

A NEW SPHENODONTIAN (LEPIDOSAURIA: RHYNCHOCEPHALIA) FROM THE MCCOY BROOK FORMATION (LOWER JURASSIC) OF NOVA SCOTIA, CANADA

HANS-DIETER SUES¹, NEIL H. SHUBIN², and PAUL E. OLSEN³

¹Department of Vertebrate Palaeontology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6, and Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1;

²Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104;

³Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964

ABSTRACT—A new sphenodontian lepidosaur referable to *Clevosaurus* Swinton, 1939, *C. bairdi*, is described from the McCoy Brook Formation (Lower Jurassic: Hettangian) of Nova Scotia, Canada. It is most closely related to *C. mcgilli* Wu, 1994 from the Dark Red Beds of the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China, and differs from the latter mainly in the absence of the hourglass-shaped constriction of the parietals, the shape of the suborbital fenestra, and in features of the marginal dentition. The new taxon is of considerable interest because it represents the first record of *Clevosaurus* from North America. Like many other early Mesozoic continental tetrapods, *Clevosaurus* had an apparently Pangaeian geographic distribution.

INTRODUCTION

The Sphenodontia are a moderately diversified clade of very lizard-like reptiles, undoubted representatives of which are first recorded from the Upper Triassic of England and Scotland (Robinson, 1973; Fraser, 1982, 1986, 1988; Fraser and Benton, 1989; Fraser and Walkden, 1983, 1984; Whiteside, 1986), Germany (Carroll, 1985; Fraser and Benton, 1989), and North America (Murry, 1987; Sues and Baird, 1993). Only a single genus, *Sphenodon*, survives today on a number of islets off the coast of New Zealand (Daugherty et al., 1990). In the past, it has frequently been cited as an example of a "living fossil" from the "Age of Reptiles," but its derived cranial structure does not support this view (Whiteside, 1986). The recovery of numerous new assemblages of Late Triassic and Jurassic small tetrapods in recent years has revealed a previously unsuspected diversity among early Mesozoic sphenodontians (Whiteside, 1986; Evans, 1988; Fraser, 1988; Fraser and Benton, 1989; Gauthier et al., 1988; Wu, 1994).

The close anatomical similarity between *Sphenodon* and lizards was first noted by its original describer (Gray, 1831, 1842) who, in fact, even referred this taxon to the lacertilian family Agamidae. Later authors, however, emphasized the retention of various plesiomorphies by *Sphenodon*, such as the presence of a complete lower temporal arch and of a quadratojugal. Thus Günther (1867:626) proposed the order Rhynchocephalia for the reception of *Sphenodon* within the Squamata. Subsequent authors, following Owen (1859) and Huxley (1869), also referred the Triassic Rhynchosauria to the Rhynchocephalia, primarily on the basis of the alleged homology between the beak-

like bony downgrowths of the premaxillae over the mandibular symphysis in rhynchososaurs and the ankylosed premaxillary "incisor" teeth in adult specimens of *Sphenodon* and related forms. Carroll (1977) revived the hypothesis that sphenodontians are indeed most closely related to squamates. Furthermore, he argued that there is no evidence to support a close relationship between rhynchososaurs and sphenodontians and that the former are, in fact, more closely related to the Archosauria. Recent work (Carroll, 1977, 1985; Benton, 1983, 1985; Evans, 1988; Gauthier et al., 1988) has provided overwhelming anatomical evidence for a sister-group relationship between the Sphenodontia and Squamata and for placement of the Rhynchosauria in the Archosauromorpha.

Large numbers of mostly dissociated but well-preserved tetrapod bones occur in the lower portion of the McCoy Brook Formation exposed at Wasson Bluff near Parrsboro, Cumberland County, Nova Scotia. The McCoy Brook Formation is the stratigraphically youngest unit of the Fundy Group (Newark Supergroup; Olsen et al., 1989). It forms an over 200 m thick sequence of red and brown fluviolacustrine clastic sedimentary rocks with locally developed eolian sandstones, lacustrine limestones, and basalt talus deposits. Schlische and Olsen (*in* Olsen et al., 1989) have reviewed the geological context of the localities at Wasson Bluff on the Bay of Fundy in detail, obviating the need for an extensive account here. The fossiliferous basal strata of the McCoy Brook Formation occur directly on top of the North Mountain Basalt. Correlations with other basins of the early Mesozoic Newark Supergroup in eastern North America, drawing on palynological data, geochemical similarities of the basalts,

and cyclostratigraphy of the associated lacustrine sedimentary rocks, indicate an earliest Jurassic (Hettangian) age for the tetrapod-bearing basal strata of the McCoy Brook Formation (Olsen et al., 1987, 1989).

Bones referable to a small sphenodontian lepidosaur are particularly abundant in two types of facies. Lake-margin and fluvial sandstones have produced the best material, including two incomplete skulls and a partial postcranial skeleton. Paleotalus deposits comprising angular clast-supported basalt breccias with a matrix of sandstone or mudstone have yielded dissociated but well-preserved sphenodontian bones.

First-hand comparisons with other Late Triassic and Jurassic rhynchocephalian lepidosaurs indicate that the Nova Scotian material represents a new sphenodontian referable to *Clevosaurus*. Olsen et al. (1987) reported the presence of two different taxa of Sphenodontia from the McCoy Brook Formation at Wasson Bluff, but the original identification of cf. *Pelecymala* sp. was based on what, after additional preparation, proved to be a fragmentary palatine referable to the new clevosaur. In this paper, we describe the excellently preserved cranial and postcranial remains of this new sphenodontian from the McCoy Brook Formation. This form is of special interest because of its bearing on problems of early Mesozoic paleobiogeography.

Following Benton (1985:147), we give preference to the name Sphenodontia Williston, 1925 (and hence the vernacular term "sphenodontian") over Sphenodontida Estes, 1983 (and its vernacular derivative "sphenodontidan"). Furthermore, we use Rhynchocephalia sensu Gauthier et al. (1988) to refer to a more inclusive clade comprising *Gephyrosaurus* Evans, 1980 (Lower Jurassic, England) and Sphenodontia. All specimens used in this study will be deposited in the Nova Scotia Museum, Halifax (denoted by the acronym NSM) and the Museum of Comparative Zoology, Harvard University (denoted by the acronym MCZ). Some of the NSM specimens will be exhibited in the Fundy Geological Museum (Parrsboro, Nova Scotia).

SYSTEMATIC PALEONTOLOGY

- LEPIDOSAURIA Haeckel, 1866
 RHYNCHOCEPHALIA Günther, 1867 sensu
 Gauthier et al., 1988
 SPHENODONTIA Williston, 1925
CLEVOSAURUS Swinton, 1939
CLEVOSAURUS BAIRDI, sp. nov.

Etymology—Named for Donald Baird, in recognition of his many important contributions to the paleontological exploration of Newark Supergroup strata in Nova Scotia, and in appreciation of his unflinching encouragement and support of our research over the years.

Holotype—NSM 988GF1.1, an excellently preserved but slightly crushed partial skull with both dentaries in occlusion, several associated but disarticulat-

ed cranial and mandibular bones, and associated articulated phalanges of three digits of the right manus.

Hypodigm—In addition to the holotype, we examined the following specimens during the course of this study: NSM 988GF2.1, incomplete left dentary; NSM 988GF4.1, complete left dentary; NSM 988GF3.1, 988GF32.1, 988GF33.1, incomplete left maxillae; NSM 988GF34.1, nearly complete right maxilla; NSM 990GF90.1, nearly complete left maxilla; MCZ 9105, dorsoventrally crushed, incomplete skull with almost complete mandible in occlusion; MCZ 9106, well-preserved partial postcranial skeleton including left humerus and ulna, articulated left hind-limb and pes, articulated distal portions of the right tibia and fibula and right pes, both ilia, and articulated partial vertebral column from the posterior dorsal to the distal caudal region; MCZ 9110, scattered palatal bones; MCZ 9112, incomplete left maxilla; MCZ 9113, incomplete left dentary and attached coronoid; MCZ 9114, complete right maxilla.

Horizon and Locality—With the exception of NSM 988GF2.1 and NSM 988GF34.1 (which were found at site F), all specimens discussed in this study were collected from sites K and K' (as designated by Schlische and Olsen in Olsen et al., 1989:fig. 11.6). The bones occur in the basal portion of the McCoy Brook Formation (Lower Jurassic: Hettangian) of the Fundy Group (Newark Supergroup) at Wasson Bluff, near Parrsboro, Cumberland County, Nova Scotia. The geographic coordinates for these exposures are latitude 45°23'40" N and longitude 64°14'00" to 30"W.

Diagnosis—Most closely related to *C. mcgilli* but differing from that taxon in the presence of but a single premaxillary "incisor" tooth in adults, the presence of three, rather than five, additional teeth in the maxilla (character of uncertain polarity), the (plesiomorphic) absence of the hourglass-shaped constriction of the parietals, and the (plesiomorphic) absence of an L-shaped suborbital fenestra.

