfrey et al. (1987). As in NSM 978 GF 53.1, the portion of the pterygoid that forms the medial margin of the adductor fossa extends well below the general surface of the palate.

The basal plate of the parasphenoid is saddle-shaped ventrally and exhibits a central denticle-bearing area with a strongly raised, wedge-shaped anterior lip. Posteriorly, this denticle field ends abruptly along a faint, parabolic ridge. Asymmetri-

cally positioned carotid foramina pierce the plate between the basiptyergoid processes. The basal plate is unusually short posteriorly. The parasphenoid is indistinguishably fused to the basisphenoid, which articulates, but does not fuse to, the basal processes of the pterygoids. The cultriform process bears faint, irregular grooves on its modestly expanded posterior base, and gradually narrows to a very thin bar anteriorly. No sutures are visible on the vomerine plate, but grooves on its posteromedian portion similar to those on the cultriform process suggest that the process may have expanded to form a portion of the posterior margin of the vomerine plate.



FIGURE 5. *Dendrerpeton acadianum*. Medial view of lower jaw.FIGURE 6. *Dendrerpeton acadianum*. Reconstruction of presacral vertebrae 15 to 21, based on NSM 978 GF 99.1.

**Mandible**—As far as exposed, the arrangement of elements is very similar to that described for NSM 978 GF 53.1 (Fig. 4). The dentary is deeper dorsoventrally, presumably due to the larger size of the specimen, restricting the small anterior splenial (presplenial) to a modest ventral exposure. The surangular extends far anteriorly as a triangular wedge between the dentary and angular. Although the posterior portion of the external surfaces of the dentary and surangular bear sculpturing that is somewhat muted as compared with the remainder of the external elements, this differential is not as marked as seen in other specimens (e.g., Carroll, 1967:fig. 7; Milner, 1980:fig. 2). Each postsplenial is pierced by two foramina (Fig. 5), one much larger than the other, in approximately the same position as the “mandibular foramen” in NSM 978 GF 53.1. Anteriorly, the postsplenial sends a narrow, triangular process between the dentary and presplenial. The latter, being much smaller than the postsplenial, allows the dentary modest medial exposure at the anterior end of the ramus. An elongate, oval Meckelian fenestra pierces the medial surface of each ramus at the junction of the angular, postsplenial, and prearticular (Fig. 5). The prearticular is inflected medially to form the medial wall of the wide adductor fossa. Ventral to the condyle, a large “para-articular” fossa contains a foramen for the chorda tympani. Matrix obscures the remainder of its medial aspect, so that neither the dorsal extent of the splenial nor the nature of the coronoids can be established.

### Vertebral Column

Seventeen closely articulated vertebrae are exposed in ventral view between the pectoral and pelvic girdles (Fig. 2). Although both the sacrum and the anterior end of the column are obscured by girdle elements, a presacral count of 24 vertebrae can be confidently estimated by reference to the positions of the skull and ilium. A presacral column of 26 or fewer vertebrae, characteristic of dissorophoids and other temnospondyls, such as *Eryops* (22; Moulton, 1974) and *Balanerpeton* (24), is considerably shorter than some aquatic temnospondyls, such as *Trimerorhachis* (31 or 32; Case, 1935) and other primitive aquatic tetrapods, such as *Greererpeton* (41; Godfrey, 1989), *Embolomeres* (32–38; Holmes, 1984, 1989), and *Crassigyrinus* (in excess of 30; Panchen 1985). This is compatible with the hypothesis (e.g., Clack, 1992; Milner, 1990) that the origin of temnospondyls was closely associated with adaptation to terrestrial habitats.

Presacral vertebrae 15 to 21 have been prepared in left lateral view, permitting the series to be reconstructed (Fig. 6). The neural arches bear short transverse processes terminating in anteroventrally elongate diapophyses. The low, sub-rectangular spines are variable in shape and height. The massive zygapophyses overlap extensively. This condition, also reported in *Balanerpeton* (Milner and Sequeira, 1994), may be primitive for temnospondyls, but may also represent a structural modification to strengthen the column.

Both intercentra and pleurocentra are remarkably well ossified externally and fit together precisely, leaving space for only a minimal layer of articular cartilage between central elements. This is in marked contrast to the condition in much larger tem-

nospondyls, such as *Eryops*, where large gaps between the ossified elements were presumably filled with considerable cartilage (Moulton, 1974). However, ossification was predominantly perichordal rather than endochondral, producing intercentra that are at most one millimeter thick in a centrum about 8.5 millimeters in diameter and leaving a large central space that was presumably occupied by cartilage and/or an essentially unconstricted notochord. The external surface of each intercentrum bears shallow concavities and a raised parapophysis on the posterolateral margin of its wedge-shaped lateral profile. Anterior to segment 12, the intercentra are separated ventrally by wedge-shaped, ventromedial extensions of the intervening pleurocentra. Posterior to this, however, the intercentra become longer, and their ventral margins approach one another, restricting the ventral extent of the pleurocentra. More complete ossification of posterior trunk centra in *Balanerpeton* and progressive enlargement of posterior intercentra in *Greererpeton* (Godfrey, 1989) and *Gephyrostegus* (Godfrey and Reisz, 1991) appear to be manifestations of the same trend. Although some of the more dorsoventrally compressed intercentra have broken along the midventral line, none shows any evidence that they were formed ontogenetically from paired elements as in *Balanerpeton* (Milner and Sequeira, 1994). The paired, rhomboidal pleurocentra, although forming much less of the external surface of the centrum, are clearly thicker than the intercentra. Each supports the pedicle of a neural arch and is closely associated with the intercentrum of the next posterior centrum, the latter bearing a concave excavation on its anterodorsal margin to receive it. In the posterior portion of the trunk, the pleurocentra reach about half way down the lateral surface of the centrum, but anterior to segment 14 the two halves begin to extend more ventrally, and anterior to segment 12, they completely separate successive intercentra with triangular processes whose cartilaginous extensions probably touched at the midventral line.

Although the first two caudal vertebrae are obscured by the ischium, articulated segments three to seven are exposed ventrally. Preservation becomes progressively poorer posteriorly, and carbonaceous material, possibly poorly preserved scales, obscures most detail. However, at least four additional disarticulated intercentra are preserved in anterior view. They are remarkable in being much more completely ossified than the presacral elements, and in being complete dorsally, thus forming thick-walled rings that constricted the notochord considerably. A similar condition, in which the presacral vertebrae are typically rhachitinous and the caudal intercentra are spool-shaped, occurs in *Parioxys ferricolus* (Moustafa, 1955). Despite the well-ossified condition of the more posterior caudal elements, their external dimensions become markedly reduced over the few preserved segments, suggesting that the tail was not long, probably consisting of no more than approximately 35 vertebrae, as in *Eryops*.

