INTRODUCTION

To date, few skeletal remains of tetrapods have been recovered from the Norian- to Rhaetian-age continental strata of the Newark Supergroup in eastern North America. It has always been assumed that these red clastic deposits are largely devoid of vertebrate fossils, and thus they have almost never been systematically prospected for such remains. During a geological field-trip in March 1995, P.E.O. discovered the partial skull of a small archosaurian reptile in the lower part of the New Haven Formation (Norian) of the Hartford basin (Newark Supergroup; Fig. 1) in Cheshire, Connecticut. Preparation of this specimen demonstrated that it is referable to Erpetosuchus Newton, 1894, which was previously known only from a skull and partial postcranial skeleton from the Lossiemouth Sandstone Formation of northeastern Scotland (Benton and Walker, 1985). Erpetosuchus provides an important new link between assemblages of Late Triassic continental tetrapods from eastern North America and western Europe.

The new fossil was preserved in a red sandy mudstone, which forms part of a sequence of gray, buff, and brown sedimentary deposits of a meandering river alternating with red overbank sediments (Horne et al., 1993; McInerney, 1993). The mudstone is intensely bioturbated by roots and invertebrate burrows (Scoyenia) and passes upward into caliche-bearing red sandy mudstone. This sequence comprises a typical paleosol profile in the lower New Haven Formation (McInerney, 1993).

Previously described reptilian skeletal material from the New Haven Formation comprises the holotype (natural mold of the dorsal dermal armor) of the stagonolepidid Stegomasus arcuatus Marsh, 1896 (middle New Haven Formation; Lucas et al., 1998), the scapula of an indeterminate phytosaur (“Belodon validus” Marsh, 1893; middle New Haven Formation), the partial skull of an indeterminate sphenodontian (Sues and Baird, 1993; upper New Haven Formation), and a skull and partial postcranial skeleton of the procolophonid Hypsognathus fenneri (Sues et al., 2000; probably from upper New Haven Formation).

The stratigraphic age of the Connecticut record of Erpetosuchus has been constrained as Norian by three independent lines of evidence. First, the basal portion of the New Haven Formation has yielded a palyno-boreal assemblage from the lower New Haven Formation (Denison, 1993). Second, using U-Pb dating, Wang et al. (1998) determined the age of pure pedogenic micritic calcite extracted from the fossil-bearing horizon as 211.9 ± 2.1 Ma, placing it in the Norian stage on recent geological time-scales (Gradstein et al., 1995; Kent and Olsen, 1999).

Third, Lucas et al. (1998) synonymized Stegomasus with Aetoso-aurus and considered the latter taxon an index fossil for continental strata of early to middle Norian age. As discussed elsewhere, we regard this as the weakest line of evidence (Sues et al., 1999).

DESCRIPTION

The fossil from Cheshire is now housed in the collections of the American Museum of Natural History, where it is cataloged as AMNH 29300. It comprises most of the right facial portion of the skull, with much of the right mandibular ramus preserved in tight occlusion, associated with several poorly preserved vertebrae and fragments of indeterminate bone (Fig. 2). The skull roof, rostral tip of the snout, left side of the face, most of the palate and the left mandibular ramus were not preserved. Slight crushing resulted in displacement of the bones forming the temporal region of the skull, and the squamosal is incompletely preserved. During preparation, the originally exposed, already weathered left side of the specimen was embedded in clear epoxy resin and then the better preserved right side was carefully exposed by mechanical preparation. We estimate the length of the skull to have been between 65 and 70 mm.

The long but low skull was transversely broad and rounded behind the orbits but narrow in the rostral region. The quadratojugal is flat, anterolaterally inclined. The long dorsal process of the latter bone extends anterodorsally along the posterior margin of the triangular infratemporal fenestra. The quadrate and quadratoid jugal are overhung posterolaterally by the squamosal, enclosing between them a distinct recess (“otic notch”). The triradiate jugal is deep below the gently rounded ventral margin of the enormous orbit and forms the posteroventral corner of the antorbital fossa. Its preorbital and postorbital processes diverge considerably from each other, and its slender infratemporal process tapers to a point posteriorly.

