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A NEW CROCODYLOMORPH ARCHOSAUR FROM THE UPPER TRIASSIC OF NORTH CAROLINA

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ABSTRACT—A new taxon of sphenosuchian crocodylomorph, *Dromicosuchus grallator*, is described on the basis of a well-preserved, largely articulated partial skeleton from Late Triassic strata in the Durham sub-basin of the Deep River basin (Newark Supergroup) of Durham County, North Carolina. The holotype was preserved directly beneath the skeleton of a rauisuchian archosaur; this association, along with apparent bite marks to the head and neck of the crocodylomorph, suggests that the two animals died and were buried together during the act of predation. *Dromicosuchus grallator* is most closely related to *Hesperosuchus agilis* from the Petrified Forest Member of the Chinle Formation (late Carnian or early Norian) of Arizona and New Mexico and *Saltoposuchus connectens* from the Middle Stubensandstein (Löwenstein Formation; middle Norian) of Württemberg, Germany. The monophyly of Sphenosuchia is only weakly supported at present.

INTRODUCTION

In September 1994, Brian Coffey and Marco Brewer, then undergraduate students at the University of North Carolina at Chapel Hill, discovered bone fragments of a Late Triassic rauisuchian archosaur in a brick-clay quarry in Durham County, North Carolina. These fossils had been uncovered during the course of commercial quarrying operations. During the following days, J. G. C., with the assistance of several students and with permission of the quarry owner, excavated the rauisuchian remains in several large blocks of matrix. Several months into the preparation of this material, it was discovered that a second, smaller reptilian skeleton was preserved underneath the pelvic region of the rauisuchian, and that additional tetrapod remains were present within the abdominal region of the rauisuchian skeleton.

The fossils represent skeletal remains referable to at least six taxa of tetrapods. The largest specimen is an incomplete but well-preserved skeleton of a new poposaurid rauisuchian closely related to *Postosuchus kirkpatricki* from the Upper Triassic Dockum Group of Texas (Chatterjee, 1985). It includes gut contents, which consist of bones (some bearing tooth marks) and osteoderms of a small stagonolepidid archosaur (*Stegomus* sp.), a snout as well as (subsequently identified) left coracoid and humerus of a traversodont cynodont (*Plinthogomphodon herpetairus* Sues et al., 1999), two articulated phalanges of a large dicynodont, and a fragment of unidentified ?temnospondyl bone. Curled up under the pelvic region of the rauisuchian skeleton, the articulated partial skeleton of a second archosaurian reptile was preserved. Based on features of its skull and postcranial skeleton, this specimen can be referred to the Sphenosuchia, a group of basal crocodylomorph reptiles (Clark et al., 2001). The left third to fifth cervical osteoderms of the sphenosuchian were largely destroyed, leaving a conspicuous gap in the cervical armor that corresponds closely in size and shape to isolated teeth of the rauisuchian. Furthermore, the posterior region of the otherwise well preserved left mandibular ramus was crushed into many small pieces of bone, presumably by an opposing tooth. The intimate association of the rauisuchian and sphenosuchian skeletons as well as the apparent injuries to the head and neck of the latter suggest that the two animals may have died and been buried together, possibly during the act of predation.

The fossils were found in a red, bioturbated sandy mudstone adjacent to a channel deposit. These strata form part of a series informally designated as Lithofacies Association II by Hoffman and Gallagher (1989) and occur in the south-central part of the Durham sub-basin of the Deep River basin (Newark Supergroup). Huber et al. (1993) regarded Lithofacies Association II as the stratigraphic equivalent of the lower Sanford Formation in the neighboring Sanford sub-basin.

Based on the occurrence of the palaeonisciform fish *Turseodus*, Olsen et al. (1989) correlated Lithofacies Association II of the Deep River basin with the Lockatong Formation of the Newark basin and the ''upper member'' of the Cow Branch Formation of the Dan River basin and thus regarded its age as late Carnian. Lucas et al. (1998) used the presence of the stagonolepidid *Stegomus arcuatus* (which they referred to *Aetosaurus*) to argue for an early to middle Norian age for what they termed the ''Neshanician land-vertebrate faunachron,'' which includes the vertebrate assemblage from Lithofacies Association II. As noted above, a partial skeleton referable to *Stegomus* was recovered from the gut contents of the rauisuchian. The type species of *Aetosaurus*, *A. ferratus*, is known from the Lower and Middle Stubensandstein (Löwenstein Formation) of Württemberg, Germany (Schoch and Wild, 1999), the Fleming Fjord Formation of eastern Greenland, and the Calcare di Zorzino of northern Italy, all of which are considered early or middle Norian in age (Lucas et al., 1998). However, regardless of a possible synonymy of *Aetosaurus* and *Stegomus*, the American specimens are taxonomically distinct from *A. ferratus* and may well have had a different stratigraphic range. Furthermore, phylogenetic analyses have consistently placed *Aetosaurus* as the sister-taxon to all other known taxa of Stagonolepididae

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(Parrish, 1994; Heckert and Lucas, 1999). Thus the *Aetosaurus* lineage must predate more derived, Carnian-age taxa such as *Stagonolepis*, and its occurrence in pre-Norian strata is to be expected.

The new poposaurid rauisuchian is closely related to *Postosuchus kirkpatricki* from the Cooper Canyon Formation (Dockum Group) of Texas (Chatterjee, 1985), which is considered early Norian in age. However, Long and Murry (1995) also referred (without further discussion) various late Carnian specimens to *P. kirkpatricki*. The traversodont cynodont *Plinthogomphodon herpetairus* is not useful for stratigraphic correlation because its phylogenetic relationships are as yet unresolved (Sues et al., 1999). The sphenosuchian described in this paper is most closely related to *Hesperosuchus agilis* from the Petrified Forest Member of the Chinle Formation (late Carnian or early Norian) of Arizona and New Mexico (Clark et al., 2001) and *Saltoposuchus connectens* from the Middle Stubensandstein (Löwenstein Formation; middle Norian) of Württemberg, Germany (Huene, 1921; Sereno and Wild, 1992; Schoch and Wild, 1999). The biostratigraphic evidence cannot definitely resolve the question whether the tetrapod assemblage from Lithofacies Association II is late Carnian or early Norian in age. Paleomagnetic sampling currently in progress by D. V. Kent and P. E. O. suggests an early Norian date for the fossil-bearing strata.

The new sphenosuchian skeleton from North Carolina is nearly complete and well preserved, and thus of considerable interest for discussions regarding the anatomy and interrelationships of basal crocodylomorph archosaurs. We present here a description of this specimen and assess its phylogenetic relationships.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; UNC, Department of Geological Sciences, University of North Carolina at Chapel Hill.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869
CROCODYLOMORPHA Hay, 1930 sensu Walker, 1970
SPHENOSUCHIDAE Haughton, 1924

Comment—The interrelationships of basal crocodylomorph archosaurs are still poorly resolved (see below), and thus it is inadvisable to offer a phylogenetic definition of Sphenosuchidae at this point.

DROMICOSUCHUS, gen. nov.

Etymology—From Greek *dromikos*, fleet, quickly walking, and *soukhos*, Greek rendering of the ancient Egyptian crocodile-headed deity Sebek or Sobk and traditional suffix for generic nomina of crocodylomorph reptiles, in reference to the inferred cursorial habits of this crocodylomorph.

Type Species—*Dromicosuchus grallator*, sp. nov. (by monotypy).

Diagnosis—As for the type and only known species, given below.

DROMICOSUCHUS GRALLATOR, sp. nov.

Etymology—Latin *grallator*, one who walks on stilts, in reference to the very long and slender limbs.

Holotype—UNC 15574, nearly complete skull with mandible in tight occlusion and partial, largely articulated postcranial skeleton (Fig. 1), comprising the vertebral column from the atlas-axis complex back to the second caudal vertebra, dorsal dermal armor, ribs and gastralia elements, left scapulocoracoid and almost complete left forelimb, partial right scapula and proximal portion of the right humerus, left ilium, left femur, distal end of the right femur, both tibiae, proximal and ?distal portions of the left fibula, incomplete left calcaneum, three left metatarsals, and fragments of several currently unidentifiable limb-bones.

Type Horizon and Locality—Mudstone facies of Lithofacies Association II sensu Hoffman and Gallagher (1989), south-central region of the Durham sub-basin of the Deep River basin, Newark Supergroup. GPS coordinates (recorded by P. E. O.): latitude 35° 52′ 28″ N; longitude 78° 53′ 81″ W. Genlee, Durham County, North Carolina, U.S.A. Age: Late Triassic (late Carnian or early Norian).

Diagnosis—Distinguished from *Saltoposuchus connectens* by the presence of paired crests separated by a median groove on the dorsal surface of the parietals and the more prominent development of the dorsolateral crest on the squamosal. Differs from *Hesperosuchus agilis* in the absence of the dorsoventral expansion of the anterior end of the dentary and the presence of a conical recess at the anterior end of the antorbital fossa. Distinguished from *Sphenosuchus acutus* and *Dibothrosuchus elaphros* by the presence of a V-shaped, rather than straight, transverse occipital crest, the presence of paired crests separated by a median groove, rather than a single median crest, on the dorsal surface of the parietals, the presence of a conical recess at the anterior end of the antorbital fossa, and the less elongated posteromedial process of the coracoid. Differs from *Kayentasuchus walkeri* in the absence of a lateral groove on the squamosal and the presence of an anterior caniniform tooth in the dentary.

DESCRIPTION

UNC 15574 comprises much of an articulated skeleton, which was recovered as a series of individual blocks as well as a number of isolated bones and bone fragments (Fig. 1). The animal was preserved with its ventral side facing up and its head folded against the left side of its neck. The left forelimb was tucked under the head and neck. The largest block (Figs. 2, 3) contains the skull, left scapulocoracoid and forelimb, and a mostly articulated series of 10 complete as well as two partial cervical and anterior dorsal vertebrae with associated ribs and 13 pairs of osteoderms. Its upper surface also preserves several segments of gastralia elements and the proximal end of the left tibia of the overlying rauisuchian skeleton. A small piece of matrix containing a partial and two complete vertebrae, together with jumbled osteoderms, indeterminate bone fragments, and a large chunk of a rauisuchian limb-bone, appears to join this block to another block, which represents the mid-dorsal region (Fig. 4). The latter contains an articulated set of three complete and three partial vertebrae with associated osteoderms (five complete and two partial pairs), ribs, and gastralia. It can be fitted to an articulated segment of vertebral column comprising the last four dorsal (the first of which is incomplete), the two sacral and the first two caudal vertebrae, which are associated with pairs of osteoderms, the left ilium, and what may be the proximal portion of the left pubis (Fig. 5). The bones of the hindlimbs and right forelimb are now completely separated from the rest of the skeleton and from each other. When the material was collected, the proximal head of the left femur still adhered to the wall of the acetabulum on the left ilium, but it was subsequently removed and reattached to the femoral shaft.

