

## A NEW SUCHIAN ARCHOSAUR FROM THE UPPER TRIASSIC OF NORTH CAROLINA

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**ABSTRACT**—A partial but largely articulated skeleton of a ‘rauisuchian’ archosaur from Late Upper Triassic strata of the Durham sub-basin, Deep River basin, Newark Supergroup, North Carolina, represents a new species of *Postosuchus* Chatterjee, 1985. It represents the first record of this taxon from eastern North America. The well preserved specimen includes cranial bones, a largely articulated right manus, right and left pedes, pubes, axis, several postaxial cervical, dorsal, and caudal vertebrae, chevron bones, osteoderms, interclavicle, clavicles, cervical ribs, a sacral rib, and a complete set of gastralia. The skeletal elements are described and compared to those of other ‘rauisuchians’. An apparent autapomorphy of *Postosuchus alisonae* includes a well developed flange on the proximal portion of metacarpal II fitting into strongly proximally grooved metacarpal I. The new specimen includes many bones previously unknown for *Postosuchus* and it allows a more complete differentiation of *Postosuchus* from other ‘rauisuchian’ genera. Diagnostic features of this genus include an axis with two ventral keels; postaxial cervical centra with strongly developed single ventral keels that are anteriorly and/or posteriorly extended into hypapophyses; short ribs on the anterior cervical vertebrae; heart-shaped cervical neural ‘spine tables’; a subrectangular, relatively short coracoid; and proportionately short manus with dorsoventrally compressed, reduced, blunt unguals on manual digits III and IV. Morphological comparisons indicate a close relationship between *Postosuchus* and *Batrachotomus* and possibly also *Tikisuchus*.

### INTRODUCTION

The partial skeleton here referred to a new species of *Postosuchus* represents the first articulated skeletal material of a ‘rauisuchian’ archosaur from the Upper Triassic of eastern North America. It was discovered in 1994 in the Triangle Brick Co. Quarry near Genlee in the Durham sub-basin of the Deep River Basin in North Carolina and was prepared and reconstructed in the Department of Geological Sciences at the University of North Carolina at Chapel Hill, between 1994 and 1998. The present specimen is the only large suchian discovered at the site. The bones of the skeleton are virtually uncrushed and, for the most part, fully or at least partially articulated. In terms of its preservation and completeness, this specimen is comparable only to the holotype of *Ticinosuchus ferox* Krebs, 1965 from southern Switzerland, and to the hypodigm of *Batrachotomus kupferzellensis* Gower, 1999 from Baden-Württemberg (Germany), and possibly the holotype and paratype of *Postosuchus kirkpatricki* (TTUP 9002) Chatterjee, 1985 from the Cooper Canyon Formation (Dockum Group) in Post, Texas. In addition to *P. kirkpatricki*, other Upper Triassic, North American ‘rauisuchians’ have been described from the Dockum Group of Texas, the Bull Canyon Formation of New Mexico, the Chinle and Moenkopi Formations of Arizona and New Mexico, and the Popo Agie Formation of Wyoming. Middle Triassic North American ‘rauisuchians’ are known from the Moenkopi Formation of Arizona. These taxa are represented by *Poposaurus* Mehl, 1915, *Arizonasaurus* Welles, 1947, *Heptasuchus* Dawley, Zawiskie, and Cosgriff, 1979,

*Postosuchus* Chatterjee, 1985, *Lythrosuchus* Long and Murry, 1995, *Chatterjeea* Long and Murry, 1995, and *Effigia* Nesbitt and Norell, 2006 (Nesbitt, 2005a; Nesbitt and Norell, 2006). Throughout much of the Middle and Late Triassic, ‘rauisuchians’ were the dominant terrestrial predators and they had a near global distribution. Their remains are known from North America, South America, Europe, Africa, and India, but not yet from Australia or Antarctica (Gower, 2000).

The abdominal region of the holotype of the new species of *Postosuchus* preserves gastrointestinal contents comprising remains of at least four different taxa of Late Triassic tetrapods including a partial skeleton of a small stagonolepidid (cf. *Stegomus*), a snout, left coracoid, and left humerus of the traversodont cynodont *Plinthogomophodon herpetairus* Sues, Olsen, and Carter, 1999, two articulated phalanges of a large dicynodont, and a fragment of an unidentified ?temnospondyl bone. These materials differ in color from the bones of UNC 15575, and some of the bones bear tooth marks and show periosteal erosion possibly caused by digestion. An articulated skull and partial postcranial skeleton of the crocodylomorph *Dromicosuchus grallator* Sues, Carter, Olsen, and Scott, 2003, was preserved underneath the skeleton of *Postosuchus* and bears tooth marks on the skull and neck.

### Previous Work on *Postosuchus*

The first known specimens of *Postosuchus* are fragments of two pelvis described by Case (1922), and referred to *Postosuchus kirkpatricki* by Chatterjee (1985). Case (1932, 1934) then discovered a series of caudal vertebrae (UMMP 13670) from Rotten Hill, Texas and a complete pelvis (UCMP V72183/

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113314) near Calgary, Texas. Camp (1932) collected the articulated surangular-articular of a 'rauisuchian' archosaur (UCMP 27492) in what is today the Petrified Forest National Park of Arizona and, during the period from 1932 to 1934, he recovered over 100 additional disassociated 'rauisuchian' bones representing at least seven individuals (UCMP A296, MNA 207C). This material was assigned to *Postosuchus kirkpatricki* (Long and Murry, 1995). During the early 1980s, Chatterjee excavated a dozen, mostly dissociated specimens of 'rauisuchian' archosaurs near Post, Texas. He designated the largest specimen (TTUP 9000) as the holotype and a slightly smaller specimen (TTUP 9002) as the paratype of his new species *Postosuchus kirkpatricki*. The remaining much smaller skeletons, considered juveniles by Chatterjee, were also assigned by him to *Postosuchus kirkpatricki*, but Long and Murry (1995) suggested that they are instead the new taxon *Chatterjeea elegans* Long and Murry, 1995. Gower (2000) and Weinbaum (2002) agreed with Long and Murry that *Chatterjeea elegans* represents a distinct taxon, although Nesbitt and Norell (2006) indicated that *Chatterjeea* is a junior synonym of *Shuvosaurus*. Long and Murry (1995) also pointed out that the hypodigm of *Postosuchus kirkpatricki* represents a chimera of three distinct 'rauisuchian' taxa: *Chatterjeea*, *Lythrosuchus*, and *Postosuchus*. The present authors found (pers. obs. of TTUP 9000 and 9002) that the material assigned to *Postosuchus kirkpatricki* is at least in part composed of associated rather than articulated bones. For example, the manus that was originally described for *Postosuchus kirkpatricki* (Chatterjee, 1985:fig. 14i) was not found in articulation but was reconstructed from various phalanges found in proximity to the *Postosuchus* material (Weinbaum, 2002). When compared to the articulated manus of the UNC *Postosuchus* it is evident that the left manus of *P. kirkpatricki* is composed of left and right phalanges and, furthermore, certain manual elements appear to belong to a different taxon (e.g., PhI-1; PhI-2; PhV-1), possibly *Chatterjeea*. Whereas most phalanges are of manual origin based on size, it is also possible that some represent distal pedal phalanges (PhII-3 and PhIII-4). Some elements closely resemble certain phalanges in the UNC *Postosuchus* whereas the placement of others remains unclear.