### Ribs

As in *Balanerpeton* and *Caerorhachis*, the ribs are short, with the longest trunk ribs being no more than two and one-half

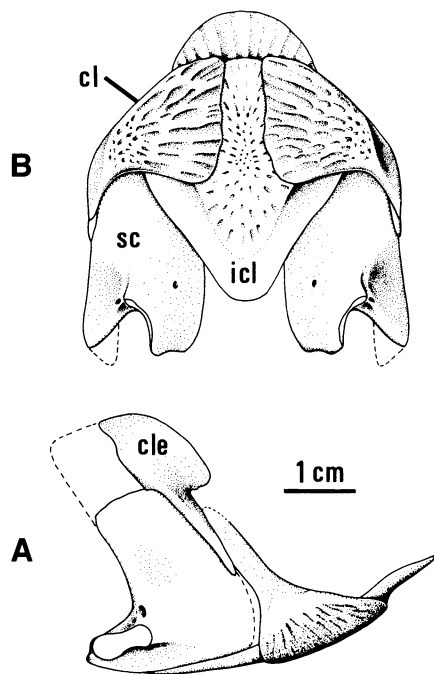


FIGURE 7. *Dendrerpeton acadianum*. Pectoral girdle in A, right lateral, and B, ventral views.

times the length of a middorsal vertebral segment (Figs. 1, 2). Capitular and tubercular facets, set off at an angle of about 65 degrees, are connected by a web of bone, obscuring the bicipital nature of the rib. Each gently curved shaft terminates in a slight swelling, suggesting that a costal cartilage was present. Posterior to the 16th vertebra, the ribs become shorter and straighter, and taper to a point distally. Anterior to vertebra 7, the vertebral column is obscured by the pectoral girdle. However, several disarticulated fragments indicate that ribs associated with at least some of the vertebrae anterior to vertebra seven were broad, flattened, and distally expanded as in *Balanerpeton* and *Caerorhachis*. Caudal ribs associated with at least the first five caudal vertebrae are as long if not longer than the longest trunk ribs, curving strongly posteriorly at their necks to lie parallel to the base of the tail.

### Pectoral Girdle and Limb

As in other temnospondyls, the scapulocoracoid appears to form from a single center of ossification. The right scapular blade is pierced by a large supraglenoid foramen. Much of the coracoid plate is covered with gastralia, but a small supracoracoid foramen is clearly visible anteroventral to the glenoid. The posterior end of the plate was eroded before recovery, and much of the glenoid has been lost.

The interclavicle is incomplete posteriorly (Fig. 2), but an impression of the internal surface of the missing portion confirms a roughly diamond-shaped outline with a modestly developed parasternal process as described in Carroll (1967) and Milner (1980). The clavicles, preserved in articulation, confirm Milner's (1980) interpretation and also indicate that the interclavicle was positioned much more anteriorly relative to the scapulocoracoid than indicated by Carroll (1967), placing the parasternal process at the level of the anterior end of the glenoid rather than projecting posterior to the coracoid plate (see also Milner, 1980). As in dissorophoids, the ventral plate of the clavicle is only modestly expanded (although it is not as narrow as

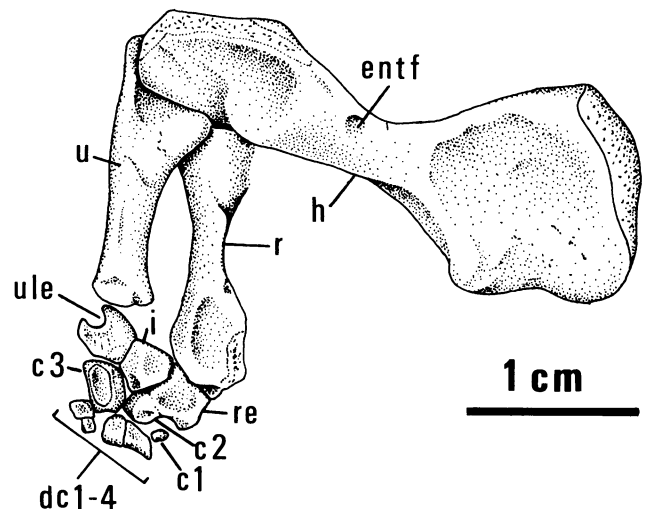


FIGURE 8. *Dendrerpeton acadianum*. Left pectoral limb of NSM 987 GF 99.1 as preserved in ventral (flexor) view.

reconstructed by Carroll, 1967), and lacks the prominent triangular anterior lamina present in many primitive tetrapods (e.g., *Crassigyrinus*, *Greererpeton*, *Saurerpeton*, and *Trimerorhachis*). Although clavicular plate width may be of phylogenetic significance, it may correlate with locomotor pattern, since all of the genera with large clavicular plates listed above are probably aquatic. The narrow stem of the cleithrum adheres to the anterior edge of the scapula. Dorsally, it forms a spoon-shaped expansion on the anterior face of the unossified suprascapula. Most of the expansion takes the form of an anterior lamina unlike the condition in dissorophoids and eryopids, in which the cleithrum produces an extensive posterior lamina that completely caps the suprascapula.

The left pectoral limb is complete except for the metacarpals and phalanges (Fig. 8). The humerus, the total length of which is equivalent to about four vertebrae, agrees with the morphology described by Carroll (1967). Both ulna and radius are about 50 percent of the humeral length. Some of the distal elements of the carpus and all of the phalanges have been lost. The three proximal carpal elements present are well ossified. This may correlate with terrestrial habits, as suggested for *Balanerpeton* (Milner and Sequeira, 1994). The ulna articulates with the ulnare only, while the radius articulates with the other two (?intermedium and radiale). There are only three centrale, one of which (C2) appears to have partially coossified with the radiale. Four small, poorly ossified elements, presumably distal carpals, are preserved distally.

### Pelvic Girdle and Limb

The pelvic girdle and limb are much as described by Carroll (1967), the main difference being the smaller size of the obturator foramen and shortness of the ischiadic plate. The long, bladelike posterodorsally directed iliac process resembles those of a variety of tetrapods, including *Caerorhachis*, *Proterogyrinus*, and *Greererpeton*, but is distinct from that of more derived temnospondyls, such as *Eryops* (Case, 1911) and *Parioxys* (Moustafa, 1955) in which the shortened blade is oriented primarily dorsally, suggesting that it represents the primitive condition for temnospondyls.

Both femora and epipodial elements are preserved, although all have sustained weathering damage, and both tarsi and feet were lost before discovery.



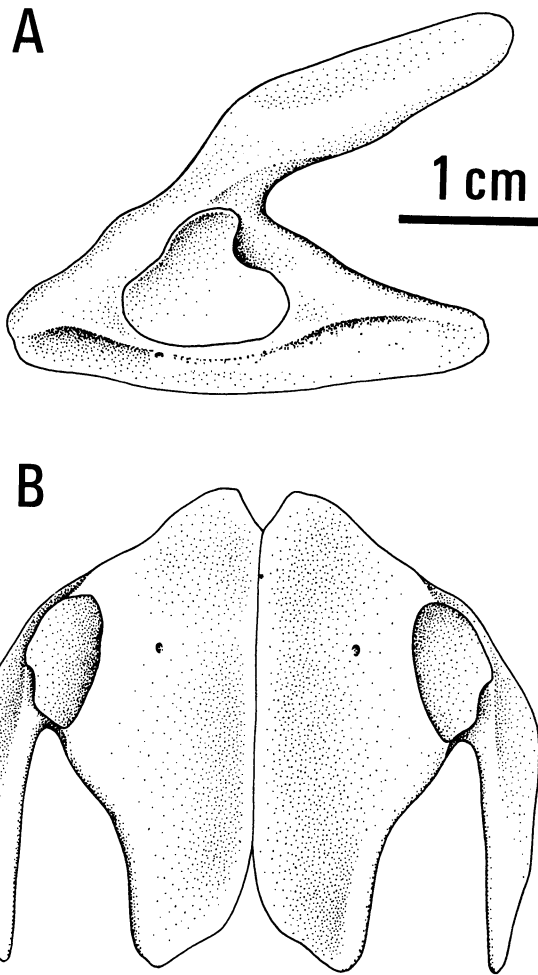


FIGURE 9. *Dendrerpeton acadianum*. Pelvic girdle in **A**, left lateral, and **B**, ventral views.

### Scales

The gastralia, damaged before recovery or lost to weathering, are represented primarily by poorly defined impressions on the matrix. However, it is possible to determine that their length is equivalent to about half of the diameter of a vertebral centrum. This is comparable to the condition in colosteids (Godfrey, 1989; Hook, 1983), but distinctly different than that of embolomeres, in which the much larger scales are equivalent to or greater than the centrum diameter. The significance of this is unknown.