DESCRIPTION

General Remarks

All known specimens of *Clevosaurus bairdi* are small. NSM 988GF1.1 and MCZ 9105 both have an estimated length of the skull roof (measured along the midline) of about 1.9 cm. Regardless of various preservational differences between these two specimens, the skull of MCZ 9105 appears more gracile in its build than that of NSM 988GF1.1.

Skull

The two incomplete skulls NSM 988GF1.1 (Figs. 1, 2) and MCZ 9105 (Figs. 3, 4) complement each other in terms of preserved structural detail and thus permit a comprehensive survey of the cranial structure in *Clevosaurus bairdi* (Fig. 5). Small-scale fracturing renders the tracing of some sutures on MCZ 9105 difficult.

In NSM 988GF1.1, each premaxilla (pm) bears a

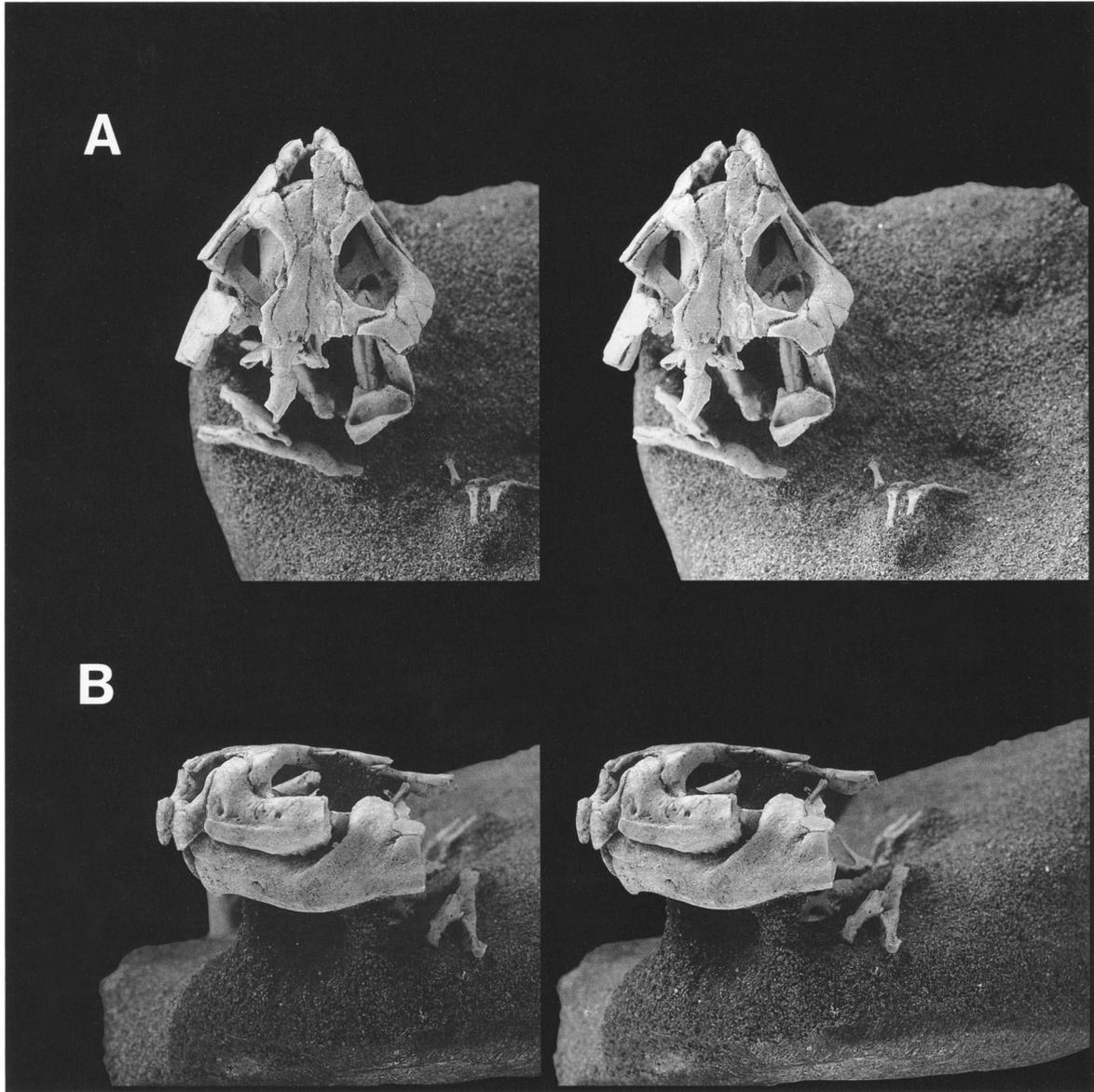


FIGURE 1. *Clevosaurus bairdi*, sp. nov., NSM 988GF1.1 (holotype). Stereophotographs of partial skull and mandible in **A**, dorsal and **B**, left lateral view. Scale bar equals 5 mm.

single robust “incisor” tooth that is completely ankylosed to the bone and forms a blunt chisel edge (Figs. 1B, 2B). As in other forms referable to *Clevosaurus* (see below), the long and slender posterior process of the premaxilla completely excludes the maxilla from participation in the posterior margin of the anterolaterally directed external naris. The apparently slender dorsal or nasal processes of the premaxillae meet the nasals posterodorsally (NSM 988GF1.1) and thus completely enclose the external nares dorsally (contra Olsen et al., 1987:fig. 3).

The anterior part of the robust, boomerang-shaped

maxilla (m) only slightly overlaps the premaxilla anteriorly (Fig. 2B). Unlike the condition in many other sphenodontian taxa, the maxilla lacks a distinct anterior or premaxillary process. The tooth-bearing portion of the maxilla is deep. Posteriorly, the marginal tooth row is distinctly inset from the lateral margin of the skull, much as in *Sphenodon*, and the maxilla forms a dorsal ledge just above the tooth row. A pronounced “lip” of secondary bone (Harrison, 1901:200; “secondary dentine” of Fraser, 1988) extends along the lateral surface of the tooth-bearing portion just above the teeth (Fig. 2B, s.b). Two distinct supralabial foram-