The first articulated 'rauisuchian' skeleton referable to *Postosuchus kirkpatricki* was collected by D. S. Berman (Carnegie Museum of Natural History) from the *Coelophys* (Whitaker) Quarry at Ghost Ranch in 1988 and 1989 and was subsequently described by Long and Murry (1995), Weinbaum (2002), and Novak (2004). It is a fairly well preserved specimen (CM73372) missing only the skull, part of the neck, most of the left scapulo-ocoroid, the distal portion of the left humerus, pubis, and the articular ends of the femur. CM 73372 differs from *Postosuchus kirkpatricki* TTUP 9000 and TTUP 9002, respectively, in the structure of the ilium (preacetabular process of CM 73372 is longer than the pubic process), bone sculpturing, and development of certain muscle attachments (Novak, 2004). Novak (2004) concluded that the differences can be explained by the fact that CM 73372 represents a much younger individual than TTUP 9002 or TTUP 9000.

Although many mostly disarticulated elements have been assigned to *Postosuchus kirkpatricki* few bones can be confidently assigned to this taxon. At this point, it is likely that at least the skull first described by Chatterjee (1985) is referable to *Postosuchus kirkpatricki* (see Gower, 2002). In the present paper, we compare the North Carolina specimen to elements in the TTUP collection (TTUP 9000; TTUP 9002; TTUP 9235) that are probably referable to *Postosuchus* based on their overall similarities to the homologous elements in the articulated specimen of *Postosuchus kirkpatricki* from Ghost Ranch (CM 73372) (Novak, 2004) and the new find from North Carolina (UNC 15575). Features in the pectoral girdle, manus, distal region of the hindlimb, and pes of the North Carolina specimen indicate that it repre-

sents a new species of *Postosuchus*, differing from *Postosuchus kirkpatricki* CM 73372, TTUP 9000, and TTUP 9002.

### Geology and Taphonomy

Rifting during the Triassic preceding the initial breakup of Pangea resulted in a series of sedimentary basins, collectively identified as the Newark Supergroup rift system, along the eastern continental margin of North America. These rift-basins were filled with fluvial and lacustrine strata with interbedded evaporitic intervals of Late Triassic to Early Jurassic age and by basalt flows of Early Jurassic age (Cornet et al., 1973; Van Houten, 1977). The *Postosuchus* remains reported in this study are from the Durham sub-basin of North Carolina, the northernmost of three sub-basins in the Deep River Basin in North and South Carolina. The Durham sub-basin lies northeast of Sanford, North Carolina.

The Durham sub-basin is a half graben (Ackermann et al., 1976), bounded to the east by the high-angle, NW-dipping Jonesboro fault (Campbell and Kimball, 1923). The western side of the basin is bounded by several NE-trending longitudinal faults (Harrington, 1948). Fanglomerates, conglomerates, sandstones, siltstones, claystones, some chert, limestone, and coal occur in the Durham sub-basin. Late Triassic sediments filling the Durham sub-basin were derived from source areas in the Piedmont highlands. Hoffman and Gallagher (1989) distinguished seven lithofacies among the Triassic sedimentary rocks in the Durham sub-basin (Southeast Durham and Southwest Durham 7.5 Minute Quadrangles) and informally grouped them into three lithofacies associations based on provenance and depositional style. The remains of UNC 15575 were recovered from a red, bioturbated, calcareous sandstone and sandy mudstone in the predominantly sandstone facies of Lithofacies Association II (Olsen and Huber, 1997). The age of the strata comprising Lithofacies Association II is late Carnian to early Norian (for further discussion see Olsen and Huber, 1997 and Sues et al., 2003).

Wheeler and Textoris (1978) concluded that the Late Triassic strata in the Deep River Basin were deposited during periods of cyclical climatic change. During warm, humid periods, swamps were present in the Sanford sub-basin and lakes in the Durham sub-basin. Semi-arid to arid climates produced caliche soil horizons formed in and along small playa lakes in the Durham sub-basin (see also Coffey and Textoris, 2003).

**Institutional Abbreviations**—**CM**, Carnegie Museum of Natural History, Pittsburgh; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Zürich; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **TMM**, Texas Memorial Museum, Austin; **TTU**, Texas Tech University, Lubbock; **UMMP**, Museum of Paleontology, University of Michigan, Ann Arbor; **UNC**, University of North Carolina, Chapel Hill.