## DISCUSSION

### Temnospondyl Amphibians From Joggins

Among the tetrapod material from Joggins, Steen (1934) recognized several species of small, primitive temnospondyls. However, the considerable variation in skull structure exhibited by the most common taxon, *Dendrerpeton acadianum*, has led to the suggestion that all described temnospondyl taxa are congeneric (Romer, 1947). This was supported by Carroll (1967), who argued that all apparent taxonomic distinctions could be accounted for either by individual variation, or damaged, incomplete, or distorted material. Sequeira and Milner (1993) have recently reopened the debate by hypothesizing the presence of at least two distinct temnospondyls at Joggins, specif-

TABLE 2. A comparison of selected skull ratios in NSM 987 GF 99.1 with average values of three hypothesized species of *Dendrerpeton* from Joggins (averages calculated from data in Milner, 1996, Table 2).

Ratios	C/D	E/G	G/H	F/G
<i>D. acadianum</i>	1.03	0.77	1.68	0.46
<i>D. confusum</i>	1.28	0.93	1.84	0.74
<i>D. helogenes</i>	0.74	0.84	2.07	0.53
NSM 987 GF 99.1	1.14–1.29	0.92	1.63	0.64

ically suggesting that at least one cochleosaurid specimen was incorporated in Carroll's (1967:fig. 3) reconstruction (see "Palate" above). Milner (1996) has argued that, although most of the temnospondyl material can be assigned to *Dendrerpeton acadianum*, two additional species can be distinguished using differences in skull proportions and size and position of the vomerine fangs. *Dendrerpeton confusum*, based on a single, very large skull, was diagnosed by the possession of very long frontals, a skull roof with a very broad interorbital region, and a long, low skull table (i.e., the cheeks are shallow). *Dendrerpeton helogenes*, represented by two relatively small skulls, (one of which is NSM 987 GF 53.1; Godfrey et al., 1987), was characterized by very short frontals forming an interorbital plate of normal (i.e., not transversely expanded) proportions, a long, low skull table, shallow otic notch, and small vomerine fangs located medial rather than anterior to the choana. Milner (1996) rejected the possibility that these differences could be attributed to allometry because there is no apparent correlation between proportional differences and absolute size of the specimens. Although the sample size is limited (13 skulls of varying completeness), morphology, expressed as skull proportions, appears to cluster around three sets of mean values with no intermediate forms, and one of the putative taxa shows distinct differences in the size and position of the vomerine fangs (Milner, 1996: table 2).

Although this considerable morphological variability may indicate the presence of multiple species of *Dendrerpeton* at Joggins, acceptance of this analysis complicates the taxonomic assignment of NSM 987 GF 99.1. If its skull proportions are compared with corresponding average values (calculated from data in Milner's table) for each of the proposed species (Table 2, this paper), unequivocal association with any of the proposed species is impossible. Although the ratio of skull table width to cheek height (G:H) is closely comparable to that of *D. acadianum*, table width to postorbital length (E:G) and frontal length to postpineal length (C:D) (even if a minimum estimate of frontal length is used) are closest to those of *D. confusum*, and the ratio of interorbital width to skull table width (F:G) is intermediate between *D. confusum* and *D. helogenes*. Furthermore, vomerine fang size and position in NSM 987 GF 99.1 are most like those of *D. helogenes*, the species to which it otherwise bears the least resemblance. Given this contradictory evidence, we have chosen to adopt a conservative position: NSM 987 GF 99.1 is assigned to *Dendrerpeton acadianum*, the species most commonly referred to in the literature. We agree with Milner that one specimen previously assigned to *D. acadianum* probably pertains to a cochleosaurid (see "Palate" above). However, in order to preserve Milner's *D. confusum* and *D. helogenes* as he diagnosed them, we would have to hypothesize that NSM 987 GF 99.1 represents yet another species with a mixture of characters seen in the other taxa. Although Milner's data are suggestive, more data will be needed to resolve more fully the taxonomy of the Joggins temnospondyls.

### The Phylogenetic Position of *Dendrerpeton*

The Dendrerpetontidae has been included traditionally within the primitive temnospondyl superfamily Edopoidea (Romer, 1947; Carroll, 1967). Milner (1980) subsequently pointed out that all characters shared with other families of the Edopoidea (Edopidae and Cochleosauridae) are plesiomorphic, and relegated the Dendrerpetontidae to Temnospondyli incertae sedis. More recently, Godfrey et al. (1987) argued that the family exhibits a primitive bauplan from which temnospondyls such as trimerorhachoids, edopoids, dissorophoids, and eryopoids could have evolved (see also Milner, 1990), although it shares no unequivocal synapomorphies with any of these groups. However, a recent phylogenetic analysis (Milner and Sequeira, 1993) hypothesizes the Dendrerpetontidae to be more derived than the Edopoidea. Although a limited number of taxa were used, their results suggest that the Dendrerpetontidae is the primitive sister-group of at least trimerorhachoids and eryopoids.

With the anatomy of *Dendrerpeton* on a secure footing, it is appropriate to reassess its place within Paleozoic temnospondyl phylogeny. However, this is not without difficulties despite new information. As with all Paleozoic groups, many temnospondyl taxa are represented by relatively few, usually incomplete specimens. Thus, many character states for particular taxa cannot be established. Although the Temnospondyli appears to be a reasonably coherent group (Milner, 1990), its specific relationships to other tetrapod groups have not been demonstrated convincingly (Panchen, 1991; Carroll, 1995). This presents difficulties in choosing the most appropriate outgroup, and renders the polarities of some of the characters used to establish internal relationships uncertain. Temnospondyls are an unusually diverse group, consisting of a large number of species (most recently estimated to number 160 genera; Milner 1990) adapted to a full range of terrestrial, aquatic, and in a few cases, even marine habitats. Unlike contemporary microsaurs and primitive amniotes, both of which were characterized by small body size, Paleozoic temnospondyls show a considerable size range. When studying a group with an established propensity for extended size range and rich adaptive diversity, it is always important to be alert to the possibility of convergence and parallelism. Particular care must be exercised in choosing characters for phylogenetic analysis.

Several characters used in recent analyses appear to be of questionable homology. For example:

1) Internarial fontanel. This character is common, but not ubiquitous, in dissorophids (being absent in *Anconastes*, *Ecolsonia*, and *Dissorophus*), suggesting a possible synapomorphy with *Dendrerpeton*. However, its sporadic occurrence in a wide variety of other temnospondyls, including zatrachydids, *Parioxys*, and even in some brachyopids and rhinosuchids (Watson, 1956, 1962), suggests that this character is of little use in establishing relationships.

2) Coronoid process. In early tetrapods, the coronoid process is absent on the lower jaw. It is present in some derived temnospondyls, although it can be formed by the surangular, posterior coronoid, or both, suggesting that it is not homologous throughout.

3) Gross skull proportions variously expressed as snout elongation and table shortening (e.g., Boy, 1990) are relative by their very nature, prone to subjective analysis, and in reality are different ways of expressing the same or closely correlated proportional changes. Snout elongation is a common trend in lower tetrapod evolution (e.g., embolomeres, archegosaurids), and is of limited use in phylogenetic analysis.

4) Shape of clavicles. In many temnospondyls, the ventral plate of the clavicle is a large triangular lamina that projects well anterior to its attachment to the clavicular stem. It may

reach the anterior end of the interclavicle. In other taxa, the ventral plate is more modest in size, expands much less medially, and does not reach the anterior end of the interclavicle. Although this variation in clavicle shape may represent a phylogenetic trend, with the more commonly seen large clavicles being the primitive condition, this configuration is usually associated with long-bodied forms with flat skulls bearing dorsally facing orbits (e.g., *Greererpeton*; *Saurerpeton*; *Trimerorhachis*; *Archegosaurus* Von Meyer, 1857; *Parotosuchus* Warren and Hutchinson, 1988), and may simply represent an adaptation to an aquatic way of life.