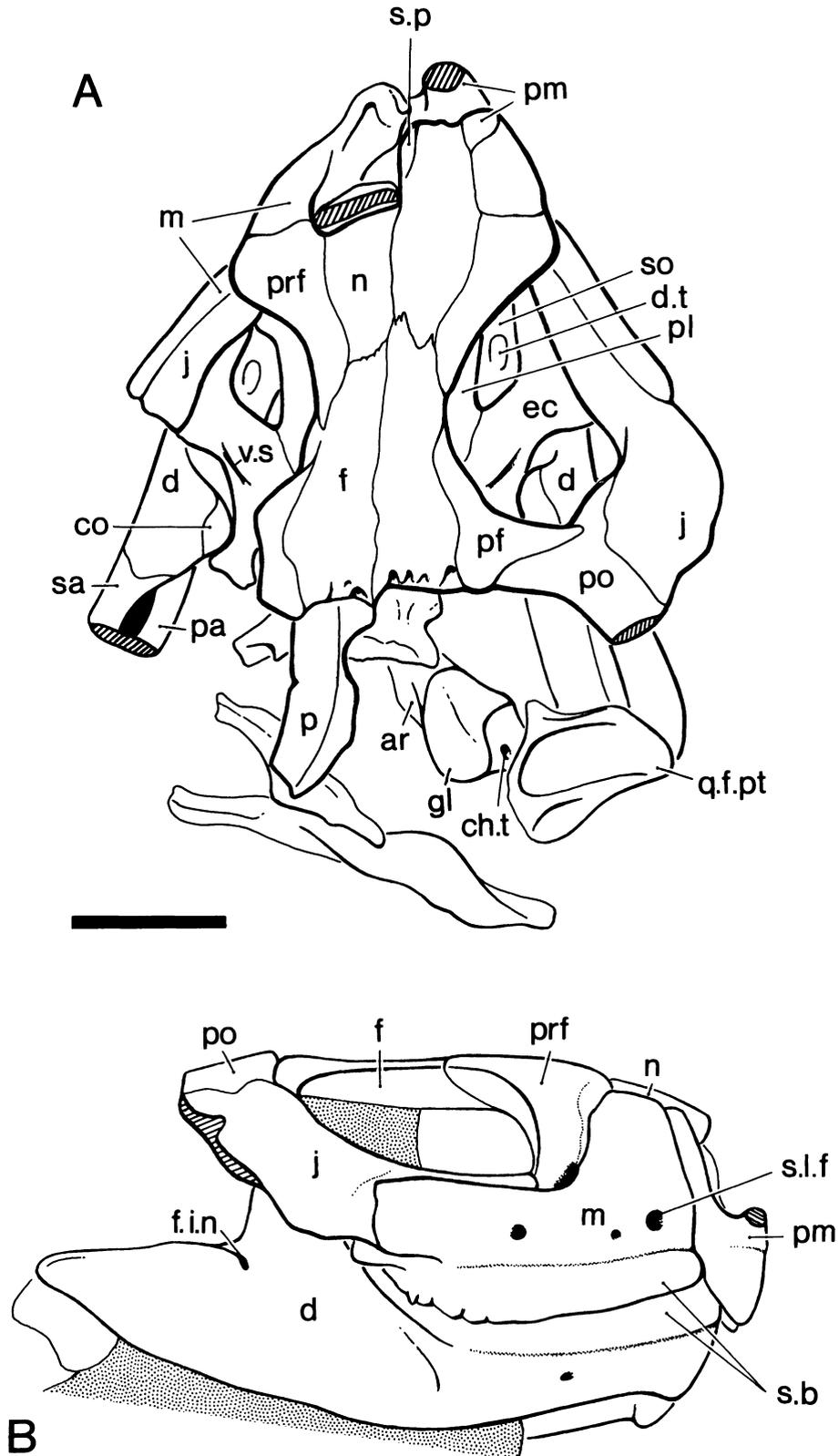


FIGURE 2. *Clevosaurus bairdi*, sp. nov., NSM 988GF1.1 (holotype). Camera lucida drawings of partial skull and mandible in A, dorsal and B, right lateral view. Scale bar equals 5 mm. Diagonal hatching denotes broken bone, mechanical stippling matrix. Abbreviations: ar, articular; ch.t, foramen for chorda tympani; co, coronoid; d, dentary; d.t, dentary tooth; ec, ectopterygoid; f, frontal; f.i.n, foramen for inferior alveolar nerve; gl, glenoid facet on articular for quadrate condyle; j, jugal;

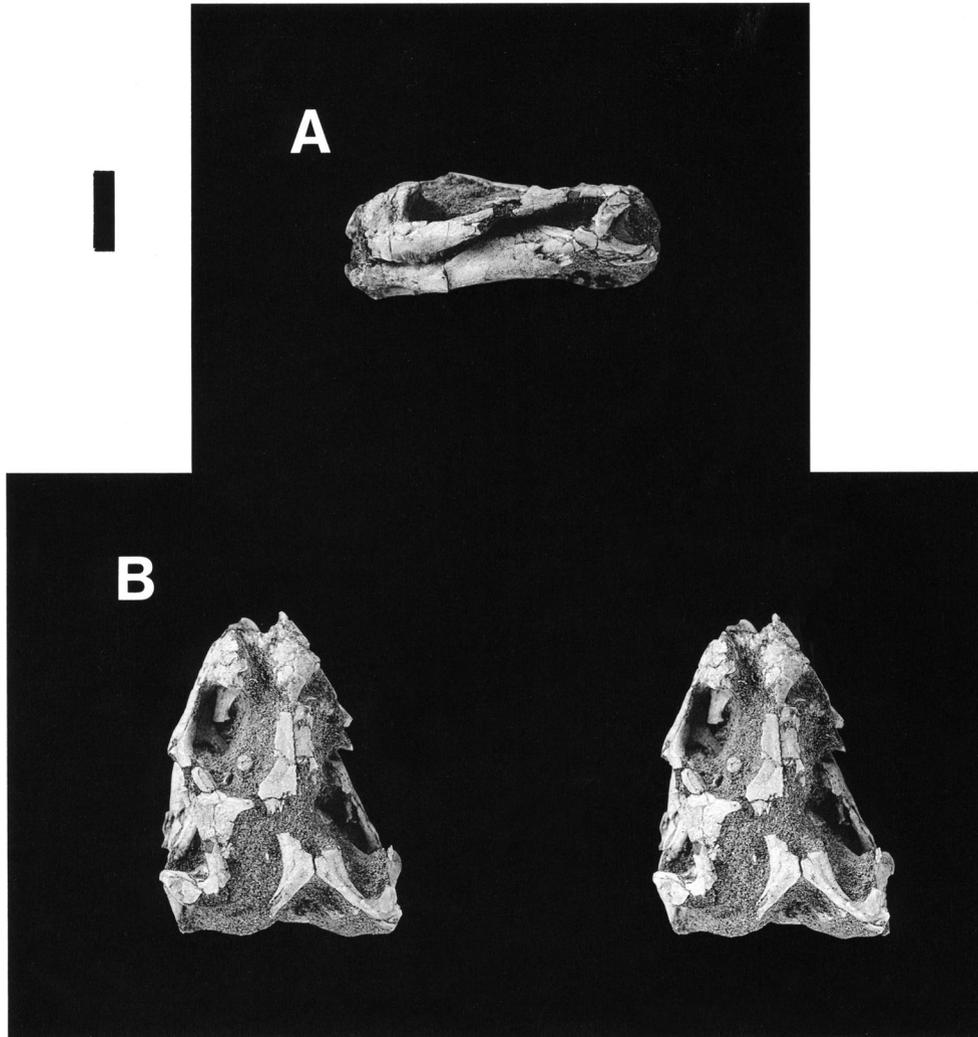


FIGURE 3. *Clevosaurus bairdi*, sp. nov., MCZ 9105. Skull in **A**, left lateral view and **B**, dorsal view (stereopair). Scale bar equals 5 mm.

ina (s.l.f) above this “lip” presumably served as exits for cutaneous branches of the superior alveolar nerve and maxillary artery, as in present-day lizards (Oelrich, 1956). The nearly vertical nasal or dorsal process of the maxilla is less broad anteroposteriorly and more distinctly offset from the tooth-bearing portion than that in *C. hudsoni* (Fraser, 1988:figs. 1b, 6).

The gently convex nasal (n) is rather large and thin.

The robust prefrontal (prf) forms the entire anterior margin of the orbit and has long sutural contacts dorsally with the nasal and frontal. The facial portion of the prefrontal (Figs. 1, 2) is much more extensive than

that in *C. hudsoni* (Fraser, 1988:fig. 7). As in other sphenodontians (Gauthier et al., 1988:25), a lacrimal is absent (contra Olsen et al., 1987:fig. 3). In NSM 988GF1.1, the large lacrimal foramen is bounded by the maxilla laterally and the prefrontal medially, much as in *Sphenodon*. Fraser’s (1988:133) inference regarding the absence of a lacrimal foramen in *C. hudsoni* was based on isolated skull bones and is probably incorrect.

Two featureless bony platelets (s) scattered in the left orbit of MCZ 9105 (Fig. 4) appear to represent scleral ossicles.

←

m, maxilla; n, nasal; p, parietal; pa, prearticular; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; prf, prefrontal; q.f.pt, quadrate process of pterygoid; s.b, secondary bone; s.l.f, supralabial foramen; s.p, sutural surface for premaxilla; sa, surangular; so, suborbital fenestra; v.s, vascular groove on ectopterygoid.

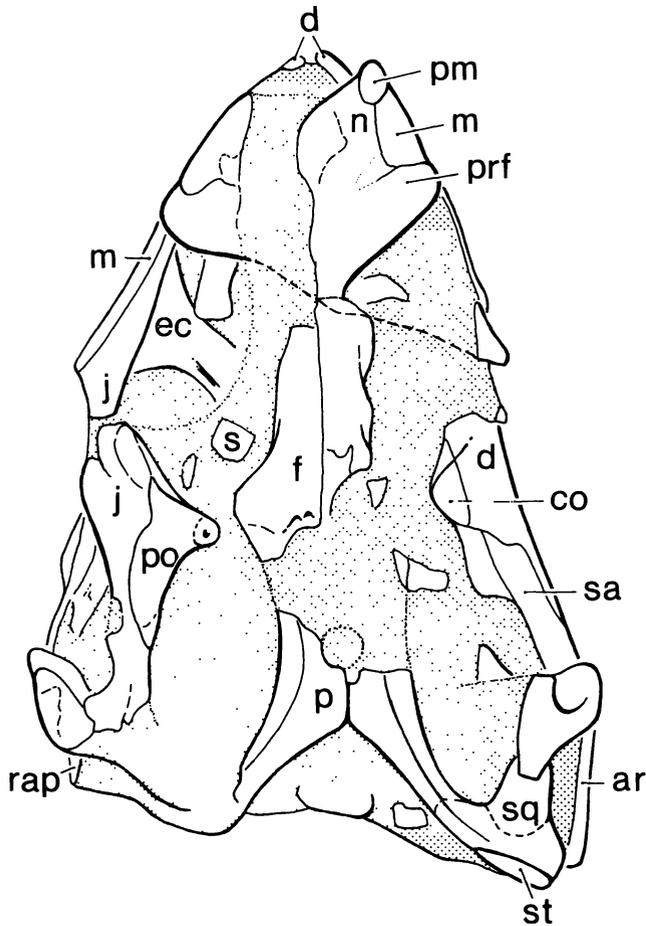


FIGURE 4. *Clevosaurus bairdi*, sp. nov., MCZ 9105. Camera lucida drawing of skull in dorsal view. Mechanical stippling denotes matrix. Scale bar equals 5 mm. Abbreviations as in Figure 2 and: rap, retroarticular process; s, scleral ossicle; sq, squamosal; st, supratemporal.