UNC 15574 is closely similar in all comparable linear dimensions to the holotype of *Hesperosuchus agilis* (AMNH 6758; Colbert, 1952:table 1). Assuming body proportions similar to those reconstructed for *Dibothrosuchus elaphros* (Wu and Chatterjee, 1993), it represents an individual with an estimated total length between 1.2 and 1.3 m. It is difficult to assess the ontogenetic stage of UNC 15574 using the standard crite-

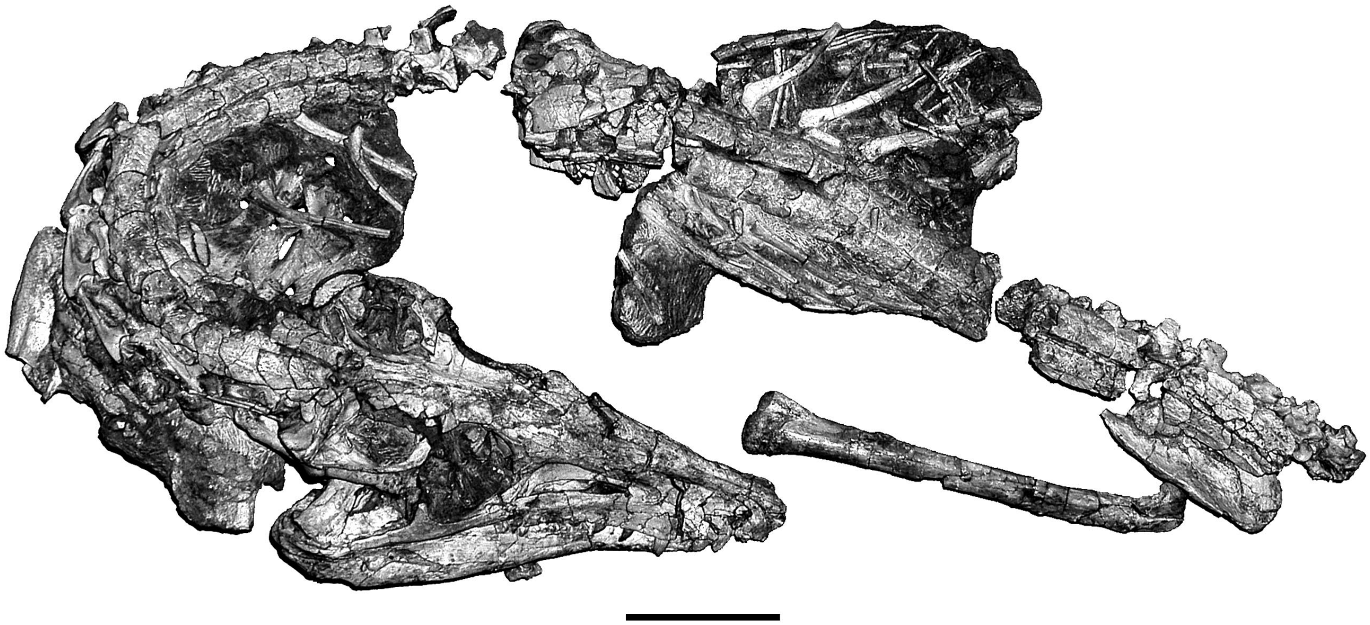

FIGURE 1. *Dromicosuchus grallator*, UNC 15574 (holotype), digital photograph of the skeleton (mostly in dorsal view) as reassembled after completed preparation. Scale bar equals 5 cm.

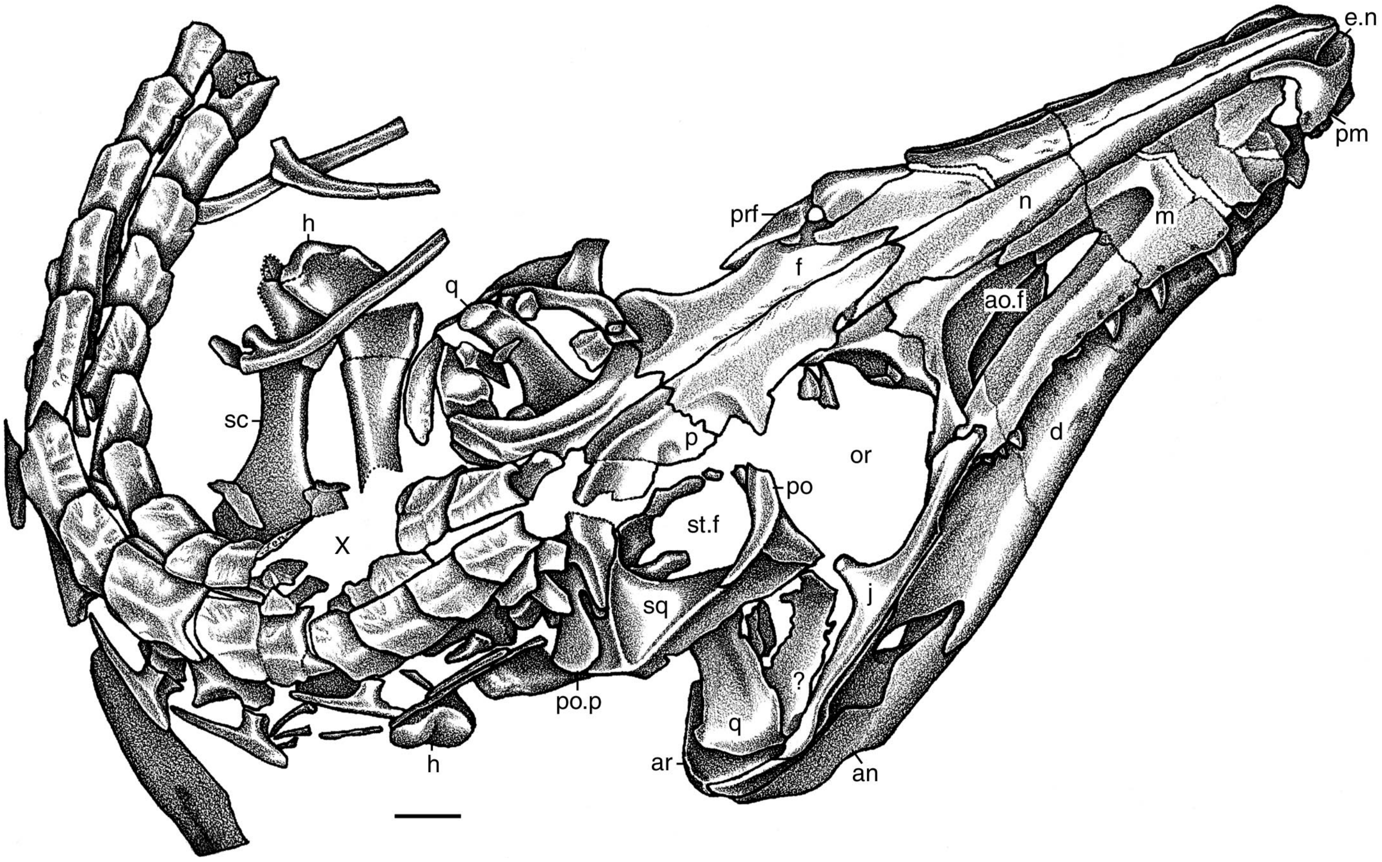

FIGURE 2. *Dromicosuchus grallator*, UNC 15574 (holotype), block with skull and anterior portion of the skeleton in dorsal view. Scale bar equals 1 cm. Areas in white represent matrix. Abbreviations: **an**, angular; **ao.f**, antorbital fossa; **ar**, articular; **d**, dentary; **e.n**, external naris; **f**, frontal; **h**, humerus; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **or**, orbit; **p**, parietal; **pm**, premaxilla; **po**, postorbital; **po.p**, paroccipital process; **prf**, prefrontal; **q**, quadrate; **sc**, scapula; **sq**, squamosal; **st.f**, supratemporal fenestra. **X** denotes apparent bite damage to cervical armor. **?** denotes possible quadratojugal.

