

A NEW SPECIMEN OF *HESPEROSUCHUS AGILIS* FROM THE UPPER TRIASSIC OF NEW MEXICO AND THE INTERRELATIONSHIPS OF BASAL CROCODYLOMORPH ARCHOSAURS

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ABSTRACT—An articulated partial skeleton, including a nearly complete skull and left forelimb, of a crocodylomorph reptile from the Upper Triassic Chinle Formation of Ghost Ranch, New Mexico, is referable to *Hesperosuchus agilis* Colbert, 1952. It contributes much new information on the skeletal structure of this previously poorly known taxon. A large, circular palpebral bone is present in each orbit. The quadratojugal is particularly well preserved and suggests a reinterpretation of this element in related taxa including *Sphenosuchus*. Previous analyses of sphenosuchian relationships reached conflicting results, and a critical review of the characters used in these analyses is presented. A phylogenetic analysis of basal crocodylomorph taxa provides weak support for sphenosuchian monophyly, placing *Hesperosuchus* with *Saltoposuchus*, *Dibothrosuchus*, and *Sphenosuchus*.

INTRODUCTION

Ghost Ranch, located 20 km NW of Abiquiu in Rio Arriba County, New Mexico, is world-renowned for an occurrence of numerous well-preserved skeletons of the theropod dinosaur *Coelophysis bauri* (Cope, 1887) at the Whitaker or *Coelophysis* quarry in strata of the Upper Triassic Chinle Formation (Chinle Group sensu Lucas, 1993) (Colbert, 1947, 1989; Schwartz and Gillette, 1994). However, skeletal remains of non-dinosaurian vertebrates, including other archosaurian reptiles and fishes (Colbert, 1989), are relatively scarce at this site.

Initial excavation of the Whitaker quarry at Ghost Ranch by Edwin H. Colbert and his team from the American Museum of Natural History (New York) in 1947 and 1948 yielded 13 blocks of bone-bearing rock. Five of these blocks were kept in New York for preparation and subsequent study, and the remainder was sent to other institutions (Colbert, 1989). Work at the site was then abandoned until the summers of 1981 and 1982, when the Whitaker quarry was reopened under the direction of and with principal funding from the Carnegie Museum of Natural History. The Museum of Northern Arizona (Flagstaff), the New Mexico Museum of Natural History (Albuquerque), the Peabody Museum of Natural History at Yale University (New Haven), Erindale College of the University of Toronto (Mississauga), and Ghost Ranch contributed personnel and financial support during various parts of the project. Sixteen blocks of various sizes were removed from the quarry and, with the exception of one very large block distributed to each of the museums in Albuquerque and Flagstaff, were shipped to Pittsburgh. The Carnegie Museum subsequently sent one large block, labeled C-3-82 (Colbert, 1989:fig. 6), to the National Museum of Natural History (Washington, DC), where it served as the center piece of a temporary exhibit showing preparation of dinosaurian bones. During the preparation of the many skeletal remains of *Coelophysis bauri* preserved in this block, Mr. Alex Downs uncovered the skull and a considerable portion of the largely articulated postcranial skeleton of a sphenosuchian reptile. This find constitutes one of the most complete and best preserved specimens of a basal crocodylomorph discovered to date. It has been accessioned into the collections of fossil vertebrates at the Carnegie Museum of Natural History as CM 29894. We present here a description of this important specimen

and assess its phylogenetic relationships to other crocodylomorph archosaurs.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BP**, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; **CM**, Carnegie Museum of Natural History; **CUP**, collections of the former Catholic University of Peking, now housed in The Field Museum, Chicago; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; **MCPUCRGS**, Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Harvard University; **P**, Department of Zoology, University College, London; **PVL**, Fundación-Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; **SAM**, South African Museum, Cape Town; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **UCMP**, University of California Museum of Paleontology, Berkeley; **YPM**, Peabody Museum of Natural History, Yale University.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869

CROCODYLOMORPHA Hay, 1930 emend. Walker, 1968

SPHENOSUCHIDAE Houghton, 1924

HESPEROSUCHUS AGILIS Colbert, 1952

Holotype—AMNH 6758, partial skeleton comprising a number of cranial bones, vertebrae, ribs, dorsal osteoderms, girdle and limb-bones.

As first pointed out by Bonaparte (1972), the holotype includes the skeletal remains of at least two individuals. The “carpus” illustrated by Colbert is actually a tarsus, but it is too large to be associated with either of the two preserved feet. This mixing of material may be explained by the manner in which the fossils were collected. A letter dated April 22, 1930 (on file at the American Museum of Natural History, New York) from the collector, Barnum Brown, to Hubert Richardson, the owner of a trading post near the type locality, is revealing: “That little reptile I collected up near Tanner Crossing is of great interest and some of it lies buried under earth I threw out of another cut. I will have to screen over this material for fragments.”

Horizon and Locality—Lower part of Petrified Forest Mem-

ber (Chinle Formation); site on the north side of the Little Colorado River, near Tanner Crossing, about 6 miles (9.6 km) SE of Cameron, Arizona. Age: Late Triassic (late Carnian).

Newly Referred Specimen—CM 29894, skull and articulated partial postcranial skeleton, described below.

Horizon and Locality for CM 29894—Upper part of Petrified Forest Member of Chinle Formation (Parrish, 1989); Whitaker Quarry, Ghost Ranch, Rio Arriba County, New Mexico. Age: Late Triassic (late Carnian or early Norian).

Revised Diagnosis—Dentary with deep symphyseal end. Other potentially diagnostic apomorphies include: single large palpebral bone in each orbit (condition unknown in related taxa); supratemporal fossa extending laterally to lateral edge of squamosal; parietal crests on medial edges of supratemporal fossae separated by narrow median sulcus.

Comments—Colbert (1952) initially classified *Hesperosuchus* as an ornithosuchid “thecodont.” Walker (1970) first established its close relationship to *Sphenosuchus*, and this assessment has since been generally accepted.

A partial braincase in the material of AMNH 6758 indicates that the posttemporal fenestrae may have been broader than in *Dibothrosuchus*. However, the squamosal is not preserved, and the opening could have been restricted by the latter bone without contacting the paroccipital process, as is the case in *Sphenosuchus* (Walker, 1990). The quadrate lacks a deep depression as in *Terrestriusuchus*. Colbert could not identify a “problematical” bone associated with AMNH 6758, but Walker (1970) interpreted it as a coracoid. It is distinctive in the presence of an elongate, mediolaterally compressed posteroventral process and closely resembles the coracoids of *Pseudhesperosuchus*, *Sphenosuchus*, and *Terrestriusuchus*. Although no coracoid foramen is evident, we accept Walker’s identification of the bone in question.

Parrish (1991) described a partial mandible and postcranial skeleton of a crocodylomorph (UCMP 129740) from the upper part of the Petrified Forest Member of Petrified Forest National Park, Arizona. He tentatively identified this specimen as cf. *Sphenosuchus* sp., citing the deep anterior end of the dentary and differences in the sculpturing on the paramedian dorsal osteoderms between his specimen and the holotype of *Hesperosuchus agilis*, AMNH 6758. Sereno and Wild (1992) and Long and Murry (1995) reinterpreted UCMP 129470 as a larger individual of *H. agilis*. The sculpturing is indeed less prominent on the dorsal osteoderms of AMNH 6758 (although not “absent,” as claimed by Parrish [1993:210]). However, some of the osteoderms of AMNH 6758 are very similar in all other features to the element figured by Parrish (1991:fig. 7), and the weaker sculpturing probably reflects the small size and thus earlier ontogenetic stage of this specimen.

The original diagnosis provided by Colbert (1952:567) for *Hesperosuchus agilis* no longer serves to distinguish this form from other archosaurian reptiles. CM 29894 shares with both AMNH 6758 and UCMP 129470 (Parrish, 1991:fig. 4A, B) the deep anterior end of the dentary, which differs from the condition in *Dibothrosuchus*, *Sphenosuchus*, and related taxa (Sereno and Wild, 1992). It further resembles AMNH 6758 in the configuration of the maxillary tooth row with a rapid increase in size of the anterior teeth from the small, slender first to the very large fourth tooth. CM 29894 is much larger than AMNH 6758 in comparable dimensions (e.g., length of humerus 138 mm vs. 94 mm).

DESCRIPTION

Skull

Although nearly complete, the skull of CM 29894 has been strongly compressed dorsolaterally during fossilization (Figs. 1, 2). Thus the flattened left side of the snout is now preserved in

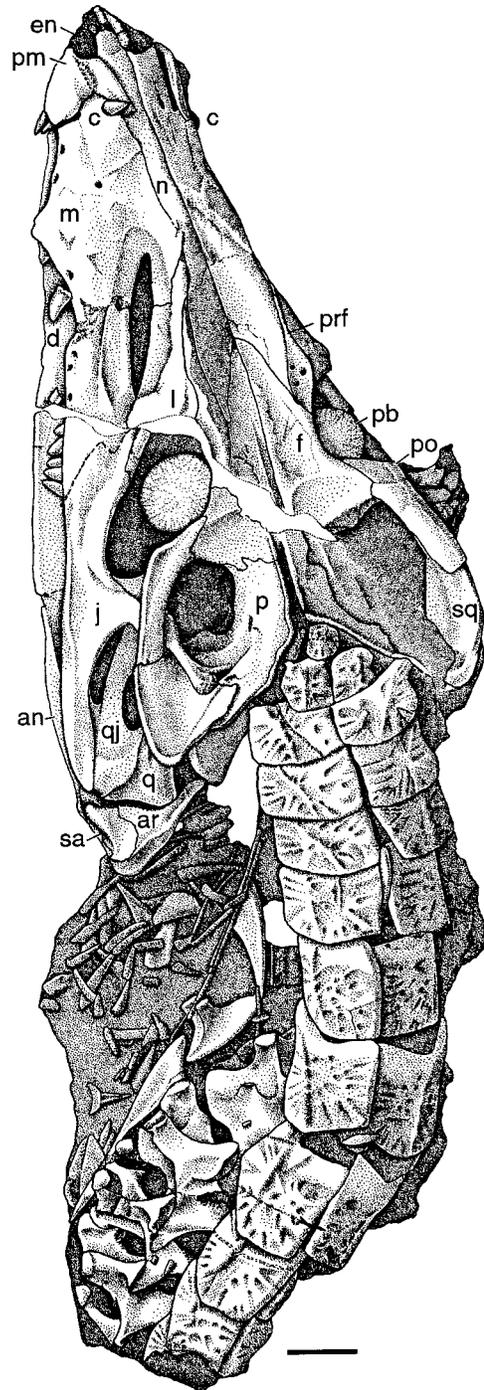


FIGURE 1. *Hesperosuchus agilis*, CM 29894, skull and cervical region in dorsal view. **Abbreviations:** an, angular; ar, articular; c, caniniform tooth in dentary; en, external narial opening; f, frontal; i, lacrima; m, maxilla; n, nasal; p, parietal; pb, palpebral; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal. Scale bar equals 1 cm.

more or less the same horizontal plane as the antorbital portion of the skull roof. It has been crushed down relative to the right side of the snout, with some separation of the bones along the midline of the skull roof. Both premaxillae, especially the right element, have been displaced downward relative to the maxillae

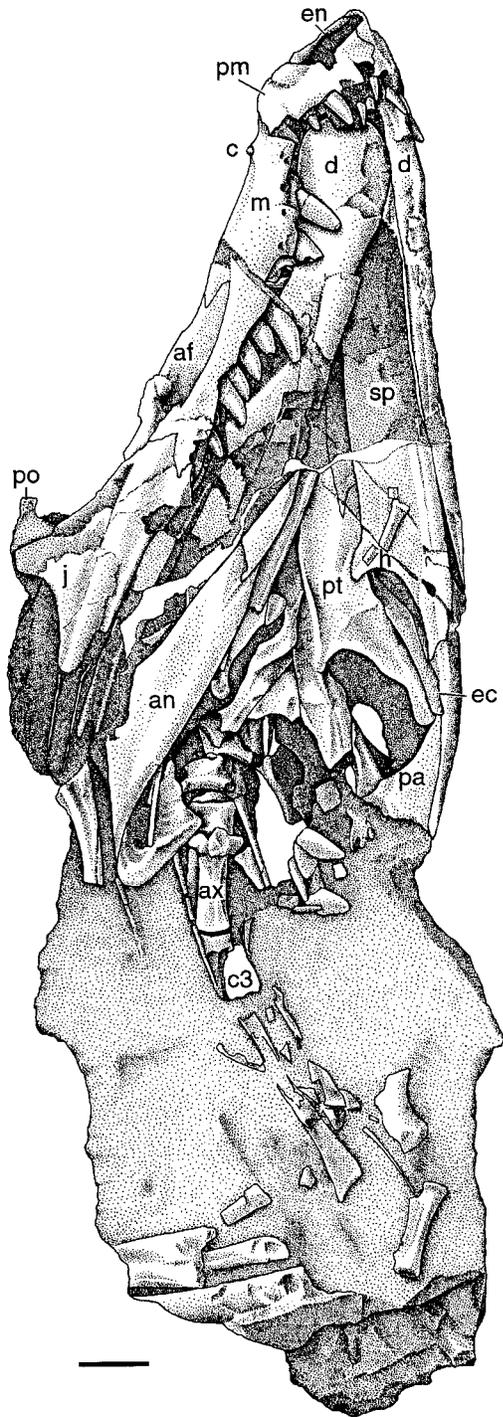


FIGURE 2. *Hesperosuchus agilis*, CM 29894, skull and cervical region in ventral view. **Abbreviations:** *af*, antorbital fossa; *an*, angular; *ax*, axis; *c*, caniniform tooth in dentary; *c3*, centrum of third cervical vertebra; *d*, dentary; *ec*, ectopterygoid; *en*, external narial opening; *pa*, prearticular; *po*, postorbital; *pt*, pterygoid; *sp*, splenial. Scale bar equals 1 cm.

by crushing. The mandible is still articulated with the skull, but its rami have been crushed into the palate and warped so that few details are apparent and most of the lower teeth are concealed from view. Due to mandibular occlusion and crushing, only the more posterior region of the palate could be exposed

during preparation. The braincase was apparently flattened dorsoventrally, and only the ventral portion of the basioccipital is clearly identifiable. Many bones show signs of plastic deformation as well as considerable small-scale fracturing. During preparation, the skull was separated into in three pieces: one piece comprises the tip of the snout and left antorbital region, a second the center of the skull roof and right antorbital and orbital regions, and the remainder of the skull is articulated with the cervical region.

The skull has a long, apparently narrow snout and a transversely broad temporal region. We estimate its original length to be about 195 mm when measured along the midline of the skull roof from the rostral end of the snout to the anterior end of the occipital embayment. The antorbital region is longer than the postorbital region. Most of the cranial bones lack sculpturing.

The posterolateral process of the extensive facial portion of the premaxilla fits into an anterolateral notch on the nasal where the latter bone is constricted to about half its maximum transverse width. It excludes the maxilla from participation in the posterior margin of the external narial fenestra. The premaxilla has a smoothly rounded posterior margin that probably very narrowly contacted the maxilla as in *Sphenosuchus* (Walker, 1990). Due to crushing, it is impossible to determine whether there was a narrow notch or an opening between the premaxilla and maxilla for the reception of the caniniform fourth tooth of the dentary as in *Dibothrosuchus* (Wu and Chatterjee, 1993). The short anterodorsal process of the premaxilla contributes to the slender internarial bar, which is largely formed by the nasal. The external narial fenestra faces laterally. The rostral portion of the premaxilla is slender. Each premaxilla holds five teeth; the fourth tooth is the largest, and the first and fifth are small.