The more or less triangular postorbital (po) broadly overlaps the squamosal posteriorly on the broad upper temporal bar. It only forms a small portion of the posterior margin of the orbit (Fig. 2A) and broadly overlaps the postfrontal medially.

The distinctly triradiate postfrontal (pf) forms an extensive median contact with the frontal, as in *C. hudsoni* and *Sphenodon* (Figs. 2A, 4). Its posterior process excludes the postorbital from contact with the parietal. The postfrontal bounds the orbit posterodorsally.

The jugal (j) is incompletely preserved posteriorly in both MCZ 9105 and NSM 988GF1.1. In MCZ 9105, a small depression on the anterolateral aspect of the quadratojugal, just dorsal and lateral to the mandibular articulation, indicates the presence of a complete lower temporal bar (Fig. 4), as reconstructed for *C. hudsoni*

(Fraser, 1988:fig. 3; contra Robinson, 1973:fig. 4A, E). Presumably the connection between the jugal and quadratojugal was rather loose. The broad and rather flat dorsal or postorbital process of the jugal is directed posterodorsally and contacts the anterior process of the squamosal, thus excluding the postorbital from participation in the dorsal margin of the lower temporal fenestra. The anterior or maxillary process of the jugal extends forward along the medial ledge of the maxilla and contacts the prefrontal (NSM 988GF1.1; Figs. 1A, 2A).

The suture between the paired frontals (f) is almost straight (Figs. 2A, 4), rather than distinctly interdigitated as in *C. hudsoni* (Fraser, 1988:fig. 8). The frontal is narrow, flat dorsally, and slightly tapered anteriorly. Its participation in the dorsal margin of the orbit is very restricted (NSM 988GF1.1; Fig. 2A). The frontal forms sutural contacts with the nasal anteriorly and the prefrontal anterolaterally. Posteriorly, it contacts the parietal along a more or less transverse suture.

The paired parietals (p) form a narrow, flat intertemporal region or "parietal table" (Figs. 2A, 4) dorsally and enclose a large pineal foramen between them anteriorly. Posteriorly, the posterolaterally diverging supratemporal process of the parietal contacts the squamosal and supratemporal.

The large squamosal (sq) forms the posterolateral portion of the upper temporal bar. A rather slender ventral or quadrate process extends ventrally along the anterolateral margin of the quadratojugal (MCZ 9105). Unlike the condition in *C. hudsoni* (Fraser, 1988:figs. 3, 11), however, it does not form a hooked end distally for contact with the jugal at the posteroventral corner of the lower temporal fenestra.

The supratemporal (st) is splint-like and dorsally placed (MCZ 9105; Figs. 3, 4).

The conjoined quadrate and quadratojugal form a conch-like structure (MCZ 9105) and enclose a small foramen (presumably for the passage of V. mandibularis; O'Donoghue, 1920:pl. 7, fig. 2) between them. The quadrate forms an extensive, anteromedially projecting pterygoid process that overlaps the deep quadrate flange of the pterygoid.

The palatine (pl) bears a single row of enlarged teeth, details of which are indistinct in NSM 988GF1.1, probably due to extensive wear. Its robust maxillary process extends anterolaterally so that the suborbital fenestra (so) is completely enclosed by the palatine and ectopterygoid. The process is perforated by the infraorbital foramen, which probably transmitted the superior alveolar nerve and artery (Oelrich, 1956).

The large, robust ectopterygoid (ec) is situated at the posterior margin of the suborbital fenestra. It forms a brace between the jugal and maxilla anterolaterally and the pterygoid posteromedially. The ectopterygoid has an extensive anterolateral process that contacts the palatine at the anterolateral corner of the suborbital fenestra (Figs. 2A, 4A). A distinct vascular groove (v.s),

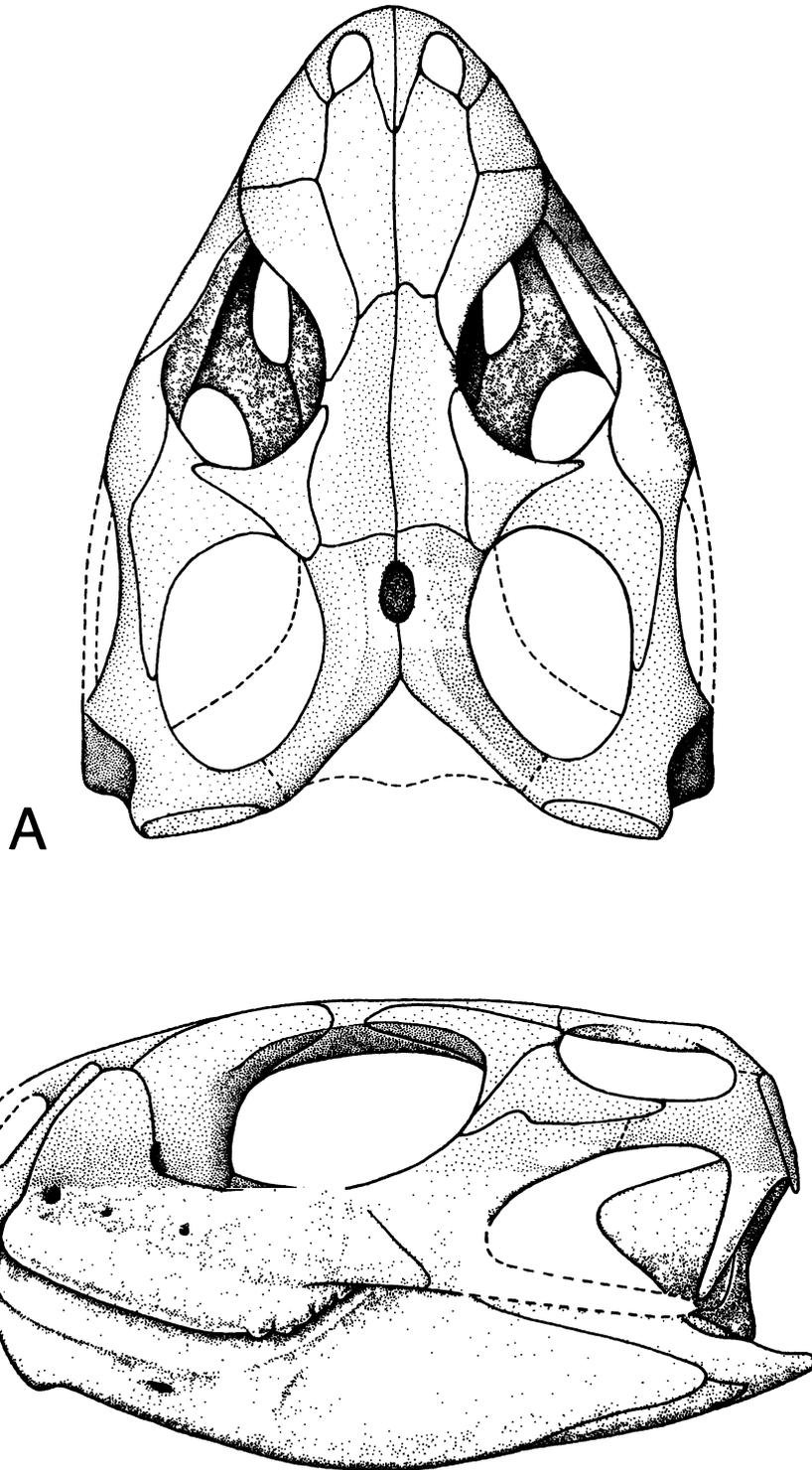


FIGURE 5. *Clevosaurus bairdi*, sp. nov. Reconstruction of the skull (based on NSM 988GF1.1 and MCZ 9105) in **A**, dorsal and **B**, left lateral view. Length of skull roof along the midline c. 1.9 cm. Missing portions (in broken lines) restored based on *C. hudsoni*.

possibly marking part of the course of *V. pterygoidea*, is present on the posterodorsal surface of the ectopterygoid.

The triradiate pterygoid has an anterolaterally directed transverse process, a fairly broad, anteriorly directed palatal process, and a thin, mediolaterally flattened quadrate process (Fig. 2A, q.f.pt). It does not enter into the margin of the suborbital fenestra.