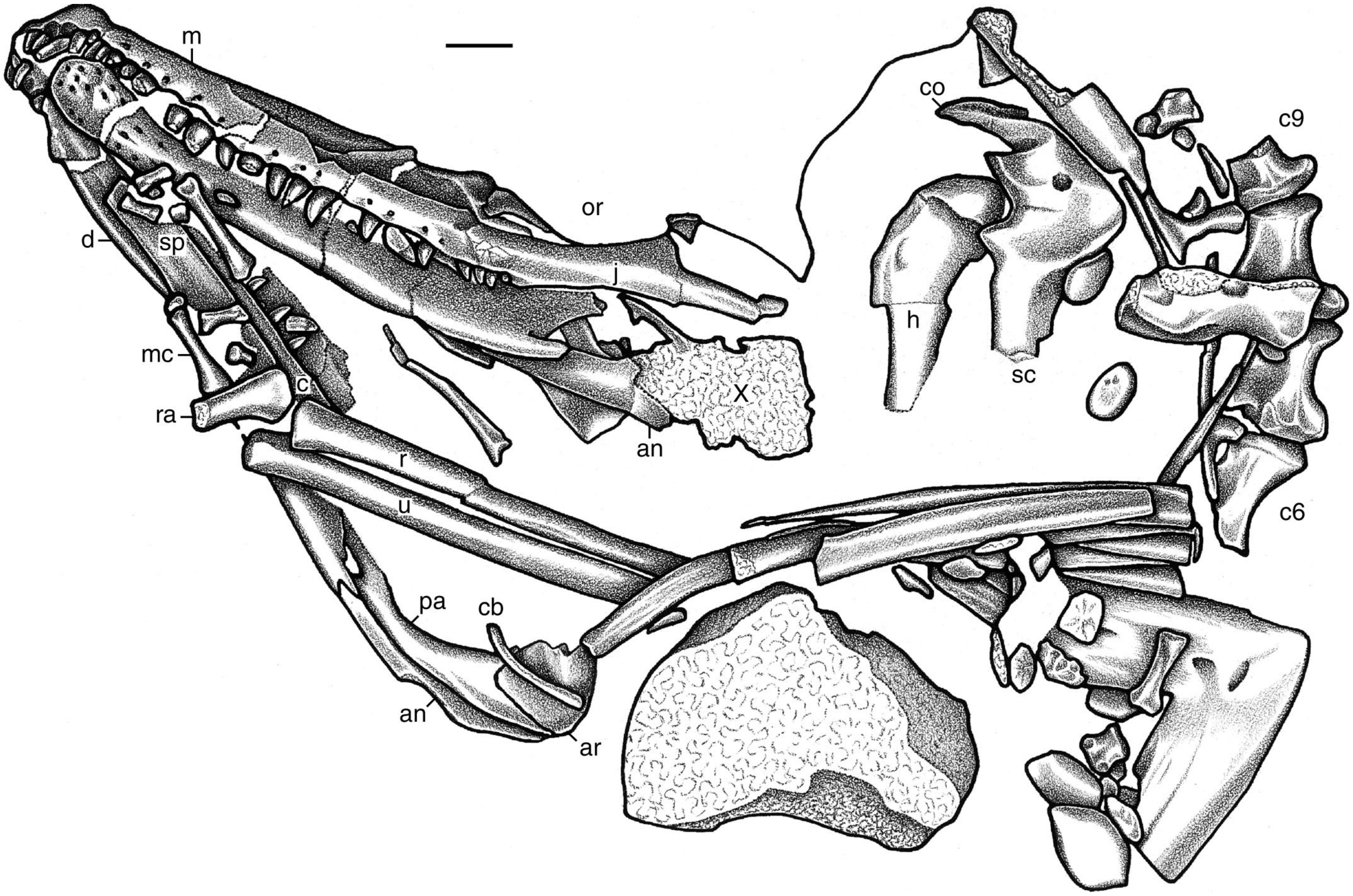

FIGURE 3. *Dromicosuchus grallator*, UNC 15574 (holotype), block with skull and anterior portion of the skeleton in ventral view. Gastralia and fragment of limb-bone in lower right corner of drawing belong to the overlying rauisuchian skeleton. Scale bar equals 1 cm. Abbreviations as in Figure 1 plus: **c**, coronoid; **c6**, **c9**, cervical 6, 9; **cb**, ceratobranchial I; **co**, coracoid; **mc**, metacarpal; **pa**, prearticular; **r**, radius; **ra**, radiale; **sp**, splenial; **u**, ulna. **X** denotes apparent bite damage to posterior region of left mandibular ramus.

rion of closure of the neurocentral sutures (Brochu, 1996). The neural arches of several dorsal vertebrae show separation from as well as some displacement relative to the centra, but it is uncertain whether this condition reflects the original presence of open neurocentral sutures. The exposed right side of the sixth cervical vertebra apparently shows a faint neurocentral suture. However, the almost complete fusion of the scapula and coracoid suggests maturity of the animal (Brochu, 1992).

Skull

The nearly complete skull of UNC 15574 (Figs. 2, 3) was obliquely crushed in a dorsolateral direction during fossilization so that its right side is now preserved in almost the same horizontal plane as the anterior portion of the skull roof. The well-preserved right side of the skull shows considerable detail, whereas compression has severely distorted the left side. Many bones are traversed by fractures. Several elements, especially along the perimeter of the orbit, were separated along their sutural contacts. The mandibular rami are tightly appressed to the skull so that the dentary teeth are largely concealed from view. The anterior end of the snout was broken off during collecting, but was recovered and readily reattached to the remainder of the skull.

The lightly built skull has a long and narrow snout and a transversely broad temporal region. It is about 150 mm long (measured along the midline of the skull roof from the anterior tip of the snout to the anterior end of the V-shaped occipital embayment). The length of the antorbital region of the skull (measured from the anterior terminus of the orbit to the tip of the snout) is more than twice that of the postorbital region (measured from the posterior end of the orbit to the level of the posterolateral termini of the occipital crests). The external nares face laterally and are separated from each other by a bony bar formed by the nasals and premaxillae. The antorbital fossa is more or less triangular in lateral view and large, with an anteroposterior length of 46 mm and a maximum height of 19 mm. The antorbital fenestra is long (31 mm) but low (4 mm). The orbit is nearly circular in outline, with an anteroposterior diameter of about 30 mm. The supratemporal fenestra is longer anteroposteriorly than wide transversely. The external surfaces of most cranial bones are devoid of sculpturing.

Premaxilla—The recurved posterolateral process of the premaxilla overlaps the nasal and maxilla on the side of the snout, excluding the latter from participation in the posterior margin of the external naris. Although damage to both sides of the snout has obscured some details of this feature, a laterally open notch is present between the posterior edge of the premaxilla and the anterior edge of the maxilla and receives an anterior caniniform tooth of the dentary. Anteriorly, the premaxilla forms the short anterodorsal portion of the slender internarial bar and the nasals make up the more posterior part. The premaxilla holds five teeth, the first of which is smaller and more slender than the others.

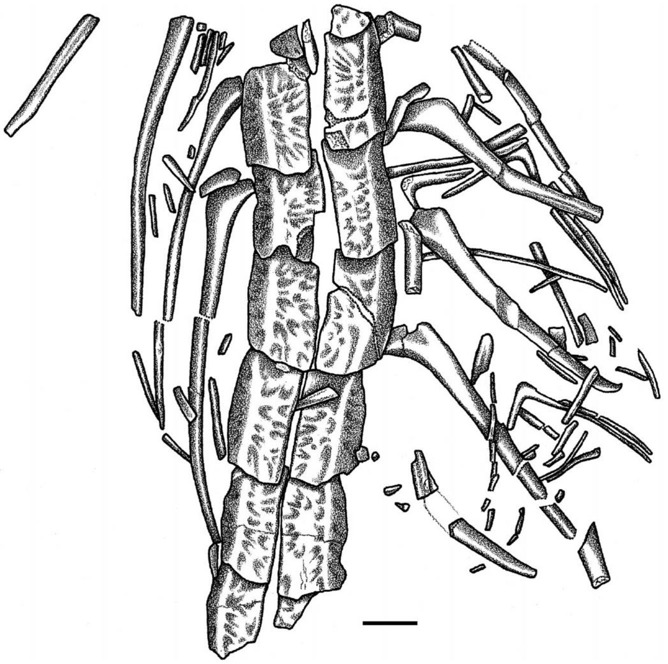

FIGURE 4. *Dromicosuchus grallator*, UNC 15574 (holotype), segment of mid-dorsal region in dorsal view. Anterior is toward the top of the figure. Scale bar equals 1 cm.

Maxilla—The long but rather low maxilla forms most of the rostral portion of the skull. Its alveolar margin is distinctly sinuous in lateral view, reaching its greatest depth at about the level of the sixth maxillary tooth. The facial portion of the maxilla extends vertically. Its ascending process projects posteriorly and slightly dorsally. It contacts the anterior ramus of the lacrimal half way along the dorsal rim of the antorbital fenestra, excluding the nasal from participation in the dorsal margin of the antorbital fossa. The anterior and ventral margins of the large, subtriangular antorbital fossa are formed by a thin medial lamina of the maxilla, which is inset relative to the remainder of the lateral surface of this bone. Anteriorly, the fossa terminates in a deep conical pit, which is largely concealed in lateral view by the lateral portion of the ascending process of the maxilla. A similar pit is present in both *Saltoposuchus* (Clark et al., 2001) and *Terrestrisuchus* (Crush, 1984). The antorbital fenestra is restricted to the more ventral portion of the antorbital fossa. The lateral surface of the maxilla bears scattered small neurovascular openings. A row of large supralabial foramina, presumably for passage of cutaneous branches of N. alveolaris superior and associated blood vessels, extends just dorsal and parallel to the alveolar margin. The more completely preserved left maxillary tooth row comprises 20 teeth (some of which have partially dropped out of their alveoli) and ends posteriorly just behind the anterior margin of the orbit.

Nasal—The nasal is narrow, thick, and long, extending from the region of the external naris back to the level of the anterior margin of the orbit. Its anterior portion forms most of the dorsal margin of the narial fenestra. In the region between the margin of the external naris and the anterior end of the antorbital fossa, the lateral portion of the nasal is somewhat deflected ventrolaterally and thus faces dorsolaterally. Although the dorsal surfaces of both nasals are slightly eroded, they appear to bear a weakly developed, irregular sculpturing of pits and longitudinal grooves, especially more anteriorly. Posteromedially, the nasals form a shallow depression along the midline of the skull roof, as in *Sphenosuchus* (Walker, 1990). The nasal forms straight lateral sutural contacts with the lacrimal and maxilla.

Lacrimal—In lateral view, the lacrimal has an inverted L-shape and is inclined forward. It forms the preorbital bar and contributes a broad, thin medial lamina to the medial wall of the antorbital fossa. Its vertical portion bears a narrow but distinct lateral crest. Anteriorly, the lacrimal is overlapped by the maxilla along the dorsal margin of the antorbital fossa. Posteriorly, it forms an extensive lateral contact with the prefrontal along the preorbital bar. The dorsal exposure of the lacrimal on the skull roof is narrow. The posterior opening of the lacrimal canal is situated about halfway up the anterior margin of the orbit on the suture between the lacrimal and prefrontal. Ventrally, the lacrimal is expanded anteroposteriorly at its contact with the jugal and maxilla.

Prefrontal—The prefrontal extends posteriorly to about midway along the dorsal rim of the orbit. Due to crushing, it is uncertain whether it extended under the frontal more posteriorly as in other sphenosuchians (Sereno and Wild, 1992). The narrow dorsal surface of the prefrontal is more or less triangular in dorsal view and set off from the ventrolateral portion of the bone by a ridge extending along the lateral edge of the skull roof. Within the anterodorsal part of the orbit, the prefrontal is considerably expanded and, as in *Sphenosuchus* (Walker, 1990), appears to form three processes: one extending ventrally along the medial aspect of the lacrimal, another projecting toward the midline of the skull, and a third extending dorsomedially toward the ventral surface of the frontal.