**Anatomical Abbreviations**—**a**, astragalus; **ap**, astragalar peg; **aq**, articular facet for quadrate; **as**, socket on the calcaneum for reception of astragalus; **asp**, dorsal process of articular; **c**, capitulum; **ca**, calcaneum; **cao**, caudal osteoderms; **cf**, coracoid foramen; **cn**, cnemial crest; **co**, coracoid; **cpol**, centropostzygapophyseal lamina; **cpri**, centroprezygapophyseal lamina; **c3**, carpal 3; **c4**, carpal 4; **dhv**, groove for dorsal head vein; **di**, diapophysis; **dpc**, deltopectoral crest; **ect**, ectepicondyle; **ent**, entepicondyle; **fft**, foramen for chorda tympani nerve; **ff**, articular facet for fibula; **fi**, fibula; **fl**, flange; **fr**, flocular recess; **ft4**, articular facet for distal tarsal 4; **gf**, glenoid fossa; **gr**, groove; **h**, humeral head; **hf**, hyposphene; **hy**, hypantrum; **i**, intermedium; **ic**, interclavicle; **mc**, Meckel's canal; **M.e.i**, M. extensor iliotibialis; **mp**, medial process of articular; **M.pp**, origin of M. protractor pterygoidei; **mt**, medial tuberosity; **n**, notch; **nc**, neural canal; **ns**, neural spine; **ob**, otic bulla; **op**, occipital condyle; **pcdl**, posterior centrodiapophyseal lamina; **pi**, pits; **podl**, postzygodiapophyseal lamina;

**poz**, postzygapophysis; **pp**, parapophysis; **ppdl**, paradiapophyseal lamina; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **ptf**, posttemporal fenestra; **pua**, pubic apron; **pub**, pubic foot; **r**, radiale; **rap**, retroarticular process; **rc**, radial condyle; **rd**, ridge; **rs**, rugosities; **ru**, rugose ridge along dorsolateral edge of skull; **s**, scapula; **sc**, supinator crest; **sls**, surface for articulation with laterosphenoid; **sp**, surface for articulation with parietal; **spr**, surface for articulation with prootic; **spra/spl**, surface for articulation with prearticular/splenic; **t**, tuberculum; **tc**, calcaneal tuber; **tf**, articular facet for tibia; **ti**, tibia; **tif**, trochanter for iliofibularis muscle; **t3**, tarsal 3; **t4**, tarsal 4; **u**, ulna; **uc**, ulnar condyle; **vafm**, ventral margin of the adductor fossa; **vk**, ventral keel; **V/mcv**, passage for branch of trigeminal nerve and/or middle cerebral vein, **V**, trigeminal nerve; **VII**, facial nerve.

#### SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869  
 CRUROTARSI Sereno and Arcucci, 1990  
 SUCHIA Krebs, 1974  
 ?RAUISUCHIDAE Huene, 1942  
 POSTOSUCHUS CHATTERJEE, 1985

**Type Species**—*Postosuchus kirkpatricki* Chatterjee, 1985.

**Revised Diagnosis**—Differs from all other 'rauisuchians' in: infratemporal fenestra divided by a forward projecting quadratojugal; comparatively large, plate-like quadratojugal; lacrimal with a dorsomedial process that separates the prefrontal from the nasal; axis centrum with two parallel ventral keels; cervical vertebrae that are constricted at mid-length to less than half the width of centrum articular surface; cervical vertebrae with well-developed keels that are developed into hypapophyses anteriorly and posteriorly; cervical vertebrae with heart-shaped 'spine tables'; very short, anterior cervical ribs; a subrectangular rather than ovate coracoid; proportionately more robust supraglenoid buttress of the scapulocoracoid; immediately narrowing scapula posterior to glenoid fossa instead of slowly grading into the scapular blade; comparatively deeper notch ventral to medioventral process of humeral head; comparatively small manus; reduced blunt unguals on manual digit III and IV; and possibly the presence of six phalanges on pedal digit IV.

*POSTOSUCHUS ALISONAE* sp. nov.  
 (Figs. 1–10)

**Holotype**—UNC 15575, partial skeleton comprising a few fragmentary cranial bones: nasal, frontal, squamosal, prootic, supraoccipital, left and right opisthotic, articular, angular, prearticular, and isolated teeth. The postcranial skeleton includes seven cervical, one dorsal, and four caudal vertebrae, with associated ribs and chevrons; partial sacral rib; cervical, dorsal, and caudal osteoderms; gastralia; right and partial left coracoid; partial left and right scapulae; interclavicle; clavicle; left and right humeri, radii, and ulnae; right carpus; nearly complete right and partial left manus; distal ends of left and right pubes; left and right tibiae, fibulae, tarsi, and pedes.

**Etymology**—Named for the late Alison L. Chambers, honoring her dedication to the popularization of paleontology in North Carolina.

**Type Locality and Horizon**—Mudstone of Lithofacies Association II sensu Hoffman and Gallagher (1989), south-central region of Durham sub-basin of Deep River Basin, Newark Supergroup. West Genlee, Durham County, North Carolina, U.S.A. Age: late Carnian or early Norian, Late Triassic.

**Diagnosis**—*Postosuchus alisonae* differs from all known 'rauisuchians' in: proximal portion of metacarpal I grooved for contact with metacarpal II. Distinguished from *Ticinosuchus ferox* in: strongly constricted axis centrum that has about the same

TABLE 1. *Postosuchus alisonae*, UNC 15575 (holotype), measurements for bones of forelimb (in mm).

Humerus	Right	Left			
Length	*300	*297			
Distal width	65.3	68.4			
Proximal width		72.5			
Shaft diameter	21.8	21.4			
Ulna	Right	Left			
Length		273			
Distal width		31.4			
Proximal width	55.2	52.3			
Shaft diameter	14.9	13.7			
Olecranon height	34.3	36.6			
Radius	Right	Left			
Length	*242	*241			
Distal width	25.3	26			
Proximal width		34.8			
Shaft diameter	11.1	11.4			
Right metacarpus	I	II	III	IV	V
Length	35.3	39.4	41.3	42.2	28.4
Shaft diameter	*6.1	6.4	5.7	6	6.9
Distal width	*9.2	12.5	12.6	12.9	13.4
Proximal width	18.3	22.5	19.6	20.8	16.5
Right manual ph.	I	II	III	IV	V
Ph1	12	12.2	p	11.5	p
Ph2	23.2	7	p	6.1	
Ph3		p	3.6	p	
Ph4			3.7		
Left manual ph.					
Ph1			11.4		
Ph2			6.5		
Ph3			3.3		
Ph4			*3.7		

All measurements are maximum length measurements, except for shaft diameters, which are minimum width measurements.

\*Estimated length.