The large facial portion of the maxilla was nearly vertically oriented. The alveolar margin of that bone has a sinuous lateral profile, reaching the greatest depth at about the level of the large fourth tooth. Its anterior margin at the broad junction to the premaxilla is convex. Dorsally, the ascending process of the maxilla contacts the lacrimal about midway along the dorsal rim of the antorbital fenestra and excludes the nasal from participation in the margin of the antorbital fossa. The ventral margin of the antorbital fossa does not form a trough, and as in *Sphenosuchus* (Walker, 1990) the maxilla lacks a lateral lamina that would conceal the medial wall of the fossa in lateral view. Unlike the condition in other known sphenosuchians, the rim of the antorbital fossa is more or less equidistant from the margin of the antorbital fenestra along the entire perimeter of the fenestra. The long axes of both the antorbital fossa and fenestra are oriented anterodorsally. The length of the antorbital fenestra is much greater than its depth. Posteriorly, the maxilla is overlapped by the anterior process of the jugal, with which it forms a W-shaped suture below the anteroventral margin of the orbit. The lateral surface of the maxilla bears scattered, small neurovascular foramina and a row of large foramina (probably for passage of cutaneous branches of N. alveolaris superior and associated vessels) just above the alveolar margin. Based on the more complete tooth row of the right element, the maxilla held at least 16 teeth. The upper tooth row ends posteriorly beneath the anterior third of the orbit. CM 29894 confirms Walker's (1970, 1990) reinterpretation of the jaw fragment of AMNH 6758 (identified by Colbert [1952:fig. 5] as a portion of the left maxilla and premaxilla) as comprising only the maxilla.

The nasal is long, transversely narrow, and thick. Anteriorly, it forms the posterodorsal margin of the external narial fenestra. Its anterodorsal surface bears sculpturing composed of fine longitudinal grooves and small foramina. The nasal is gently concave along its long lateral contact with the maxilla, but is flat or slightly concave posterodorsally. The frontals project far an-

teriorly along the midline of the skull roof between the posterior ends of the nasals.

The lacrimal has an inverted L-shape in lateral view. It extends forward almost to the anterior end of the dorsal margin of the antorbital fenestra, and forms the posterior and postero-dorsal margins of the antorbital fossa. Anteriorly, the lacrimal is overlapped by the maxilla within the antorbital fossa; poor preservation prevents detailed description of this region. The lacrimal forms an extensive lateral contact with the prefrontal along the preorbital bar. Its exposed dorsal surface is narrow. The position of the lacrimal duct cannot be determined with certainty.

The prefrontal extends posteriorly to about midway along the dorsal margin of the orbit where it is thick and slightly sculptured. Its posterior portion inserts on the anteroventral surface of the frontal. The narrow dorsal surface of the prefrontal bears three deep pits or foramina and is set off from the ventrolateral portion forming the orbital rim by a low, laterally projecting crest. The prefrontal is convex laterally and concave ventrally.

The triradiate jugal is almost twice as deep below the orbit than it is below the infratemporal fenestra. Its posterior or infratemporal process is slender and tapers toward the jaw joint. The dorsal process of the jugal appears to be wide anteroposteriorly although this configuration may be exaggerated by crushing. The lateral surface of the jugal bears a pronounced but low longitudinal ridge, extending from beneath the orbit and fading into the infratemporal process posteriorly. The sutural contact between the jugal and the lacrimal cannot be definitely identified due to poor preservation on both sides of the skull, but, as in other crocodylomorph archosaurs, the jugal apparently did not enter into the antorbital fossa.

Medial to the jugal, the quadratojugal apparently extends anteriorly to meet the postorbital bar and expands along the posterior edge of the latter. Crushing has displaced the quadratojugal slightly ventromedially. The short dorsal process of the quadratojugal extends along the lateral margin of the quadrate and tapers to a point. Unlike previous reconstructions of other taxa such as *Sphenosuchus* (Walker, 1990), the dorsal process ends well below the postorbital, suggesting a new interpretation for the fragmentary bones in this region of the holotype of *S. acutus* (see below). The quadratojugal has only limited lateral exposure and does not participate in the formation of the jaw joint. There is no trace of a foramen between the quadrate and quadratojugal.

The quadrate closely resembles that of *Sphenosuchus* (Walker, 1990:figs. 13, 16) in having a distinct lateral ridge along its anterior margin. Just medial to this ridge, a shallow depression is developed on the posterior surface of the bone. The quadrate slopes steeply anterodorsally so that its proximal end is placed well forward of the transversely expanded distal articular surface for the mandible. There is no evidence of a division of the pterygoid ramus of the quadrate into a pterygoid process and an orbital process, as reconstructed in *Sphenosuchus* by Walker (1990:fig. 16).

The frontals form a distinct but narrow (6 mm wide) median crest, which fades into the bone anteriorly. This condition closely resembles that in AMNH 6758 (Colbert, 1952:fig. 3b) and in *Sphenosuchus* (Walker, 1990). In *Dibothrosuchus*, the median crest is flanked by another ridge on either side, and the three ridges converge anteriorly and posteriorly (Wu and Chatterjee, 1993). A ridge curves laterally from the posterior end of the median crest and defines the anterior margin of a shallow depression of the supratemporal fossa on the frontal. The frontal forms most of the dorsal orbital rim and enters the anterior margin of the supratemporal fenestra. The orbital rim is nearly flat. Posteriorly, the frontals contact the parietals along an almost straight transverse suture. The posterolateral edge of the frontal is overlapped by the postorbital. Distinct cristae border

a median channel for the olfactory tracts on the ventral surface of the frontals.

Posteriorly, the parietals form a distinctly V-shaped embayment in the occipital margin so that the occipital crests extend posterolaterally, unlike the transverse, almost straight occipital crest in *Dibothrosuchus* (Wu and Chatterjee, 1993) and *Sphenosuchus* (Walker, 1990). A sagittal crest, composed of two ridges separated by a median gutter, extends along the entire length of the parietals. This differs from the narrow sagittal crest in *Dibothrosuchus* and *Sphenosuchus*. (Parrish [1991:table 3] claimed absence of a sagittal crest in *Hesperosuchus*, but the parietals are not preserved in AMNH 6758.) The two ridges, separated along the midline by about 4 mm, form the medial borders of the adjacent large supratemporal fossae. The interparietal suture extends in the median gutter between the ridges. The two ridges diverge posterolaterally and continue as occipital crests, which delimit the supratemporal fossae posteriorly. Anteriorly, the parietal contacts the long medial process of the postorbital behind the frontal.

The long, narrow postorbital forms the anterior half of the dorsal margin of the supratemporal bar and overlaps the squamosal posteriorly. Its thick lateral ridge overhangs the postorbital bar. The anterior end of the postorbital turns medially to end in a fork-like margin embracing the posterolateral end of the frontal.

A thick, subcircular palpebral bone is preserved in each orbit. This element has not been previously reported in any basal crocodylomorph archosaur. The longest diameter of the palpebral bone is 20 mm. Its gently convex dorsal surface bears fine, radiating sculpturing.

Anteriorly, the squamosal extends ventral to the postorbital to form part of the postorbital bar. Its anterior portion is broad transversely and overhangs the infratemporal fenestra laterally. A distinct dorsal ridge along its lateral edge forms a continuation of the ridge along the dorsolateral margin on the postorbital and the ridge on the occipital margin of the parietal, delimiting the posterolateral margin of the supratemporal fossa. This ridge sharply demarcates the skull table. Posteriorly, the squamosal forms a channel-like groove that receives the distal end of the paroccipital process. Its lateral, anteriorly directed flange projects ventrally and contacts the process. The paroccipital process formed by the otoccipital (fused exoccipital and opisthotic) is slightly expanded distally. Its posterior surface is gently convex dorsoventrally.

The pterygoid closely resembles that in *Sphenosuchus* (Walker, 1990:fig. 3A). Its transverse flange has a concave postero-medial edge, and its distal end projects posteriorly. As in *Sphenosuchus*, the pterygoid forms a distinct medial flange, which expands into a deep, posterolaterally directed quadrate ramus.

The ectopterygoid has a very long medial portion, which extends back along the anterolateral margin of the transverse flange of the pterygoid, ending just short of the distal tip of the latter. In ventral view, the anterolateral margin of the pterygoid overlies the medial portion of the ectopterygoid anteriorly, whereas the relationship is reversed posteriorly. The ectopterygoid contacts the medial surface of the jugal just anterior to the postorbital bar, but without contributing to the latter.

Due to the extensive dorsoventral crushing of the skull, few details of the braincase and basicranial region are apparent. That part of the basioccipital comprising the ventral portion of the occipital condyle, the basal tubera, and the region immediately anterior to the latter is exposed in ventral view. The bases of the tubera are linked by a transverse ridge of bone, as in *Sphenosuchus* (Walker, 1990:fig. 20). Recesses are present just anterior to this ridge, of which only the left is clearly visible. Pieces of the long, slender ceratohyalia were preserved, but most were removed in order to expose the palate and basicranial region.

Mandible

The long dentary is deep at its anterior (symphyseal) end, where the alveolar margin at the level of the enlarged third or fourth dentary tooth is situated well above that of the more posterior teeth. Neither the number nor the configuration of the dentary teeth can be determined due to the crushing and occlusion of the mandibular rami. The mandibular symphysis is long, extending posteriorly almost to the level of the anterior margin of the antorbital fossa. The lateral surface of the anterior portion of the dentary is marked by numerous neurovascular foramina. They are rounded in the expanded anterior region, but gradually become anteroposteriorly elongate behind the symphysis, particularly along the ventrolateral margin of the dentary.

The gently concave dorsal edge of the angular probably formed the ventral margin of a large mandibular fenestra, as in *Sphenosuchus* (Walker, 1990:fig. 31A), but the outline of this opening has been obscured by crushing on both sides.

The prearticular, which is exposed in medial and ventral view on both mandibular rami, gradually becomes deeper dorsoventrally toward its posterior contact with the articular.

The surangular forms the lateral third of the mandibular articular facet of the jaw joint and a low, conical process at the posterolateral corner of that facet. It is broadly exposed on the posterodorsal surface of the mandibular ramus and projects laterally over the angular.

The transversely expanded articular forms a finger-like dorsomedial process, which projects anteriorly and above the level of the articular facet of the jaw joint. The posterodorsal surface of the articular lies in the same plane as the posterodorsal surface of the quadrate. An irregular, rugose ridge extends along the posterodorsal surface of the bone, nearly horizontal dorsomedially and curving ventrolaterally. Unlike the condition in *Dibothrosuchus* (Wu and Chatterjee, 1993), there appears to be no foramen aërum.

The splenial is badly damaged on both mandibular rami. It covers much of the medial surface of the dentary, but details of its outline and structure have been obscured by crushing and poor preservation.

Teeth

The premaxillary and more anterior maxillary teeth have slightly recurved, labiolingually flattened crowns with convex anterior and nearly straight posterior carinae. The first maxillary tooth is small and slender. The anterior maxillary teeth rapidly increase in size up to the very large fourth tooth. The fourth to sixth teeth are large. Immediately behind this group, the maxillary teeth abruptly decrease in size. The crowns of the five posterior teeth in the left maxilla are not recurved and have convex anterior and posterior carinae. They are shorter but anteroposteriorly broader than those of the preceding teeth. The anterior and posterior carinae on the crowns of all teeth are serrated from the base to the tip of the crown, with an average count of eight serrations per mm. The fourth dentary tooth, best exposed on the right side, was tall and caniniform, and the tip of its crown is pushed up through the maxilla on both sides of the snout due to postmortem crushing.

Postcranial Axial Skeleton

The vertebral column is preserved more or less in articulation from the atlas-axis to the posterior portion of the dorsal series, although several of the more posterior cervical vertebrae and ribs were displaced post mortem. Most of the vertebrae are concealed by the overlying dermal armor dorsally and, in the trunk region, by the gastralia ventrally.

The atlas has a short centrum, whereas that of the axis is rather long but transversely narrow. The well-developed para-

pophyseal and diapophyseal facets are pendant on all exposed cervicals. The diapophyseal facet is located on the anterior margin of the centrum on the axis and third cervical, but, beginning with the fifth cervical, shifts more posteriorly and dorsally toward the neural arch. In lateral view, the ventral surface of all exposed cervical centra is distinctly concave anteroposteriorly, unlike the condition in *Terrestriisuchus* (Crush, 1984:fig. 10A). All centra are compressed mediolaterally, constricted at mid-length, and lack a ventral keel. The zygapophyses are large and robust.

The first and second cervical ribs are rod-like and extend posteriorly at least to the posterior end of the third cervical vertebra. Beginning with the third cervical rib, the ribs are short and of typically archosaurian form. Each is double-headed and forms a distinct, flange-like anterior projection. The few exposed dorsal ribs have rather straight, somewhat flattened shafts with at least anterior flanges developed on the proximal portion of the shaft.

The gastralia are slender, V-shaped elements with the median angle pointing forward. There are at least 25 densely packed gastralia, which, for the most part, are still preserved in association.

Dermal Armor

With the exception of an unpaired cervical osteoderm immediately behind the apex of the V-shaped occipital emargination of the skull roof, the dorsal dermal armor comprises two rows of paramedian osteoderms over the neck and trunk region (Figs. 1, 3A), as in other basal crocodylomorph archosaurs. At least 22 pairs of osteoderms are preserved in CM 29894. The dorsal surface of each osteoderm bears a well-developed sculpturing of irregular pits separated by ridges radiating from a prominent longitudinal ridge close to the lateral margin; the ventral surface is smooth.

The first osteoderm is small and subrectangular. It occupies a median position in the V-shaped embayment of the posterior margin of the skull roof. Although this osteoderm bears sculpturing it lacks ridging. Each plate of the paired second osteoderm is pentagonal with the longest side along the midline and bears a longitudinal ridge, which is less prominent than those on the more posterior osteoderms. Anteriorly, it is slightly overlapped by the first osteoderm. The second osteoderm is only about half as wide as the third (15 mm vs. 26 mm) and lacks a peg at the anterolateral corner. Osteoderms 3 to 5 are wider transversely than long anteroposteriorly. Each osteoderm forms a short, unsculptured anterolateral process, which projects anteriorly below the preceding plate. A distinct longitudinal ridge extends obliquely posterolaterally on the flat dorsal surface from the medial end of the articular process to the posterolateral corner of the osteoderm. Each osteoderm overlaps the anterior end of the succeeding plate. The sixth osteoderm is slightly wider than long and deflected ventrolaterally from the dorsolateral ridge. Osteoderms 7 to 22 are more or less rectangular, and their anterolateral articular pegs are longer and placed more anteriorly than on the third osteoderm. The anterior portion of the dorsal surface of each osteoderm is devoid of sculpturing and gently raised, marking the area of overlap by the preceding osteoderm. The dorsal ridge extends parasagittally close to the lateral margin and marks the division of each osteoderm into a horizontal medial and a slightly ventrolaterally deflected lateral portion that gives each plate in end view the appearance of a widely opened, inverted V. The anterior margin of each osteoderm is concave and its lateral edge is distinctly convex. The more posterior osteoderms have a notch in the posterolateral corner.