The perimeter of the large antorbital fossa is marked by distinct bony ridges. The thin anteromedial wall of the fossa, formed by the ascending process of the maxilla, is marked by irregular, shallow depressions. The lateral surfaces of the maxilla and the portion of the jugal below the orbit form a broad lateral shelf with a narrow, dorsolaterally facing surface and a broad, obliquely ventrally and slightly laterally facing surface. These two surfaces meet laterally to form a prominent ridge. The maxillary tooth row is confined to the anterior end of the maxilla
FIGURE 1.  A, stratigraphic division of the Late Triassic–Early Jurassic strata of the Hartford basin (Newark Supergroup) in Connecticut and Massachusetts.  B, geological map of the Hartford basin.

and is deeply inset from the lateral margin of the skull. It comprises only five or six teeth. The first tooth, just posterior to the suture between the maxilla and premaxilla, was only preserved as an impression, and the second, fourth, and fifth are represented by complete crowns. The recurved, conical crowns of the preserved teeth are oval rather than labiolingually flattened in transverse section. Anteriorly, the maxilla forms a nearly vertical sutural contact with the premaxilla, a small fragment of which is preserved.

The mandibular ramus is slender and has a long, low external mandibular fenestra. A distinct lateral ridge curves from the ventral margin of the ramus just behind the external mandibular fenestra to the posterior end of the lower jaw, delimiting an obliquely ventrolaterally facing surface formed by the surangular, angular, and presumably prearticular.

The partial skull AMNH 29300 is remarkably similar to the skull of the holotype of Erpetosuchus granti (Natural History Museum, London, BMNH R3139) from the Lossiemouth Sandstone Formation of northeastern Scotland (Newton, 1894; Benton and Walker, 1985). We refer AMNH 29300 to Erpetosuchus because it exclusively shares the following apomorphies with E. granti among known archosaurian reptiles: (1) maxillary tooth row restricted to the anterior end of the maxilla; (2) jugal forms a broad lateral shelf with a narrow, dorsolaterally facing surface and a broad, obliquely ventrally and slightly laterally facing surface; (3) perimeter of large antorbital fossa formed by prominent bony ridges; and (4) presence of lateral ridge on the postdentary portion of the mandibular ramus behind the external mandibular fenestra. There are several minor differences between the two skulls, such as the relatively smaller antorbital fenestra, the more gently rounded ventral margin of the orbit, and the size of the maxillary teeth in AMNH 2930. They probably reflect individual variation and preservational features rather than taxonomically significant characters, and we identify AMNH 29300 as Erpetosuchus sp.

FIGURE 2. Partial skull and mandible of Erpetosuchus sp., AMNH 29300, in right lateral view. The first maxillary tooth was preserved only as an impression in the matrix. **Abbreviations:** an, angular; ao.f, antorbital fenestra; d, dentary; j, jugal; l, lacrimal; lt.f, infra-or laterotemporal fenestra; m, maxilla; m.f, external mandibular fenestra; or, orbit; pm, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal. Scale bar equals 1 cm.

The phylogenetic relationships of Erpetosuchus have remained unresolved since the original description of E. granti by Newton (1894). Most authors (e.g., Romer, 1956) referred Erpetosuchus to the Thecodontia. Since the pioneering phylogenetic analysis by Gauthier (1984), most authors have considered “Thecodontia” a paraphyletic assemblage of only distantly related basal archosaurian taxa. Walker (1968) noted the crocodile-like configuration of the temporal region of the skull in Erpetosuchus and placed it, along with the poorly known Dyoplax arenaceus from the Upper Triassic Schilfsandstein of southern Germany, in a suborder Erpetosuchia of his order “Crocodilomorpha” [sic]. Subsequently, Walker (1970:367) considered Erpetosuchus “a pseudosuchian at best only distantly related to crocodiles,” and interpreted its skull as displaying “a remarkable example of convergence towards the crocodilian condition in the attitude of the quadrate and formation of an otic notch” (Walker, 1970:368). However, neither
of Walker’s hypotheses has ever been tested in a rigorous phylogenetic fashion.