**Abbreviation:** p, presence inferred from articulation surfaces or other manus.

length as the postaxial cervical vertebrae; no accessory caudal neural spines; small, possibly ventral or distal dorsal osteoderms that are not waisted and concave posteriorly; a subrectangular coracoid; more prominent olecranon process; proportionately shorter manus; more reduced manual unguals. Distinguished from *Fasolasuchus tenax* in: much smaller overall size; less expanded spine tables on the dorsal vertebrae; less pronounced olecranon process. Distinguished from *Yarasuchus deccanensis* in: presence of only a single median keel on the ventral surface of the cervical centra. Distinguished from *Prestosuchus chiniquensis* in: presence of a longer postglenoid process on the coracoid. Distinguished from *Rauisuchus tiradentes* in: more pronounced nasal ridge; scapular blade narrows immediately posterior to the glenoid fossa; presence of posterior lip on the proximal end of the fibula; single prominent insertion for M. iliofibularis. Distinguished from *Batrachotomus kupferzellensis* in: presence of a dorsally flat frontal; nearly flat medial portion of the posterodorsal surface of the supraoccipital; no median ridge on the dorsal surface of the small osteoderms; a subrectangular coracoid; absence of a well-developed muscle insertion on the scapula; more strongly developed olecranon process.

#### DESCRIPTION

##### Skull

Only a few disarticulated and mostly incomplete craniomandibular elements are known for the holotype of *Postosuchus alisonae*. Identifiable bones include incomplete frontal, nasal, and prootic, both paroccipital processes, supraoccipital, articular, prearticular, and angular; and several fragments possibly belonging to the prefrontal, postorbital, and squamosal.

TABLE 2. *Postosuchus alisonae*, UNC 15575 (holotype), measurements for bones of hindlimb (in mm).

Tibia	Right	Left			
Length		300			
Distal width	62.4	63.2			
Proximal width		70.6			
Shaft diameter	26.1	28.2			
Fibula	Right	Left			
Length	291	298			
Distal width	50.2	46.1			
Proximal width	43.5	43.6			
Shaft diameter	17.2	17.7			
Right metatarsus	I	II	III	IV	V
Length	19.3	130	137	117	81
Shaft diameter	11.1	11.9	13.6	11.5	
Distal width	21.4	23.7	25.5	22.8	11.2
Proximal width	35.7	42.7	47.6	44.4	44.4
Left metatarsus	I	II	III	IV	V
Length	110	130.7	136	117.3	77.5
Shaft diameter	11.9			11.2	
Distal width	19.3	26	23.1	22.3	
Proximal width	36.3	39.7	44.3	39.2	41.8
Right pedal ph.	I	II	III	IV	V
Ph1	32	42.3	39.4	34.1	
Ph2	38.8	26.8	21.9	17.3	
Ph3		34.7	20.2	18.4	
Ph4			28.1	7.4	
Ph5				10.4	
Ph6				1.9	
Left pedal ph.	I	II	III	IV	V
Ph1	36.2	40.8	40.7	34.2	18.8
Ph2	38.7	27.7	22.4	19.7	7.6
Ph3		35.1	19	19	1.9
Ph4			26.8		
Ph5					

All measurements are maximum length measurements, except for shaft diameters, which are minimum width measurements.

**Nasal**—The anterior portion of the left nasal, clearly anterior to the antorbital fenestra, has a concave dorsal surface that is laterally bounded by a pronounced, roughened dorsolateral ridge. Its dorsal surface forms an angle of almost 90° with its lateral surface (Fig. 1A). Ventral to this ridge on its lateral side, the nasal has obliquely inclined rugosities that terminate along the suture with the maxilla. A more anteriorly placed, smaller piece of the right nasal has a dorsal surface that does not exceed a mediolateral width of 4 mm. The dorsolateral ridge in that part of the nasal is very thin (Fig. 1B). Strongly ridged nasal bones, with distinct marginal rugosities and nearly perpendicular dorsal and lateral surfaces, are present in *P. kirkpatricki* (TTUP 9002) (Chatterjee, 1985), and *Batrachotomus* (Gower, 1999). A somewhat less pronounced nasal ridge is present in *Rauisuchus* (Huene, 1942), but this feature is absent in *Arizonasaurus* (Nesbitt, 2005a).

**Squamosal**—A somewhat smaller, equally rugose ridge adorned the postolateral margin of what appears to be the left squamosal (Fig. 1C). Ornamentation in the form of ridges is present along the lateral ridge.

**Frontal**—A strongly rugose, thick, slightly domed bone fragment represents part of the left frontal (Fig. 1D). Dorsally, the ornamentation extends transversely, forming a rough ridge at its sutural margin with the lacrimal, prefrontal, or postorbital. Similar dorsally ornamented frontals are present in *P. kirkpatricki* (TTUP 9002) and *Batrachotomus* (Gower, 2000), but the frontals have a smooth dorsal surface in *Arizonasaurus* (Nesbitt, 2005a). Towards the median suture, the ventral face of this bone is slightly pitted but otherwise smooth. A slightly domed frontal is also present in *P. kirkpatricki* (TTUP 9002) and differs from the frontal in *Batrachotomus*, which bears a median crest (Gower, 1999).

**Opisthotic**—Both paroccipital processes (formed largely by the opisthotics) are nearly complete distally but are missing their proximal bases (Fig. 1E). They are fairly short with anteroposteriorly flattened, much expanded distal ends. Anteriorly, a medial ridge spans the extension of the bone starting at the point where the process becomes dorsoventrally narrow. Ventral to that ridge and farther medially the opisthotic is overlapped by the prootic. Posteriorly, a shallow, laterally directed foramen pierces the paroccipital process near the ventral border. Several smaller pits are visible dorsal to this foramen.

**Prootic**—The prootic, represented by the left element, has a thick main portion and a thin, posterolaterally extending flange, which extensively overlapped the opisthotic and participates in the formation of the paroccipital process (Fig. 1F). The posterodorsal edge of the prootic at the junction of these two portions is distinctly concave, presumably forming part of the margin of the posttemporal fenestra. The main portion of the prootic encloses a large, posteriorly facing foramen for passage of the trigeminal nerve (V). This foramen and associated lateral depression are bordered by two lateral, nearly horizontal ridges. The ventral ridge may represent the site of origin of *M. protractor pterygoidei* (Gower, 2002). The anterior margin of the prootic bears a small notch anterodorsal to the trigeminal foramen; in medial view, this notch is connected to the trigeminal foramen by a short groove, which may have carried a branch of the trigeminal nerve and/or the middle cerebral vein. Dorsal to the trigeminal foramen, the medial surface of the prootic bears a shallow depression, which represents part of the floccular (auricular) recess. A foramen at the anterior end of the floccular depression may be related to the course of the middle cerebral vein (Gower, 2002). Posterior and ventral to the trigeminal foramen, a smaller opening in the medial surface of the prootic represents the internal entrance of the canal for passage of the facial nerve (VII), but, due to damage to the ventrolateral region of the prootic, the external opening of this canal cannot be confidently identified.