Other continuously variable proportional features may represent evolutionary trends in temnospondyls, but because either they are difficult to quantify or cannot be objectively assigned to classes, cannot be incorporated easily into a system that is designed to accommodate discrete character states. For example:

5) Relative size of interpterygoid vacuities. The relative size of the interpterygoid vacuities is extremely variable in temnospondyls. In the few cases where growth series are known (e.g., Credner, 1886; Boy, 1988; Warren and Hutchinson, 1988), increase in the dimensions of the vacuity appears to be isometric, so it is not surprising that many workers have attempted to utilize this character in phylogenetic analyses (e.g., Milner, 1980, 1990; Sequeira and Milner, 1993). Although quantification of this character is relatively straightforward, its continuous nature makes it impossible to break it up objectively into discrete size classes. Nevertheless, it is still possible to incorporate vacuity size into the analysis, since it is closely linked to the morphology of the vomers and pterygoid (characters 9, 13, and 14 below; Table 3) that can be defined less ambiguously.

6) Size of cleithrum. In most primitive tetrapods, the cleithrum is a light splint of bone adhering to the anterior border of the scapula (e.g., anthracosaurs, *Crassigyrinus*). It is only slightly expanded dorsally. In more derived temnospondyls, there is a tendency for the dorsal expansion to extend posteriorly over the suprascapula, and in some forms, completely cap it. However, the cleithrum is not preserved in many temnospondyls. In derived groups where it is preserved, (e.g., dissorophoids), it is the larger taxa (e.g., *Cacops* Williston, 1910) that show the largest cleithra; the smaller taxa (e.g., *Amphibamus* (Carroll, 1964a)) show the "primitive" condition, suggesting that its relative size and development may be related at least partly to absolute size or growth (ontogenetic data in *Sclerocephalus* Meckert, 1993 suggest the latter).

### Characters Used in the Analysis

Although a complete phylogenetic analysis of temnospondyls is beyond the scope of this paper, it is necessary to place *Dendrerpeton* within a phylogenetic framework. To this end, we have attempted to identify characters that clarify its position with respect to the major taxa within the order. A number of particularly well-described taxa, each representing a different family of Paleozoic temnospondyls, have been scored (Table 3) using the following sources: *Chenoproscopus* and *Zatrachys* (Langston, 1953), *Edops* (Romer and Witter, 1942), *Capetus* (Sequeira and Milner, 1993), *Balanerpeton* (Milner and Sequeira, 1994; Sequeira, in press; Watson, 1956), *Saurerpeton* (Milner, 1982; Romer, 1947), *Eryops* (Case, 1911; Miner, 1925; Sawin, 1941), *Parioxys* (Carroll, 1964b; Moustafa, 1955), *Sclerocephalus* (Boy, 1988; Meckert, 1993; Watson, 1962), *Eoscopus* (Daly, 1994). Characters were polarized using both *Greererpeton* (Godfrey, 1989) and *Proterogyrinus* (Holmes, 1984) as outgroups.

The following characters have been included in the analysis because, unlike the characters listed above, they are binary and/

TABLE 3. Data matrix showing the distribution of 18 characters and their states in 14 representative temnospondyls. Characters represented by numbers are identified and discussed in the text.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 <i>Chenoprosopus</i>	1	1	1	0	1	1	?	0	0	0	0	0	0	0	0	0	?	0
2 <i>Edops</i>	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	?	0
3 <i>Dendrerpeton</i>	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
4 <i>Balanerpeton</i>	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
5 <i>Trimerorhachis</i>	1	1	0	1	0	0	1	1	0	1	—	0	1	0	0	0	0	0
6 <i>Capetus</i>	1	1	0	0	0	0	?	1	1	0	0	0	0	0	?	0	?	0
7 <i>Eryops</i>	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	1	1	0
8 <i>Greererpeton</i>	0	0	0	1	0	0	0	0	0	—	—	0	—	—	0	0	0	0
9 <i>Proterogyrinus</i>	0	0	1	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0
10 <i>Saurerpeton</i>	1	1	1	1	0	0	1	0	1	1	—	0	1	1	?	0	0	0
11 <i>Paryoxys</i>	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1
12 <i>Zatrachys</i>	1	1	0	0	1	0	?	1	0	1	0	0	0	0	1	1	?	1
13 <i>Eoscopus</i>	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1
14 <i>Sclerocephalus</i>	1	1	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0

or discrete, generally do not occur in taxa outside the analysis, are consistent within each taxon, and can be scored in most or all taxa.

1) Small, laterally facing external naris with its ventral rim located very close to the jaw margin (i.e., distance between its ventral rim and the jaw margin less than the diameter of the opening) (0). Large, dorsolaterally facing external naris (with the distance between its ventral rim and the jaw margin greater than the diameter of the opening) (1) (Milner and Sequeira, 1994). Laterally placed external nares set close to the jaw margin occur in a variety of primitive tetrapods including colosteids, loxommatids (Beaumont 1977), anthracosauroids, and *Ichthyostega* (Jarvik 1980), and is almost certainly a primitive condition for tetrapods. All temnospondyls are characterized by larger external nares that have migrated to some extent dorsally away from the jaw margin.

2) Interpterygoid vacuities narrow and slit-like or absent (0). Interpterygoid vacuities rounded and well developed (1). The presence of well-developed, rounded interpterygoid vacuities is accepted as one of the diagnostic characters of temnospondyls (Milner and Sequeira, 1994).

3) Ectopterygoid forms part of the border of the subtemporal fenestra (0). Pterygoid-jugal contact excludes ectopterygoid from subtemporal fenestra (1). This character is directly linked to the specific interrelationship of the maxilla, quadratojugal, and jugal. Primatively, the maxilla maintains contact with the quadratojugal, excluding the jugal from the ventral margin of the cheek and preventing the formation of a jugal-ptyergoid contact. In some derived forms, the maxillary-quadratojugal contact is lost, exposing the jugal along the ventral cheek margin and permitting a contact between the ventromedial edge of the jugal and the lateral edge of the pterygoid. This character, in combination with a closed parietal foramen in large individuals, muted sculpturing on depressed areas of the skull, and triangular, anteriorly broad choanae, supports the monophyly of the Cochleosauridae (Godfrey and Holmes, 1995). This condition also occurs in at least some saurerpetontids (Romer, 1947; Foreman, 1990), and anthracosaurs (Panchen, 1970; Holmes, 1984; 1989), suggesting that it is prone to convergence.

4) Squamosal embayment present (0). Embayment absent (1). The embayment, present in many Paleozoic amphibians, is generally considered to be derived from the spiracular cleft of sarcopterygians. This implies that it is a primitive tetrapod character (Clack, 1993), and its absence in some aquatic temnospondyls such as trimerorhachoids is secondary (e.g., Milner, 1980). However, this interpretation has been complicated by the traditional assumption that the embayment supported a tympanum (e.g., Romer, 1947), which in turn implied the presence of

a sound-conducting stapes. Within this paradigm, the presence of a large hyomandibula-like stapes in the primitive, embaymentless tetrapod *Greererpeton* was interpreted as indicating that reception of air-borne sound did not arise with the first tetrapods (Carroll, 1980). Subsequent discoveries of large stapes clearly unsuitable for conducting air-borne vibrations in a variety of embayment-bearing Paleozoic tetrapods (Clack, 1983, 1989) has forced a decoupling of structure and hypothesized function. With the breakdown of a functional connection between the presence of an embayment and perception of air-borne sound, the purported late appearance of an impedance matching middle ear ceases to have a bearing on the polarity of the embayment. Rather than functioning in hearing, the embayment may have supported a functional spiracle in the first tetrapods (Clack, 1989, citing Carroll). This hypothesis is consistent with the wide distribution of the embayment in primitive tetrapods regardless of stapes structure, and supports the suggestion that its presence is plesiomorphic.