The epipterygoid is rod-like dorsally but becomes flattened and expanded ventrally where it contacts the medial surface of the quadrate process of the pterygoid dorsal to the basiptyergoid joint (NSM 988GF1.1).

Mandible

The stout symphysis projects distinctly downward. Behind it, the ventral margin of the robust dentary (d) is convex in side view and rounded up to the level of the coronoid process, where it becomes sharp. In some specimens (e.g., MCZ 9105), fine longitudinal striations extend anteroposteriorly along the ventral margin of the dentary. Medially, the dentary bears an open groove for Meckel's cartilage along its entire length. There is definitely no splenial (NSM 988GF1.1). The mediolaterally flattened tooth-bearing ramus of the dentary is distinctly curved inward anteriorly toward the symphyseal facet. Its lateral surface bears a prominent "lip" of secondary bone (s.b) just below the teeth. Up to three mental foramina, presumably for cutaneous branches of the inferior alveolar nerve, are situated below this lip. The prominent coronoid process of the dentary is positioned lateral to the posterior end of the tooth row and forms the lateral portion of the coronoid eminence of the mandible. A shallow depression, which presumably reflects the extent of the pars superficialis of *M. adductor mandibulae externus*, is developed anteriorly on the lateral aspect of the coronoid portion of the dentary. Posterior to the coronoid eminence, the dentary continues as a tall, thin, and somewhat tapering lamina that overlaps the surangular portion of the articular complex. A small mandibular foramen (f.i.n), presumably for passage of a cutaneous branch of the inferior alveolar nerve, is enclosed by the dentary and surangular.

A separate coronoid bone (co; NSM 988GF1.1 and MCZ 9113) forms the medial portion of the coronoid eminence of the mandible and projects slightly above the coronoid process of the dentary (Fig. 2).

Prearticular, articular, and surangular appear to be fused into a single compound bone. The presumed prearticular portion is slender and, together with the articular, forms a long, tapering retroarticular process (rap) posteriorly (Figs. 3, 4). This process forms a slightly raised lateral edge, which apparently corresponds to the tympanic crest in lizards. The articular forms the glenoid facet for contact with the quadrate condyle. The glenoid facet (Fig. 2A, gl) is divided by a distinct anteroposterior ridge; the resultant lateral and medial facets are placed at a slight angle to each other, the medial one being distinctly inclined inward. The length of the facet is more or less equal to its transverse width.

Just behind the glenoid facet, a small foramen (ch.t) on the medial portion of the retroarticular process probably transmitted the chorda tympani nerve.

Dentition

As in *Clevosaurus hudsoni* (Fraser, 1986, 1988) and other sphenodontian lepidosaurs (Harrison, 1901; Robinson, 1976), the acrodont marginal dentition of *C. bairdi* exhibits pronounced regional differentiation. Early in ontogeny, the anterior teeth of both the dentary and maxilla are completely worn away (Fig. 6B), and, in these regions, the jaw bones form sharp bony ridges that functionally replace the teeth.

The premaxillary dentition is known only in the mature specimen NSM 988GF1.1, where each premaxilla holds a single large "incisor" tooth with a blunt chisel edge.

Anteriorly, the fragment of a small maxilla MCZ 9112 bears three small teeth between which smaller denticles are developed; these teeth appear to represent the hatchling dentition (sensu Robinson, 1976). In MCZ 9112 there is an anterior additional tooth with a low, somewhat elongate crown with an oval base; in larger specimens, there are several teeth of this type (Fig. 6A). Behind this anterior series of additional teeth, there are up to three large, flanged teeth. Each flanged tooth consists of an anterior cusp and a blade-like, obliquely posterolingually directed flange ("talon" of Cocude-Michel, 1963), which slightly overlaps the tooth behind it lingually. The tooth crown is covered by thick, darkly colored enamel with distinct vertical wrinkling. In MCZ 9105, the three flanged additional teeth in the maxilla are well worn and are followed behind by two small conical teeth. In NSM 988GF1.1, wear has nearly obliterated the upper teeth.

The anterior teeth are heavily worn (NSM 988GF2.1) or completely obliterated (e.g., MCZ 9113) on all dentaries found to date. In side view, the additional teeth have more or less triangular, anteroposteriorly somewhat elongate crowns with blunt apices. In NSM 988GF4.1, the crown of a replacement tooth is visible medially below the occlusal level at the posterior end of the tooth row.

Wear produced steeply inclined facets along the lingual aspect of the maxillary tooth crowns. The thick enamel on the labial aspect of the crowns of the posterior additional teeth formed a cutting edge that generated deep scoring marks on the lateral face of the tooth-bearing ramus of the dentary (e.g., NSM 988GF2.1). When the jaws are closed the dentary teeth are completely hidden in lateral view. The flanged additional teeth of the maxilla occluded obliquely with the lateral aspect of the dentary. The steeply oblique inclination of the wear facets on the maxillary additional teeth appears to reflect an emphasis on shearing, rather than crushing or piercing. The pattern of tooth wear indicates that *Clevosaurus* had simple orthal jaw motion without a significant anteroposterior component, unlike *Sphenodon* (Robinson, 1976; Fraser, 1988).

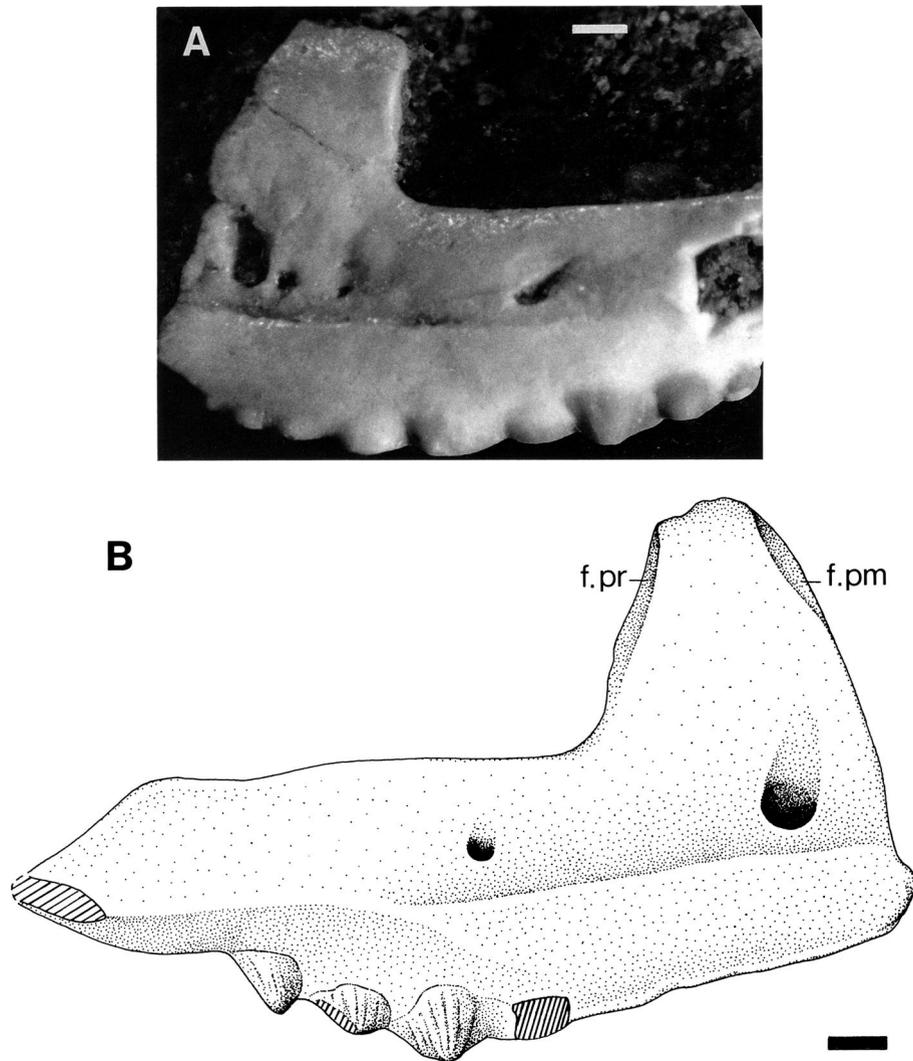


FIGURE 6. *Clevosaurus bairdi*, sp. nov. **A**, left maxilla (NSM 988GF35.1) with complete tooth row in lateral view. **B**, right maxilla (MCZ 9114) with additional teeth; the more anterior teeth are obliterated by wear. Cross-hatching denotes damaged areas. Abbreviations: **f.pm**, facet for premaxilla; **f.pr**, facet for prefrontal. Scale bars each equal 1 mm.

The sharp anterior edges of the jaw bones presumably functioned in the manner of scissor blades.