**Supraoccipital**—The supraoccipital is slightly wider transversely than tall dorsoventrally (Fig. 1G). Its posterodorsal (occipital) surface is nearly flat, lacking a distinct median ridge. Anterolateral articular facets for contact with the parietals are clearly visible, especially on the right side of the supraoccipital. On the right side, just behind the parietal facet, the supraoccipital preserves a bony sheet that partially covered the paroccipital process (Gower, 2002). The posteroventral end of the supraoccipital formed the dorsal margin of the foramen magnum. The anterior (internal) surface of the supraoccipital bears a deep, nearly vertically extending groove that contains a foramen, possibly for the dorsal head vein.

**Articular**—The articular, represented by the nearly complete right element, is robust. With the exception of the lateral extremity, it forms most of the saddle-shaped articular facet for the quadrate condyles (Fig. 2A). The posterior edge of this facet is bounded by a deep transverse groove, posterior to which is the mediolaterally compressed, deep retroarticular process and, anteromedial the latter, an ascending process, of which only the base is preserved. The prominent, flange-like medial process of the articular has a dorsally slightly concave surface and is perforated near its anterior end by an anteroventrally extending canal for passage of the chorda tympani. On the lateral side of the articular, the broken surface indicates the former position of the surangular.

**Angular**—The angular is known from a partial left element (Fig. 2B). Only its ventral margin is nearly complete. The angular bears a ventrolateral facet that presumably was for contact with the dentary. The medial surface of the element bears a pronounced ridge and, ventral to the latter, an extensive surface for contact with the prearticular and splenial. The ventral margin of the more posterior portion of the angular is slightly rugose.

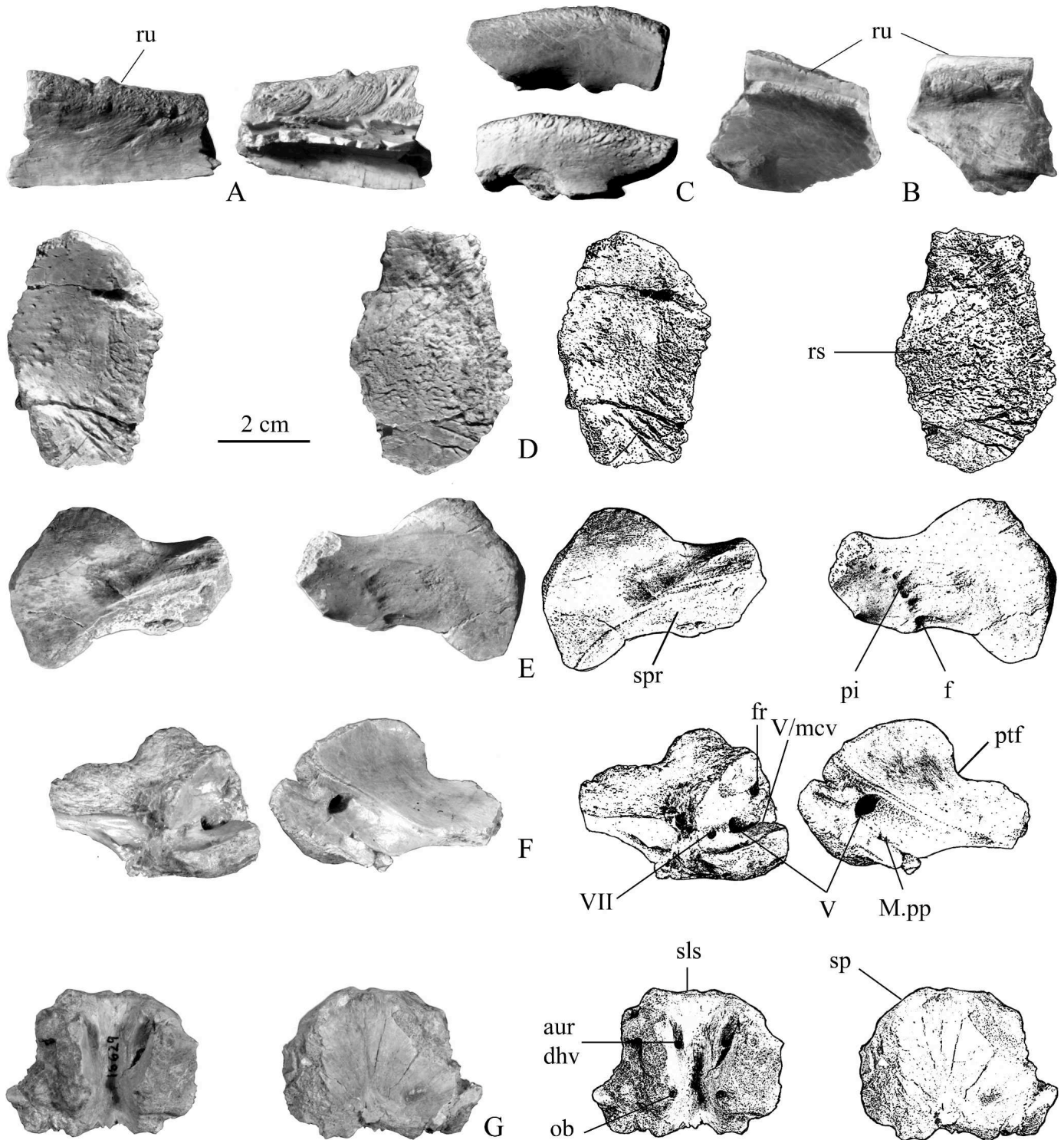


FIGURE 1. *Postosuchus alisonae*, UNC 15575 (holotype), cranial bones. **A**, left nasal in dorsal and ventral view; **B**, right anterior portion of left nasal in medial and dorsolateral view; **C**, left squamosal in ventral and dorsal view; **D**, frontal in ventral and dorsal view; **E**, right paroccipital process in posterior and anterior view; **F**, left prootic in medial and lateral view; **G**, supraoccipital in anteroventral and posterodorsal view.