A numerical cladistic analysis, using the exhaustive search option of PAUP (version 3.1.1; Swofford and Begle, 1993) and based on 33 characters and 7 taxa (see Appendix 1 and Table 1), yielded a single most parsimonious tree with a length of 44 steps, a Consistency Index (CI) of 0.795 (CI excluding uninformative characters: 0.757), and a Retention Index (RI) of 0.727. Stagonolepis was used as the outgroup. Character-states for *Erpetosuchus* were scored using the original account by Olsen (1989), a reconstruction of the skull published by Walker (1970:fig. 12D), and inspection of new casts of the holotype. Interpretation of the skull of *E. granti* is complicated by the fact that the specimen is preserved as a natural mold. Most of the cranial sutures shown in Walker’s reconstruction are not evident on the casts examined by us, and thus we could not verify many of his interpretations.

In our analysis, *Erpetosuchus* is the proximate sister-taxon of Crocodylomorpha (Fig. 3). Unambiguous synapomorphies linking *Erpetosuchus* and Crocodylomorpha are medial contact of the maxillae to form a secondary bony palate (3.1), absence of a postfrontal (8.1), and parietals fused without a trace of an interparietal suture (15.2). However, increasing tree length by only two steps to 46, we obtained a polytomy that only retained the interparietal suture (15.2). In our analysis, *Erpetosuchus* has a longer biostratigraphic range than previously assumed, persisting across the Carnian-Norian boundary. Third, the actual age of the Lossiemouth Sandstone Formation is early Norian rather than late Carnian (as was indeed argued by Benton and Walker [1985]), in which case rhynchosaurs also ranged into the Norian. In the latter two possibilities, one or two additional family-level taxa of terrestrial vertebrates did not become extinct at the Carnian-Norian boundary.

**DISCUSSION**

The presence of *Erpetosuchus* in the New Haven Formation of Connecticut has implications for the timing and magnitude of early Mesozoic faunal changes. Benton (1991, 1993, 1994) argued that either the largest or “ecologically key” extinction event during the early Mesozoic occurred at the Carnian–Norian boundary rather than at the Triassic-Jurassic boundary as postulated by other authors (e.g., Olsen and Sues, 1986). According to Benton and other authors, the stratigraphically youngest known rhynchosaurs (*Hyperodapedon*), which occur with *Erpetosuchus* in the Lossiemouth Sandstone Formation, are of late Carnian age, contributing to the magnitude of the Carnian-Norian faunal changes. However, the presence of *Erpetosuchus* in apparently Norian-age strata in Connecticut can be interpreted in three different ways. First, the Connecticut fossil could actually be Carnian in age, in which case all three lines of age-diagnostic data for that part of the New Haven Formation are incorrect. We consider this interpretation highly unlikely. Second, *Erpetosuchus* had a longer biostratigraphic range than previously assumed, persisting across the Carnian-Norian boundary. Third, the actual age of the Lossiemouth Sandstone Formation is early Norian rather than late Carnian (as was indeed argued by Benton and Walker [1985]), in which case rhynchosaurs also ranged into the Norian. In the latter two possibilities, one or two additional family-level taxa of terrestrial vertebrates did not become extinct at the Carnian-Norian boundary.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


Corbet, B. 1977. The palynostratigraphy and age of the Newark Super-

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**TABLE 1. Character-taxon matrix showing the distribution of character-states for 33 characters (see Appendix) for seven archosaurian taxa.**

<table>
<thead>
<tr>
<th>Character</th>
<th>Stagonolepis</th>
<th>Gracilisuchus</th>
<th>Postosuchus</th>
<th>Erpetosuchus</th>
<th>Sphenosuchus</th>
<th>Protosuchus</th>
<th>Alligator</th>
</tr>
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<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
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<td>00100</td>
<td>00000</td>
<td>00000</td>
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<td>00000</td>
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<td>?0?000</td>
<td>01101?</td>
<td>00007?</td>
<td>0??000</td>
<td>071?</td>
<td>011?</td>
</tr>
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<td>??0000?</td>
<td>01102?</td>
<td>011??</td>
<td>0??000?</td>
<td>00000?</td>
<td>??01</td>
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</table>

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**FIGURE 3.** Single most parsimonious tree depicting a hypothesis of relationships for *Erpetosuchus*, Crocodylomorpha, and selected other archosaurian taxa, based on numerical cladistic analysis (using the exhaustive search option of PAUP, version 3.1.1) of character-states for 33 characters in 7 taxa (see Table 1).