Postcranial Skeleton

The postcranial axial skeleton of *Clevosaurus bairdi* does not differ appreciably from that of *C. hudsoni*, as described and illustrated by Fraser (1988). The partial postcranial skeleton MCZ 9106 (Fig. 7) appears to preserve two posterior dorsal, two sacral, the proximal 14 caudal, and at least two more distally placed caudal vertebrae in articulation; in addition, there are two or three disarticulated vertebrae that probably belong to the presacral column. The sacral vertebrae bear low neural spines and robust sacral ribs. The second sacral rib is bifurcated distally. The proximal caudal vertebrae have large transverse processes that are dorso-

ventrally flattened and curve slightly forward. Autotomy septa are apparent from the eighth caudal back, as is typically the case in *Sphenodon* (Howes and Swinerton, 1901:pl. 1, fig. 18).

The appendicular skeleton of *Clevosaurus bairdi* also closely resembles that of *C. hudsoni*. Of the forelimb, only the disarticulated left humerus and ulna are preserved in MCZ 9106 (Fig. 7). The pelvic girdle is documented by both ilia. Both hind-limbs are preserved in MCZ 9106; the left one is essentially complete, articulated, and sharply flexed at the knee and ankle. A slender shaft separates the much expanded proximal and distal articular ends of the humerus (h), which are set at almost a right angle to each other. The large entepicondylar foramen opens in a ventral depression above the distal articular end. The prominent olecranon epiphysis is suturally separated from the slender

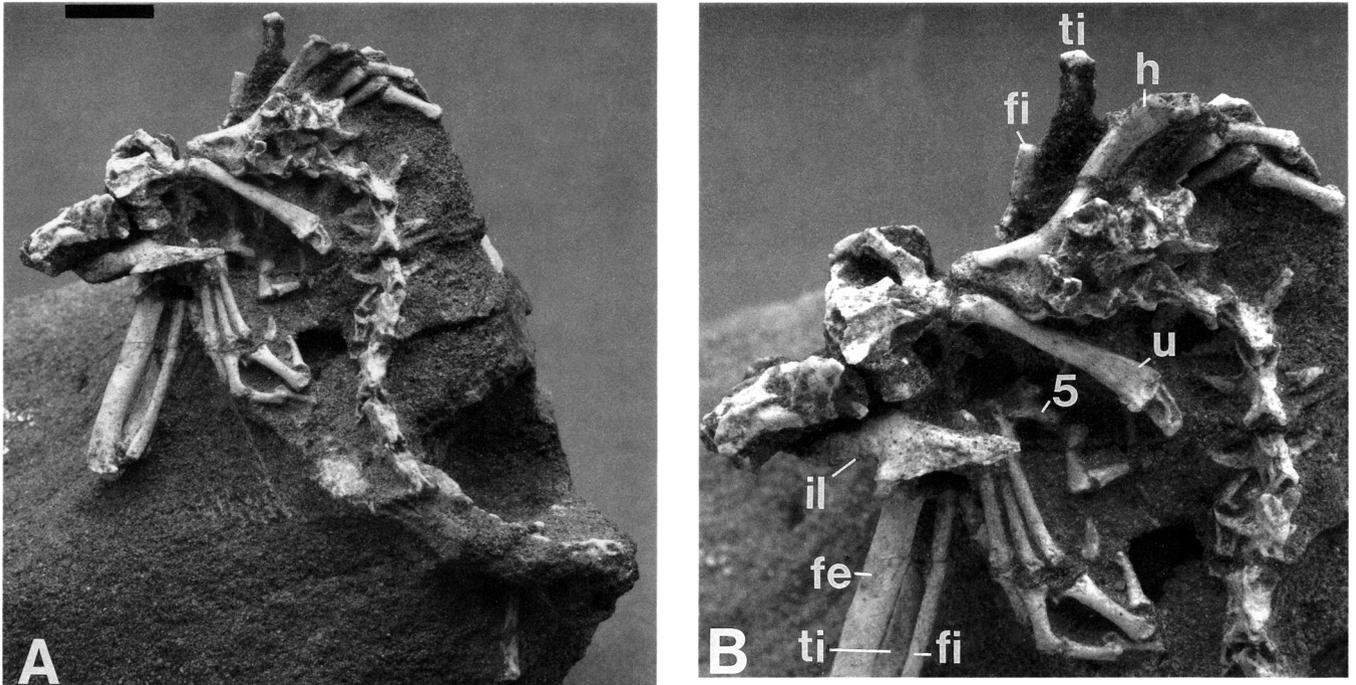


FIGURE 7. *Clevosaurus bairdi*, sp. nov., MCZ 9106. Partial postcranial skeleton. **A**, oblique left lateral view. **B**, detail of **A**. Abbreviations: fe, femur; fi, fibula; h, humerus; il, ilium; ti, tibia; u, ulna; 5, metatarsal V. Scale bar equals 5 mm.

diaphysis of the ulna (u). The blade of the ilium (il) is not vertically oriented as in *Sphenodon*. The femur (fe) has a gently sigmoidally curved shaft. Its flattened distal end has an irregular surface suggestive of an epiphyseal contact. The stout tibia (ti) has an expanded proximal articular end and a robust shaft. The delicate fibula (fi) is mediolaterally flattened. Its proximal end articulates with a recess on the dorsal aspect of the fibular condyle of the femur. The poorly preserved astragalus and calcaneum appear to be fused into a single compound element. The robust metatarsal V is distinctly hooked (Fig. 7) and bears distinct lateral and medial plantar tubercles; it closely resembles the homologous bone in *Sphenodon* (Howes and Swinerton, 1901:pl. 6, fig. 18). The slender metatarsals I to IV have slightly thickened proximal articular ends. Metatarsal III was apparently slightly longer than metatarsals II and IV. The phalangeal formula of the pes is 2-3-4-5-4.

DISCUSSION

Relationships of *Clevosaurus bairdi*

The cladistic hypothesis of sphenodontian interrelationships developed by Fraser and Benton (1989) and

modified by Wu (1994) served as the framework for our assessment of the phylogenetic relationships of the new sphenodontian from the McCoy Brook Formation. The character states for 34 cranial and dental characters modified from the compilation by Wu (1994; see Appendix) were scored for the new species and 12 other taxa of Rhynchocephalia sensu Gauthier et al. (1988). We re-scored several characters used by Fraser and Benton (1989) and Wu (1994) as (unordered) multi-state characters. The resulting matrix (Table 1) was analyzed using PAUP 3.0s on a Macintosh IIci. Using the branch-and-bound search option, we found seven trees, each with a length of 54 steps, a consistency index (C.I.) of 0.667 (C.I. excluding uninformative characters: 0.633), a homoplasy index (H.I.) of 0.333 (0.367), and a retention index (R.I.) of 0.760; the seven trees and the strict consensus tree (Fig. 8) yielded consistent results for the subset of taxa to be discussed here.

We refer the new sphenodontian to *Clevosaurus* Swinton, 1939 on the basis of character 1.1 (presence of a long posterior process of the premaxilla that excludes the maxilla from participation in the margin of the external naris). This character state cannot be determined for the holotype and only known specimen of *C. petilus* (Yang, 1982) from the Dull Purplish Beds

FIGURE 8. Strict consensus tree computed from seven trees for *Clevosaurus bairdi* and 12 other rhynchocephalian taxa based on PAUP analysis of the data matrix in Table 1. See text for discussion.