No trace of ventral osteoderms is preserved. Small, scale-like

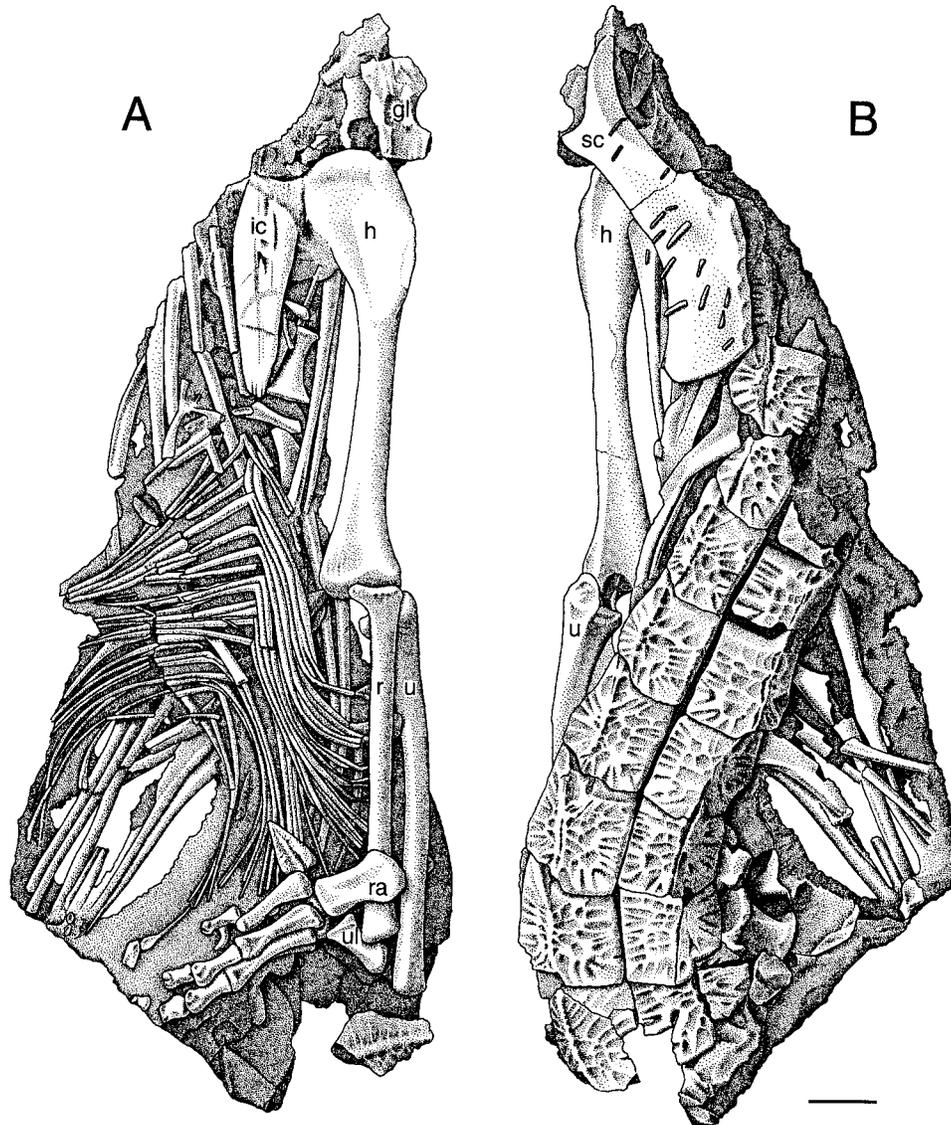


FIGURE 3. *Hesperosuchus agilis*, CM 29894, trunk and left forelimb in **A**, dorsal and **B**, ventral views. **Abbreviations:** **gl**, glenoid fossa; **h**, humerus; **ic**, interclavicle; **r**, radius; **ra**, radiale; **sc**, scapula; **u**, ulna; **ul**, ulnare. Scale bar equals 1 cm.

platelets, particularly on the lateral surface of the left scapula (Fig. 3A), may represent remains of a light appendicular armor.

Shoulder Girdle and Forelimb

The shoulder girdle is represented by an almost complete left scapula and the posterior part of the interclavicle (Fig. 3A). The elongate scapula consists of a flattened blade that is constricted between the much expanded dorsal portion (the anterior edge of which has been damaged) and the less expanded proximal end, which is greatly expanded at its contact with the coracoid. Flattening of the scapular blade has been somewhat exaggerated by crushing. The anteroventral portion of the scapula bears a distinct acromial ridge. Its thickened posterior edge forms the concave, posteroventrally facing glenoid facet. The interclavicle is elongated, with a flat ventral surface and more or less parallel lateral margins. Neither coracoid is preserved.

The almost complete and articulated left forelimb (Fig. 3B) is gracile. The humerus, radius, and ulna are slender, and each

is longer than the scapula. The humerus has a straight shaft and expanded proximal and distal articular ends. Its proximal end bears a well-developed, anteromedially reflected deltopectoral crest (the medial edge of which has been damaged) and a distinct internal tuberosity. There is no oval depression on the dorsal surface of the proximal end as there is in *Dibothrosuchus* (Wu and Chatterjee, 1993). The rounded distal condyles are well separated from one another, the medial one being the larger of the two. The slender radius (length: 107 mm) and ulna (length: 127 mm) are somewhat shorter than the humerus (length: 138 mm). The radius is moderately expanded at both articular ends, with the proximal end being T-shaped in lateral view. It has a nearly straight shaft, which is oval in transverse section. The ulna has a robust proximal end with a short olecranon process and a slightly expanded distal end that extended beyond that of the radius. Its anteroposteriorly somewhat flattened shaft has a gently sigmoidal curvature. Its distal end is distinctly concave along the medial margin.

The left carpus and manus have been displaced medially relative to the remainder of the forelimb and are exposed in dorsal view. The elongated radiale and ulnare appear to be proportionately more robust than those in *Dibothrosuchus* and *Terrestriisuchus*. The dorsoventrally flattened radiale has an expanded proximal and a less expanded distal end. It is only slightly longer than metacarpal III (28 mm vs. 27.6 mm). The smaller, much less massive ulnare (length 19 mm) appears to be equally expanded at both articular ends. A single distal carpal is situated over the proximal ends of metacarpals II and III. Only portions of manual digits I–IV are preserved. The “bundled” disposition of the metacarpals and digits indicates that the manus was digitigrade. Metacarpals II and III are subequal in length and longer than metacarpal I. The distal portion of the displaced metacarpal IV is concealed by metacarpal III. The proximal portions of metacarpals I–III are expanded, and their distal ends bear extensor pits, as do those of the two preserved phalanges in digits II and III. Manual digit I is short and apparently comprises only two phalanges.

COMMENTS ON OTHER TAXA REFERRED TO SPHENOSUCHIA

Since the original description of *Sphenosuchus acutus* by Haughton (1915), various crocodile-like archosaurs of Late Triassic or Jurassic age have been explicitly compared and related to that taxon (Walker, 1970; Bonaparte, 1972; Clark, 1986). Bonaparte (1972, 1982) proposed a suborder Sphenosuchia for the reception of these “crocodile-like thecodonts,” which he considered broadly ancestral to crocodylians (Bonaparte, 1982). Below we present a brief review of the various taxa that have been referred to Sphenosuchia.

Pseudhesperosuchus jachaleri Bonaparte, 1969

The holotype and only known specimen of *Pseudhesperosuchus jachaleri* (PVL 3830) from the Upper Triassic (Norian) Los Colorados Formation of Argentina has been described in detail by Bonaparte (1972). It consists of a nearly complete but poorly preserved skull with articulated mandible and associated postcranial skeleton including most of the vertebral column, the shoulder girdle and greater part of the forelimb, and some bones of the hind-limb. The palatal region of the skull is poorly preserved, and most of the sutures are difficult to identify and trace. Bonaparte (1972) noted its crocodylomorph features and recognized its relationships to *Sphenosuchus*.

The lateral temporal region is poorly preserved, and comparison with better preserved cranial material of other sphenosuchian taxa supports an interpretation different from those offered by Bonaparte (1972:fig. 22) and Parrish (1993:fig. 9C). A feature interpreted by these authors as the suture between the quadrate and quadratojugal is in the same position as a depression or fenestra on the posterior surface of the quadrate in *Dibothrosuchus*, *Sphenosuchus*, and *Terrestriisuchus*. In Bonaparte's (1972:fig. 22) drawing, the foramen indicated between the quadrate and quadratojugal most likely represents this depression. The suture between the quadrate and quadratojugal, illustrated as dorsal to this feature, appears to be a narrow crack (JMC, pers. obs.). A small piece of the quadratojugal is preserved in the ventral part of the temporal region, adhering to the anterior edge of the quadrate, but this is the only fragment of this bone definitely present. According to our reinterpretation (Fig. 4), this region may not differ from that in other sphenosuchians.

A small, unexpanded basiptyergoid process adheres to the left pterygoid and can be seen in outline in Bonaparte's (1972:fig. 24) drawing, where it is identified as part of the pterygoid. The surangular is broken off on the posterior part of the left mandibular ramus. It probably continued posteriorly at the same

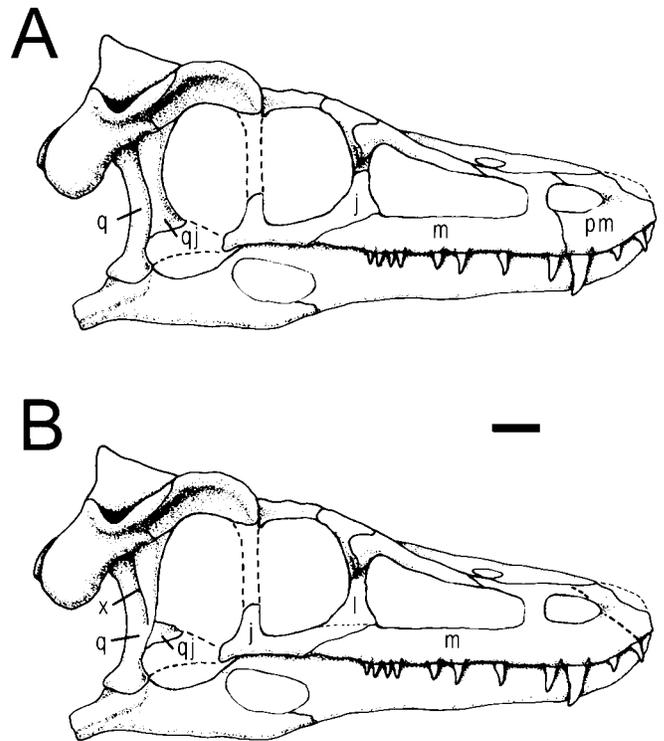


FIGURE 4. Reconstructions of the skull of *Pseudhesperosuchus jachaleri* in right lateral view. **A**, reconstruction by Parrish (1993); **B**, reconstruction proposed in the present paper. Note that the quadrate is interpreted here as including much of what was previously identified as the quadratojugal, and the supposed suture is considered a crushed depression (x) on the posterior surface of the quadrate. **Abbreviations:** j, jugal; l, lacrimal; m, maxilla; pm, premaxilla; q, quadrate; qj, quadratojugal; x, depression on posterior surface of quadrate. Scale bar equals 1 cm.

level as the anterior part, indicating that the depression in the posterior part of the lower jaw illustrated by Bonaparte (1972:fig. 22) and Parrish (1993:fig. 9C) is not natural. The location and even the presence of the posttemporal fenestrae are uncertain; the openings identified as such by Bonaparte (1972:fig. 24) occupy unusual positions, being too far lateral in comparison with most other archosaurs except birds. Although the depressions medial to these openings do not open anteriorly, they are in the appropriate positions for posttemporal fenestrae. The sutural pattern in this region indicated in Bonaparte's illustration would be unlikely if this is indeed the posttemporal fenestra, since the latter is never enclosed within the squamosal. However, it is impossible to determine the actual sutural pattern on the original specimen. The squamosal, and probably the parietal, clearly has a broad occipital exposure.

The small openings between the maxilla and nasal dorsal to the antorbital fenestra (Bonaparte, 1972:fig. 23) may be artifacts because they are asymmetrically placed on either side of the specimen and differ in size. The ventral edge of the lacrimal within the antorbital fossa is straight on the right side of the specimen, and the concave edge on the left side illustrated by Bonaparte (1972:fig. 22) is probably the result of a break. It is impossible to determine whether the jugal borders the antorbital fenestra, as figured by Bonaparte (1972) and Parrish (1993), because (as Bonaparte indicated through the use of a dotted line) the contact between the jugal and lacrimal cannot be traced on the fossil. The anterior part of the palate has not been

prepared, and thus it is impossible to determine whether the maxillae formed a secondary bony palate as in other crocodylomorphs.

The premaxilla and circumnarial region, as reinterpreted by Parrish (1993), are unlike those in any other sphenosuchian, and comparison with other sphenosuchians suggests an alternative reconstruction. Although Parrish reconstructed an unusually large premaxilla with a very large dorsomedial process and narial opening, examination of the holotype of *Pseudhesperosuchus jachaleri* indicates that the suture between the premaxilla and maxilla is in the more anterior position indicated by Bonaparte (1972). As noted by Bonaparte (1972:60): "en la diagnosis preliminar de este género (Bonaparte, 1969) interpreté a estas aberturas preorbitarias adicionales como las narinas externas, interpretación que rectifico ahora dado que la mejor preparación del ejemplar permite ver la extensión y relaciones de los nasales y premaxilares. Las narinas externas de *Pseudhesperosuchus* son de posición terminal y más bien chicas." We also note that the prefrontal has been mislabeled as the postfrontal by Parrish (1993:fig. 9C).

Saltoposuchus connectens Huene, 1921

Saltoposuchus connectens is represented by several well-preserved specimens from the Upper Triassic (Norian) Stubensandstein of Baden-Württemberg (Germany). The partial skeleton SMNS 12597 is the holotype of *S. connectens*. Sereno and Wild (1992) demonstrated that two partial skulls, one with an associated articulated manus (SMNS 12352), previously attributed to the small theropod dinosaur *Procompsognathus triassicus* from the same horizon, actually belong to *S. connectens*. They also followed Crush (1984) and Parrish (1991) in considering *Saltoposuchus longipes* a subjective junior synonym of *S. connectens*. Walker (1970) and Crush (1984) corrected a number of Huene's (1921) original identifications of individual bones, but no comprehensive revision of the entire hypodigm of *Saltoposuchus connectens* is as yet available.

Terrestrisuchus gracilis Crush, 1984

Terrestrisuchus gracilis from Late Triassic (Norian) fissure-fillings in Wales was described in detail by Crush (1984), having earlier been the subject of a brief communication by Kermack (1956). The specimens referred to this taxon vary considerably in completeness, ranging from isolated bones to associated but scattered skeletal remains and fragments of skulls. All of the known skeletal material is comparable in size to *Pseudhesperosuchus* and *Saltoposuchus*. Many aspects of the structure of the skull still remain unknown, and several features described by Crush are open to different interpretations.

Based on an isolated pterygoid, Crush (1984:138) inferred the presence of an interpterygoid vacuity because "[the pterygoid] did not suture to its counterpart." The anterior portions of the pterygoids in extant crocodylians, dorsal to the narial passage, are also not sutured together even though they do not enclose a vacuity between them. Furthermore, the medial edge of the bone in *Terrestrisuchus* is flat rather than curving posterolaterally (Crush, 1984:138; JMC, pers. obs.). Thus it is unclear whether an interpterygoid vacuity was present or absent. The articular was probably distorted on the specimen illustrated by Crush (1984:fig. 5), although the medial process is clearly present. The peculiar dorsal orientation of the retroarticular process is presumably the result of distortion, because it would prevent mandibular depression to the degree seen in related taxa. The large size of the posttemporal fenestrae is most likely due to breakage of the occipital portion of the parietal, but this cannot be confirmed on the currently available material. The feature on the dorsal surface of an osteoderm labeled as a "muscle scar" by Crush (1984:fig. 10C) is probably incorrect,

as no muscles attach to either the dorsal or the ventral surfaces of the osteoderms and only ligaments attach to the ventral surfaces of the osteoderms in extant crocodylians (Frey, 1988).

Terrestrisuchus gracilis is very similar to *Saltoposuchus connectens*. Crush (1984:152) offered only a single feature to distinguish the former taxon from the latter, viz. "the maxilla of *Saltoposuchus* lacks the fossa found in this bone of *Terrestrisuchus*." In his description of the maxilla of *Terrestrisuchus*, Crush (1984: 134) stated that "[a] conical fossa is present in the facial plate anterior to the antorbital fenestra. This fossa is directed anteroventrally and is of moderate depth." Clark (in Benton and Clark, 1988) noted that the holotype of *Saltoposuchus connectens* (SMNS 12597) has the same fossa, and he suggested that the two forms may be synonymous.

Sereno and Wild (1992) rejected the synonymy proposed by Clark and listed several autapomorphies to distinguish *Terrestrisuchus* from *Saltoposuchus*, specifically the more elongated distal caudal centra, the extremely slender limb-bones, and the presence of an antitrochanter on the acetabular margin of the ischium. Regarding the elongated distal caudals, however, comparison between these two taxa is difficult because the only known specimen of *Saltoposuchus* with preserved caudal vertebrae (SMNS 12597) includes only 24 vertebrae and may not be complete (note that Sereno and Wild [1992:fig. 11] inferred approximately twice as many caudal vertebrae), whereas the tail of *Terrestrisuchus* was reconstructed by Crush (1984:150) as comprising approximately 70 vertebrae. It is the distal caudal vertebrae that are elongate in *Terrestrisuchus*, and comparing them with the proximal 24 caudal vertebrae of *Saltoposuchus* is dubious. The caudal series of SMNS 12597 suggests that there were far fewer vertebrae in *Saltoposuchus* than in *Terrestrisuchus*, but more complete material is required to be certain. Regarding the antitrochanter on the ischium of *Saltoposuchus*, the only specimen preserving this element (SMNS 12596) is not prepared on the lateral surface in the region where an antitrochanter would be present, and thus the presence or absence of this feature cannot be ascertained at present.

