FIRST RECORD OF *ERPETOSUCHUS* (REPTILIA: ARCHOSAURIA) FROM THE LATE TRIASSIC OF NORTH AMERICA

PAUL E. OLSEN[1], HANS-DIETER SUES[2], and MARK A. NORELL[3]

[1]Lamont-Doherty Earth Observatory, Columbia University,
Palisades, New York 10964;
[2]Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6 and
Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 3G5;
[3]Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street,
New York, New York 10024

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 *Stegomus 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 palynoflorule dated as latest Carnian to early Norian (Cornet, 1977). 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 $\pm$ 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 *Stegomus* with *Aetosaurus* 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 catalogued 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 quadrate and quadratojugal are steeply inclined anterodorsally. The long dorsal process of the latter bone extends anterodorsally along the posterior margin of the triangular infratemporal fenestra. The quadrate and quadratojugal 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
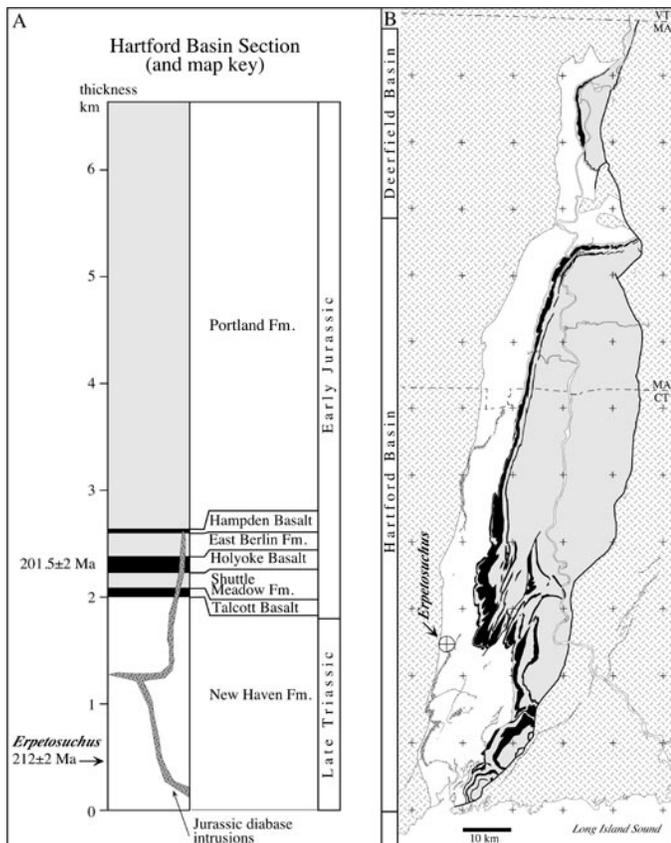
FIGURE 1.   **A**, stratigraphic division of the Late Triassic–Early Jurassic strata of the Hartford basin (Newark Supergroup) in Connecticut and Massachusetts. **B**, geological map of the Hartford basin.

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.

PHYLOGENETIC POSITION OF *ERPETOSUCHUS*

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

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.
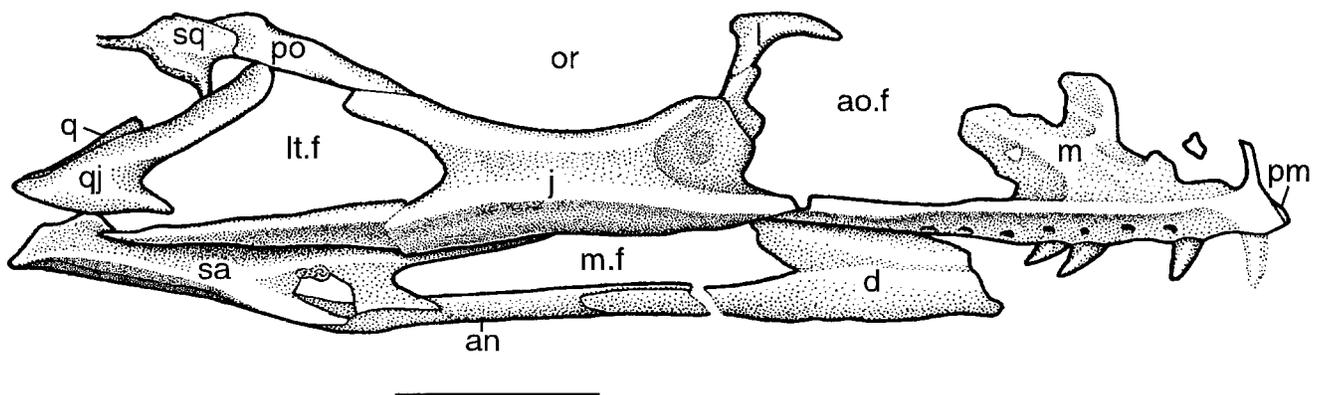