Jugal—The jugal is slender and triradiate. Its lateral surface bears a low ridge that extends back from below the orbit and fades into the posterior or infratemporal process posteriorly. The infratemporal process tapers toward the jaw joint. The dorsal process of the jugal is very slender. The anterior process forms the entire ventral margin of the orbit but does not extend to the posteroventral corner of the antorbital fenestra anteriorly. It overlaps the ventral part of the lacrimal.

Frontal—The frontal is much longer than wide and forms much of the roof as well as the slightly raised rim of the orbit. Its dorsal surface is concave transversely. A low ridge extends along the median suture between the frontals, fading into the bones more anteriorly. Posterolaterally, the supratemporal fossa continues forward onto the dorsal surface of the frontal, forming a distinct depression on the latter. Anteriorly, the frontals extend far forward between the posterior ends of the nasals along the midline of the skull roof, resulting in a V-shaped suture, and, posteriorly, they contact the parietals along a transverse suture.

Parietal—Dorsally, the parietals bear paired crests, which are separated by a median longitudinal groove. Each crest forms the posteromedial edge of the adjacent supratemporal fossa. The interparietal suture extends in the median groove between the two crests. This condition differs from the single median crest on the parietals in *Dibothrosuchus*, *Saltoposuchus*, and *Sphenosuchus*, but closely resembles the paired parietal crests in *Hesperosuchus* (Clark et al., 2001). In a partial skull referred to *Saltoposuchus connectens*, the dorsal surface of the parietals is flat between the medial margins of the supratemporal fenestrae (Sereno and Wild, 1992:fig. 5A). The posterolateral wings of the parietals in UNC 15574 diverge posteriorly, forming a V-shaped embayment in the occipital margin of the skull roof, as in *Hesperosuchus* and *Saltoposuchus* but unlike the transverse occipital crest in *Dibothrosuchus* and *Sphenosuchus*.

Postorbital—The postorbital is triradiate in lateral view. It forms the anterior half of the supratemporal bar and overlaps the squamosal posteriorly. A prominent anterolateral ridge overhangs the ventral process for contact with the jugal. Anteromedially, the postorbital contacts the posterolateral end of the frontal.

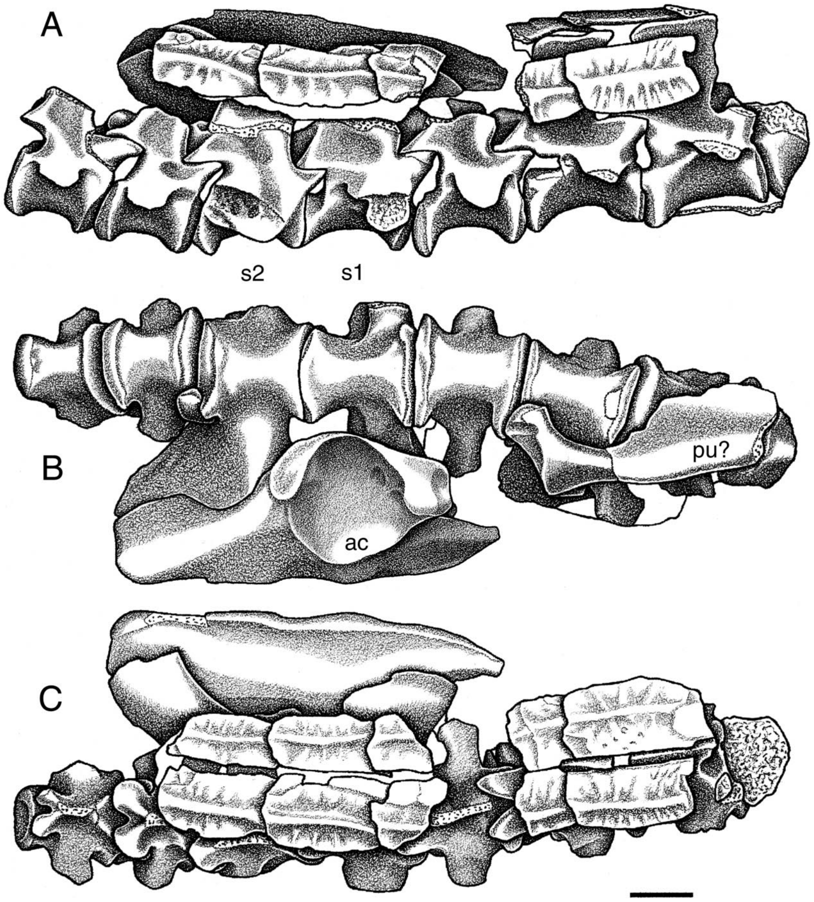

FIGURE 5. *Dromicosuchus grallator*, UNC 15574 (holotype), articulated segment of vertebral column consisting of posterior four dorsal, two sacral, and first two caudal vertebrae, with articulated left ilium and disarticulated proximal portion of left ?pubis in **A**, right lateral, **B**, ventral and **C**, dorsal views. Scale bar equals 1 cm. Abbreviations: **ac**, acetabulum; **pu?**, possible pubis; **s1**, **s2**, sacral vertebra 1, 2.

Squamosal—The squamosal forms the posterolateral corner of the skull table and overhangs the infratemporal region and suspensorium laterally. It is rather thin and ventrally concave. Laterally, the squamosal is deflected so that this portion of the bone probably assumed a nearly vertical oriention. Anteriorly, it extends ventral to the postorbital to participate in the formation of the postorbital bar. A prominent crest extends along the posterolateral margin of the supratemporal fossa on the dorsal surface of the squamosal, continuing the anterolateral ridge on the postorbital and the parasagittal ridge on the parietal. Together, these ridges surround most of the supratemporal fossa and sharply demarcate the skull table from the occiput and the sides of the skull. In *Saltoposuchus*, the squamosal appears to be wider transversely and has a less prominent posterolateral crest (Sereno and Wild, 1992:fig. 5A).

Quadrate—The quadrate is steeply inclined anterodorsally so that its proximal end is situated well forward of its distal mandibular condyles. A lateral ridge extends along the anterior margin of the bone. Medial to this ridge, the posterior surface of the quadrate bears a distinct, oval depression. On the left side of the skull, postmortem crushing has pushed the quadrate in a dorsolateral direction through the supratemporal fenestra, clearly exposing the single, anteroposteriorly elongate proximal head of the quadrate. The right quadrate has been similarly displaced.

?Quadratojugal—On the right side of the skull, bone is visible in the infratemporal fenestra anterior to the quadrate and medial to the somewhat displaced jugal. This bone probably represents the quadratojugal, but details are obscured by fracturing and displacement.

Braincase—The crushing of the skull during fossilization has destroyed and/or obscured most of the palate and braincase. The distal end of the paroccipital process formed by the otoccipital (fused exoccipital and opisthotic) is distinctly expanded vertically. The posterior surface of the process is gently convex dorsoventrally.

Hyoid—A curved fragment of rod-like bone, which is appressed to the medial surface of the right articular, probably represents a ceratobranchial I (cornu branchiale I).

Mandible

The mandibular rami are long and slender (Figs. 2, 3). Few structural details can be discerned due to crushing on both rami. The large external mandibular fenestra was bounded by the dentary anteriorly and dorsally, the surangular posterodorsally, and the angular ventrally.

Dentary—The dentary is long and low. Its anterior (symphyseal) end lacks the distinct dorsoventral expansion diagnostic for *Hesperosuchus* (Clark et al., 2001). Although details are obscured by crushing and displacement of the mandibular rami, the symphysis apparently did not extend much posterior to the region of the third or fourth dentary tooth. The lateral surface of the anterior portion of the dentary, especially in the symphyseal region, bears numerous scattered neurovascular foramina. The number of teeth in each dentary cannot be determined due to the tight contact between the mandibular rami and the skull.

Coronoid—On the lingual surface of the right mandibular ramus, a long and very slender coronoid bone extends just ventral and parallel to the alveolar margin of the dentary and ventrally contacts the splenial, much as in *Sphenosuchus* (Walker, 1990:fig. 31). Wu and Chatterjee (1993) reported the presence of a crescentic coronoid bone in *Dibothrosuchus*, but that interpretation requires confirmation.

Splenial—The flat splenial covers most of the medial surface of the dentary including the Meckelian groove. Due to breakage along its anterior edge, it is not clear whether the splenial contributed to the formation of the mandibular symphysis.

Surangular—The surangular overlaps the articular laterally and extends back to the posterior end of the mandibular ramus. It makes a small contribution to the lateral portion of the articular facet for the mandibular condyles of the quadrate.

Angular—The angular forms the ventral margin of the external mandibular fenestra and overlaps the prearticular and surangular more posteriorly.

Prearticular—The expanded posterior portion of the prearticular contacts the articular posteromedially. The curved dorsal edge of this bone delimits the adductor fossa ventromedially.

Articular—The articular is inserted between the surangular laterally and the prearticular medially. It is wide transversely and bears a prominent, dorsomedially directed process just posteromedial to the articular facet for the mandibular condyles of the quadrate, as in *Dibothrosuchus* (Wu and Chatterjee, 1993: fig. 8). Unlike in extant crocodylians (Iordansky, 1973), there is no long, dorsally curving retroarticular process.

Dentition

All teeth have labiolingually flattened crowns with finely serrated anterior (mesial) and posterior (distal) carinae. The premaxillary and more anterior maxillary teeth have slender, only slightly flattened and recurved crowns. Behind the small first maxillary tooth, the tooth crowns rapidly increase in size back to the sixth tooth, which is the largest of the tooth row. Immediately behind the latter, the tooth crowns decrease again in size and the posterior maxillary teeth are the smallest ones. The crowns of the more posterior teeth are somewhat recurved and have convex anterior and gently concave or straight posterior carinae. One of the anterior dentary teeth, probably either the third or fourth, is enlarged and fits into the notch between the premaxilla and maxilla visible on the left side of the snout.