**Prearticular**—The prearticular is known from only a single fragment of the left element. The anterior and posterior ends of the bone are missing. The prearticular gradually narrows anteriorly; posteriorly, where it contacts the articular, it is deep dorsoventrally (Fig. 2C). Its slightly curved dorsal edge forms the ventral margin of the adductor fossa. In contrast, the ventral

margin of the adductor fossa is strongly curved in *P. kirkpatricki* (TTUP 9000) and *Batrachotomus* (Gower, 1999). The lateral surface of the prearticular is longitudinally excavated for Meckel's cartilage. Laterally, along its ventral margin, the prearticular has a pronounced rim for the contact with the surangular and angular.

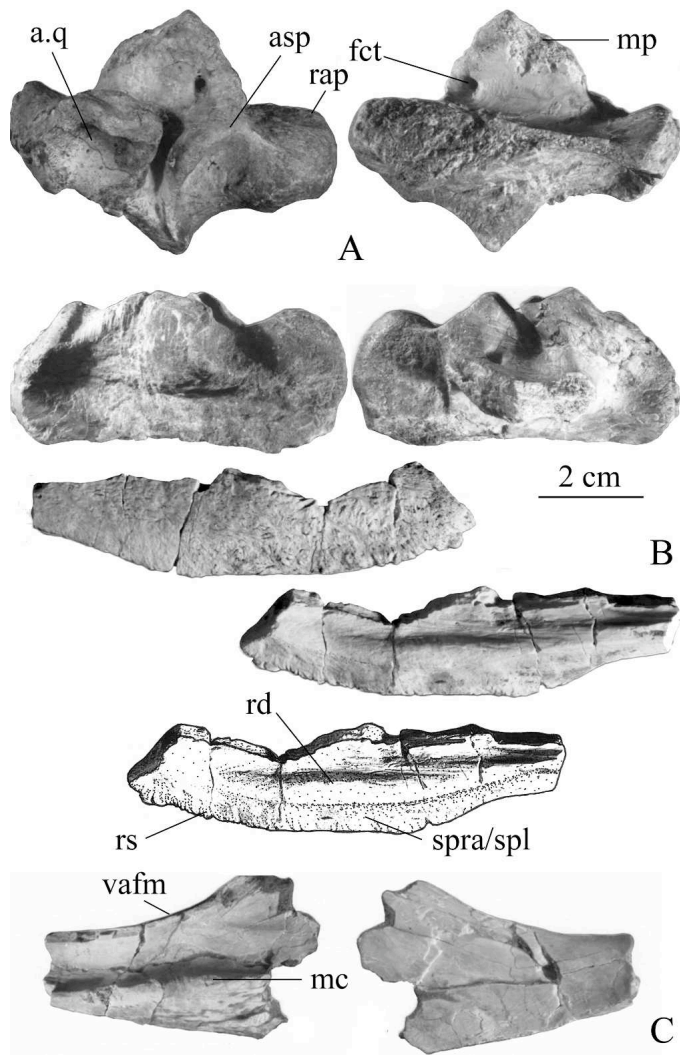


FIGURE 2. *Postosuchus alisonae*, UNC 15575 (holotype), mandibular bones. **A**, left articular in dorsal, ventral, lateral, and medial view; **B**, left angular in lateral and medial view; **C**, left prearticular in lateral and medial view.

**Dentition**—One complete, possibly anterior tooth and a partial posterior tooth are preserved. The dentition of *P. alisonae* is typical for carnivorous archosaurs, with labiolingually compressed, recurved tooth crowns that have finely serrated anteromedial and posterolateral edges (carinae). The complete tooth measures 7.2 cm in height, of which the crown comprises 3 cm. The denticles diminish 1.8 cm above the gum line of the tooth. The second tooth is more labiolingually compressed and has a greater anteroposterior width than the more anterior tooth. The denticle density in both teeth averages 16 or 17 per 5 mm and is comparable to *P. kirkpatricki* (TTUP 9002) (15–16 per 5 mm; J. Weinbaum, pers. comm.), the Moroccan ‘rauisuchian’ *Arganasuchus* Jalil and Peyer 2007 (16 per 5 mm; MNHN AZA 408-2), *Tikisuchus* Chatterjee and Majumdar, 1987 (15 per 5 mm) and *Bromsgroveia* (16–22 per 5 mm; Benton and Gower, 1997), but lower than in *Rauisuchus* (20–25 per 5 mm; Huene, 1942).

#### Postcranial Axial Skeleton and Dermal Armor

The preserved axis and six consecutive cervical vertebrae indicate that the neck of *P. alisonae* comprised at least eight cer-

vical vertebrae. One complete mid-dorsal vertebra and an isolated as well as three articulated caudal vertebrae are also preserved. Isolated centra and neural spines representing about 30 additional cervical, dorsal, and caudal vertebrae are too incomplete to allow their precise placement in the vertebral column. No intercentra were found between the cervicals, dorsals, and caudals and probably were absent except possibly in the atlas-axis complex. Fragments of at least four chevrons are present, two of which comprise a consecutive set in close association with several articulated small osteoderms from the caudal region. No sacral vertebrae were recovered.

**Cervical Vertebrae**—The axis centrum is anteroposteriorly slightly shorter than the following cervical centra. The anterior articular surface is strongly convex, whereas the posterior articular surface is concave (Fig. 3A, B), as in *P. kirkpatricki* (TTUP 9235; Long and Murry, 1995:fig. 128) and *Teratosaurus silesiacus* (Sulej, 2005). A pronounced oval depression occupies most of the lateral side of the centrum. Two distinct ventral keels extend along the length of the centrum. Two distinct ventral keels could also be identified in *P. kirkpatricki* (TTUP 9235). In comparison, there is a single primary keel, which is accompanied by two secondary keels posteriorly, in *Arizonasaurus* (Nesbitt, 2005a). The neural arch and neural spine of the axis are not preserved. No rib facets are present on the axis centrum and thus the rib head probably articulated with the intercentrum of the axis. The axis centrum is similar to that of *Postosuchus* (Long and Murry, 1995:fig. 126A), *Teratosaurus silesiacus* (Sulej, 2005) and *Fasolasuchus* (Bonaparte, 1981), but differs from the axis centrum in *Ticinosuchus* (PIMUZ T2817), which is much shorter than those of the following cervical vertebrae and just barely laterally constricted. The centrum of the axis of *Arizonasaurus* is very long, longer than most other cervical centra (Nesbitt, 2005a).