FIGURE 2.   Partial skull and mandible of *Erpetosuchus* sp., AMNH 29300, in right lateral view. The first maxillary tooth was preserved only as an impression in the matrix. **Abbreviations**: **an**, angular; **ao.f**, antorbital fenestra; **d**, dentary; **j**, jugal; **l**, lacrimal; **lt.f**, infra- 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.

TABLE 1. Character-taxon matrix showing the distribution of character-states for 33 characters (see Appendix) for seven archosaurian taxa. "0" denotes plesiomorphic character-state, "1" and "2" denote apomorphic character-states. "?" indicates unknown character-state. "N" indicates that scoring is inapplicable due to transformation; in such instances, the character-state was treated as unknown in the analysis. See Clark et al. (2000) for details regarding coding.

	Character						
		1		2		3	
Taxon	12345	67890	12345	67890	12345	67890	123
Stagonolepis	00000	00000	00100	00100	00000	00000	000
Gracilisuchus	?1?10	??000	01101	000??	??0??	000?0	0?1
Postosuchus	01000	??000	1?000	11000	00000	00000	0??
Erpetosuchus	0110?	??100	?10?2	011??	????0	000??	?01
Sphenosuchus	00111	01111	11112	11111	11001	011??	???
Protosuchus	11111	0?101	10012	10121	2211N	012?1	011
Alligator	1N1N1	10101	10012	10121	2011N	00201	000

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).

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 Newton (1894), 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 pairing *Protosuchus + Alligator* (Crocodyliformes) and left the position of *Erpetosuchus* unresolved. It is to be hoped that a detailed redescription of the holotype of *Erpetosuchus granti* will lead to a more refined understanding of the skeletal structure and phylogenetic position of this distinctive archosaurian reptile.

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
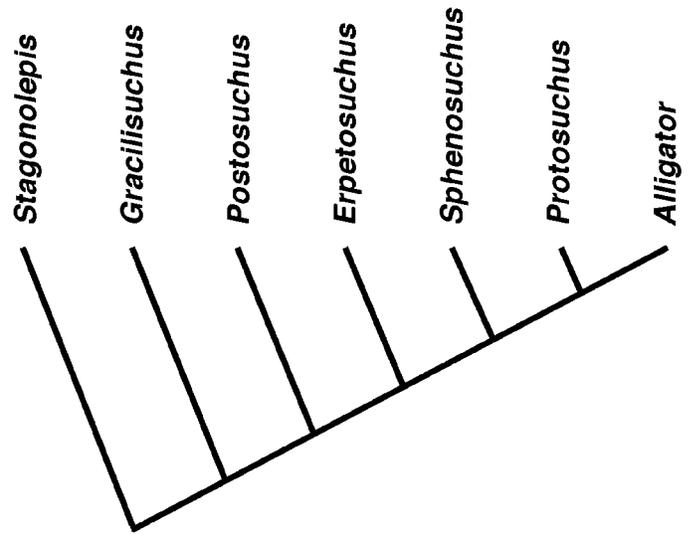
of age-diagnostic data for that part of the New Haven Formation are incorrect. We consider this interpretation highly unlikely. Second, *Erpetosuchus* had a longer biostratigraphic range than previously assumed, persisting across the Carnian-Norian boundary. Third, the actual age of the Lossiemouth Sandstone 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

LITERATURE CITED

Benton, M. J. 1991. What really happened in the Late Triassic? Historical Biology 5:263–278.

——— (ed.). 1993. The Fossil Record 2. Chapman & Hall, London, 845 pp.

——— 1994. Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern; pp. 366–397 *in* N. C. Fraser and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge and New York.

———, and A. D. Walker. 1985. Palaeoecology, taphonomy, and dating of Permo–Triassic reptiles from Elgin, north-east Scotland. Palaeontology 28:207–234.

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

group. Ph.D. dissertation, Pennsylvania State University, State College, Pennsylvania, 505 pp.

Clark, J. M., H.-D. Sues, and D. S Berman. 2000. A new specimen of *Hesperosuchus* from the Upper Triassic of New Mexico, and the interrelationships of basal crocodylomorph archosaurs. Journal of Vertebrate Paleontology 20:683–704.