Vertebrae and Ribs

Much of the vertebral column, from the atlas-axis complex back to the second caudal vertebra, was found articulated (Figs. 1–5). It consists of at least 23 presacral, two sacral, and the first two caudal vertebrae. One or perhaps two presacral vertebrae may now be missing as there are small gaps between consecutive blocks. The complete presacral series of the partial skeleton referred to *Dibothrosuchus* by Wu and Chatterjee (1993) comprises 24 vertebrae, and Crush (1984) inferred the same number for *Terrestrisuchus*. Bonaparte (1972) reported 23 presacral vertebrae in *Pseudhesperosuchus*, but noted that the total count could be as high as 26.

Due to local displacement within and damage of the vertebral column as well as concealment by adjacent bones or overlying osteoderms, few vertebrae are sufficiently exposed for detailed examination. All centra are amphicoelous and laterally constricted at mid-length.

Cervical Vertebrae—Of the atlas, the neural arch and atlantal intercentrum are partially exposed on the right side. The axis has short prezygapophyses, and its parapophyseal facet is situated low on the centrum. The post-axial cervical centra are almost twice as long as high and are transversely compressed. The ventral surface of each centrum is distinctly concave and bears a well-developed median keel; the former feature is shared by *Hesperosuchus* but the latter is not (Long and Murry, 1995). The ventrolaterally facing diapophyseal facets are well-developed and separated from the parapophyseal facets by a groove along the lateral surface of the centrum. The prezygapophyses are not as elongated as on the cervical vertebrae of *Hesperosuchus* (Colbert, 1952:fig. 15). The neural spines in the mid-cervical region are laterally compressed and lack apical expansion.

The number of cervical vertebrae is uncertain. Walker (1990) inferred the presence of nine cervicals in *Sphenosuchus*, based on the condition in extant crocodylians, and Wu and Chatterjee (1993) identified the same number in *Dibothrosuchus*. In UNC 15574, the ninth and tenth presacral vertebrae are incompletely preserved; thus the position of the cervicodorsal junction is uncertain.

Dorsal Vertebrae—The dorsal centra are longer than high. Their ventral surfaces are not keeled and become rather flat more posteriorly along the column. The bases of the neural spines are laterally constricted. On what appears to be the 13th presacral vertebra, the dia- and parapophysis have become confluent. Where visible between the overlying osteoderms, the neural spines appear to be of moderate height.

Sacral Vertebrae—There are two sacral vertebrae. The centrum of the first is more laterally constricted than that of the second, and the first sacral rib is restricted to the anterior half of the centrum. The second sacral rib is shaped like the head of a hatchet and much wider anteroposteriorly than the first, occupying most of the length of the centrum. Proximally, the ribs were inserted into sockets on the sides of the centra and the pedicles of the neural arches; these sockets are visible on the right side of the two vertebrae where the ribs were not preserved.

Caudal Vertebrae—The centra of the first and second caudal vertebrae are only slightly longer than high. They have flattened ventral surfaces and bevelled rims anteriorly and posteriorly. The transverse processes are dorsoventrally flattened and slightly deflected. The bases of the (broken) neural spines are laterally constricted. The first chevron facet is located on the second caudal.

Based on the elongation of the centrum, a nearly complete isolated vertebra and an isolated centrum represent distal caudals.

Ribs—The first and second cervical ribs each have a single proximal head and a very long, rod-like shaft. The second rib extends along the dorsal edge of the first. Starting at the third cervical vertebra, the ribs become double-headed and ‘‘plough-shaped,’’ with a more or less horizontal shaft, which extends more or less parallel to the vertebral centrum and is continued anteriorly as a short, tapering process. The posterior end of the rib shaft contacts the anterior tip of the anterior process of the succeeding rib.

The capitulum and tuberculum on the dorsal rib-heads are widely separated. The proximal portion of the slender shaft on the more completely preserved mid-dorsal ribs bears a small anterolateral process similar to that in *Hesperosuchus* (Colbert, 1952). Two disarticulated but well-preserved anterior dorsal ribs each have a posterior flange extending along the proximal region of the shaft.

Gastralia—Gastralia are represented by a number of disarticulated pieces in the mid-dorsal region, including one V-shaped median segment.

Dermal Armor

As in other basal crocodylomorph archosaurs, two rows of paramedian dorsal osteoderms cover the neck, trunk, and presumably tail (most of which is not preserved in UNC 15574) (Figs. 1, 2, 4, 5). Unlike in *Hesperosuchus* (Clark et al., 2001), there is no unpaired first osteoderm immediately behind the median occipital margin of the skull roof. At least 28 pairs of osteoderms are preserved in the region from the craniocervical junction to the base of the tail. Each osteoderm overlaps the anterior end of its successor and forms an unsculptured anterolateral process, which projects anteriorly below the preceding osteoderm; this process is short on the first cervical osteoderm. A low longitudinal ridge extends obliquely posterolaterally on the dorsal surface from the medial end of the anterolateral process to the posterolateral corner of each osteoderm. It marks the division of the osteoderm into a horizontal medial and a slightly ventrolaterally deflected lateral portion. The dorsal surface of the osteoderm bears a distinct sculpturing of irregular pits separated by ridges originating from the longitudinal ridge, whereas the ventral surface is smooth. The anterior margin of each plate is concave, and its lateral edge is convex. A shallow notch is developed in the posterolateral corner of the more posterior osteoderms. The straight medial border forms the longest side of each plate. With the exception of the first pair of more or less pentagonal plates, the osteoderms are longer than wide and become more rectangular further posteriorly; the disparity between osteoderm length and width appears to be most pronounced in the mid-dorsal region and decreases again in the pelvic region.

A small, irregularly shaped piece of bone is preserved attached to the medial aspect of the distal portion of the left femur and possibly represents an appendicular osteoderm.

Pectoral Girdle and Forelimb

The left scapulocoracoid and forelimb (Figs. 2, 3) are nearly completely preserved. The right scapulocoracoid and forelimb are apparently represented only by a partial scapular blade and two fragments of the humerus.

Scapulocoracoid—The proximal portion of the strongly curved scapula broadly contacts the coracoid. The two bones are almost completely fused to each other, with sutural separation persisting only for a short distance anterior to the glenoid. The anterior end of the scapula bears a distinct acromial ridge laterally. The distal portion of the scapular blade is flattened and greatly expanded, especially anteriorly so that the anterior margin of the blade is distinctly concave in lateral view. The posterior margin of the bone is less concave and becomes thicker proximally where it supports the posterolaterally and ventrally facing scapular glenoid facet. Just above the buttress for the glenoid facet, the scapula bears a rugose thickening, which probably marks the origin of the caput scapulare of M. triceps brachii as in extant crocodylians (Fürbringer, 1876).

The anterior portion of the coracoid is thin, plate-like, and perforated by a large foramen. The posterolaterally and dorsally facing glenoid facet of the coracoid is gently convex and has a posterolateral 'lip.' The coracoid forms a prominent, posteromedially directed process behind the glenoid region. This process is shorter than the body of the coracoid, unlike the greatly elongated process in *Dibothrosuchus* (Wu and Chatterjee, 1993) and *Sphenosuchus* (Walker, 1990), and tapers posteriorly. Its ventral surface bears a deep groove, which is delimited dorsally by a more or less horizontal ridge and probably contacted the interclavicle medially (Walker, 1990).

Humerus—The complete left humerus is 89 mm long. Its slender, hollow shaft is round in transverse section between the expanded proximal and distal articular ends. The proximal portion lacks the round depression on the anterior surface of the proximal end reported in *Dibothrosuchus* (Wu and Chatterjee, 1993). Its medial margin is strongly arched. The head of the humerus is reflected and forms a distinct, rounded articular surface. The well-developed deltopectoral crest projects anteromedially, rising just distal to the head to a median apex and terminating in the proximal third of the bone. A distinct ridge extends anterolaterally where the deltopectoral crest turns anteromedially. The distal end of the humerus bears two condyles, which are separated by a groove and together form a slightly saddle-shaped articular surface for the radius and ulna.

Radius and Ulna—The left ulna is 102 mm long and thus distinctly longer than the humerus (89 mm; 114.6%). The radius appears to be shorter than the ulna (although its proximal end could not be fully exposed during preparation), and its shaft is slightly more slender than that of the latter. Both bones are slender and have only slightly expanded distal ends. The proximal end of the ulna bears a well-developed olecranon process.

Carpus and Manus—The carpus and manus are largely disarticulated, resulting in the loss of a number of smaller bones. Both the radiale and ulnare are columnar and elongated in typically crocodylomorph fashion. Although its distal end is damaged, the radiale is more robust than the ulnare; its estimated length is 18 mm. The preserved metacarpals are long and slender. Based on the preserved, mostly scattered phalanges, the manus was small.

Pelvic Girdle and Hindlimb

The left ilium is still preserved in articulation with the two sacral vertebrae. A fragment of bone just anterior to the left ilium is possibly the proximal portion of the left pubis. The hindlimbs are represented by the complete left femur and the distal end of the right femur, both tibiae, the proximal and ?distal portions of the left fibula, an incomplete left calcaneum and (associated with the latter) three metatarsals from the left pes.

The hindlimb is much longer than the forelimb; the ratio of the combined length of femur and tibia (274 mm) to that of humerus and ulna (191 mm) is 1.43.

Ilium—The slightly ventrolaterally inclined blade of the ilium (Fig. 5) is clearly set off from the acetabular region. It is long anteroposteriorly but low dorsoventrally. The more or less horizontal dorsal margin of the blade is thickened, especially more anteriorly. The preacetabular process of the ilium is more slender than the postacetabular one and tapers anteriorly in lateral view. (Its anterior tip is not preserved.) Medially, the postacetabular process bears a prominent ridge along its ventral margin, which is in contact with the broadly flaring second sacral rib. The deeply concave acetabulum is partially overhung by a broad supra-acetabular crest, the central portion of which continues dorsally as a thick vertical ridge. The crest is widest anteriorly but does not extend to the posterior end of the acetabulum. The ventral margin of the acetabular wall between the anterior and posterior peduncles is gently convex rather than concave. The articular surfaces for contact with the pubis and ischium are broad. Just anterior to the lateral margin of the facet for contact with the ischium, there is a distinct, slightly rugose area, which probably represents an antitrochanter.