However, the squamosal embayment of temnospondyls may nevertheless have supported a tympanum. The embayment of embolomeres, *Crassigyrinus*, and loxommatids presents a triangular outline in lateral view that is roughly comparable to the configuration in rhipidistian fish such as *Eusthenopteron*, suggesting that it represents a spiracular cleft (functional, larval, or vestigial). In contrast, the embayment of temnospondyls has a broadly curved margin (Fig. 10), although positive allometric growth of the suspensorium in larger taxa such as *Eryops* tends to obscure this. This shape, although difficult to quantify satisfactorily, appears to be unique among Paleozoic amphibians, and may indicate that, unlike most if not all other contemporary amphibians, temnospondyls had a functional tympanum.

Establishing the morphology of the stapes would help to corroborate this hypothesis, but this element is not preserved in many taxa (e.g., of the 14 taxa in this analysis, it is known only in *Edops*, *Dendrerpeton*, *Balanerpeton*, *Trimerorhachis*, *Sclerocephalus*, *Eryops*, and *Greererpeton*). In the notchless *Greererpeton* (here designated an outgroup), it shows the putative primitive form, bracing the braincase against the suspensorium (Carroll, 1980). In all other taxa included in this analysis except *Dendrerpeton*, it is smaller, lighter (although there is considerable variation in size, in all cases it is much larger than the stapes of a modern alligator with an equivalent sized skull), and apparently directed towards the center of the embayment as would be predicted if it were an impedance-matching ear ossicle. *Dendrerpeton* and *Trimerorhachis* are anomalous, the former in possessing a primitive stapes (Clack, 1983) despite the presence of a rounded embayment, the latter in possessing a small, possibly sound-conducting stapes while possessing a

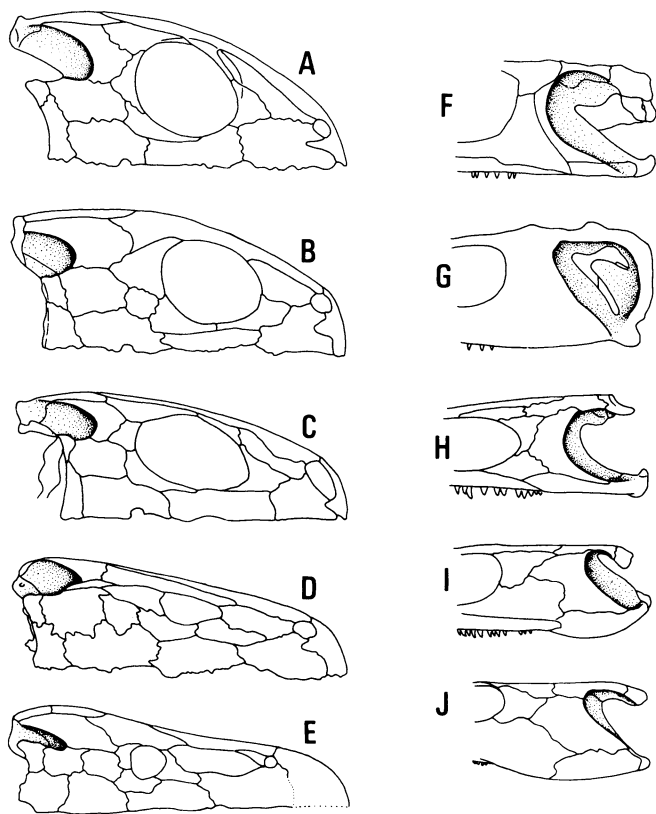


FIGURE 10. The otic region of selected temnospondyls in dorsal (A–E) and lateral (F–J) views. The region of the squamosal embayment is stippled for emphasis. A and H, *Eoscopus* (from Daly, 1994). B, *Balanerpeton* (from Milner and Sequeira, 1994). C, *Doleserpeton* (from Bolt, 1969). D and I, *Dendrerpeton*. E and J, *Cochleosaurus* (from Godfrey and Holmes, 1995; and personal observation). F, *Dissorophus* (from Carroll, 1964a). G, *Cacops* (from Willison, 1910).

very shallow embayment. The orientation of the stapes in *Dendrerpeton* is unknown. However, the shape of the associated embayment suggests that it may nevertheless have functioned (presumably inefficiently) as an ear ossicle. If, as Clack (1992) suggests, a sound-conducting stapes and tympanic notch evolved in the first temnospondyls as part of a general adaptation to a terrestrial habitus, then the trimerorhachoid condition can be interpreted as the loss of the tympanum and retention of a (?nonfunctional) ear ossicle in a secondarily aquatic lineage. Recent reinterpretation of the otic region of trimerorhachoids, indicating that an embayment was present primitively, but lost in more derived members of the group (Sequeira and Milner, 1996), supports this hypothesis.

Two analyses were performed with respect to the form of the stapes: one included stapes morphology, the other did not. The resulting tree topologies were the same (i.e., data on stapes morphology does not affect the analysis). This character was therefore omitted from the analysis.

5) Simple, rectangular premaxilla not projecting far anterior to the external naris (0). Anteroposteriorly elongated premaxilla extending at least 15% of the total skull length anterior to the naris (1). Most temnospondyls conform to the primitive state. The derived state appears to be restricted to edopoids (sensu Godfrey and Holmes, 1995; Milner and Sequeira, 1994).

6) Lacrimal forms part of the orbital margin (0). Lacrimal is excluded from the orbital margin by a jugal-prefrontal contact (1). This character, in one form or another, has been used in

most recent phylogenetic analyses of temnospondyls (e.g., Boy, 1990; Milner, 1990; Milner and Sequeira, 1994; Sequeira and Milner, 1993). The exclusion of the lacrimal from the orbital margin appears to be correlated with snout elongation in some primitive tetrapods. This occurs in most embolomeres (only in the relatively short-faced *Proterogyrinus* and *Gephyrostegus* does the lacrimal enter the orbit), eryopoids, and edopoids. However, orbital exposure of the lacrimal is maintained in relatively long-snouted taxa such as *Capetus* and trematopids. Furthermore, in the few cases where reasonably complete growth series are known (e.g., *Sclerocephalus*) there is no evidence of ontogenetic exclusion of the lacrimal from the orbital margin during snout elongation. This suggests that, although the exclusion of the lacrimal from the orbital margin may be prone to convergence, it can corroborate relationships supported by other characters.

7) Entepicondylar foramen present (0). Entepicondylar foramen absent (1), see Milner and Sequeira (1994). The derived state appears to diagnose a clade comprising at least eryopoids, dissorophoids, and trimerorhachoids. However, in many taxa, the humerus is not preserved, limiting the usefulness of this character.

8) Alar process of premaxilla absent (0). Alar process of premaxilla present (1). The possession of this small triangular process lying over the nasal appears trivial, but is apparently a consistent character of more derived temnospondyls. This character, along with characters 1 and 2 above, were presented as a single character in Milner and Sequeira (1994). However, since there is no obvious functional or phylogenetic connection between them, they are treated as discrete characters.

9) Septomaxilla forms part of the external surface of the snout (0). Septomaxilla lies completely within the naris (1). This feature has been defined variously as a sculptured triangular septomaxillary sutured into the dermal roof of the snout (Milner 1980; Godfrey et al., 1987), a free septomaxillary in the naris (Sequeira and Milner, 1993) and a septomaxilla with a dermal portion (Boy, 1990).