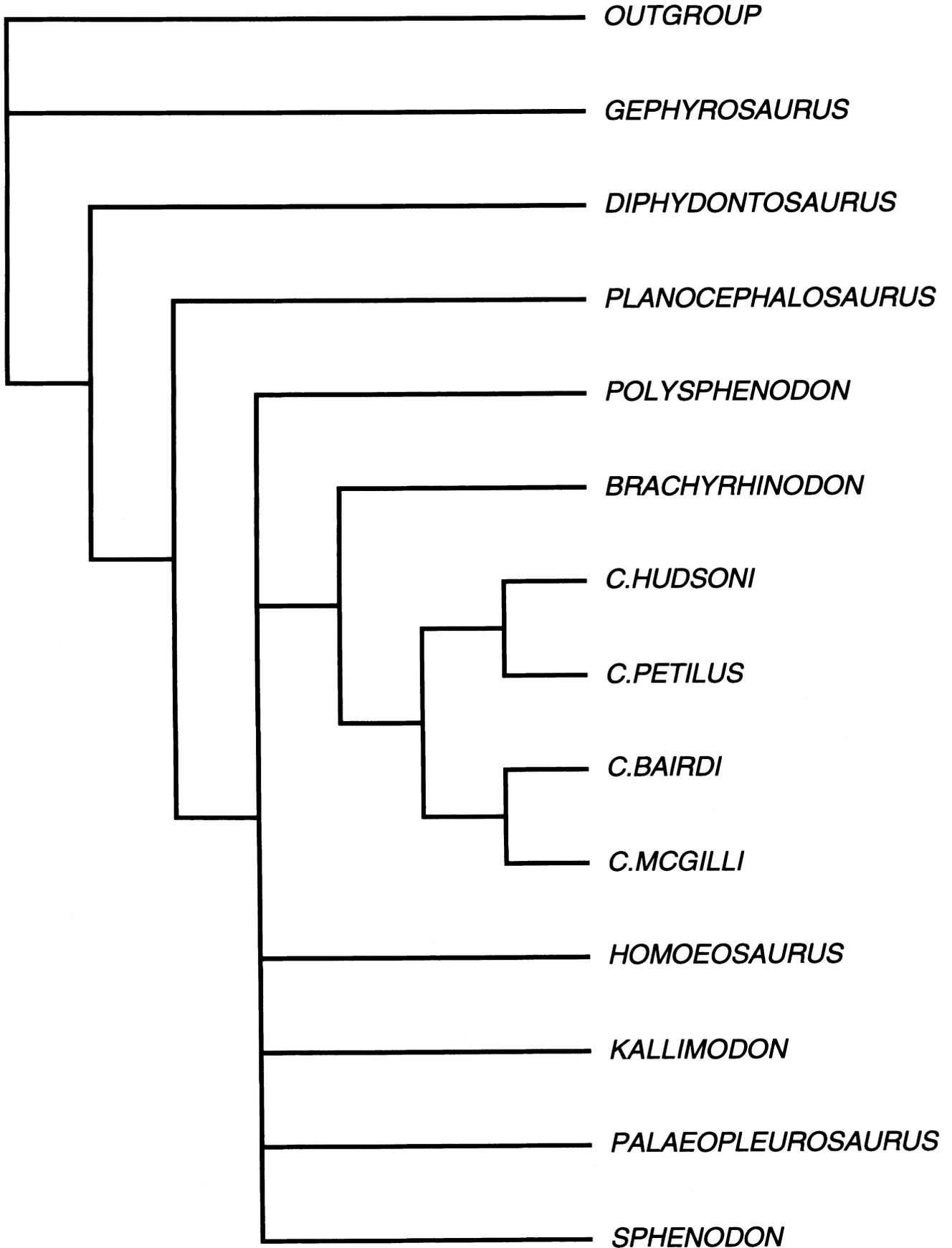


TABLE 1. Distribution of character states for 34 cranial and dental features (see Appendix) in 13 taxa of Rhynchocephalia. "0" denotes primitive character state and "1" and "2" derived character states; "9" indicates missing data.

Taxon	Character						
	5	1 0	1 5	2 0	2 5	3 0	
Outgroup	00000	00000	00000	00000	00000	00000	0000
<i>Gephyrosaurus</i>	00001	10010	00101	00000	00000	10000	0000
<i>Diphydontosaurus</i>	00101	00010	10111	00011	00000	10000	0000
<i>Planocephalosaurus</i>	00101	10010	00111	10012	01010	10000	0000
<i>Polysphenodon</i>	99100	00090	90111	19912	11199	11109	0190
<i>Brachyrhinodon</i>	01100	00090	21111	10912	11199	11100	0990
<i>Clevosaurus hudsoni</i>	11100	01000	11111	10012	11111	11100	0110
<i>C. bairdi</i>	11110	01000	21111	10012	11111	11100	9110
<i>C. petilus</i>	11100	90000	11111	90012	91111	11101	1110
<i>C. mcgilli</i>	11110	90000	21111	90012	11111	11110	0110
<i>Homoeosaurus</i>	00100	00011	00111	11912	11111	11110	0100
<i>Kallimodon</i>	09100	01111	01111	10912	11111	11910	0100
<i>Palaeopleurosaurus</i>	00100	11110	01110	00012	11111	11101	0000
<i>Sphenodon</i>	00100	01111	11111	11112	11111	11111	0101

of the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China (Wu, 1994). The antorbital length of the skull is about 30 percent of the total skull length (character 11.1) in both *C. hudsoni* Swinton, 1939, from fissure-fillings of Late Triassic age in southwestern Britain, and *C. wangi* Wu, 1994, from the Dark Red Beds of the Lower Lufeng Formation (Lower Jurassic) of Yunnan. In *Brachyrhinodon*, *Clevosaurus mcgilli*, and *C. bairdi*, the antorbital length is less than 25 percent of the total skull length (character 11.2); again, this character state cannot be scored for the holotype of *C. petilus*. Despite a slight difference in stratigraphic age, we regard *Clevosaurus wangi* as a subjective junior synonym of *C. petilus* (Yang, 1982). Both share character 31.1 (presence of distinct ventral depression on the parabasisphenoid), which may diagnose *C. petilus*. Wu (1994) distinguished *C. petilus* from *C. wangi* based on its possession of "oval supratemporal fenestrae that are diagonally oriented," a jugal with a "very short anterior process," and "very slender basiptyergoid processes." Differences in post-mortem crushing between the skulls of the two forms are obvious in Wu's excellent illustrations, and they could at least partially account for the reported differences in the shape and orientation of the supratemporal fenestrae. The exact length of the anterior process of the jugal is difficult to determine, but it does not appear to be distinctly shorter in *C. petilus* than in *C. wangi* (see Wu, 1994).

The Nova Scotian sphenodontian is most closely related to *Clevosaurus mcgilli* from the Dark Red Beds of the Lower Lufeng Formation of Yunnan (Wu, 1994), with which it shares the presence of a contact between the prefrontal and jugal (character 4.1). Both taxa also share an anteroposteriorly broad dorsal process of the jugal, a prominent row of palatine teeth that extends more or less parallel to the maxillary tooth row, and the roughly T-shaped outline of the postorbital. The

articular facets for the prefrontal and jugal on isolated maxillae of *C. hudsoni* indicate that the infraorbital process of the jugal closely approaches the ventral portion of the prefrontal in this taxon (H.-D.S., pers. obs.). *C. bairdi* lacks two diagnostic features of *C. mcgilli* (Wu, 1994): the distinct, hourglass-like constriction of the parietals and the L-shaped outline of the suborbital fenestra (elsewhere found only in *Sphenodon*). Furthermore, *C. bairdi* has only a single premaxillary "incisor" tooth, rather than two (in skulls of similar length), and three, rather than five, flanged additional teeth in the maxilla; these differences may well be invalidated by larger samples for both taxa. In *C. mcgilli*, the frontal also appears to contribute more extensively to the dorsal margin of the orbit.

Biogeographic Significance

The new sphenodontian is of considerable interest because it represents the first record of *Clevosaurus* from North America and because it most closely resembles *C. mcgilli* from the Lower Jurassic of Yunnan (Wu, 1994). The type species, *C. hudsoni* Swinton, 1939, is known from fissure-fillings of Late Triassic age in southwestern Britain (Fraser, 1988). Fraser (1988) distinguished two additional taxa among the British material: *C. minor* Fraser, 1988 and a still inadequately known form provisionally referred to as *C. sp.* by Fraser (1988:161). Gow and Raath (1977) briefly reported on several isolated jaw fragments of a *Clevosaurus*-like sphenodontian from the Lower Jurassic Forest Sandstone of Zimbabwe, which can be correlated with the upper part of the Stormberg Group of South Africa and Lesotho. A partial skull referable to *Clevosaurus* from the upper Stormberg Group of South Africa is virtually indistinguishable from *C. bairdi* (Sues and Reisz, unpubl. data). This wide geographic distribution of *Clevosaurus* is consistent with the recorded ranges

for the other tetrapod taxa from the McCoy Brook Formation, notably the tritheledontid cynodont *Pachygenelus* (Shubin et al., 1991) and the crocodyli-form archosaur *Protosuchus* (Sues et al., unpubl. data), both of which also occur in strata of the upper Stormberg Group in southern Africa.