?Pubis—A fragment of bone preserved adjacent to the last three dorsal vertebrae possibly represents the proximal portion of the left pubis (Fig. 5B). Its identification is based on its resemblance to the pubes of *Saltoposuchus* (Huene, 1921:fig. 19) and *Terrestrisuchus* (Crush, 1984:fig. 8).

Femur—The complete left femur (Fig. 6) is 144 mm long. Its proximal portion is flattened transversely and twisted relative to the long axis of the bone so that the distinct head projects anteromedially. The femoral head is set at a right angle to the shaft, suggesting a fully erect posture of the hindlimb in life. Its terminal articular surface is gently convex medially and extends posterolaterally across the proximal end of the femur. The posteromedial margin of the facet forms a distinct tubercle. A low, thick, and rugose ridge just distal to the lateral end of the

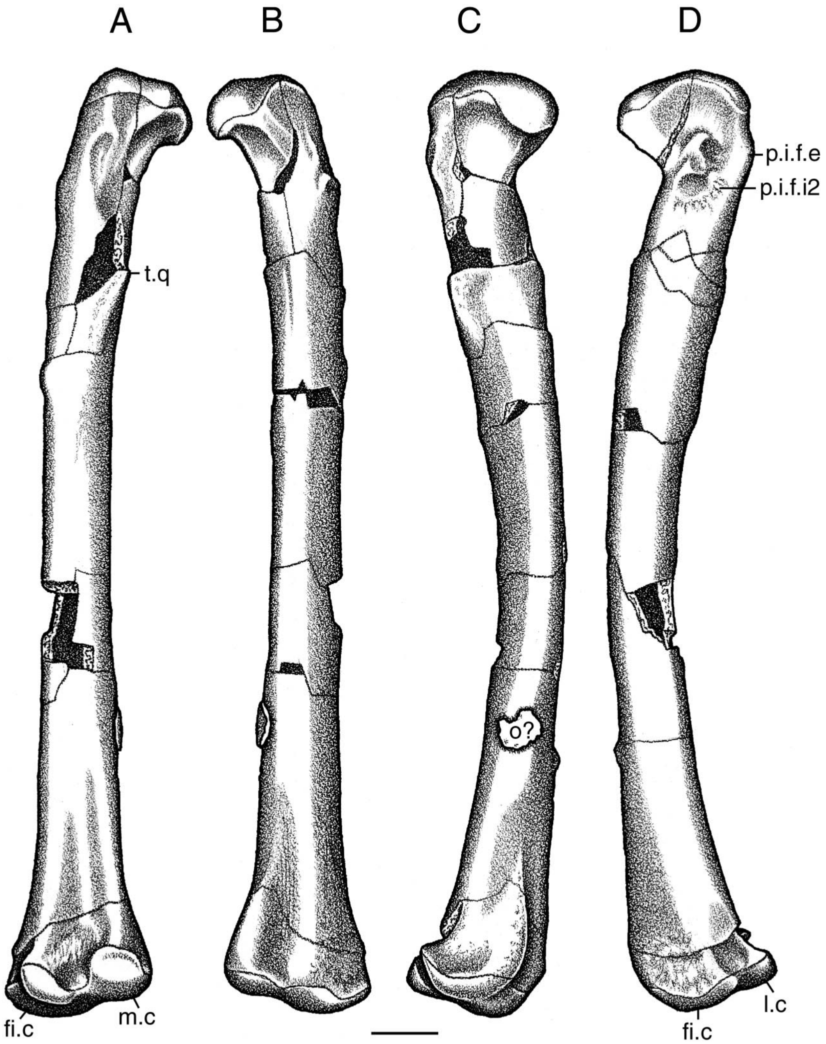

FIGURE 6. *Dromicosuchus grallator*, UNC 15574 (holotype), left femur in **A**, posterior; **B**, anterior; **C**, medial; and **D**, lateral views. Scale bar equals 1 cm. Abbreviations: **fi.c**, fibular condyle; **l.c**, lateral condyle; **m.c**, medial condyle; **o?**, possible appendicular osteoderm; **p.i.f.e**, insertion for M. puboischiofemoralis externus; **p.i.f.i2**, insertion for M. puboischiofemoralis internus 2; **t.q**, fourth trochanter (insertion for M. caudifemoralis longus).

proximal articular surface probably represents the site of insertion for M. puboischiofemoralis externus, as in extant crocodylians (Romer, 1923; ‘‘pseudointernal trochanter’’ sensu Walker [1970]). A rugose area on the anterolateral surface of the proximal end presumably served as the point of insertion for M. puboischiofemoralis internus 2 (Romer, 1923; Hutchinson, 2001); it appears to be homologous to the ‘‘lesser trochanter’’ identified on the femur of *Hallopus* by Walker (1970:fig. 6). A prominent ridge on the posteromedial surface of the shaft, situated about one-fourth of the length of the femur distal from the head, represents the fourth trochanter for the insertion of M. caudifemoralis longus. In lateral view, the slender, hollow shaft of the femur is distinctly bowed forward. Because its proximal quarter is nearly straight, the shaft lacks the sigmoid flexure characteristic of crocodyliform femora. It is flattened transversally proximally but becomes more robust toward the distal end of the bone. The well-developed distal condyles of the femur, especially the lateral one, project posteriorly. They are separated by a deep intercondylar sulcus posteriorly and a slightly more shallow patellar groove anteriorly. As in *Hesperosuchus* (Parrish, 1991), a distinct fibular condyle is developed just anterior and lateral to the lateral condyle and is separated from the latter by a mediolaterally extending sulcus.

Tibia—The tibia (Fig. 7) is shorter than the femur (130 mm vs. 144 mm; 90.27%). Its slender, hollow shaft is bowed anteriorly as well as slightly medially toward the distal end of the bone. The transversely broad, robust proximal end bears a prominent, medially directed process. The proximal surface for contact with the femoral condyles slopes slightly laterally. It is divided into two articular surfaces by a low ridge. In articular view, the transversely expanded distal end for contact with the astragalus has a convex anterior and a deeply concave posterior margin. Its articular surface is divided into two distinct facets, which are separated posteriorly by a deep sulcus. The flat lateral facet faces posterodistally and forms a slight lateral rim. The medial facet descends farther distally than the lateral one and has a convex, anteroposteriorly longer surface. The posterior surface of the distal end is concave above the articular surface. The shaft of the right tibia bears a distinct swelling along its lateral margin at about mid-length; this feature appears to be pathological in origin.

Fibula—Only the proximal end of the left fibula (Fig. 8) can

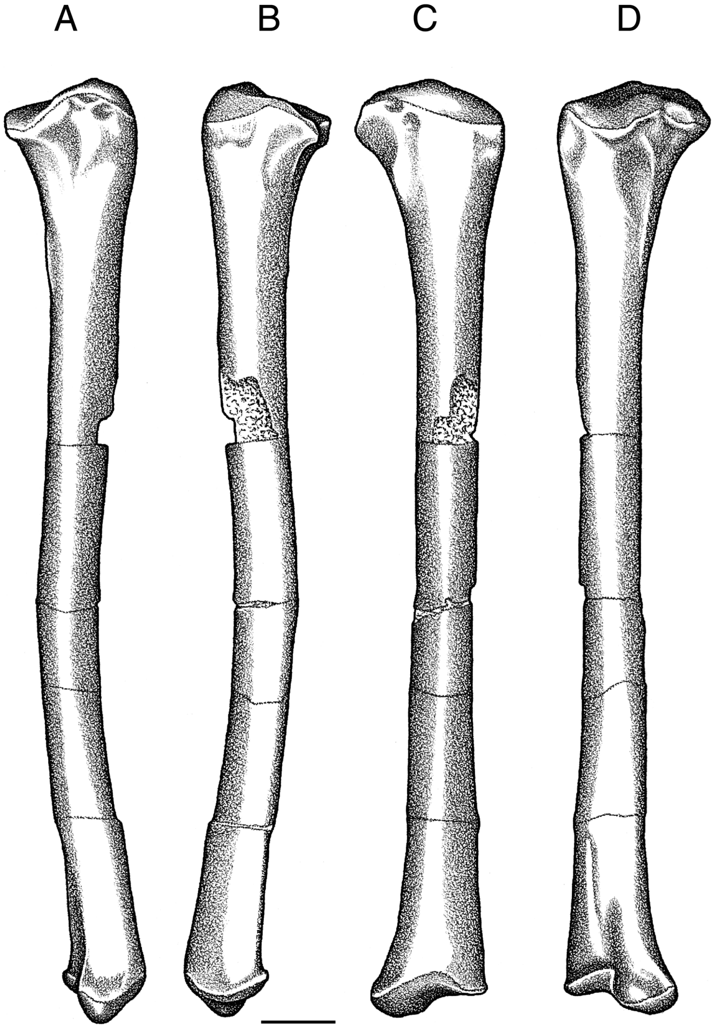

FIGURE 7. *Dromicosuchus grallator*, UNC 15574 (holotype), left tibia in **A**, medial; **B**, lateral; **C**, anterior; and **D**, posterior views. Scale bar equals 1 cm.

be identified with certainty. A fragment of a mediolaterally flattened limb-bone may represent the distal end of the same bone, but it cannot be joined to the proximal segment. The proximal portion is expanded, mediolaterally flattened, and curves posteriorly in the sagittal plane. Its lateral surface bears a ridge anteriorly, probably for the insertion of M. iliofibularis (Huene, 1921).

Calcaneum—The calcaneum (Fig. 9) bears a robust tuber. The tuber was broken off during recovery and can no longer be precisely fitted onto the body of the calcaneum. Its base is flattened dorsoventrally and appears to be relatively wider transversely than in extant crocodylians. The medial surface of the calcaneum bears a deep, round pit for the reception of the lateral ''peg'' of the astragalus (which is not preserved) and was delimited posteriorly by a distinct, medially projecting process. The lateral surface of the calcaneum is concave, especially in the region of the calcaneal condyle.

Pes—Three bones found in association with the left calcaneum are metatarsals that probably belong to the left pes (Fig. 10). They are long and have straight shafts. The longest probably represents metatarsal III.