10) Vomers excluded from the rim of the interpterygoid vacuities by parasphenoid and/or pterygoids (0). Vomers form anterior margins of the vacuities (1). The state of this character no doubt correlates with the size of the vacuity, but unlike the latter, it is possible to describe the presence or absence of a vomerine contribution as discrete states.

11) Embayment supported ventrally by the squamosal (0). Enlarged embayment supported in part by the quadratojugal and/or quadrate (1). In most temnospondyls possessing an embayment, it is supported dorsally by the supratemporal (and sometimes tabular) and anteriorly and ventrally by the squamosal. Its shape and size are not unlike those of *Balanerpeton* (Fig. 10B) and to a lesser extent the more distantly related *Cochleosaurus* (Fig. 10E, J). However, in *Dendrerpeton* and *Eoscopus*, the ventral margin of the enlarged embayment extends onto the quadratojugal and turns medially onto the quadrate. This morphology occurs in other dissorophoids (Milner, 1980; Fig. 10), and may represent a synapomorphy. However, this morphology also tends to occur in other small skulls (e.g., *Branchiosaurus*; Boy, 1976), and may be pedomorphic.

12) Quadrate bears no pronounced process dorsal to the medial condyle (0). Quadrate bears a dorsally or anterodorsally directed process dorsal to the medial condyle (1) (Bolt, 1969). In some dissorophoids (e.g., *Cacops* and *Acheloma*), this process forms a large anterodorsally directed flange that reaches the posteroventral process of the tabular to close the squamosal embayment from behind. In most other (generally smaller) taxa (*Tersomius*, *Ecolsonia*, *Phonerpeton*, *Micropholis*), the process is little more than a simple knob. *Dendrerpeton* bears on its quadrate a protuberance very similar to that seen in smaller dissorophoids. However, absence of complex morphology pro-

vides little basis for the detailed comparisons necessary to establish homology with any degree of certainty.

13) Palatal ramus of pterygoid reaches at least as far anteriorly as the anterior margin of the interpterygoid vacuity (0). Palatal ramus of pterygoid does not extend to the anterior end of the vacuity (1). The posterior retreat of the palatal ramus of the pterygoid (Milner, 1990) may have evolved in association with increasing size of the interpterygoid vacuities (all taxa showing this feature also have large vacuities), although some taxa with large vacuities (e.g., *Balanerpeton* and *Dendrerpeton*) show the primitive condition.

14) Palatine bordered medially by the pterygoid, excluding it from the interpterygoid vacuity margin (0). A pterygoid-vomer contact is absent, permitting the palatine to form part of the border of the vacuity (1). The incorporation of the palatine into the vacuity rim is correlated with the shortening pterygoid (see character 13). However, in trimerorhachids and *Dvinosaurus* (Bystrow 1938), a posterior process of the vomer maintains contact with the posteriorly retreating pterygoid, resulting in the retention of the plesiomorphic condition (Milner, 1990). Both the retreat of the pterygoid (character 13) and exposure of the palatine on the vacuity margin occur in the possibly neotenic branchiosaurs *Branchiosaurus* and *Micromelerpeton* (Boy, 1971; 1976), suggesting that these features are paedomorphic, and as such capable of evolving in distantly related adults sharing a common larval bauplan. Although the derived state is shared by saurerpetontids and most dissorophoids, at least *Phonerpeton*, *Anconastes*, and *Ecolsonia* show the primitive condition. Although this may represent a reversal, it is also possible that the derived condition evolved independently within several dissorophoids, underscoring the need to use this character cautiously.

15) Occipital condyle formed mostly by basioccipital (0). Occipital condyle formed mostly by exoccipitals (bilobed) (1). The derived condition occurs in *Eryops*, *Parioxys*, *Sclerocephalus*, *Zatrachys*, and *Eoscopus* (Milner, 1990), and with character 16 (absence of the intertemporal; see below) supports the monophyly of this clade.

16) Intertemporal present (0). Intertemporal absent (1). This character has long been included in discussion of temnospondyl evolution and relationships (e.g., Romer, 1947). However, the loss of the intertemporal bone has occurred in other tetrapod groups. For example, most specimens of the primitive colosteid amphibian *Greererpeton* lack it, although it is present on one side of at least one specimen (Smithson, 1982). It is present in the primitive loxommatid genera *Loxomma* and *Baphetes*, but has been lost in the more derived *Megaloscephalus* (Beaumont, 1977). The same trend occurs in saurerpetontids (the primitive *Saurerpeton* has an intertemporal (Romer, 1947), while the more derived *Acroplous* (Foreman, 1990), does not). The apparent ease with which this bone is lost suggests that its absence may be a convergent feature in several groups of temnospondyls (compare Boy, 1990 with Milner and Sequeira, 1994 for opposing views of the significance of this feature). Nevertheless, it is congruent with other features (loss of the entepicondylar foramen, elaboration of a double occipital condyle) and is accepted as a synapomorphy of derived temnospondyls.

17) Iliac blade distally tapered and posterodorsally directed (0). Iliac blade short and expanded dorsally (1). It should be noted that the form and orientation of the blade can change somewhat during growth or simply exhibits individual variation (e.g., Carroll, 1967:fig. 16; Boy, 1972:fig. 49), or may be partly size related, since within at least dissorophoids, short, expanded blades occur most commonly in large taxa.

18) Squamosal and tabular separated by a lateral flange of the supratemporal (0). Squamosal-tabular contact attained laterally or ventrolaterally to the supratemporal (Boy, 1990). This feature, seen in almost all dissorophoids (except the paedo-

morphic or larval *Doleserpeton* (Bolt, 1969) and some specimens of *Tersomius* (Daly, 1994)), is correlated with the development of the diagnostic supratympanic flange (Bolt, 1974a). However, a similar configuration also occurs in a number of non-dissorophoid taxa (e.g., zatrachyids and *Parioxys*) in the absence of a supratympanic flange. In saurerpetontids, in which the squamosal embayment is lacking, the posterodorsal corner of the squamosal approaches the tabular. In one juvenile specimen, a contact between the two bones is established (Milner, 1982), but in larger specimens, the tabular becomes relatively smaller, and the contact does not appear to persist to adulthood (Foreman, 1990; Romer, 1947).

### Phylogenetic Analysis

The data matrix (Table 3) was assembled using MacClade 3 (Maddison and Maddison, 1992). Both *Proterogyrinus* and *Greererpeton* were designated as outgroups. The matrix was processed using PAUP 3.1 (Swofford, 1993) using the ACCT-RAN option and branch and bound search setting. Three shortest trees of 34+ steps and a C.I. of 0.53 were generated (Fig. 11).

Although the interrelationships of *Dendrerpeton*, *Balanerpeton*, and trimerorhachoids are not resolved in a strict consensus tree (Fig. 11d), the analysis generally supports the hypothesis (Milner and Sequeira, 1994) that *Dendrerpeton* is the primitive sister-group of trimerorhachoids and eryopoids. However, *Dendrerpeton* moves up the comb and with *Balanerpeton* forms the sister-group of all "higher temnospondyls." This occurs because (unbeknownst to Milner and Sequeira, 1994) it shares with these taxa an alar process of the premaxilla (character 8; reversed in *Saurerpeton* and *Parioxys*). In addition to the alar process, *Dendrerpeton* shares with "post-edopoid" temnospondyls a septomaxilla not incorporated into the external surface of the snout (character 10; reversed in *Trimerorhachis* and *Zatrachys*), and with all but the most plesiomorphic "post-edopoid" temnospondyl, *Capetus*, vomers that form part of the margin of the interpterygoid vacuities (character 9; reversed in *Parioxys*). However, this hypothesis is supported by few characters, two of which have been reversed in some derived taxa, and must be viewed as tentative.