Gauthier, J. A. 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California at Berkeley, 564 pp.

Gradstein, F. M., F. P. Agterberg, J. G. Ogg, J. Hardenbol, P. Van Veen, J. Thierry, and Z. Huang. 1995. A Triassic, Jurassic and Cretaceous time scale; pp. 95–126 *in* W. A. Berggren, D. V. Kent, M.-P. Aubry, and J. Hardenbol (eds.), Geochronology, Time Scales and Stratigraphic Correlation. Society of Economic Paleontologists and Mineralogists Special Publication no. 54.

Horne, G. S., N. G. McDonald, P. M. LeTourneau, and J. Z. deBoer. 1993. Paleoenvironmental traverse across the early Mesozoic Hartford Rift Basin, Connecticut; pp. 1–26 *in* J. T. Cheney and J. C. Hepburn (eds.), Field Trip Guidebook for the Northeastern United States. Geological Society of America Annual Meeting, Boston, Massachusetts, October 25–28, 1993, vol. 2.

Kent, D. V., and P. E. Olsen. 1999. Astronomically tuned geomagnetic polarity time scale for the Late Triassic. Journal of Geophysical Research 104:12831–12841.

Lucas, S. G., A. B. Heckert, and P. Huber. 1998. *Aetosaurus* (Archosauromorpha) from the Upper Triassic of the Newark Supergroup, eastern United States, and its biochronological significance. Palaeontology 41:1215–1230.

Marsh, O. C. 1893. Restoration of *Anchisaurus.* American Journal of Science (3) 45:169–170.

———— 1896. A new belodont reptile (*Stegomus*) from the Connecticut River sandstone. American Journal of Science (4) 2:59–62.

McInerney, D. P. 1993. Fluvial architecture and contrasting fluvial styles of the lower New Haven Arkose and mid-upper Portland Formation, early Mesozoic Hartford Basin, central Connecticut. M.S. thesis, University of Massachusetts, Amherst, 271 pp.

Newton, T. E. 1894. Reptiles from the Elgin Sandstone—Description of two new genera. Philosophical Transactions of the Royal Society of London, B, 185:573–607.

Olsen, P. E. 1980. Comparison of the vertebrate assemblages from the Newark and Hartford basins (Early Mesozoic, Newark Supergroup) of eastern North America; pp. 35–53 *in* L. L. Jacobs (ed.), Aspects of Vertebrate History. Museum of Northern Arizona Press, Flagstaff.

————, and H.-D. Sues. 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic–Jurassic tetrapod transition; pp. 321–351 *in* K. Padian (ed.), The Beginning of the Age of Dinosaurs. Cambridge University Press, Cambridge and New York.

Romer, A. S. 1956. Osteology of the Reptiles. The University of Chicago Press, Chicago, XXII + 772 pp.

Sues, H.-D., and D. Baird. 1993. A skull of a sphenodontian lepidosaur from the New Haven Arkose (Upper Triassic: Norian) of Connecticut. Journal of Vertebrate Paleontology 13:370–372.

————, P. E. Olsen, and J. G. Carter. 1999. A Late Triassic traversodont cynodont from North Carolina. Journal of Vertebrate Paleontology 19:351–354.

————, D. M. Scott, and P. S. Spencer. 2000. Cranial osteology of *Hypsognathus fenneri,* a latest Triassic procolophonid reptile from the Newark Supergroup of eastern North America. Journal of Vertebrate Paleontology 20:275–284.

Swofford, D. L., and D. Begle. 1993. Phylogenetic Analysis Using Parsimony. Version 3.1.1. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, DC.

Walker, A. D. 1968. *Protosuchus, Proterochampsa,* and the origin of phytosaurs and crocodiles. Geological Magazine 105:1–14.

———— 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Philosophical Transactions of the Royal Society of London, B 257:323–372.

Wang, Z. S., E. T. Rasbury, G. N. Hanson, and W. J. Meyers. 1998. Using the U-Pb system of calcretes to date the time of sedimentation of clastic sedimentary rocks. Geochimica et Cosmochimica Acta 62:2823–2835.

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 lacrimal or maxilla (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. Exoccipitals broadly 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 dorsoventrally tall and distinctly expanded distally (0) or process narrower dorsoventrally, 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. Symphyseal 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 posteromedially (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 osteoderms straight (0) or with anterior process (1).
33. Paramedian dorsal osteoderms flat (0) or with distinct longitudinal bend near lateral edge (1).