PHYLOGENETIC RELATIONSHIPS OF *DROMICOSUCHUS*

Walker (1968, 1970) demonstrated conclusively that certain Late Triassic and Jurassic crocodile-like archosaurs, which had traditionally been referred to the grade ''Thecodontia,'' were closely related to ''true crocodilians'' (Crocodyliformes sensu Clark, 1986). Thus he proposed Crocodylomorpha for the reception of both groups. Ever since Haughton's (1915) original report on *Sphenosuchus acutus* from the Lower Jurassic Elliot Formation of South Africa, various ''crocodile-like thecodontians'' of Late Triassic and Jurassic age have been explicitly compared to that form. Bonaparte (1972, 1982) established a suborder Sphenosuchia for these taxa, which he interpreted as broadly ancestral to crocodylians. The first phylogenetic analyses (Clark, 1986; Parrish, 1991) considered Sphenosuchia a paraphyletic assemblage of basal Crocodylomorpha, with some sphenosuchians being more closely related to Crocodyliformes than others. However, Sereno and Wild (1992) and Wu and Chatterjee (1993) independently argued for the monophyly of Sphenosuchia. Most recently, Clark et al. (2001) discussed the interrelationships of basal crocodylomorph archosaurs in detail.

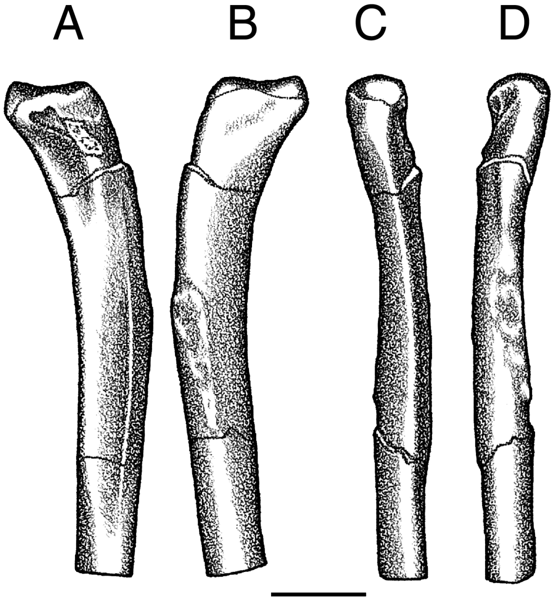

FIGURE 8. *Dromicosuchus grallator*, UNC 15574 (holotype), proximal portion of left fibula in **A**, medial; **B**, lateral; **C**, posterior; and **D**, anterior views. Scale bar equals 1 cm.

They critically reviewed the previously published character evidence and found only weak support for the monophyly of Sphenosuchia in their own analysis (see also Clark and Sues, 2002).

We assessed the phylogenetic position of UNC 15574 using a modified version of the character-taxon data matrix compiled by Clark et al. (2001) for selected taxa of basal crocodylomorph archosaurs (see Appendix and Table 1). First, several character-states for BP/1/5237 (Gow and Kitching, 1988) were rescored after further cleaning and re-examination of the skull of this specimen (Clark and Sues, 2002). Second, we added character-states for one additional taxon, *Kayentasuchus* from the Lower Jurassic Kayenta Formation of Arizona (Clark, 1986; Clark and Sues, 2002). Third, character 13 was added. Fourth, character 26 of Clark et al. (2001) was deleted because the derived character-state represents an autapomorphy for *Hesperosuchus* and thus is uninformative for the purpose of the present analysis. The matrix was analyzed invoking the branch-and-bound search option of PAUP 3.1.1 (Swofford, 1993) and with characters 16, 20, 22 and 23 treated as ordered. The analysis yielded 20 equally most parsimonious trees (MPTs), each with a length of 63 steps, a Consistency Index (CI) of 0.619, and a Retention Index (RI) of 0.680. Both strict consensus and Adams consensus trees were calculated for this set of trees (Fig. 11). The former contains only those monophyletic groupings shared by all trees, whereas the latter provides the highest possible ‘‘resolution’’ among multiple trees (Adams, 1972).

In the strict consensus, UNC 15574 is placed with *Hesperosuchus*, *Saltoposuchus*, *Dibothrosuchus*, *Sphenosuchus* and *Kayentasuchus* (Fig. 11). The Adams consensus shows a node comprising UNC 15574, *Hesperosuchus*, and *Kayentasuchus*; in turn, that grouping forms a trichotomy with *Saltoposuchus* and *Dibothrosuchus* + *Sphenosuchus* (Fig. 11). However, tree support is very weak, and if tree length is increased by only a single step to 64, the strict consensus no longer provides any resolution among Crocodylomorpha.

UNC 15574 differs from *Saltoposuchus connectens* Huene, 1921 from the Middle Stubensandstein (Löwenstein Formation; middle Norian) of Württemberg, Germany primarily in the presence of paired crests separated by a median groove on the dorsal surface of the parietals and the more prominent development of the posterolateral crest on the squamosal (Sereno and Wild, 1992). It shares these character-states with *Hesperosuchus agilis* Colbert, 1952 from the Petrified Forest Member of the Chinle Formation (late Carnian or early Norian) in Arizona and New Mexico (Clark et al., 2001). However, like *Saltoposuchus*, UNC 15574 is distinguished from *Hesperosuchus* by the absence of the dorsoventral expansion of the symphyseal portion of the dentary and the presence of a conical recess at the anterior end of the antorbital fossa. Based on the account by Long and Murry (1995), there are also differences in the structure of the cervical vertebrae. Furthermore, *Hesperosuchus* has a large palpebral bone (Clark et al., 2001), but the absence of this element in other known sphenosuchian specimens may simply be a taphonomic artifact. UNC 15574 differs from *Sphenosuchus acutus* Haughton, 1915, from the Lower Jurassic Elliot Formation of South Africa (Walker, 1990), and *Dibothrosuchus elaphros* Simmons, 1965, from the Lower Jurassic Lower Lufeng Formation of Yunnan, China (Wu and Chatterjee, 1993), in the presence of a V-shaped, rather than straight, transverse occipital

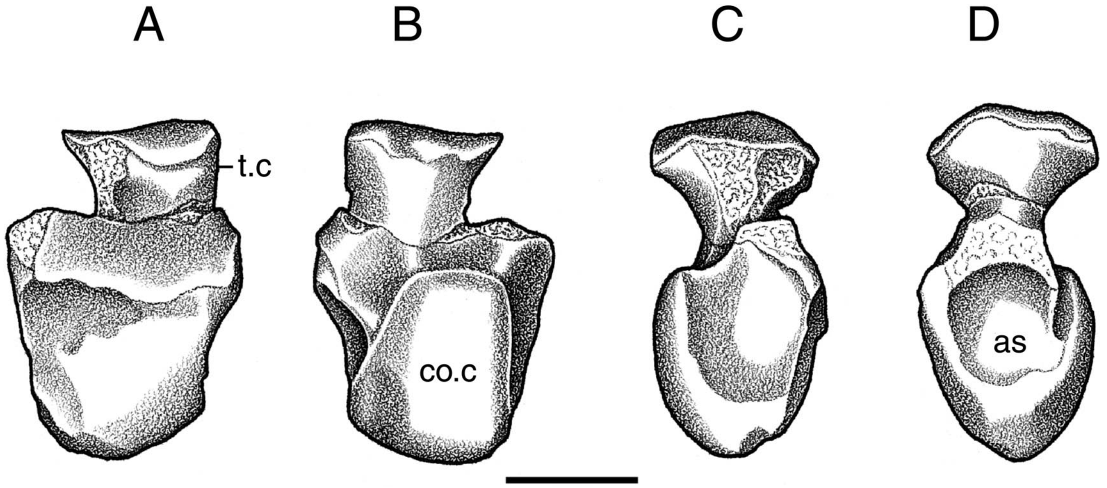

FIGURE 9. *Dromicosuchus grallator*, UNC 15574 (holotype), incomplete left calcaneum in **A**, ventral; **B**, dorsal; **C**, lateral; and **D**, medial views. The tuber was accidentally broken off during preparation and can no longer be precisely fitted onto the body of the bone. Abbreviations: **as**, pit for lateral ‘‘peg’’ of astragalus; **co.c**, calcaneal condyle; **t.c**, calcaneal tuber. Scale bar equals 1 cm.

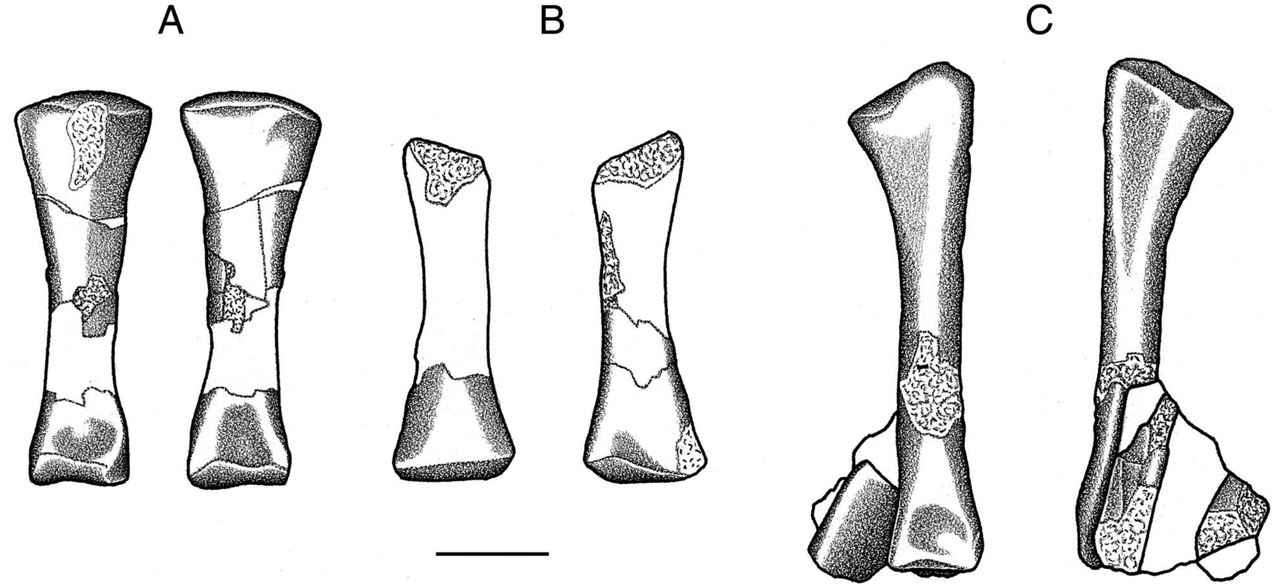

FIGURE 10. *Dromicosuchus grallator*, UNC 15574 (holotype), three metatarsals (each illustrated in two views) found in association with left calcaneum. White areas represent reconstructed portions of the bones based on impressions in the matrix. Scale bar equals 1 cm.