### *Dendrerpeton* and the Dissorophoidea

*Dendrerpeton*, with its large skull and short trunk, absence of lateral line canals, large, laterally facing orbits, deep squamosal embayment, well-developed limbs and generally terrestrial appearance, is strikingly similar to many dissorophoids. It is therefore not surprising that some form of relationship has been hypothesized (e.g., Carroll, 1967; Milner, 1980). Although diagnosis of the Dissorophoidea is not without difficulties, the following derived characters are present in most or all members (see Dilkes, 1990): 1) a median narial flange formed from contributions of the nasal, prefrontal, and lacrimal; 2) a dorsally or anterodorsally directed quadrate process, (apparently associated with a posteromedial process of the quadratojugal (Bolt, 1969)); 3) a large otic notch with a supratympanic flange; 4) lateral exposure of the palatine, ectopterygoid, or both to form part of the ventral margin of the orbit; and 5) a semilunar curvature on the ventral surface of the squamosal to form a convexity that projects into the otic notch. In addition, the presence of a ventral prefrontal process forming part of the anterior wall of the orbit medial to the lacrimal and articulating ventrally with the palatine has been proposed as a synapomorphy of dissorophids (Daly, 1994), but this feature also occurs in other Paleozoic amphibians (Bolt, 1974b), making its taxonomic significance uncertain.

An internarial fenestra is present in many dissorophoids. However, it is absent in at least *Anconastes* (Berman et al.,

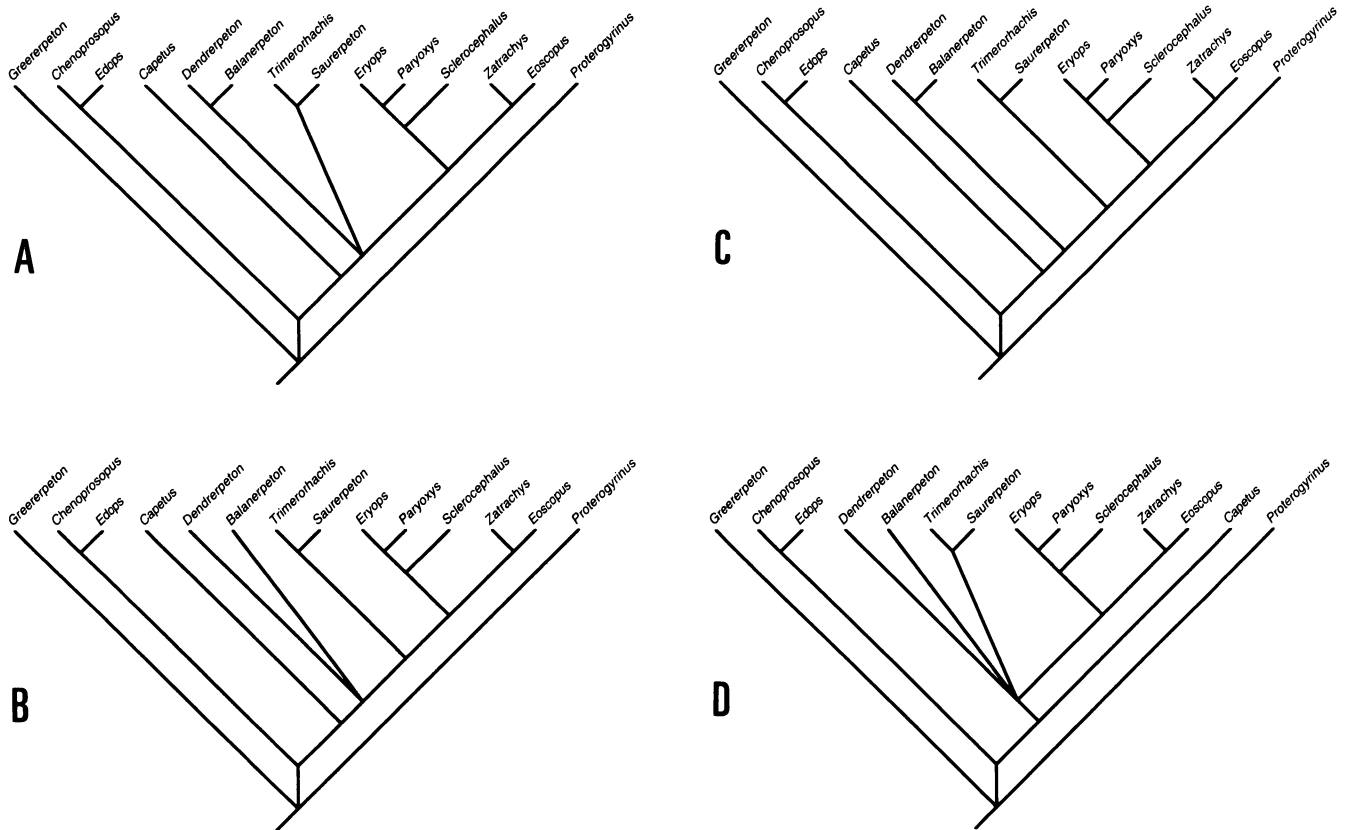


FIGURE 11. Hypothesis of relationships of selected Paleozoic temnospondyls. A–C, Shortest trees, 34+ steps, C.I. of 0.53. D, Strict consensus tree (50 percent majority rule tree is identical to C).

1987), *Ecolsonia* (Berman et al., 1985), *Cacops* (Williston, 1910), and *Tersomius texensis* (Carroll, 1964a), and appears sporadically in a variety of non-dissorophoids (e.g., zatracheids (Langston, 1953; Boy, 1989); some branchiosaurs (Boy, 1986; 1987); *Parioxys* (Moustafa, 1955); *Crassigyrinus* (Panchen, 1985); and rhinosuchids (Watson, 1962)). Although this in itself does not prove that the character was not uniquely derived within dissorophoids (Dilkes, 1990, for example, uses it to diagnose the trematopsid clade *Acheloma*+*Phonerpeton*), it is of limited use unless supported by other, more consistent synapomorphies.

*Dendrerpeton* does not possess dissorophoid characters (4) and (5). The otic notch, although large, lacks a supratympanic flange (3). The presence of a narial flange (1), a character unique to dissorophoids (Dilkes, 1990), cannot be confirmed on the basis of the preserved material. The only potential synapomorphy is the presence of an incipient dorsal quadrate process (2). The quadratojugal wraps around the posterior surface of the quadrate, but does not extend under the quadrate process, and so is not closely comparable to the condition in dissorophids. Posteromedial development of the quadratojugal is known in other amphibian groups (e.g., *Cochleosaurus* (Godfrey and Holmes, 1995); *Parioxys* (Moustafa, 1955)) and its presence in *Dendrerpeton* may be of no taxonomic significance. An internarial fenestra is present, but as noted above, its significance in the taxonomy of dissorophoids is uncertain. Hence, *Dendrerpeton* cannot be included within the Dissorophoidea as it is presently defined, nor does phylogenetic analysis support a sister-group relationship between *Dendrerpeton* and dissorophoids (Fig. 11). Various attempts to establish this relationship have no doubt been prompted by general or superficial similarities. For example, the short, broad snout, large orbits, and large

otic notch all produce a superficial resemblance to some members, in particular of the family Amphibamidae. These features, also present in a variety of “branchiosaurs” (Boy, 1972) are arguably associated with small size. In typical “long-snouted” temnospondyls for which we have ontogenetic data (e.g., “*Branchiosaurus*” and *Archegosaurus* (Romer, 1939)), these features disappeared as the skull grew (orbits and notch become smaller, and the snout elongates and becomes narrower). It has been pointed out by Milner (1980) that these trends are not exhibited by *Dendrerpeton*. Although the orbits become somewhat smaller as the animal grew, the snout does not elongate, and the notch grows at about the same rate as the rest of the skull. Although it is possible that the skull of *Dendrerpeton* was constrained to dissorophoid-like proportions during growth, and this in turn indicates a dissorophoid-*Dendrerpeton* relationship, this argument is based on overall similarity rather than specific characters, and is in itself unconvincing. Large interpterygoid vacuities, although common to *Dendrerpeton* and dissorophoids (Milner, 1980), are found in a variety of unrelated amphibian groups. Since the development of lateral exposure of the palatine and/or ectopterygoid in dissorophoids was presumably correlated with reduction and ultimate truncation of the anterior (suborbital) ramus of the jugal (which in turn correlates with the presence of large orbits), the slender suborbital ramus in *Dendrerpeton* is suggestive of dissorophoid affinities (Milner, 1980). Nevertheless, the ramus is always complete, and neither palatal element is ever exposed laterally. Therefore, despite the presence of large, laterally-facing, superficially dissorophoid-like orbits, no discrete diagnostic character associated with the orbit can be identified.