ACKNOWLEDGMENTS

We thank the authorities of the Nova Scotia Museum, Halifax, especially R. Ogilvie and R. Grantham, for permission to collect in the Province of Nova Scotia and for varied assistance. W. W. Amaral, C. J. Banach, J. Dunham, S. H. Orzack, C. R. Schaff, W. P. Stevens, and A. Werth provided invaluable help in fossil collecting. Special thanks are due to W. W. Amaral for his superb preparation of the principal specimens used in this study; A. W. Crompton and F. A. Jenkins, Jr. generously facilitated his participation in our study. We are indebted to N. C. Fraser and Wu X. for discussions and for access to important comparative material. S. E. Evans and N. C. Fraser provided helpful comments on a draft of the manuscript. V. Krantz and B. Boyle took the photographs. J. Mulock prepared the drawings for Figure 5. Field work in Nova Scotia was supported by grants from the National Geographic Society (to P.E.O. and N.H.S.) and from the Barbour Fund of the Museum of Comparative Zoology, Harvard University (to N.H.S.). H.-D.S. gratefully acknowledges support for this research from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

- Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, B*, 302:605–720.
- 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97–164.
- Carroll, R. L. 1977. The origin of lizards; pp. 359–396 in S. M. Andrews, R. S. Miles, and A. D. Walker (eds.), *Problems in Vertebrate Evolution*. Linnean Society Symposium Series 4. Academic Press, London.
- 1985. A pleurosauro from the Lower Jurassic and the taxonomic position of the Sphenodontida. *Palaeontographica, A*, 189:1–28.
- Cocude-Michel, M. 1963. Les rhynchocéphales et les sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 7:1–187.
- Daugherty, C. H., A. Cree, J. M. Hay, and M. B. Thompson. 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). *Nature* 347:177–179.
- Estes, R. 1983. *Sauria terrestria, Amphisbaenia*. *Handbuch der Paläoherpetologie, Part 10A*. Gustav Fischer Verlag, Stuttgart and New York, XXII + 249 pp.
- Evans, S. M. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society* 70:203–264.
- 1988. The early history and relationships of the Diapsida; pp. 221–260 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Vol. 1: Am- phibians, Reptiles, Birds*. Systematics Association Special Volume 35A. Clarendon Press, Oxford.
- Fraser, N. C. 1982. A new rhynchocephalian from the British Upper Trias. *Palaeontology* 25:709–725.
- 1986. New Triassic sphenodontids from south-west England and their classification. *Palaeontology* 29:165–186.
- 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London, B*, 321:125–178.
- and M. J. Benton. 1989. The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. *Zoological Journal of the Linnean Society* 96:413–445.
- and G. M. Walkden. 1983. The ecology of a late Triassic reptile assemblage from Gloucestershire, England. *Palaeogeography, Palaeoclimatology, Palaeoecology* 42:341–365.
- and ——— 1984. The postcranial skeleton of *Planocephalosaurus robinsonae*. *Palaeontology* 27:575–595.
- Gauthier, J. A., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha; pp. 15–98 in R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford University Press, Stanford, California.
- Gow, C. E., and M. A. Raath. 1977. Fossil vertebrate studies in Rhodesia: Sphenodontid remains from the Upper Trias of Rhodesia. *Palaeontologia Africana* 20:121–122.
- Gray, J. E. 1831. Note on a peculiar structure in the head of an Agama; pp. 13–14 in J. E. Gray, *The Zoological Miscellany*. Privately published, London.
- 1842. Descriptions of two hitherto unrecorded species of reptiles from New Zealand; presented to the British Museum by Dr. Dieffenbach; p. 72 in J. E. Gray, *The Zoological Miscellany*. Privately published, London.
- Günther, A. 1867. Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). *Philosophical Transactions of the Royal Society of London* 157:595–629.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen*. Zweiter Band: Allgemeine Entwicklungsgeschichte der Organismen. Georg Reimer, Berlin, CLX + 462 pp.
- Harrison, H. S. 1901. The development and succession of teeth in *Hatteria punctata*. *Quarterly Journal of Microscopical Science* 44:161–213.
- Howes, G. B., and H. H. Swinnerton. 1901. On the development of the skeleton of the Tuatara, *Sphenodon punctatus*, with remarks on the egg, on the hatching, and on the hatched young. *Transactions of the Zoological Society of London* 16:1–86.
- Huxley, T. H. 1869. On *Hyperodapedon*. *Quarterly Journal of the Geological Society of London* 25:138–152.
- Murry, P. A. 1987. New reptiles from the Upper Triassic Chinle Formation of Arizona. *Journal of Paleontology* 61:773–786.
- O'Donoghue, C. H. 1920. The blood vascular system of the Tuatara, *Sphenodon punctatus*. *Philosophical Transactions of the Royal Society of London, B*, 210:175–252.
- Oelrich, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications, Museum of Zoology, University of Michigan* 94:1–122.
- Olsen, P. E., R. W. Schlichte, and P. J. W. Gore (eds.). 1989. *Tectonic, Depositional, and Paleocological History of Early Mesozoic Rift Basins, Eastern North America*. 28th International Geological Congress, Field Trip T351,

- Guidebook. American Geophysical Union, Washington, D.C., X + 174 pp.
- , N. H. Shubin, and M. H. Anders. 1987. New Early Jurassic tetrapod assemblages constrain Triassic-Jurassic tetrapod extinction event. *Science* 237:1025–1029.
- Owen, R. 1859. Note on the affinities of *Rhynchosaurus*. *Annals and Magazine of Natural History* (3)4:237–238.
- Robinson, P. L. 1973. A problematic reptile from the British Upper Trias. *Journal of the Geological Society of London* 129:457–479.
- 1976. How *Sphenodon* and *Uromastix* grow their teeth and use them; pp. 43–64 in A. d'A. Bellairs and C. B. Cox (eds.), *Morphology and Biology of Reptiles*. Linnean Society Symposium Series 3. Academic Press, London.
- Shubin, N. H., A. W. Crompton, H.-D. Sues, and P. E. Olsen. 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. *Science* 251:1063–1065.
- 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.
- Swinton, W. E. 1939. A new Triassic rhynchocephalian from Gloucestershire. *Annals and Magazine of Natural History* (11)4:591–594.
- Whiteside, D. I. 1986. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London*, B, 312: 379–430.
- Williston, S. W. 1925. *The Osteology of the Reptiles*. Harvard University Press, Cambridge, Massachusetts, XIII + 300 pp.
- Wu X. 1994. Late Triassic-Early Jurassic sphenodontians from China and the phylogeny of the Sphenodontia; pp. 38–69 in N. C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, New York.
- Yang Z. 1982. [On a new reptilian fossil from Lufeng, Yunnan]; pp. 36–37 in [Selected Works of Yang Zhongjian.] Science Press, Beijing. [Chinese]

Received 10 February 1993; accepted 14 May 1993.

APPENDIX. List of 34 craniodental characters of Rhynchocephalia (= *Gephyrosaurus* + Sphenodontia) used for cladistic analysis. "0" denotes primitive character state, "1" and "2" derived character states. Modified from Wu (1994).

1. Maxilla entering into margin of external naris (0) or excluded from margin of external naris by posterodorsal process of premaxilla (1).
2. Premaxillary process of maxilla: elongate (0), short (1).
3. Lacrimal: present (0), absent (1).
4. Prefrontal: no contact with jugal (0), in contact with jugal (1).
5. Frontals: unfused (0), fused (1).
6. Parietals: unfused (0), fused (1).
7. Intertemporal width of parietals: greater than interorbital width (0), less than interorbital width (1).
8. Parietal crest: absent (0), present (1).
9. Supratemporal: present (0), absent (1).
10. Parietal foramen: posterior to transverse line across anterior margins of supratemporal fenestrae (0), extends to or crosses line (1).
11. Antorbital length/total length of skull: more than 33 percent (0), 25 to 33 percent (1), less than 25 percent (2).
12. Supratemporal fenestra/orbit length ratio: less than 75 percent (0), more than 75 percent (1).
13. Posterior process of dentary: short (0), elongate (1).
14. Coronoid process of dentary: absent or short (0), pronounced (1).
15. Lower temporal bar: aligned with maxillary tooth row (0), bowed out laterally (1).
16. Lower temporal bar: incomplete (0), secondarily complete (1).
17. Retroarticular process: pronounced (0), short (1).
18. Quadrate–quadratojugal conch: pronounced (0), reduced (1).
19. Marginal dentition: pleurodont (0), some degree of acrodonty (1).
20. Premaxillary teeth: more than seven (0), four to seven (1), three or fewer (2).
21. Premaxilla: discrete teeth in adult (0), teeth fused to form "chisel" in adult (1).
22. Posterior maxillary teeth: simple conical crowns (0), presence of posterolingual flange or ridge (1).
23. Wear facets on marginal teeth: absent or poorly defined (0), well-defined on both dentary and maxillary teeth (1).
24. Anterolabial flanges on dentary teeth: absent (0), flanges on at least one tooth (1).
25. Posterolingual flanges on some maxillary teeth (at least as long as tooth cone): absent (0), present (1).
26. Lateral tooth row on palatine: small (0), enlarged (1).
27. Palatine tooth row: more than one tooth row (0), a single large lateral tooth row (1).
28. Pterygoid teeth: more than two rows (0), two rows or none (1).
29. Palatine: tapered posteriorly (0), relatively wide posteriorly (1).
30. Central portion of pterygoid between three rami: short (0), elongate (1).
31. Parabasisphenoid depression: absent (0), present (1).
32. Pterygoid: entering into margin of suborbital fenestra (0), excluded from margin of suborbital fenestra (1).
33. Suborbital fenestra: enclosed by more than two bones (0), enclosed only by ectopterygoid and palatine (1).
34. Jaw motion: orthal (0), propalinal (1).