APPENDIX 1

Characters and character-states for crocodylomorph archosaurs and various related taxa (from Clark et al., 2000).

1. Posterodorsal process of premaxilla overlapping anterodorsal surface of maxilla (0) or dorsal process of premaxilla vertical, strongly sutured to maxilla (1).

2. Facial portion of maxilla anterior to anterior edge of antorbital fenestra equal in length or longer than portion posterior to anterior edge of fenestra (0) or shorter than posterior portion (1).

3. Maxillae do not meet on palate (0) or meet on palate to form secondary bony palate anterior to choana (1).

4. Jugal participates in posterior edge of antorbital fenestra (0) or is excluded by lachrymal or frontal (1).

5. Descending process of prefrontal absent (0) or present (1).

6. Descending process of prefrontal not contacting palate (0) or contacting palate (1).

7. Prefrontal not underlying anterolateral edge of frontal to a significant degree (0) or with distinct posterior process underlying frontal dorsal to orbit (1).

8. Postfrontal present (0) or absent (1).

9. Dorsal surface of frontal flat (0) or with longitudinal ridge along midline (1).

10. Squamosal not significantly overhanging lateral temporal region (0) or with broad lateral expansion overhanging lateral temporal region (1).

11. Descending process of squamosal anterior to quadrate present (0) or absent (1).

12. Squamosal without ridge on dorsal surface along edge of supratemporal fossa (0) or with ridge (1).

13. Quadratojugal extends anterodorsally to contact postorbital (0) or does not contact postorbital (1).

14. Quadrate does not contact prootic (0) or contacts prootic (1).

15. In presumed adults, parietals separate (0), interparietal suture partially obliterated (1), or interparietal suture absent (2), [ordered]

16. Posteroventral edge of parietals extends more than half the width of occiput (0) or less than half the width of occiput (1).

17. Medial extent of supratemporal fossa on lateral surface of parietal separated on midline by broad, flat area (0) or by “sagittal crest” (which may be divided by interparietal suture) (1).

18. Occipital margin of parietals V-shaped in dorsal view (0) or straight (1).

19. Exoccipital bones widely separated dorsal to foramen magnum (0), approach midline without contacting (1), or contacting below supraoccipital (2), [ordered]

20. Prootic broadly contacting anterior surface of paroccipital process (0) or not in broad contact (1).

21. Depression for mastoid antrum: absent (0), present on lateral surface of prootic dorsal to otic capsule (1), or entering into prootic and connecting with opposite through supraoccipital (2), [ordered]

22. Depression for posterior tympanic recess: absent (0), depression posterior to fenestra ovalis on anterior surface of the paroccipital process (1), penetrating prootic and paroccipital process (2), [ordered]

23. Paroccipital process dorsosventrally tall and distinctly expanded distally (0) or process narrower dorsosventrally, distal end only slightly expanded (1).

24. Basipterygoid processes of basisphenoid present (0) or absent (1).

25. Basipterygoid processes simple, without large cavity (0) or greatly expanded, with large cavity (1).

26. Suprasymphyseal region of dentary with straight ventral margin (0) or with deep “swelling” extending ventrally below level of ventral margin of postsymphyseal portion of dentary (1).

27. Articular without dorsomedial projection posterior to the glenoid fossa (0) or with dorsomedial projection (1).

28. Coracoid subcircular in lateral view (0), with elongate post-glenoidal process postero medi ally (1), or with elongate ventromedial process expanded ventrally (2).

29. Proximal ends of metacarpals overlap (0) or abut one another without overlapping (1).

30. Proximal head of femur confluent with shaft (0) or with distinct, medially directed head set off from shaft (1).

31. Tibia/femur length ratio: less than 1 (0) or more than 1 (1).

32. Anterior edge of paramedian dorsal osteoderm series straight (0) or with anterior process (1).

33. Paramedian dorsal osteoderm s flat (0) or with distinct longitudinal bend near lateral edge (1).