The postaxial cervical centra are taller than long, with oval, vertically elongated, and slightly concave articular faces (Fig. 3A). The anterior face of the centrum is positioned slightly more dorsal than the posterior face of the centrum in the anterior cervicals. In contrast, the anterior and posterior faces of the posterior cervicals are generally level. The centra appear more or less equal in length throughout the preserved cervical series with the third and fourth cervicals being somewhat longer than other elements in the series. This differs from the condition in *Arizonasaurus* (Nesbitt, 2005a) where the anterior cervicals are about twice as long as the posterior ones. The centra are laterally constricted and hourglass-shaped in ventral view (Fig. 3D). The diapophyses of the anterior cervicals are directed laterally and, starting at the fifth cervical, they are directed posteroventrally. The parapophyses are located on the anterolateral surface of the centrum throughout the cervical series. As in other ‘rauisuchians’ and many other archosaurs (Nesbitt, 2005a) the diapophyses are connected to the centrum by four bony laminae: the prezygodiapophyseal lamina, the postzygodiapophyseal lamina, the posterior centroprezygodiapophyseal lamina, and the paradiapophyseal lamina (Fig. 3A, E). Another lamina, possibly the centroprezygodiapophyseal lamina (Wilson, 1999), arises on the prezygodiapophyses and ends at the anterior end of the neurocentral junction. In lateral and posterior aspect, another lamina arises at the neurocentral junction posterior to the diapophysis and terminates on the ventral face of the postzygodiapophysis; this feature is interpreted here as the centropostzygodiapophyseal lamina (Wilson, 1999). A fossa opens on either side of the centrum, ventral to the diapophysis. These fossae are ventrally bounded by an anteroposterior ridge. As in *P. kirkpatricki* (Long and Murry, 1995:fig. 126B–N), *Teratosaurus silesiacus* (Sulej, 2005), *Prestosuchus chiniquensis* (Huene, 1942), and *Rauisuchus* (Huene, 1942), a single pronounced keel extends anteroposteriorly for the entire length of the centrum. The keel passes anteriorly and, on some centra, also posteriorly into a hypapophysis (Fig. 3A, E). In *Yarasuchus* the midline keel does not extend to the pos-

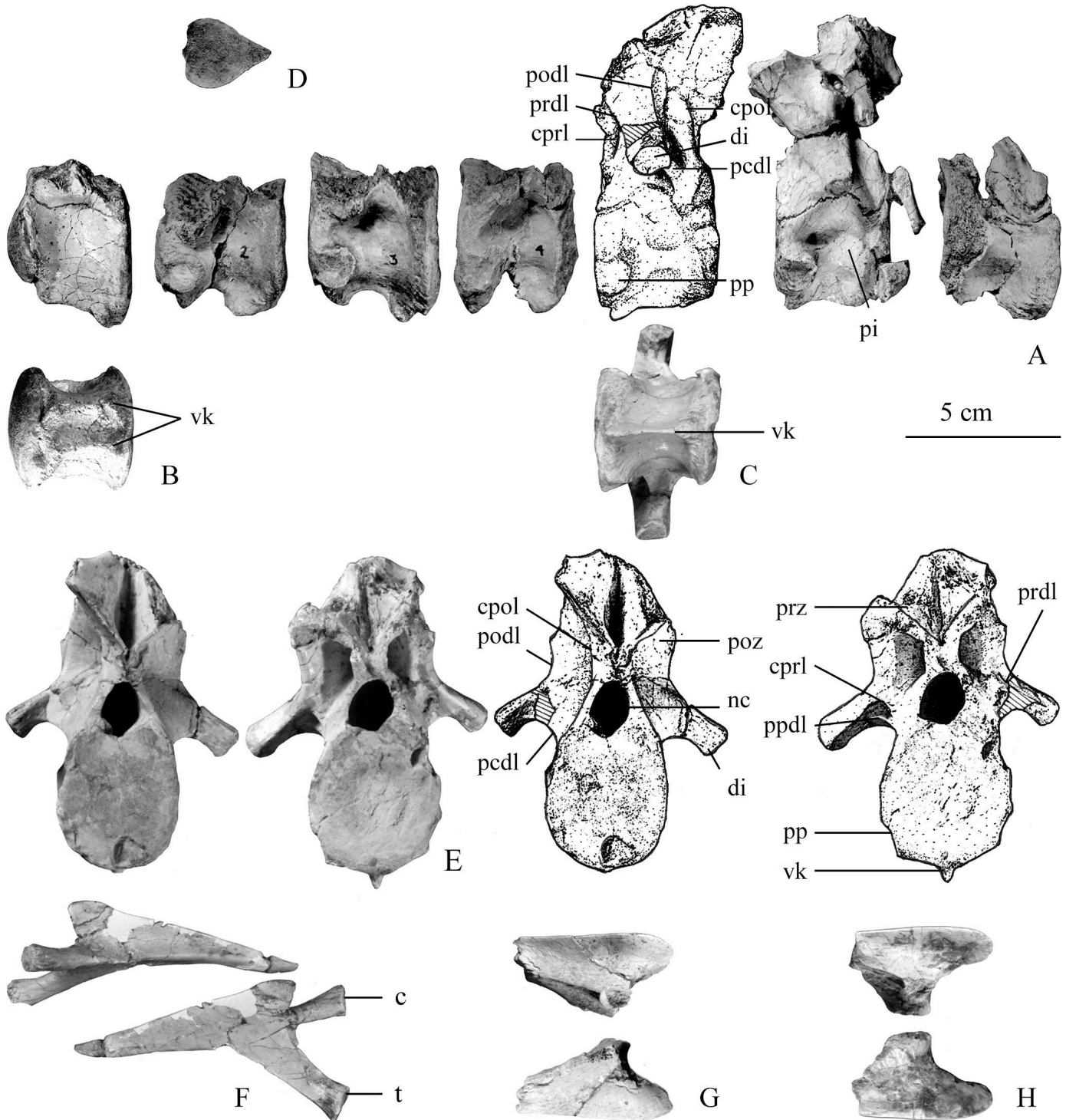


FIGURE 3. *Postosuchus alisonae*, UNC 15575 (holotype), cervical vertebrae and ribs. **A**, axis and postaxial cervical vertebrae 3-8 in lateral view; **B**, axis in ventral view; **C**, sixth cervical vertebra in ventral view; **D**, cervical neural spine in dorsal view; **E**, sixth cervical vertebra in posterior and anterior view; **F**, sixth cervical rib in posterior and anterior view; **G**, **H**, anterior cervical ribs.

terior end of the centrum, but two additional keels originate near the middle of the centrum and continue posteriorly (Sen, 2005). The cervical neural arches are of moderate height. The neural canal is deeply excavated (Fig. 3E) as in *P. kirkpatricki* (TTUP 9235), *Heptasuchus* (Dawley et al., 1979), *Yarasuchus* (Sen, 2005), and *Prestosuchus chiniquensis* (Huene, 1942).