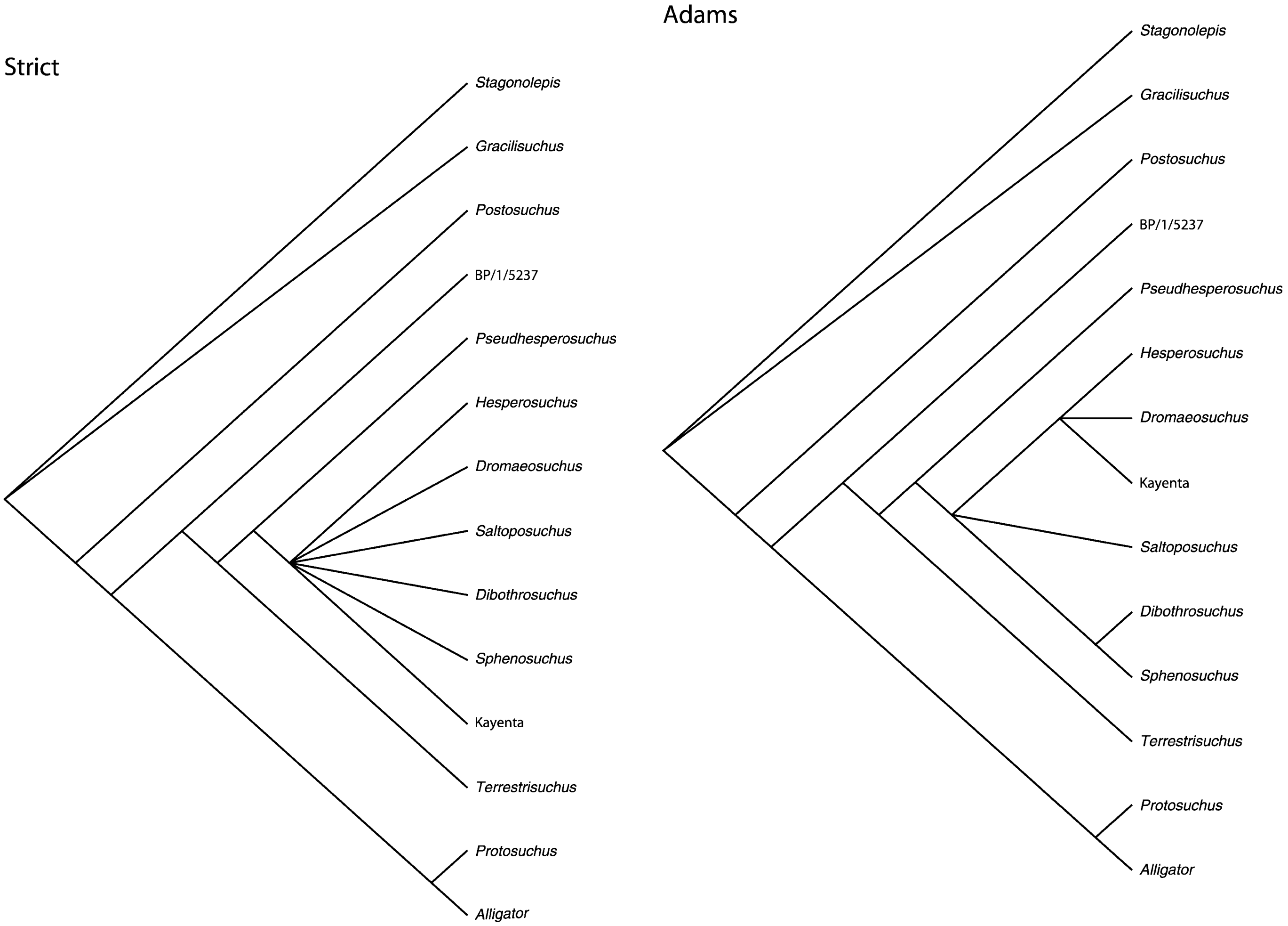

FIGURE 11. Strict consensus and Adams consensus of 20 most parsimonious trees (MPTs) generated by PAUP analysis of the character-taxon matrix in Table 1. Each MPT has a length of 63 steps, a Consistency Index (CI) of 0.619, and a Retention Index (RI) of 0.680.

TABLE 1. List of character-states for three outgroup taxa and 11 taxa of Crocodylomorpha, modified from Clark et al. (2001). ‘‘0’’ denotes primitive, ‘‘1’’ and ‘‘2’’ denote derived character-states. ‘‘X’’ and ‘‘N’’ represent transformational changes of uncertain polarity, both of which were treated as ‘‘?’’ in the PAUP analysis.

	Character						
	00000	00001	11111	11112	22222	22223	3333
Taxon	12345	67890	12345	67890	12345	67890	1234
Outgroup taxa							
Stagonolepis	0000X	XX000	00010	00010	0XX00	00?X0	0000
Gracilisuchus	?1?10	N?000	01010	1000?	???0?	?0?0?	00?1
Postosuchus	01000	N?000	1?000	01100	00000	00000	00??
Ingroup taxa							
BP/1/5237	00?1?	?1101	?00??	1100?	???0?	?101?	????
Pseudhesperosuchus	01??1	1?101	110??	0?10?	????0	0??1?	?0??
Dromicosuchus	00?1?	??111	110??	0?10?	???0?	?111?	1011
Saltoposuchus	00?1?	?1101	110??	0?10?	?????	??1?1	1011
Terrestrisuchus	?111?	?1101	100?0	0?001	1??0?	?101?	11??
Hesperosuchus	00?1?	?1111	1101?	0?10?	???00	11111	1?11
Dibothrosuchus	00111	10111	1?012	21111	12000	11?11	??00
Sphenosuchus	00111	01111	11011	21111	11100	11?1?	????
Kayentasuchus	0010?	???11	111?1	?1001	11???	1?1??	1?11
Protosuchus	11111	0?101	10101	21012	12211	N112?	1011
Alligator	1N1N1	10101	10101	21012	12011	N0120	1000

margin of the skull roof and the presence of paired sagittal crests on the parietals. Furthermore, the posteromedial process of the coracoid is less elongate than that in the latter two taxa. Finally, UNC 15574 differs from *Kayentasuchus* from the Lower Jurassic Kayenta Formation of Arizona (Clark and Sues, 2002) in the absence of a lateral groove on the squamosal and the presence of an anterior caniniform tooth in the dentary.

Although the analysis indicates that UNC 15574 is most closely related to *Hesperosuchus agilis* it differs from the latter in several features, especially the absence of the dorsoventral expansion of the symphyseal end of the dentary. In view of the distinctive character combination exhibited by this specimen, we propose a new Linnean binomen, *Dromicosuchus grallator*, for its reception. However, we have not yet identified autapomorphies to support the strict monophyly of this taxon.

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APPENDIX

List of characters and their character-states for the phylogenetic analysis of crocodylomorph archosaurs (modified from Clark et al. [2001]).

1. Posterodorsal process of the premaxilla overlaps anterodorsal surface of the maxilla (0) or dorsal process of premaxilla vertical, strongly sutured to maxilla (1).
2. Facial portion of maxilla anterior to anterior edge of antorbital fenestra equal in length or longer than portion posterior to anterior edge of fenestra (0) or shorter than posterior portion (1).
3. Maxillae do not meet on palate (0) or meet on palate to form secondary bony palate anterior to choana (1).
4. Jugal participates in posterior margin 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 does not contact palate (0) or contacts 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 median 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. Lateral edge of squamosal without (0) or with longitudinal groove (1).
14. Quadratojugal extending anterodorsally to contact postorbital (0) or not contacting postorbital (1).
15. Quadrate not in contact with prootic (0) or contacting prootic (1).
16. In presumed adults, parietals separate (0), interparietal suture partially obliterated (1), or interparietal suture absent (2). [Ordered.]
17. Posteroventral edge of parietals extending more than half the width of the occiput (0) or less than half the width of the occiput (1).
18. Medial margins of supratemporal fossae on lateral surfaces of parietals separated on midline by broad, flat area (0) or by sagittal crest (which may be divided by median sulcus) (1).
19. Occipital margin of parietals V-shaped in dorsal view (0) or straight (1).
20. Exoccipitals broadly separated dorsal to foramen magnum (0), approaching midline without contacting (1), or contacting below supraoccipital (2). [Ordered.]
21. Prootic broadly contacting anterior surface of paroccipital process (0) or not in broad contact (1).
22. Depression for mastoid antrum: absent (0), present on lateral surface of prootic dorsal to otic capsule (1), or entering into prootic and connecting with each other through supraoccipital (2). [Ordered.]
23. Depression for posterior tympanic recess: absent (0), depression posterior to fenestra ovalis on anterior surface of paroccipital process (1), or penetrating prootic and paroccipital process (2). [Ordered.]
24. Paroccipital process dorsoventrally tall and distinctly expanded distally (0) or process narrower dorsoventrally, distal end only slightly expanded (1).
25. Basipterygoid processes of basisphenoid present (0) or absent (1).
26. Basipterygoid processes simple, without large cavity (0) or greatly expanded, with large cavity (1).
27. Articular without dorsomedial projection posterior to glenoid fossa (0) or with dorsomedial projection (1).
28. Posterior edge of maxillary and more posterior dentary teeth concave or straight (0) or distinctly convex (1).
29. Coracoid subcircular in lateral view (0), with elongate post-glenoidal process posteromedially (1), or with elongate ventromedial process expanded ventrally (2).
30. Proximal ends of metacarpals overlap (0) or abut one another without overlapping (1).
31. Proximal head of femur confluent with shaft (0) or with distinct, medially directed head set off from shaft (1).
32. Tibia/femur length ratio: less than 1 (0), greater than 1 (1).
33. Anterior edge of paramedian dorsal osteoderms straight (0) or with anterior process (1).
34. Paramedian dorsal osteoderms flat (0) or with distinct longitudinal bend near lateral edge (1).