The known limb bones of *Saltoposuchus* have thicker shafts than those of *Terrestrisuchus*. For example, the left femur of the holotype of *Terrestrisuchus gracilis*, P47/21 and 22 (part and counterpart), is 56 mm long but has a minimum mid-shaft diameter of only 3.2 mm (length/diameter ratio: 17.5). By comparison, the left femur of *Saltoposuchus connectens* (SMNS 12596) is 108.5 mm long and has a minimum mid-shaft diameter of 10.6 mm (length/diameter ratio: 10.24). However, this difference may simply reflect the larger size of *Saltoposuchus*, because limb-bones become more robust at larger sizes in extant *Alligator mississippiensis* (Dodson, 1975; for example, the allometric coefficient for femoral length in the latter is 0.97, but that for femoral diameter is 1.09). The lack of large specimens of *Terrestrisuchus* and small specimens of *Saltoposuchus* precludes assessment of allometry in these taxa.

Allometry may also be responsible for the difference in proportions of the tibia relative to the femur between *Saltoposuchus* and *Terrestrisuchus*. In *Terrestrisuchus*, the tibia is longer than the femur (the length of the left femur of the holotype of *T. gracilis* is 56 mm and that of the right tibia is 59.4 mm), whereas the femur is longer than the tibia in *Saltoposuchus* (the length of the left femur of SMNS 12596 is 108.5 mm and that of the left tibia is 91.5 mm). In *Alligator mississippiensis*, the tibia is negatively allometric relative to the femur (Dodson, 1975), and the femur is relatively longer in larger, more mature individuals.

The squamosals of *Saltoposuchus* and *Terrestrisuchus* differ in that the dorsal surface of the squamosal of the former bears a distinct ridge, which marks the posterolateral edge of the supratemporal fossa. Although Sereno and Wild (1992:448) regarded the absence of this ridge on the known squamosals of

Terrestri-suchus as due to poor preservation, the absence of such a ridge on the well-preserved squamosal of a specimen (BP/1/5237) referred to *Pedeticosaurus* by Gow and Kitching (1988) indicates that this feature may indeed be absent in *Terrestri-suchus*.

The maxilla of *Saltoposuchus* differs from that of *Terrestri-suchus* in being proportionately shorter but with a more extensive facial portion anterior to the antorbital fossa. In this feature, *Terrestri-suchus* is more similar to *Pseudhesperosuchus*.

The proximal head of the femur of *Saltoposuchus* (e.g., SMNS 12596) may be more distinctly inturned than that of *Terrestri-suchus*, but there exists some variation among the specimens referred to the former (e.g., SMNS 12597).

Thus there exist differences that may distinguish *Terrestri-suchus gracilis* from *Saltoposuchus connectens*, but they may simply reflect the larger size of known specimens for the latter taxon.

Sphenosuchus acutus Houghton, 1915

The holotype of *Sphenosuchus acutus* (SAM 3014) consists of a nearly complete, well-preserved skull and partial postcranial skeleton from the Lower Jurassic Elliot Formation of South Africa. Based on careful preparation of this specimen, Walker (1990) published a meticulous redescription to which readers are referred for further details.

The quadratojugal of *Sphenosuchus* was reconstructed by Walker (1990:fig. 18A) as extending anterodorsally beneath the squamosal anterior to the quadrate. However, Walker's (1990:figs. 13D, 19B, 56) drawings and photograph of this region in the holotype of *Sphenosuchus acutus* as preserved present a pattern more similar to that in CM 29894 (see also Walker [1970:fig. 12c]), where the quadratojugal does not extend dorsally more than about half way up the anterior edge of the quadrate (Fig. 5). The bone identified as the dorsal portion of the right quadratojugal (Walker, 1990:fig. 7H, I) is in a position comparable to the anterodorsal process of the quadrate in other sphenosuchians, such as *Dibothrosuchus* (Wu and Chatterjee, 1993).

Clarencea gracilis Brink, 1959

This taxon was based on a small partial skull (BP/1/288) from the Lower Jurassic Elliot Formation of South Africa. (The subsequent change in the spelling of the generic nomen to "*Clarensia*" made by Gow and Kitching [1988] is not valid under the rules of the International Code of Zoological Nomenclature.) The specimen consists of an articulated snout and mandible; the braincase is not preserved. Brink considered *Clarencea* an ornithosuchid thecodont, but Cooper (1982) and Gow and Kitching (1988) suggested protosuchian affinities. Much of what Brink figured as bone is actually matrix, and some of what he interpreted as sutures are cracks. Indeed, so many cracks penetrate the specimen that only the most obvious sutures can be identified with certainty. Gow and Kitching (1988:fig. 11) presented a new interpretation of the specimen. Contrary to Brink's description, the contact between the maxilla and jugal cannot be identified with certainty, the prefrontal does not overhang the orbit, the dentary is longer than figured by Brink, the mandibular symphysis is not "massive" but is very similar to that in most sphenosuchians, and the alleged ectopterygoids probably represent parts of the pterygoids. The rostrum is similar to that of *Sphenosuchus*, and we consider it possible that the holotype of *Clarencea gracilis* represents a juvenile individual of *S. acutus*. There is nothing to indicate affinities with basal crocodyliforms, as claimed by Cooper (1982) and Gow and Kitching (1988). Because the holotype has no features that distinguish it from other taxa such as *Spheno-*

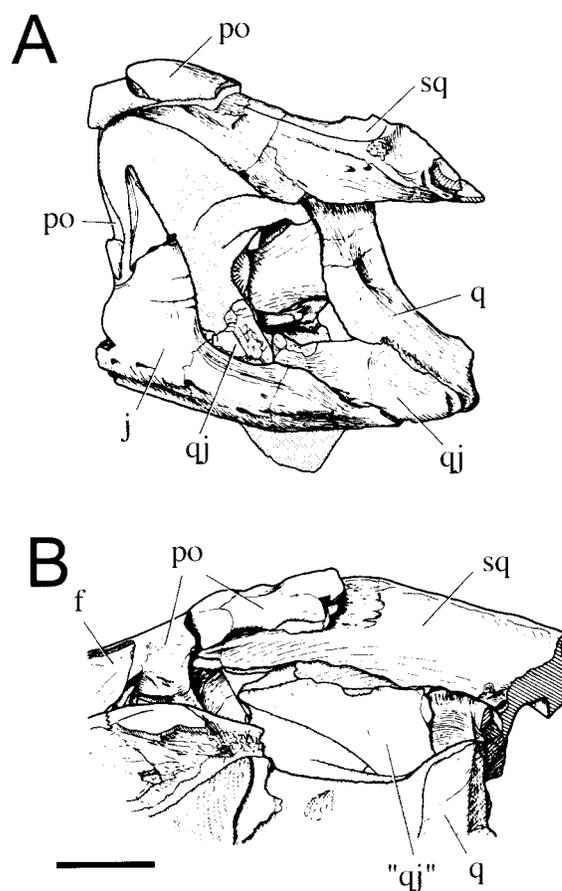


FIGURE 5. Temporal region of the skull of the holotype of *Sphenosuchus acutus* as figured by Walker (1990:fig. 7A, H). A, left infratemporal region in lateral view; B, right supratemporal region in dorso-medial view. The bone labeled "qj" in the lower figure was identified as the quadratojugal, but it is in the same position as an anterior extension of the quadrate on CM 29894. The limited dorsal extent of the quadratojugal seen on the left side in the upper figure is also comparable to that of CM 29894. **Abbreviations:** f, frontal; j, jugal; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal. Scale bar equals 1 cm.

suchus or *Hesperosuchus*, we consider *Clarencea gracilis* a nomen dubium.

Dibothrosuchus elaphros Simmons, 1965

Simmons (1965) described *Dibothrosuchus elaphros* from the Lower Jurassic Lower Lufeng Formation of Yunnan (China) and referred it to the Ornithosuchidae. At that time, this taxon was known only from the holotype (CUP 2081), which comprises skull fragments, including parts of the frontals, maxilla, infratemporal arcade, and most of the mandible, most of the vertebral column, a coracoid, and some fragmentary limb-bones. Simmons and most later authors considered *Dibothrosuchus* an ornithosuchid, but Crush (1984) tentatively allied it to the Sphenosuchia. An almost complete skull and associated partial skeleton (IVPP V7907) from the Lower Lufeng Formation (Wu, 1986; Wu and Chatterjee, 1993) confirmed reference of *Dibothrosuchus* to the Sphenosuchia. Wu and Chatterjee (1993) presented an excellent description of this specimen, but we disagree with their interpretation of some features.

Some of the highly unusual features of the skull of IVPP V7907 may be the result of postmortem crushing. Thus the

anterior position of the quadrate, exposing much of the otic region laterally, may be due to warping of the quadrate by dorsoventral crushing. The broad contact of the descending process of the prefrontal with the palate may also be a result of the obvious dorsoventral crushing of the rostrum. The ventrolateral contact between the premaxilla and maxilla may be an artifact of crushing, and the recess between these bones may have been open ventrally; there certainly exists no evidence for a "ball-and-socket" articulation in this region.

We could not confirm the presence of the quadratojugal in the dorsal part of the infratemporal fenestra, as claimed by Wu and Chatterjee (1993:64).

The right coracoid of IVPP V7907 has flat surfaces where it terminates posteroventrally and on its ventral edge, which Wu and Chatterjee (1993) considered articular surfaces for the sternum. They also identified a biceps tubercle at the anterior end of the supposed sternal facet. However, our examination of the coracoid indicates that these edges are broken, and that the bone is incomplete in this region. The biceps tubercle may merely be an artifact produced by this breakage.

***Barberenasuchus brasiliensis* Mattar, 1987**

The holotype and only known specimen of *Barberenasuchus brasiliensis*, MCPUCRGS-220, from the Upper Triassic (Carnian) Santa Maria Formation of Rio Grande do Sul (Brazil), comprises a poorly preserved, apparently badly crushed skull and mandible with an associated axis vertebra. Most sutures are uncertain and are only indicated by broken lines in Mattar's (1987) drawings. The skull apparently closely resembles that of *Pseudhesperosuchus*. The supposed presence of teeth on the pterygoid is unusual for a derived archosaurian reptile.

***Hallopus victor* (Marsh, 1877)**

The holotype and only known specimen of *Hallopus victor* (YPM 1914) probably came from the Upper Jurassic Morrison Formation of Colorado, although the debate about its geographic and stratigraphic provenance continues to the present day (Ague et al., 1995). It consists of dissociated but well-preserved postcranial elements, including an articulated hind-limb and most of the forelimb. Walker (1970) redescribed the specimen, and our observations are fully consistent with his meticulous description. *Hallopus* was traditionally considered a coelurosaurian dinosaur, but Walker convincingly demonstrated its crocodylomorph affinities. A splint of bone lying medial to the left second metatarsal may not be the first metatarsal, as suggested by Walker, but this is a plausible interpretation of the material.

***Trialestes romeri* (Reig, 1963)**

This taxon was founded by Reig (1963, under the preoccupied generic nomen *Triassolestes*, for which Bonaparte [1982] proposed the replacement name *Trialestes*) on the basis of two specimens, the holotype (PVL 2561) and a referred specimen (PVL 2559), from the Upper Triassic (Carnian) Ischigualasto Formation of northwestern Argentina. PVL 2561 consists of a partial skull lacking the skull roof and braincase, portions of two forelimbs including a scapula, a humerus, a radius, ulnae, a radiale and an ulnare, and several cervical and 16 caudal vertebrae. PVL 2559 now comprises a partial articulated pes. Reig (1963) provided measurements for a pubis, astragalus, and cervical and sacral vertebrae of this specimen, but JMC could not locate these elements in the collections of the Instituto Miguel Lillo in 1985. The forelimb elements of the holotype were associated with the skull. However, because the carpals are elongate, Reig considered it unlikely that a skull devoid of crocodylian characters would be associated with a forelimb exhibiting such a characteristic crocodylian feature. Instead, because

he interpreted *Proterochampsia* from the same horizon as a crocodylian (Reig, 1959; see also Sill, 1967), he referred the limbs to that taxon (Reig, 1963:15). With the realization that *Proterochampsia* was not closely related to Crocodylomorpha (Walker, 1968), there is no reason that the limbs should not be referred to the same animal as the skull of *Trialestes* (Bonaparte, 1972). A third specimen from the same horizon (PVL 3889) was subsequently referred to this taxon by Bonaparte (1978). It includes portions of the forelimb other than the carpus, most of the pelvis and hind-limb, and several vertebrae. The pelvis and hind-limb have features considered diagnostic for dinosaurs, including a perforated acetabulum with a well-developed supraacetabular crest, an inturned femoral head that is more distinct than that in sphenosuchians, a mesotarsal ankle joint and a functionally tridactyl pes. The vertebral centra have excavated lateral surfaces.

Although the forelimbs of both specimens are very similar, nearly all of their similarities can be interpreted as plesiomorphic character-states or features that are found in both crocodylomorphs and basal dinosaurs. However, the limb proportions are indeed striking and deserve attention. In particular, the great length of the radius and ulna relative to the humerus is very unusual. The radius and ulna are significantly longer than the humerus in both specimens (1.15 times in PVL 2559). In no other basal archosaur known to us are the radius and ulna significantly longer than the humerus. Either the two specimens represent two different taxa, one a basal crocodylomorph and the other a basal dinosaur, but both converging in forelimb structure, or the two specimens represent the same taxon, which combines dinosaurian and crocodylomorph characteristics. Considering the latter possibility, it is not clear that this taxon would be referable to the Crocodylomorpha. The only apparent crocodylomorph feature is the elongation of the radiale and ulnare, whereas at least four different dinosaur-like features are present in the hind-limb and vertebrae. The simplest solution would be to refer this taxon to the Dinosauria and to interpret the elongate radiale and ulnare as the result of convergent evolution. However, if the specimens actually represent two different taxa, then PVL 2561 is a basal crocodylomorph and PVL 3889 a dinosaur. The problem posed by these two specimens is intriguing, but its resolution must await the discovery of additional material including both the carpus and hind-limb.

***Parrishia mcreai* Long and Murry, 1995**

We have not had the opportunity to study material assigned to this taxon, which is known only from isolated vertebrae (mostly centra) from the Upper Triassic Chinle, Dockum, and Santa Rosa formations of the American Southwest. Long and Murry (1995) compared the material mainly with *Hesperosuchus*, and distinguished *Parrishia* from the latter as being more robust and having a straight, rather than anterodorsally curved, neck. Photographs of anterior cervical vertebrae (Long and Murry, 1995:fig. 174A–L) show that the anterior and posterior articular surfaces of the centra are not inclined, but also show that the anterior surface is situated more dorsally than the posterior surface. This is similar to the condition in *Hesperosuchus* (Colbert, 1952:fig. 15), and indicates an anterodorsally curved neck. The vertebrae of *Parrishia* appear to be more robust, but this taxon is best considered a nomen dubium until more complete material is discovered.