*Dendrerpeton* also resembles some dissorophoids with re-



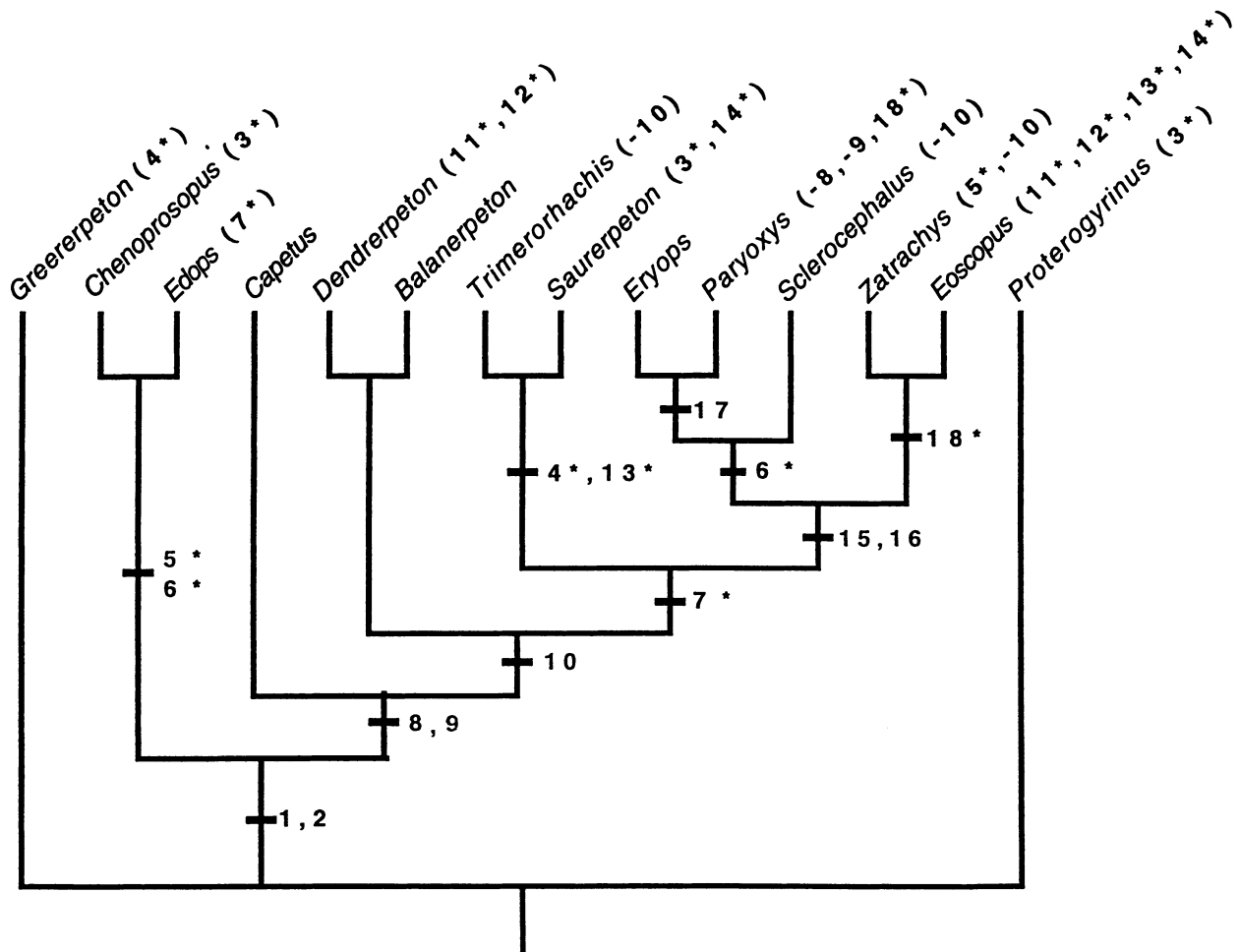


FIGURE 12. Distribution of characters from Table 3 on majority rule consensus tree. \* indicates homoplasy, – indicates character reversal.

spect to vertebral structure. In particular, the pleurocentral halves approach each other ventrally in the anterior part of the presacral column. However, this feature is quite variable in dissorophoids, ranging from typically rhachitinous in *Micropholis* to fully gastrocentrous in *Doleserpeton*. A presacral count of 24 segments falls within the typical dissorophoid count of 26 or fewer, but some non-dissorophoid temnospondyls also have short columns (e.g., *Eryops* (Moulton, 1974) and *Balanerpeton* (Milner and Sequeira, 1994); with 22 and 24 respectively). Other proportional similarities such as long, well-ossified limbs (Berman et al., 1985), although contributing to an overall similarity to dissorophoids, are difficult to quantify objectively, and in any case can be explained plausibly as convergence in animals with similar ways of life.

In summary, the present phylogenetic analysis suggests that similarities between *Dendrerpeton* and dissorophoids (including some characters used in this analysis (see Fig. 12)) represent homoplasies and that *Dendrerpeton* is better considered the primitive sister-group of an as yet poorly defined clade consisting of temnospondyls above the edopoid (Edopidae and Cochleosauridae) level. Its generalized anatomy makes it a suitable ancestral morphotype for trimerorhachoids and/or eryopoids (sensu Carroll, 1988), but the present lack of convincing synapomorphies makes it impossible to propose a more precise hypothesis of relationship.

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#### APPENDIX 1. Abbreviations used in illustrations.

**ang**, angular; **art**, articular; **asp**, anterior splenial; **c1–c3**, centralia 1–3 of carpus; **car**, foramen for carotid artery; **cl**, clavicle; **cle**, cleithrum; **d**, dentary; **dc 1–4**, distal carpals; **ec**, ectopterygoid; **entf**, entepicondylar foramen; **f**, frontal; **h**, humerus; **ic**, intercentrum; **icl**, interclavicle; **inf**, internarial fontanel; **iptv**, interpterygoid vacuity; **it**, intertemporal; **j**, jugal; **Mf**, Meckelian fenestra; **mndf**, mandibular foramina; **n**, nasal; **na**, neural arch; **p**, parietal; **pa**, parasphenoid; **paf**, para-articular fossa; **pal**, palatine; **pc**, pleurocentrum; **pf**, prefrontal; **pm**, premaxilla; **pof**, postfrontal; **posp**, postsplenial; **pp**, postparietal; **pra**, prearticular; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, radius; **re**, radiale; **sc**, scapulocoracoid; **sm**, septomaxilla; **sq**, squamosal; **sqem**, squamosal embayment; **st**, supratemporal; **t**, tabular; **u**, ulna; **ule**, ulnare; **v**, vomer.