***Dyoplax arenaceus* O. Fraas, 1867**

The holotype of *D. arenaceus* (SMNS 4760) comprises a sandstone cast of much of the skeleton, missing only the distal portion of the tail and most of the limb-bones, from the Schilf-sandstein (Upper Triassic: lower Carnian) of Stuttgart-Feuerbach, Baden-Württemberg (Germany). The specimen was re-

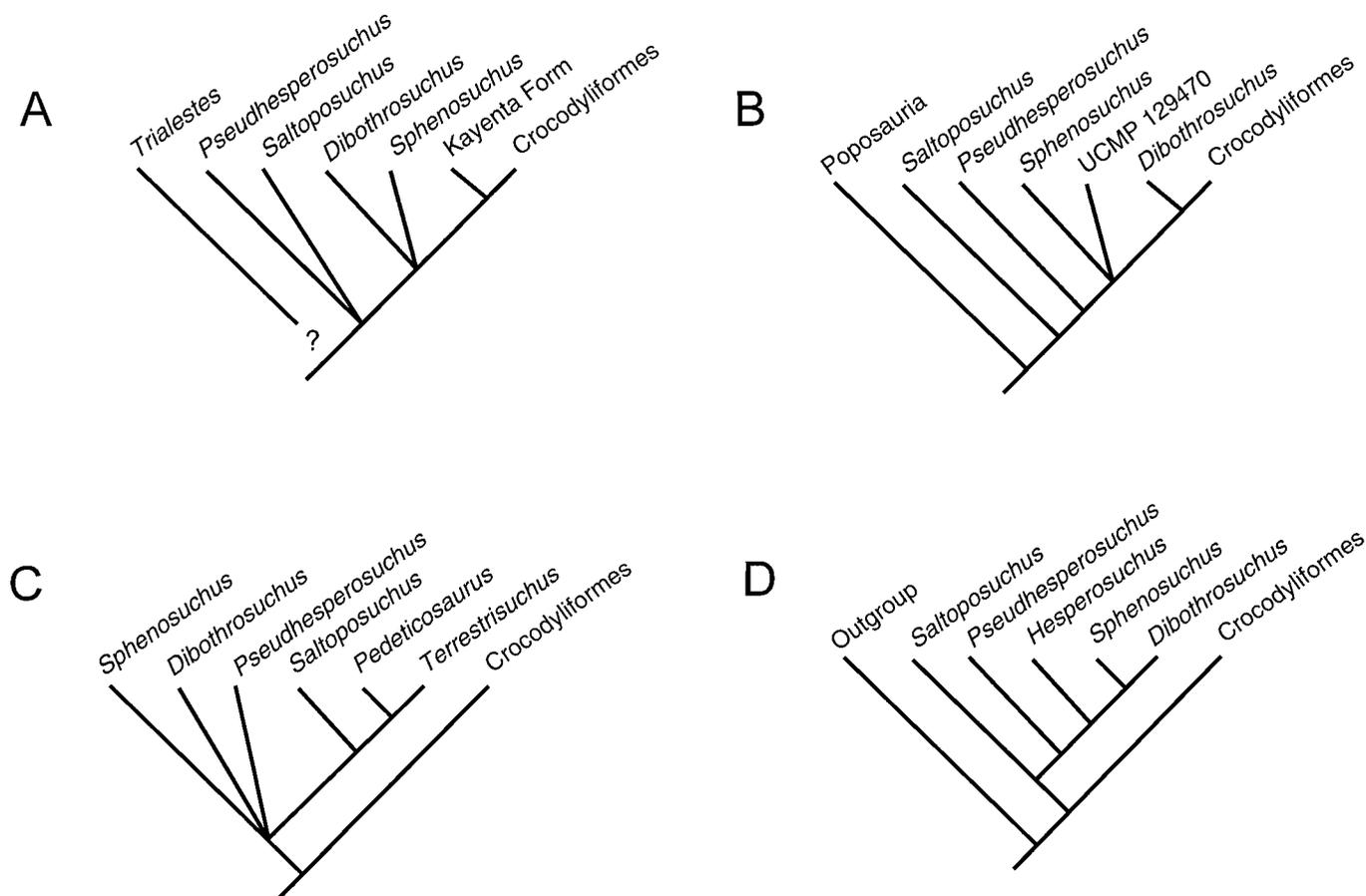


FIGURE 6. Phylogenetic hypotheses proposed for basal crocodylomorph archosaurs: **A**, Benton and Clark (1988); **B**, Parrish (1993); **C**, Sereno and Wild (1992); and **D**, Wu and Chatterjee (1993).

cently redescribed and illustrated in detail by Lucas, Wild, and Hunt (1998) who reinterpreted *Dyoplax* as a sphenosuchian. However, it is impossible to verify most of their inferences concerning cranial structure on the poorly preserved cast of the skull. *Dyoplax* may be a crocodylomorph and is of great interest due to its stratigraphic age, but there currently exists little evidence to support sphenosuchian affinities.

PHYLOGENETIC RELATIONSHIPS

Clark (1986 and in Benton and Clark, 1988), Parrish (1991), Sereno and Wild (1992), and Wu and Chatterjee (1993) have reviewed the interrelationships of basal crocodylomorph archosaurs in explicitly cladistic terms. The phylogenetic analyses by Clark and Parrish both generated a paraphyletic arrangement of Sphenosuchia, with some taxa more closely related to Crocodyliformes than others, whereas Sereno and Wild (1992) and Wu and Chatterjee (1993) independently hypothesized the monophyly of Sphenosuchia (Fig. 6). The latter two studies reviewed the earlier analyses by Clark and Parrish. However, many characters listed by Wu and Chatterjee require reassessment, and several character codings appear to have been based on published reconstructions of certain taxa (such as *Pseudhesperosuchus jachaleri*) that include features not preserved and/or not identifiable in the original material. Furthermore, several characters used by Sereno and Wild misinterpreted the corresponding character-states in basal crocodyliforms, and their use of a composite "ancestor" outgroup and a composite assemblage

Crocodyliformes obscured variation within these groups. Therefore, we present a detailed review of the characters used by Sereno and Wild (1992) and Wu and Chatterjee (1993) below, and provide a revised list of characters and their respective states as well as a character-taxon matrix in Appendix 1.

Characters used by Wu and Chatterjee (1993)

The character list provided by Wu and Chatterjee (1993) summarizes those published by Clark (in Benton and Clark, 1988) and Parrish (1991) and adds many new characters. It therefore provides a useful basis for the discussion in this paper. The character numbers are those of Wu and Chatterjee, followed in brackets by those cited from Clark (hyphenated) or Parrish (not hyphenated).

1 [6]. "External naris: longer than tall (0), taller than long (1)." This character is not considered here because we are not certain that it is variable among sphenosuchians. Wu and Chatterjee scored only one sphenosuchian taxon, "*Saltoposuchus*" (*Terrestri-suchus*), as exhibiting the derived condition. However, according to Crush (1984:fig. 1B), the premaxilla of *Terrestri-suchus* (and thus the anterior border of the external narial fenestra) is not preserved in the available material, and no complete premaxilla is known for *Saltoposuchus* (Sereno and Wild, 1992).

2 [7]. "Lateral articulation of premaxilla/maxilla: ball-and-socket (0), suture (1)." Parrish (1991) stated that *Dibothrosuchus* shares with crocodyliforms a condition in which the ven-

tral part of the premaxilla is sutured to the maxilla, whereas he interpreted *Sphenosuchus* as having a “ball-and-socket” joint similar to that present in many rauisuchian archosaurs. Wu and Chatterjee, however, interpreted the ventral contact of the premaxilla and maxilla in *Dibothrosuchus* as lacking a suture and instead comprising a “ball-and-socket” joint, although they do not note this in their description. JMC could not identify this kind of joint during his recent examination of IVPP V7907. Indeed, it is unclear whether a “ball-and-socket” joint between the premaxilla and maxilla is present in any sphenosuchian (Walker, 1990:12) and whether the ventral contact on the skull surface is different in those crocodyliforms with this contact (e.g., *Orthosuchus*) and in sphenosuchians. The structure of this region is variable within some taxa, such as *Orthosuchus*, where the holotype of *O. stormbergi* shows a ventral contact on the right side and no contact on the left (Nash, 1975). *Protosuchus* was interpreted by Wu and Chatterjee as having a sutural contact, but in all specimens examined by us there is no contact between the premaxilla and maxilla ventral to the notch (see also Crompton and Smith, 1980). Furthermore, although Parrish (1991) interpreted *Gracilisuchus* as lacking the ball-and-socket joint and *Postosuchus* as indeterminate, Wu and Chatterjee considered both taxa to have the ball-and-socket joint (which is definitely absent in *Gracilisuchus*, MCZ 4117).

With regard to this character, a more striking difference between crocodyliforms and sphenosuchians concerns the posterodorsal process of the premaxilla, which overlaps the maxilla in sphenosuchians, whereas the two bones abut in a strong suture in crocodyliforms, a character considered by Clark (1986) but not by other authors. There is also considerable variation in the presence, size, and shape of the notch formed between the premaxilla and maxilla, but vagaries of preservation often make it difficult to interpret this region with confidence.

3 [8]. “Ascending process of maxilla: vertical (0), angled posteriorly (1).” The portion of the facial process of the maxilla that extends posterodorsally above the antorbital fenestra is shorter and extends vertically in basal crocodyliforms.

4. “Maxilla terminating behind anterior border of orbit in lateral view (0), in front of anterior border of orbit (1).” More accurately expressed, the jugal covers the posterior end of maxilla in the derived condition, as the maxilla extends beneath the orbit in all sphenosuchians in which this condition can be determined. Among sphenosuchians, the only taxon scored for the derived condition is *Pseudhesperosuchus*, but poor preservation in this area on the skull of the holotype of *P. jachaleri* makes this assessment questionable.

5. “Preantorbital part of maxilla: shorter than postantorbital part in lateral view (0), longer than postantorbital part (1).” As stated, this character is confusing in that it does not specify whether the antorbital fenestra or antorbital fossa forms the point of reference. Furthermore, the region posterior to the posterior edge of either the fossa or fenestra is not longer than the region anterior to the anterior edge in any taxon known to us. We interpret this character as referring to whether the portion of the maxilla anterior to the anterior edge of the fenestra is shorter or longer than the portion posterior to the anterior edge of the fenestra. This is related to the size of the maxilla and antorbital fenestra, and thus to the character used by Clark (1986) to describe the shape of the fenestra.

6. “Palatal processes of maxilla in front of choana: separate (0), meeting one another (1).” In other words, the maxilla does or does not form part of the secondary bony palate.

7. “Maxillary component of secondary palate: short (0), enlarged (1).” The extent of the secondary bony palate is difficult to characterize in several taxa, although there are undoubtedly differences. In *Sphenosuchus*, for example, the secondary bony palate is much longer along the midline than it is further laterally and anterior to the choana. In other taxa, such as *Ter-*

restrisuchus, it is unclear whether the entire median portion is preserved on any specimen. In *Dibothrosuchus* (IVPP V7907), the palatal portion of the maxilla extends back to the level of the fifth or sixth maxillary alveolus. Contra Wu and Chatterjee (1993), this character cannot be scored in *Pseudhesperosuchus*. Although the secondary palate of *Terrestrisuchus* appears to be shorter than in other taxa (i.e., less than 25% of the length of the maxilla), this is due to the unusual length of the posterior part of its maxilla. For example, the secondary bony palate terminates posteriorly between the fourth and fifth maxillary teeth in both *Sphenosuchus* (Walker, 1990:fig. 4e) and *Terrestrisuchus* (Crush, 1984).

8 [1–1]. “Jugal contributing to border of antorbital fenestra: yes (0), no (1).”

9 [51]. “Quadratojugal/postorbital contact: no (0), yes (1).” Walker (1990) reconstructed an extensive dorsal process of the quadratojugal that contacts the postorbital dorsal to the infratemporal fenestra in *Sphenosuchus*, but the holotype of *S. acutus* does not offer conclusive evidence in support of this reconstruction (Walker, 1990:figs. 15, 17). In *Dibothrosuchus* (IVPP V7907), a reported quadratojugal fragment near the postorbital cannot be recognized (JMC, pers. obs.). We have argued above that the bone identified as the quadratojugal in *Pseudhesperosuchus* may actually represent a portion of the quadrate, with the apparent suture between the two parts created by the crushing of a depression similar to that on the quadrate of *Terrestrisuchus*; this ambiguity precludes identification of the character-state in this taxon. To date, only the specimen of *Hesperosuchus* reported here includes a well-preserved quadratojugal, and there is no evidence that this element differs from that in other basal crocodylomorphs (including *Protosuchus*).

10. “Descending process of prefrontal reaching palate medially: no (0), yes (1).” The descending process of the prefrontal in *Dibothrosuchus* apparently contacts the palate broadly, similar to the condition in eusuchian crocodyliforms, but the condition may be partially due to dorsoventral crushing of the snout in IVPP V7907. The process is delicate in *Pseudhesperosuchus* and a substantial sutural contact is not apparent in the poorly preserved and only known specimen of that taxon (contra Wu and Chatterjee, 1993).

11. “Longitudinal frontal crest(s): absent (0), present (1).” A median frontal crest is present in *Dibothrosuchus*, *Hesperosuchus*, and *Sphenosuchus*. *Dibothrosuchus* is distinguished by the presence of a second longitudinal ridge on either side of the median one.

12[1–b]. “Postfrontal: present (0), absent (1).”

13. “Postorbital: forming much of anterodorsal border of infratemporal fenestra (0), nearly excluded from infratemporal fenestra (1), no relationship to infratemporal fenestra (2).” This character requires revision because it is closely related to character 9, which concerns the contact between the quadratojugal and the postorbital. *Gracilisuchus* is the only taxon scored as having character-state 2, apparently based on Romer’s (1972) reconstruction of this region. Brinkman (1981) claimed that the relationship of the postorbital to the infratemporal fenestra in this taxon is not unusual. However, Parrish (1993) accepted Romer’s reconstruction based on his examination of the MCZ material and material at the Instituto Miguel Lillo in Tucuman, Argentina, and it is further supported by examination of MCZ 4117. As for the supposed similarity between *Postosuchus*, *Protosuchus*, and *Stagonolepis* in this feature, the former two are similar in sharing the derived condition of character 9, dorsal elongation of the quadratojugal, whereas in *Stagonolepis* the exclusion of the postorbital from the infratemporal fenestra is due to the close proximity of the squamosal and postorbital.

14 [2–b]. “Parietals: separate (0), fused (1).” Contra Parrish (1991) and Wu and Chatterjee (1993), the parietals of the ho-

lotype of *Hesperosuchus agilis* are not preserved and thus cannot be scored.

15 [1-bb]. “Parietal: relatively narrow on occiput, squamosal relative [sic] wide: no (0), yes (1).” “No” presumably means that the parietal is broad and the squamosal has a more limited exposure on the occiput. Contra Wu and Chatterjee, this condition cannot be scored in either *Pseudhesperosuchus* or *Hemiprotosuchus*. Furthermore, the parietal of *Postosuchus*, as figured by Chatterjee (1985), is narrower than the homologous element in *Gracilisuchus* and *Stagonolepis* and comparable in width to that in *Sphenosuchus* (Walker, 1990:fig. 19).

16 [53]. “Sagittal crest on parietal: absent (0), present (1).” We differ from Wu and Chatterjee in the interpretation of this character. The important landmark is the dorsomedial edge of the attachment area for the fascia covering the adductor jaw musculature within the supratemporal fossa. In extant tetrapods, the fascia attaches to the parietal along a distinct crest on the dorsolateral edge of the bone. Three conditions are found among sphenosuchians: either the crests from both sides abut along the midline, forming a single median crest, or they are separated by a narrow median sulcus, or the two crests are separated broadly by a flat midline area. The parietals are not preserved in the holotype of *Hesperosuchus agilis*, and it is not clear on what basis this taxon was scored by Parrish or by Wu and Chatterjee.

17. “T-shaped crest on dorsal surface of parietal and squamosal: no (0), yes (1).” We interpret this character description as distinguishing between the condition in which the crest along the dorsal edge of the occiput is straight and transverse and the condition in which it is V-shaped, extending further anteriorly along the midline (character 18 of Sereno and Wild). Contra Wu and Chatterjee, we interpret *Pseudhesperosuchus* as having the latter condition.

18 [9]. “Interparietal: present (0), absent (1).” An interparietal has only been reported in *Gracilisuchus* (Romer, 1972; MCZ 4117), and is unknown among crocodylomorphs.

19 [3-a]. “Lateral edge of squamosal with groove: no (0), yes (1).”

20 [2]. “Descending process of squamosal: present (0), absent (1).”

21 [12]. “Lateral flange on squamosal: absent (0), present (1).” Restated, the squamosal does or does not overhang the infratemporal region laterally.

22 [1-2, modified]. “Quadrate foramen: at quadrate/quadratojugal junction (0), within quadrate (1), absent (2).” We interpret this character as comprising two separate characters. In many extinct reptiles and in *Sphenodon*, a foramen is present between the quadrate and quadratojugal, through which V. capitis lateralis passes in *Sphenodon*. The depression on the quadrate of many sphenosuchians is comparable in position to fenestrae in the quadrate of crocodyliforms that, in extant forms, house extensions of the middle ear cavity. A foramen between the quadrate and quadratojugal is not known in any basal crocodylomorph, and thus this feature is not included in this analysis. The area with the “foramen” in *Dibothrosuchus* (IVPP V7907) is damaged, and it is not clear whether there was a depression or an opening (JMC, pers. obs.).

23 [56]. “Quadrate shift anteriorly: no (0), yes (1).” According to Parrish (1991:210), this character refers to the articulation of the quadrate with the prootic, which Wu and Chatterjee treated as a separate character (24). They may have intended this character description to refer to the posterior position of the quadrate in *Pseudhesperosuchus* as reconstructed by Bonaparte (1972). However, our interpretation of this region in the latter taxon is that it does not differ from other sphenosuchians, and we therefore ignore this character.

24 [1-f]. “Primary contact of quadrate with prootic: no (0), yes (1).” A contact between the quadrate and prootic is present

in crocodylomorph archosaurs (Walker, 1970), although it does not necessarily form the “primary” contact.

25. “Anterodorsal [process] of quadrate: absent (0), present (1).” Restated, the quadrate extends further anteriorly beneath the squamosal than in outgroup taxa. This is related to the absence of a descending process of the squamosal (character 20), as it occupies the same region and would seem to preclude the latter.

26. “Dorsomedial process of quadrate: absent (0), present (1).” Unfortunately, this region of the quadrate is either damaged or covered by the squamosal in sphenosuchians other than *Dibothrosuchus*. For example, although the quadrate of *Sphenosuchus* was reconstructed by Walker (1990) as lacking such a process, Walker’s illustrations of the specimen indicate that the quadrate is damaged in this region. *Terrestrisuchus* may lack such a process, but it is unclear from the description by Crush (1984) whether this part of the quadrate is sufficiently well preserved in the known material to determine the presence or absence of a dorsomedial process.

27. “Great anterior extent of anterodorsal process of quadrate: no (0), yes (1).” This is related to characters 25 and 20, such that taxa without an anterodorsal process are coded as inapplicable. According to Wu and Chatterjee (and confirmed by JMC), *Dibothrosuchus* uniquely shares the derived character-state with crocodyliforms, but it is not clear that the quadrate of the holotype of *Sphenosuchus acutus* is well enough preserved to allow determination of its anterior extent beneath the squamosal. According to our interpretation of *Pseudhesperosuchus*, the quadrate extends much further anteriorly than was inferred by Wu and Chatterjee.

28. “Anteroventral surface [of] quadrate body hollowed out and marked by an oblique crest extending from articular condyle to ventral edge of pterygoid ramus: no (0), yes (1).” This condition is present in *Protosuchus*, and, in our opinion, in a modified form in extant crocodylians. The condition in *P. richardsoni* (Clark, 1986) is very similar to that of sphenosuchians, whereas the quadrate in extant crocodylians is somewhat more elongate than in more basal crocodylomorphs but nevertheless has a depression bounded by a crest in the same position (Iordansky, 1973:fig. 10).

29 [22]. “Ectopterygoid/jugal and/or maxilla junction: planar (0), ball-and-socket (1).” It is unclear that a ball-and-socket joint is present in any crocodylomorph. For example, Wu and Chatterjee (1993:64) described the ectopterygoid in *Dibothrosuchus* as “butt-jointed to the jugal,” and Walker (1990:fig. 11G) clearly figured the contact surfaces of this suture in *Sphenosuchus* as being flat. We therefore ignore this character.

30 [23, modified]. “Ectopterygoid junction with: jugal/maxilla (0), jugal (1).” In other words, the ectopterygoid does or does not contact the maxilla. This character does not vary among basal crocodylomorphs.

31 [20]. “Basipterygoid trough: absent (0), present (1).” According to Parrish (1993:300), this term refers to “a posteroventrally open trough formed by elongated and conjoined basipterygoid processes” that is present in rauisuchians and Crocodylomorpha. The basipterygoid processes are absent in Crocodyliformes, but Parrish (pers. comm.) argues that a trough is nonetheless present in *Protosuchus* and *Orthosuchus*. However, this is not the case in specimens of *Protosuchus* examined by us (Fig. 6). In any case, this feature is not considered by Parrish to vary among basal crocodylomorphs.

32 [1-g]. “Pneumatic space in body of basisphenoid: no (0), yes (1).” *Gracilisuchus* cannot be scored for this feature at present, and thus the character shows no variation among the taxa listed by Wu and Chatterjee (1993).

33. “Dorsoventrally expanded lateral end of paroccipital process reaching to the outermost edge of occiput and interlocked with squamosal: no (0), yes (1).” As stated, this character in-

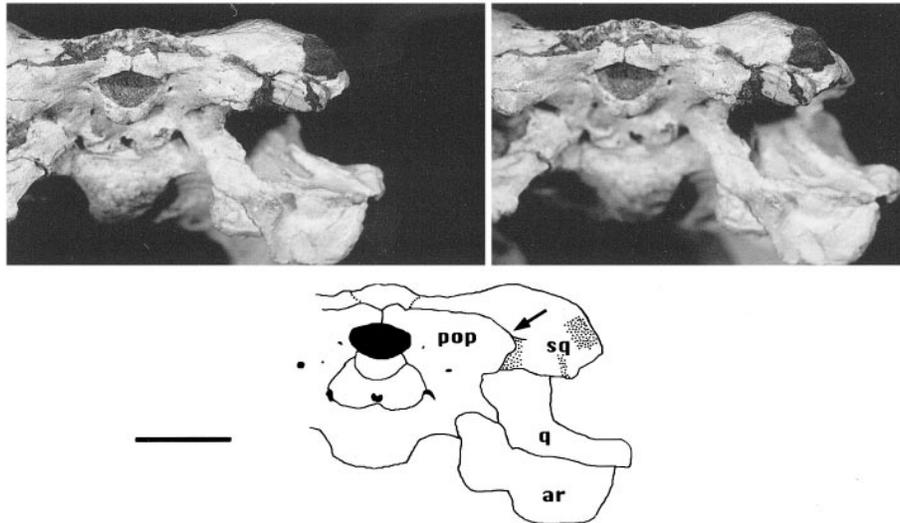


FIGURE 7. Stereophotograph and explanatory sketch of the occiput of *Protosuchus richardsoni*, UCMP 131827, in posterior view, showing the descending flange of the squamosal articulating with the paroccipital process. **Abbreviations:** ar, articular; pop, paroccipital process; q, quadrate; sq, squamosal. Scale bar equals 1 cm.

cludes several features. Sereno and Wild (1992) also focused on some of these features, and an extended discussion is necessary. We would argue that three separate characters are involved: 1) the lateral extent of the paroccipital process, 2) the degree of expansion of the distal end of the paroccipital process, and 3) the nature of the articulation between the paroccipital process and squamosal.

In Crocodyliformes, the squamosal forms a posterolateral extension not present in sphenosuchians or crocodylomorph outgroups, and, although the paroccipital process is as laterally extensive relative to other bones as in sphenosuchians, it is separated from the lateral edge of the occiput by this extension of the squamosal. Thus the lateral extent of the paroccipital process does not differ in sphenosuchians and crocodyliforms, but the posterolateral extent of the squamosal does. Apparent differences between crocodylomorphs and outgroup taxa indicate an apomorphic condition in Crocodylomorpha, but more detailed comparisons of this region in *Gracilisuchus*, *Postosuchus*, and Stagonolepididae are required.

The distal end of the paroccipital process is expanded in the outgroups, as Wu and Chatterjee acknowledged, and they noted that the process in crocodyliform archosaurs is "narrow dorsoventrally" (Wu and Chatterjee, 1993:83). We therefore consider this a valid character, although it does not vary among known sphenosuchian taxa.

The nature of the articulation between the squamosal and paroccipital process is considered apomorphic in sphenosuchians by Wu and Chatterjee (1993) and by Sereno and Wild (1992), but the apomorphic condition is characterized in different ways in the two papers. Wu and Chatterjee (1993) referred to the paroccipital process and squamosal simply as "interlocked," but did not explain how this differs from the condition in crocodyliforms. Sereno and Wild (1992:448) stated that in sphenosuchians the portion of the squamosal articulating with the paroccipital process is "deeply cleft, rather than simply grooved, and has tongue-shaped anterior and posterior processes. The anterior flange projects ventrally and the posterior flange is directed ventromedially." They claimed that Crocodyliformes lack this modification, and illustrated this region of the skull in the basal crocodyliform *Protosuchus richardsoni* in support of this claim. However, these structures are present in

Crocodyliformes, including the taxon illustrated by them, *Protosuchus richardsoni*. Sereno and Wild (1992:fig. 10) figured a dorsal view of the squamosal in this taxon, but they misidentified a structure lying lateral to the squamosal as the paroccipital process. They cited Colbert and Mook (1951) as the source for their illustration, but, in that paper, the structure in question is correctly identified as the quadrate. Furthermore, in two specimens of *P. richardsoni* (UCMP 13060 and 131827; see Clark [1986]) the squamosal is cleft, and a broad, "tongue-shaped" anterior process covers much of the anterior surface of the paroccipital process (Fig. 7). As in sphenosuchians, the posterior process is less extensive than the anterior process. In *Protosuchus*, the orientation of the posterior process is ventral, rather than ventromedial, because the occiput is flat rather than V-shaped as in some sphenosuchians (cf. character 17). In none of the specimens examined by us does the paroccipital process extend beyond the squamosal, as illustrated by Sereno and Wild.

34. "Pentagonal supraoccipital with a ventral process: no (0), yes (1)." This character cannot be scored for *Hemiprotosuchus*, *Hesperosuchus*, or *Pseudhesperosuchus* (contra Wu and Chatterjee, 1993). It is not clear that a ventral process is present in any taxon, but the appearance of such a process is created by the posterior overlap of the exoccipitals onto the ventrolateral edges of the supraoccipital. We consider this character redundant with character 35.

35. "Supraoccipital: forming dorsal margin of foramen magnum (0), nearly excluded from margin of foramen magnum (1), without any contribution to margin of foramen magnum (2)." *Pseudhesperosuchus* and *Hemiprotosuchus* cannot be scored for this character. The decision by Wu and Chatterjee (1993) not to order this character has important implications for their results. Thus the ventral restriction of the supraoccipital in sphenosuchians, to nearly exclude it from the dorsal margin of the foramen magnum (state 1), and the complete exclusion of the supraoccipital (state 2) in crocodyliforms are not interpreted as evidence of phylogenetic relationship between the two taxa. Instead, the presence of character-state 1 is considered to provide evidence for sphenosuchian monophyly, and the similarity shared by character-states 1 and 2 is ignored.

36 [1-d]. "Prootic having no broad contact with anterior sur-

face of paroccipital process: yes (0), no (1).” *Gracilisuchus* and *Hemiprotosuchus* cannot be scored for this character (contra Wu and Chatterjee, 1993).

37 [1-h, modified]. “Mastoid antrum: absent (0), depression (1), entering into prootic and connecting with opposite through supraoccipital (2).” The mastoid antrum is equivalent to the structure termed the superior tympanic recess (e.g., Witmer, 1990). This character cannot be scored for *Gracilisuchus* or *Hemiprotosuchus* (contra Wu and Chatterjee, 1993). It is unclear whether state 1 or 2 is present in the holotype of *Hesperosuchus agilis*, as noted by Wu and Chatterjee (1993:85), and it is puzzling why they scored it as having state 1 in their matrix. Because Wu and Chatterjee did not order character-states, the evidence for relationships provided by the presence of a mastoid antrum itself, as indicated by states 1 and 2, is ignored.

38. “Posterior tympanic recess: absent (0), depression (1), penetrating prootic and paroccipital process (2).” This character cannot be identified in the available specimens of *Gracilisuchus* (contra Wu and Chatterjee, 1993). Not ordering this character has the same effect as in characters 35 and 37, ignoring the similarity between states 1 and 2.

39 [19]. “Eustachian tube: absent (0), present (1).” This presumably refers to the structure often termed the passage for the “lateral eustachian tube”, as opposed to the “median eustachian tube” (passing through the foramen intertympanicum). Its presence or absence cannot be determined in either *Gracilisuchus* or *Hemiprotosuchus* (contra Wu and Chatterjee, 1993).

40 [11]. “Posttemporal fenestrae: present (0), absent (1).” This cannot be scored for *Hemiprotosuchus*, in which the occiput is eroded. In *Pseudhesperosuchus*, the sutures on the occiput cannot be identified, and it cannot be determined whether one of the several openings on the occiput is the posttemporal fenestra. Contra Parrish (1991) and Wu and Chatterjee (1993), posttemporal fenestrae are present (but small) in nearly all Crocodyliformes (Iordansky, 1973). The position of the fenestra differs due to the recession of the occipital portion of the parietal, and the ventral edge is modified to form a synovial joint in extant Crocodylia, but it is nevertheless present.

41 [16]. “Parasphenoid rostrum: rodlike (0), wedge-shaped (1).” Presumably this refers to the short, blunt, dorsoventrally broad process characteristic of Crocodyliformes. This character cannot be scored for *Gracilisuchus*. According to Walker (1990: fig. 21A), the cultriform process is rod-like in *Sphenosuchus*, but Parrish (pers. comm.) suggests that this area is too poorly preserved to identify this process. Wu and Chatterjee (1993:68) described the parasphenoid rostrum in *Dibothrosuchus* only as “incomplete”, but they later contended that it is complete enough to score as being wedge-shaped. Examination of IVPP V7907 by JMC failed to find any portion of the parasphenoid rostrum. We question whether the parasphenoid rostrum (cultriform process) is well preserved enough in any sphenosuchian to determine its shape.

42. “Retroarticular process transversely broad and with a pronounced dorsomedial projection at its posteromedial edge: no (0), yes (1).” This is a combination of two separate characters, the breadth of the retroarticular process and the presence or absence of a dorsomedial projection. The width of the process in *Postosuchus* is similar to that in sphenosuchians, and, in *Protosuchus*, this area is similarly broad and has the dorsomedial projection, although it is modified by the anteroposterior shortening of the process (personal communication from JMC cited by Wu and Chatterjee [1993:84]). Furthermore, *Stagonolepis* has a narrow process, which appears to have a short dorsomedial projection. We consider the width of the process a synapomorphy for *Postosuchus* and Crocodyliformes and the presence of a dorsomedial projection a crocodyliform apomorphy.

43 [13]. “Interdental plates: absent (0), present (1).” Only *Postosuchus* is scored as having them. The poor preservation of the holotype of *Pseudhesperosuchus jachaleri* makes their identification uncertain. The presence or absence of interdental plates is a controversial character in the literature. In undisputed examples of these plates, which are formed from interalveolar septa, their edges are separate from the dentary, but, in many taxa, grooves and lines of small foramina are interpreted as indicating the edges of these plates (e.g., Currie, 1987). Among Crocodyliformes, such interdental plates have been reported in *Sphenosuchus* (Walker, 1990:13), *Hesperosuchus* (Colbert, 1952:figs. 5, 10), and *Protosuchus* (Sues et al., 1996). We regard this feature as uninformative for elucidating relationships among basal crocodyliform archosaurs.

44 [58]. “Teeth with swollen crowns: no (0), yes (1).” This presumably refers to the anteroposterior expansion of teeth, possibly including a lack of a concave posterior margin. Parrish (1991:210) added the descriptive comment of “convex to straight posterior margins” to his characterization of the derived character-state. Posterior, but not anterior, maxillary teeth of *Saltosuchus* were described by Sereno and Wild (1992) as exhibiting the derived condition, but their illustration (Sereno and Wild, 1992:fig. 5C) does not show swelling of the crowns of the posterior teeth. The character cannot be scored for *Pseudhesperosuchus*.

45 [26]. “Proximal anterolateral flange on dorsal ribs: absent (0), present (1).” Chatterjee (1985) did not describe *Postosuchus* as having the derived character-state, but it was scored as present by Wu and Chatterjee (1993).

46 [44]. “Postglenoid process of coracoid: absent (0), small knob (1), elongate process (2).” Several taxa of basal crurotarsal archosaurs exhibit character-state 1 (Parrish, 1993), and it was described for the stagonolepidid *Neoaetosauroides* (Bonaparte, 1972); its absence in *Stagonolepis* may be apomorphic for that taxon. Because character 46 was considered unordered by Wu and Chatterjee, it had the effect of treating state 1 of this character as irrelevant to state 2; thus, the “small knob” and “elongate process” are not considered homologous. Furthermore, state 2 and character 48 together form a multi-state character. Depending upon whether the assumptions of ordered multi-state characters are accepted (i.e., that the similarity shared by an intermediate condition with an extreme condition provides evidence of group membership), either characters 46 and 48 should be combined into a single unordered character or character 46 should be ordered. Furthermore, crocodyliforms have a ventrally elongate coracoid, but are scored as having the plesiomorphic condition for character 48; presumably this refers to the abbreviated posterior extent of the coracoid in these taxa, but this is a confusing way of describing this condition.

47. “Sternal facet of coracoid: along posteromedial margin of body (0), along medial margin of broad postglenoid process (1), along posteromedial margin of elongate postglenoid process (2).” The only difference between the character-states 0 and 2 is the presence of a postglenoid process in the latter condition. Therefore, this character serves to identify the character “elongate postglenoid process,” as opposed to “broad postglenoid process,” and is redundant with character 46. Furthermore, it is not clear that the sternal articulation in non-crocodyliform archosaurs is only posteromedial. This character needs to be redefined in terms of coracoid shape, rather than the position of the facet.

48. “Postglenoid process of coracoid: shorter than body (0), longer than body (1).” As noted by Bonaparte (1972:72), the holotype of *Pseudhesperosuchus jachaleri* shows variation in this feature between the elements from right and left side of the body. Furthermore, as illustrated by Wu and Chatterjee (1993: fig. 17), the coracoid of *Hesperosuchus* shows a condition intermediate between the two extremes. We therefore hesitate to

ascribe any phylogenetic significance to this character (see also discussion of character 46).

49 [45]. "High, narrow scapula: absent (0), present (1)." Presumably the primitive condition is a short and broad scapula. It is unclear that there is a significant difference between Stagonolepididae and other archosaurian taxa in this character (Bonaparte, 1972).

50 [41]. "Distal end of pubis: flat plate (0), knob (1), foot (2)." The distal end of the pubis is slightly expanded in crocodyliforms. Wu and Chatterjee (1993) interpreted two sphenosuchians, *Hesperosuchus* and *Saltoposuchus*, as sharing character-state (2) with crocodyliforms. However, the distal end of the pubis of *Terrestrisuchus* (Crush, 1984:fig. 8) lacks any expansion. Furthermore, the pubis is not preserved in the holotype of *H. agilis*, the only other sphenosuchian scored by Wu and Chatterjee for this character. The pubis of the specimen referable to *Hesperosuchus* and described by Parrish (1991) can be interpreted as having an expanded distal end, although we would agree with Parrish that it is probably due to the larger size compared with known specimens of *Saltoposuchus* and *Terrestrisuchus*. Wu and Chatterjee, however, followed Parrish in considering that specimen referable to *Sphenosuchus*. The prominent distal "foot" (or "boot") on the pubis of *Postosuchus* may be autapomorphic for that taxon (Parrish, 1993). This character is only informative as a crocodyliform autapomorphy.

51 [59]. "Obturator foramen: yes (0), no (1)." That is, the foramen is present or absent.

52 [42]. "Ischium shape: flat, horizontal trough (0), downturned with a thin profile (1)." The derived condition is only known in *Gracilisuchus* (Parrish, pers. comm.).

53 [24]. "Crocodylomorph femoral head: absent (0), present (1)." According to Parrish (1991), this character refers to a medially directed femoral head that is set off from the shaft. Contrary to the statements by Wu and Chatterjee (1993) and to Parrish (1991), the head of the femur in *Protosuchus* and extant crocodylians such as *Alligator* is not medially directed or differentiated from the shaft, at least not to the extent found in certain sphenosuchian taxa. The proximal end of the femur of *Pseudhesperosuchus* more closely resembles that of crocodyliforms.

54 [50]. "Elongate radiale/ulnare: no (0), yes (1)." The holotype of *Hesperosuchus agilis* cannot be scored for this character, but the derived character-state is present in the new specimen.

55 [33]. "Median groove on calcaneal tuber: absent (0), present (1)." Only *Stagonolepis* lacks this condition (Walker, 1961).

56 [52, modified]. "Lateral expansion of distal end of calcaneal tuber: modest swelling (0), prominent flange (1)."

57 [32]. "Fifth metatarsal: unreduced (0), reduced to a splint (1)." This refers to the reduction in width of the proximal portion of the fifth metatarsal, in comparison with Stagonolepididae.

58 [46]. "Fewer than four phalanges on pedal digit V: no (0), yes (1)." Although the stagonolepidid *Stagonolepis* has four phalanges in pedal digit V (Walker, 1961), only two have been reported in *Neoaetosauroides* (Bonaparte, 1972).

59 [49]. "Fewer than three phalanges on pedal digit V: no (0), yes (1)." The only taxon scored as having four phalanges is *Stagonolepis*, but all others have two or less, making this character redundant with character 58. Wu and Chatterjee (1993) inexplicably scored *Saltoposuchus* as unknown for this character but as having the derived condition in character 58.

60 [I-i]. "Pedal digit IV with four phalanges: no (0), yes (1)." The primitive condition is the presence of five phalanges. Only four phalanges are preserved on pedal digit IV of the holotype of *Hesperosuchus agilis*, but Colbert (1952:585) reconstructed a fifth based on comparison with the basal archo-

sauriform *Euparkeria*. Furthermore, it is unclear whether this pes is correctly referred to the holotype, as it is proportionately much larger than expected. We therefore consider the condition in *Hesperosuchus* unknown.

61 [55]. "Sculptured osteoderms: no (0), yes (1)." Contra Parrish (1991) and Wu and Chatterjee (1993), the osteoderms of the holotype of *Hesperosuchus agilis* are lightly sculptured. Parrish (1991:207) first described the sculpturing as "not well developed" and then as absent, and he scored this feature as absent in his data matrix. In the text of his paper, he hinted that the difference in degree of sculpturing may reflect ontogenetic differences between specimens, and we concur. The well-developed sculpturing on the osteoderms in the specimen described here, which is considerably larger than the holotype, corroborates this explanation. Furthermore, contrary to the claim by Wu and Chatterjee, the osteoderms of *Gracilisuchus* were described as being "highly sculptured" (Romer, 1972:17).

62 [48]. "Osteoderms wider than long: no (0), yes (1)." *Postosuchus* cannot be scored for this character (Chatterjee, 1985). This character presumably refers to the post-cervical dorsal osteoderms, as those from the cervical region are always narrow. Most of the osteoderms in the holotype of *Hesperosuchus agilis* and all osteoderms preserved in the specimen of *Dibothrosuchus* (IVPP V7907) described by Wu and Chatterjee (1993) are derived from the cervical region. It is unclear from which region the two isolated, unusually shaped osteoderms of *Sphenosuchus* are derived, or whether they indeed represent dorsal osteoderms.

63 [27]. "Paramedian osteoderms with anterior lappets: absent (0), present (1)." This refers to a short process extending from the anterior edge of the lateral part of dorsal osteoderms, which is lacking in the cervical osteoderms of *Dibothrosuchus*.

64 [28]. "Paramedian osteoderms with posterior lappets: absent (0), present (1)." Contra Wu and Chatterjee (1993), osteoderms of *Protosuchus* lack this condition and only have an anterolateral process.

65 [3-b]. "Osteoderms rectangular: no (0), yes (1)." This may refer to whether the osteoderms have straight edges, because character 62 describes whether they are wider than long, and some of the taxa scored as lacking the latter condition are scored as being rectangular (e.g., *Hesperosuchus*). However, the two preserved osteoderms in the holotype of *Sphenosuchus acutus* are not rectangular and lack straight edges, whereas in specimens of *Hesperosuchus*, the lateral edge is distinctly convex and the overall shape of the osteoderm is subquadrangular, making the exact meaning of this character unclear.

Characters used by Sereno and Wild (1992)

1. "Nasal margin of antorbital fossa: present (0), absent (1)." Although Sereno and Wild scored this character as absent in the hypothetical "ancestor" (a composite based upon *Postosuchus*, *Gracilisuchus*, *Saurosuchus*, and "various aetosaurs"), only *Gracilisuchus* (which has a very large antorbital fossa; MCZ 4117) was described as definitely having this condition. This condition may be present in *Saurosuchus* (Sill, 1974), but it is definitely absent in the stagonolepidid *Desmotosuchus* (Parrish, 1993).

2. "Postfrontal: present (0), absent (1)."

3. "Jugal margin of antorbital fossa and fenestra: present (0), absent (1)."

4. "Shape of anterior process of squamosal: narrow (0), transversely broad (1)." Sereno and Wild (1992:446) criticized the observation by Clark (1986 and in Benton and Clark, 1988) that "crocodylomorphs are unique in the degree to which the squamosal overhangs the quadrate and laterotemporal fenestra" and then restated the same character as their character 4. The

width of the anterior process determines how far it overhangs the temporal region.

5. “Shape of squamosal-paroccipital process articulation: overlapping (0); tongue-and-groove (1).” See discussion of Wu and Chatterjee’s character 33 above.

6. “Ulnare and radiale: cuboid or ovoid (0), elongate with shafts (1).”

7. “Articulation of posterior process of prefrontal: prefrontal overlaps frontal (0), prefrontal turns under frontal (1).” The discussion of this character (Serenó and Wild, 1992:447–448) conflicts with the character description in their Appendix 1, where the prefrontal of *Crocodyliformes* is described as having “. . . a shorter, blunt posterior process that articulates with an interdigitating suture on the anterior margin of the orbit . . .” Thus it neither overlaps nor turns under the frontal, and differs from the supposed plesiomorphic condition. Among sphenosuchians, *Dibothrosuchus* was figured and described by Wu and Chatterjee (1993) as lacking the derived condition, whereas Sereno and Wild considered it indeterminate (cf. Sereno and Wild, 1992:fig. 8B). In *Gracilisuchus*, contrary to Sereno and Wild (1992:448), it is unlike the blunt condition of the crocodyliform prefrontal, and Romer (1972:figs. 1, 2) figured it as having two processes, one overlapping the frontal and the other turning under it. In *Postosuchus*, the prefrontal is described as having only a medial contact with the frontal, and no posterior contact. Thus (contra Sereno and Wild, 1992) the condition in this taxon is not comparable to that of crocodylomorphs. Gow and Kitching (1988) neither figured nor described the prefrontal in “*Pedeticosaurus*” in sufficient detail to score this character (contra Sereno and Wild, 1992). Regarding *Crocodyliformes*, Sereno and Wild (1992) cited Clark (1986) in support of their contention that the prefrontal of crocodyliforms lacks a posteroventral process beneath the frontal, but Clark did not discuss this feature. Furthermore, to our knowledge this feature cannot be determined in the available material of *Protosuchus* or other basal crocodyliforms, so that Sereno and Wild’s coding of *Crocodyliformes* as having the plesiomorphic condition is unfounded.

8. “Squamosal (dorsal view): L-shaped (0), arcuate (1).” According to Sereno and Wild (1992:448), “in sphenosuchians, the squamosal curves from the occiput to the postorbital bar and does not form an angular posterolateral corner on the skull table, as in crocodyliforms and crocodylomorph outgroups.” We find little difference in overall shape between the squamosals of sphenosuchians and most crocodyliforms, except that the squamosal in *Crocodyliformes* extends further posterolaterally along the paroccipital process than in any other crurotarsal archosaur. This is not true of crocodylomorph outgroups (contra Sereno and Wild, 1992), all of which lack this posterolateral extension. We therefore do not consider this a valid character except with regard to crocodyliform monophyly.

9. “Squamosal margin of supratemporal fossa: rounded (0), bounded in part by rim (1).” Contra Sereno and Wild, the derived condition is present in the outgroups. *Gracilisuchus* and *Postosuchus* both have such a rim, as does *Erpetosuchus* (Newton, 1894), but because their squamosal is narrower than in crocodylomorphs the rim is not as distinctly set off from the body of the squamosal. Furthermore, we do not ascribe its absence in *Terrestrisuchus* to preservation (see above).

10. “Posterior process of squamosal: grooved (0), forked (1).” Sereno and Wild misinterpreted this region in *Protosuchus* (see discussion of Wu and Chatterjee’s character 33 above), which shares the apomorphic condition with sphenosuchians. We are uncertain that the condition in *Gracilisuchus* can be determined on the basis of the available material, and the condition in *Postosuchus*, as described by Chatterjee (1985), is quite unusual.

11. “Ventral margin of antorbital fossa: laterally exposed (0), trough-shaped (1).” It is unclear that the “trough” of the de-

rived state is present in any sphenosuchian, including *Saltoposuchus* (Serenó and Wild, 1992:fig. 7A), *Dibothrosuchus* (Wu and Chatterjee, 1993), *Terrestrisuchus* (Crush, 1984), or *Pseudhesperosuchus* (Bonaparte, 1972).

12. “Postorbital bar width: narrow (0), very slender (1).” We hesitate to ascribe significance to the subtle differences in the width of this structure between taxa represented by specimens that differ so greatly in overall size. All of the specimens with “very slender” postorbital bars are much smaller than those with “narrow” postorbital bars. Sereno and Wild did not score this character in *Dibothrosuchus* (IVPP V7907), although it preserves most of the postorbital bar.

13. “Quadrate shaft: without (0), with (1) lateral rim.” Contra Sereno and Wild, the quadrate of *Sphenosuchus* has a structure corresponding to the lateral rim (Walker, 1990:fig. 15F). In extant crocodylians a ridge is often present in a position comparable to the lateral rim, but more dorsally situated due to the more horizontal position of the quadrate (Iordansky, 1973; JMC, pers. obs.), and is the attachment site for the tympanic membrane. In basal crocodyliforms such as *Protosuchus*, the quadrate is heavily fenestrated, and the presence or absence of a rim cannot be definitely established.

14. “Metacarpal 2–5 length and configuration: stout with spreading metacarpus (0), elongate with compact metacarpus (digitigrady) (1).” The description by Sereno and Wild of the derived condition of the metacarpals as “compact” (Serenó and Wild, 1992:appendix 1) or having “subparallel shafts” (Serenó and Wild, 1992:449) refers to the positions of the metacarpals relative to one another, rather than their structure, and therefore relies upon interpretive reconstruction of the manus. Several features are mentioned as indicative of the derived condition, including whether the proximal ends abut rather than overlap, whether the metacarpals are gracile or stout, and whether metacarpal I is significantly shorter than metacarpal II. These appear to be separate, although perhaps functionally related, features. In any case, it is not clear to us that either *Dibothrosuchus* or *Pseudhesperosuchus* possesses the plesiomorphic condition (contra Sereno and Wild). Although Wu and Chatterjee (1993:fig. 13F) reconstructed the manus of *Dibothrosuchus* in a spreading, plantigrade posture, they stated in their description that the manus is digitigrade, and the latter interpretation is supported by the specimen, IVPP V7907 (JMC, pers. obs.). In proximal view, the first three metacarpals of the right manus abut rather than overlap each other (metacarpal IV having been displaced). Furthermore, the more gracile proportions of the manus in *Saltoposuchus* and *Terrestrisuchus* may simply reflect the smaller overall size of these animals. Although Sereno and Wild referred to the reconstruction of the manus of *Protosuchus* by Colbert and Mook (1951:fig. 9) to support their contention that this form had a spreading manus, the actual specimen on which it is based (Colbert and Mook, 1951:fig. 13) is too incomplete and disarticulated to show whether the metacarpals abutted or overlapped.

15. “Pubic shaft: rod-shaped (0), blade-shaped (1).” Sereno and Wild (1992:449) considered the pubes of *Terrestrisuchus* and *Saltoposuchus* blade-like rather than rod-like in comparison with outgroups and crocodyliforms, but they noted that “given the scarcity of comparative information among sphenosuchians [this condition] does not carry great phylogenetic weight.” We concur with this assessment.

16. “Obturator opening: small (0), large (1).” The basis for this character is the larger size of the foramen in *Terrestrisuchus* and *Saltoposuchus* than in *Postosuchus*, an animal approximately five times the length of the former two. The pubis of *Stagonolepis* has a small dorsal and a large ventral foramen (Walker, 1961:fig. 16). Furthermore, in many archosaurian pelvises, the bone surrounding this foramen is thin and thus easily broken. This may explain the large size of the opening in the

TABLE 1. Revised character-taxon matrix used for analyzing the interrelationships of basal crocodylomorph archosaurs in this study.

Taxon	Character						
	12345	1 67890	12345	2 67890	12345	3 67890	123
Outgroup taxa							
<i>Stagonolepis</i>	00000	00000	00100	00100	00000	00000	000
<i>Gracilisuchus</i>	?1?10	??000	01101	000??	??0??	000?0	??1
<i>Postosuchus</i>	01000	??000	1?000	11000	00000	00000	0??
Ingroup taxa							
BP/1/5237	?0???	??101	?0??1	100??	??0??	0?1??	???
<i>Pseudhesperosuchus</i>	01???	1?101	11??0	?10??	??000	0?1??	0??
<i>Hesperosuchus</i>							
AMNH 6758	?????	??1?1	?????	?????	??0??	1?1?1	?11
CM 29894	00?1?	?1111	111?0	?10??	??001	11?1?	?11
UCMP 129470	?????	?????	?????	?????	?????	1?1?1	?11
Combined	00?1?	?1111	111?0	?10??	??001	11111	?11
<i>Saltosuchus</i>	00?1?	?1101	11??0	?10??	?????	0??11	011
<i>Terrestrisuchus</i>	?111?	?1101	10??0	?0011	??0??	011?1	1??
<i>Dibothrosuchus</i>	00111	10111	1?112	11111	20101	0111?	?00
<i>Sphenosuchus</i>	00111	01111	11112	11111	11001	011??	???
<i>Protosuchus</i>	11111	0?101	10012	10121	2211N	012?1	011
<i>Alligator</i>	1N1N1	10101	10012	10121	2011N	00201	000

N = inapplicable due to transformation, treated as unknown.

Notes

Character 1: The premaxilla of *Gracilisuchus* (MCZ 4117) forms a vertical sutural contact with the maxilla, but differs from that in crocodyliform archosaurs in not being strongly sutured. This may be an autapomorphy, and we scored the character-state as “?”

Character 4: Although Romer (1972) reconstructed the jugal of *Gracilisuchus* as entering into the margin of the antorbital fenestra, Brinkman (1981) reinterpreted it as being excluded from the margin of the fenestra. Based on examination of MCZ 4117 by H-DS, we concur with Brinkman's interpretation.

Character 13: In *Alligator*, the quadratojugal contacts the postorbital, but this is not the case in *Crocodylus* (pers. obs.).

Character 18: The occipital crest of BP/1/5237 is gently concave forward rather than V-shaped as, for example, in *Hesperosuchus*, but it is not straight as in *Dibothrosuchus* or *Sphenosuchus*.

Character 32: The femur of BP/1/5237 is incomplete, and thus the tibia/femur ratio cannot be determined with certainty (contra Gow and Kitching [1988] and Sereno and Wild [1992]).

two small sphenosuchians. We are reluctant to place much significance on this character.

17. “Parietal sagittal crest: absent (0), present along entire length of parietal (1).” See discussion with character 16 of Wu and Chatterjee. CM 29894 and an undescribed sphenosuchian from the Upper Triassic of North Carolina (H-DS, pers. obs.) clearly demonstrate that fusion of the parietals and the presence of a sagittal crest are indeed separate characters, as originally argued by Clark (1986) but rejected by Sereno and Wild (1992).

18. “Occipital crest: V-shaped (0), straight (1).”

19. “Maxillary and dentary crown shape: recurved (0), bulbous (1).” As noted by Sereno and Wild (1992:450), there is variation in crown shape within the tooth rows of sphenosuchians (see also discussion of Wu and Chatterjee's character 44 above.) The condition in *Sphenosuchus* is not clear because almost all of the functional tooth crowns were damaged in the holotype of *S. acutus* (Walker, 1990). Most of the teeth in *Dibothrosuchus elaphros* (IVPP V7907) are badly preserved and/or were damaged by preparation, and their crown shapes cannot be determined with certainty. Because of the variability of tooth shape among, and sometimes within, these taxa, we consider this character unreliable for phylogenetic analysis.

20. “Tibia/femur length ratio: less than 1 (0), more than 1 (1).”

Phylogenetic Analysis

Our analysis was based on a revised set of 33 characters (Appendix 1). We selected the stagonolepidid *Stagonolepis robertsoni* (Walker, 1961), the poposaurid *Postosuchus kirkpatricki* (Chatterjee, 1985), and *Gracilisuchus stipanicorum* (Romer, 1972; MCZ 4117) as outgroup taxa, rooting with *Stagonolepis*. These taxa have been hypothesized as close relatives of Cro-

codylomorpha in recent phylogenetic analyses (Clark in Benton and Clark, 1988; Parrish, 1993; Wu and Chatterjee, 1993), which also found *Gracilisuchus* and *Postosuchus* to be more closely related to Crocodylomorpha than is *Stagonolepis*. For Crocodyliformes, we included the basal taxon *Protosuchus richardsoni* and the extant *Alligator mississippiensis*. We identified character-states for all three specimens referred here to *Hesperosuchus agilis* and scored them individually. A partial skeleton of a small, gracile crocodylomorph (BP/1/5237) referred to *Pedeticosaurus leviseuri* by Gow and Kitching (1988) was also included in our analysis (although we do not consider it referable to *P. leviseuri* because the holotype of the latter is not diagnostic). We did not have the opportunity to examine the poorly preserved holotype and only known specimen of *Barberenasuchus brasiliensis*, and thus did not include this taxon in the analysis.

The character-taxon matrix (Table 1) was analyzed using PAUP, version 3.1.1 (Swofford and Begle, 1993), invoking the branch-and-bound option. When all taxa were included, the analysis generated three equally parsimonious cladograms, for which a strict consensus cladogram is illustrated in Figure 8A. Two of these cladograms differed only in arbitrarily resolving relationships among the three *Hesperosuchus* specimens, however, and we will consider only the two cladograms lacking this arbitrary resolution. The three specimens referred to *Hesperosuchus* form a clade, but the only autapomorphy identifiable in all three is the great depth (“swelling”) of the symphyseal region of the dentary (26.1). An analysis with all three specimens referable to *Hesperosuchus* coded as a single taxon produced two equally parsimonious cladograms with the same strict consensus cladogram. Re-running the data matrix with three multi-state characters (21, 22, and 28) re-coded as pairs of binary characters also yielded the same topologies.

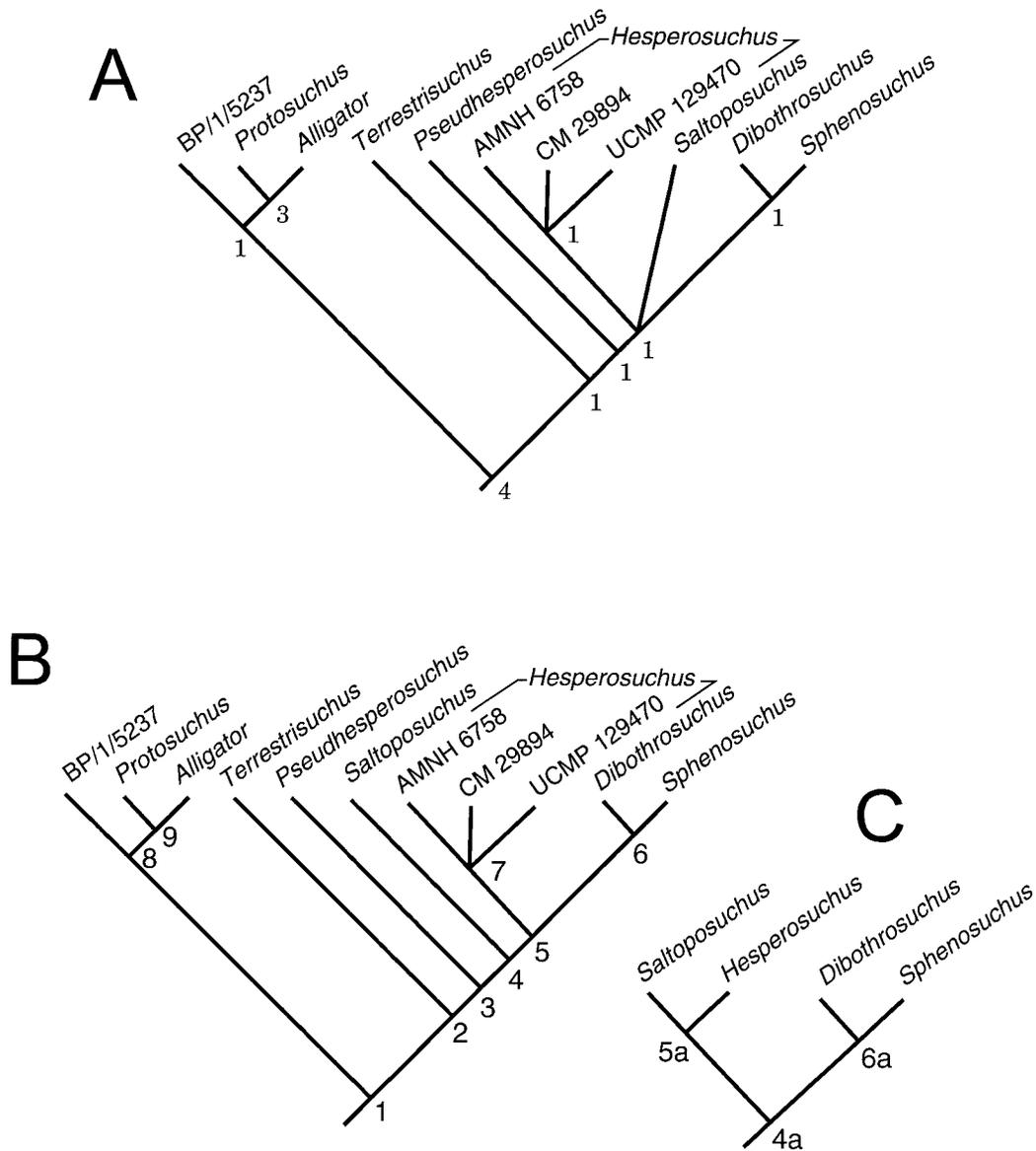


FIGURE 8. Results of the phylogenetic analysis of the data used in this study (Table 1). **A**, strict consensus cladogram of three equally parsimonious cladograms, **B**, one of the two of the equally parsimonious cladograms, and **C**, the relevant part of the second equally parsimonious cladogram (a third cladogram identified by PAUP arbitrarily resolves relationships among the specimens of *Hesperosuchus*). Including two autapomorphic characters, the length of each cladogram is 60 steps, the Consistency Index (CI) is 0.633, and the Retention Index (RI) is 0.707. The complete cladogram (B) is the only one found when the results of the analysis with equal weights are reweighted according to the rescaled consistency indices of the characters. Numbers on upper cladograms represent decay indices (Bremer, 1994), numbers on lower cladograms refer to the list of apomorphies presented in Appendix 2.

The strict consensus with all taxa is generally concordant with that of Sereno and Wild (1992) and Wu and Chatterjee (1993) in finding a monophyletic taxon Sphenosuchia, but BP/1/5237 groups with the two crocodyliforms. The two equally parsimonious cladograms differ only in the placement of *Hesperosuchus* with *Saltoposuchus* or with a clade *Dibothisuchus* + *Sphenosuchus*. Reweighting the characters based upon their rescaled consistency index (Carpenter, 1988), thus down-weighting more homoplastic characters, and repeating the analysis yielded a single cladogram with *Hesperosuchus* placed with *Dibothisuchus* + *Sphenosuchus*.

Sphenosuchian monophyly is corroborated by one unambiguous and two ambiguous apomorphies. The unambiguous de-

rived character-state is 7.1 (distinct posterior process of the prefrontal underlying the frontal). However, this feature is absent in *Dibothisuchus*, and the condition in *Protosuchus* is not known. The ambiguous apomorphies are 13.1 (quadratojugal not in contact with postorbital; condition unknown in several sphenosuchians) and 29.1 (proximal ends of metacarpals abutting; condition unknown in *Protosuchus*). The relationships of all sphenosuchian taxa remained unresolved in a strict consensus of the cladograms only one step longer than the two most parsimonious cladograms.

Terrestrisuchus is placed outside a group comprising other sphenosuchians, but the derived character-states supporting the latter clade may be size-related. The two supporting apomor-

phies, 12.1 (squamosal with ridge bordering supratemporal fossa) and 17.1 (medial edge of parietal with ridge along supratemporal fossa), both relate to the formation of a bony ridge along the edges of the fascia covering the adductor jaw musculature in the supratemporal fossa. The latter is weakly developed in BP/1/5237, but this specimen and *Terrestrisuchus* are smaller than all other known sphenosuchian specimens (although similar in size to some specimens of *Protosuchus richardsoni* with well-developed ridges). If these two characters are deleted from the analysis, *Pseudhesperosuchus* and *Terrestrisuchus* form an unresolved trichotomy with other sphenosuchians in the strict consensus cladogram.

Pseudhesperosuchus and *Terrestrisuchus* are placed outside a group comprising other sphenosuchians that is supported by one unambiguous and one ambiguous apomorphy. The larger facial portion of the maxilla (character-state 2.1) is an unambiguous apomorphy, and the expanded basipterygoid processes (25.1; condition unknown in *Saltoposuchus* and *Terrestrisuchus*) are an ambiguous apomorphy.

The relationships of *Hesperosuchus* lie either with *Saltoposuchus* or with a clade *Dibothrosuchus* + *Sphenosuchus*. Support for a relationship with *Saltoposuchus* comes from a single unambiguous apomorphy (32.1, presence of anterior process on dorsal osteoderms) and a single ambiguous one (33.1, dorsal osteoderms with ventrolateral bend). Both of these characters are unknown in *Sphenosuchus*, *Terrestrisuchus*, and *Pseudhesperosuchus*, and *Dibothrosuchus* has the primitive condition (although its osteoderms appear unusual in several respects). A relationship between *Hesperosuchus* and a clade *Dibothrosuchus* + *Sphenosuchus* is supported unambiguously by character-state 9.1 (median ridge on frontal).

Support for a clade comprising *Saltoposuchus*, *Hesperosuchus*, *Dibothrosuchus* and *Sphenosuchus* differs in the two equally parsimonious cladograms. When *Saltoposuchus* and *Hesperosuchus* group together, monophyly of the clade comprising the four aforementioned taxa is supported unambiguously by character-states 2.0 (long facial portion of maxilla) and 25.1 (expanded basipterygoid processes) and ambiguously by 9.1 (midline ridge on frontal). When *Hesperosuchus* groups with *Dibothrosuchus* and *Sphenosuchus*, support for the four-taxon clade is provided unambiguously only by character-state 2.0, with 25.1 being ambiguous.

The results of the phylogenetic analysis should be considered tentative in view of the small samples and incomplete material currently available for the various sphenosuchian taxa as well as the differences in size among them.

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APPENDIX 1
Revised Characters and Character-states.

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 to 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 midline ridge (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 or gently rounded 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), or 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-glenoid process posteromedially (1), or with elongate ventromedial process expanded ventrally (2). [UNORDERED]
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).

APPENDIX 2

Diagnostic character-states for the nodes and terminal taxa of the three most parsimonious cladograms found with the primary data set (Fig. 8). Equivocal character-states are indicated by parentheses, and are optimized with accelerated transformation. The numbers for the respective character and character-state are separated by a period (e.g., 31.1).

BP/1/5237: 2.0

Protosuchus: (6.0), 22.2

Alligator: (27.0), (32.0), 33.0

Terrestrisuchus: 31.1

Pseudhesperosuchus: none

Saltoposuchus: none

Hesperosuchus AMNH 6758: none

Hesperosuchus CM 29894: none

Hesperosuchus UCMP 129470: none

Dibothrosuchus: 7.0, 23.1

Sphenosuchus: (6.0), (21.1), 22.1

Node 1: 3.1, (4.1), 5.1, 8.1, 10.1, 14.1, 19.1, 20.1, 21.2, (27.1), 28.1, 30.1

Node 2 (*Sphenosuchia*): 7.1, (13.1), (29.1)

Node 3: 12.1, 17.1

Node 4: 2.0, (25.1)

Node 5 (*Sphenosuchidae*): 9.1

Node 6 (*Sphenosuchinae*): 15.2, 18.1, (32.0), (33.0)

Node 7 (*Hesperosuchus*): 26.1

Node 8: (1.1), 15.1, (19.2), (24.1)

Node 9 (*Crocodyliformes*): 15.2, 18.1, 23.1, 28.2

Node 4a: 2.0, (9.1), 25.1

Node 5a: 32.1, (33.1)

Node 6a: 15.2, 18.1