One complete and several incomplete cervical neural spines

are preserved. The bases of the neural spines are narrow anteroposteriorly with nearly equal lengths at their base and tip. They are situated on the posterior portion of the centrum. The cervical neural spines are tall, and their apices are massive and transversely expanded. Viewed from above, these expanded apices form heart-shaped 'spine tables' with the pointed end projecting posteriorly (Fig. 3D). A similarly heart-shaped spine table is

present on a spine associated with a large specimen of *P. kirkpatricki* (TTUP 9235) (Long and Murry, 1995:fig. 128). Where preserved, the cervical vertebrae have prezygapophyses with articular surfaces that are inclined steeply towards the midline and postzygapophyses with articular surfaces facing steeply away from the midline.

**Dorsal Vertebrae**—One complete mid-dorsal vertebra is preserved (Fig. 4A). Fragments of several disarticulated dorsals are present but are difficult to place more precisely in the dorsal series. Like the cervical centra, the dorsal centra are shorter than tall, with a length/height (anterior) ratio of 0.94; they are slightly longer than the cervicals, which have a length/height ratio of 0.80. Ventral keels are absent or reduced to a sharp edge in the mid- to posterior dorsal vertebrae as in *P. kirkpatricki* (TTUP 9002) and most other well known 'rauisuchians'. The articular faces are slightly inclined relative to the long axis of the centra and as on the more cranially placed cervical centra, the anterior and posterior articular surfaces are set at different levels. The articular ends are concave and only slightly oval. The centra are even more laterally constricted than the cervical centra. The neural arch is low, and the diapophysis extends almost horizontally and is connected to the parapophysis by the paradiapophyseal lamina. The other three laminae connecting the diapophysis with the prezygapophysis (prezygodiapophyseal), the postzygapophysis (postzygodiapophyseal) and the posterior margin of the neurocentral junction (posterior centrodiapophyseal) are still developed on this mid-dorsal vertebra. As in *Bromsgroveia* (Benton and Gower, 1997) and *P. kirkpatricki* (TTUP 9002), a pit opens just ventral to the diapophysis. The neural spines are blade-like, barely transversely expanded at their apices, and generally much longer anteroposteriorly at their distal end than at their base. The largest neural spine present has an anteroposterior length more than twice that of a cervical neural spine. The neural spines are about as tall as the centrum and neural arch combined, but generally not taller than the cervical neural spines. Dorsal vertebrae with tall, distally anteroposteriorly expanded neural spines and only slightly expanded spine tables are also present in *Rauisuchus* (Huene, 1942:pl. 26, fig. 10A), *Lythrosuchus* (Long and Murry, 1995), and *P. kirkpatricki* (TTUP 9002). In contrast, more expanded spine tables are characteristic of the dorsals of *Saurosuchus* (Sill, 1974), *Fasolasuchus* (Bonaparte, 1981:figs. 10–11), and *Ticinosuchus* (PIMUZ T2817). The articular surfaces of the pre- and postzygapophyses are only slightly inclined mediolaterally. A hyosphenehypantrum is clearly visible on the preserved dorsal vertebra.

**Caudal Vertebrae**—The caudal region is represented by seven vertebrae from different regions of the tail. The centra decrease in height and increase in length/height ratio toward the distal end of the tail (Fig. 4B). Three articulated and one isolated vertebra form the mid-caudal series each are about twice as long as high, whereas two incomplete caudal vertebrae, closer to the distal end of the tail, have a reconstructed length three times their height. Only a partial centrum from the more anterior caudal series is present. Prezygapophyses on the mid- and posterior caudal vertebrae are directed anteriorly and have steeply medially inclined articular facets, as on the cervical vertebrae. The postzygapophyses are also steeply inclined. The prezygapophyses overhang the centrum anteriorly whereas the shorter postzygapophyses are level with the articular surface of the centrum. Transverse processes are absent on the mid-caudal and posterior caudal vertebrae. These vertebrae bear a pronounced, slightly arched, anteroposteriorly extending ridge on the lateral surfaces of their centra. The ventral surfaces of the centra are smooth and slightly convex. The neural spines are short and do not rise above the zygapophyses in the mid- and more posterior caudal vertebrae. Accessory caudal neural spines have been reported for *Ticinosuchus* (Krebs, 1965) and *Teratosaurus silesiacus* (Sulej 2005:fig. 1K) but they appear to be absent in *P. kirkpatricki* (Long and

Murry 1995:fig. 130; UCMP A269/124890) and in *P. alisonae* as far as can be inferred from fragments of preserved caudal vertebrae. All of the recovered caudal centra have slightly concave, dorsally inclined articular surfaces.

**Cervical Ribs**—Three nearly complete cervical ribs are present. The left fifth cervical rib is more than twice as long as the corresponding cervical centrum. Its shaft tapers distally (Fig. 3F). The capitulum and somewhat longer tuberculum enclose an angle of 50°. Their articular ends are circular in outline. Anteriorly, the rib has a pronounced, anteriorly projecting keel, which descends 1 cm below the shaft where the articular heads meet, and then slowly decreases in height towards the posterior end of the rib. Two slightly incomplete ribs from the right side of the neck are similar in size, with a maximum length of 3 cm (Fig. 3G, H). Their size implies that they were associated with cervicals anterior to the fifth vertebra. Each has a broad keel, two articular heads, and a relatively short posterior shaft.

**Dorsal Ribs**—The distal segments of five right dorsal ribs were found in association with the gastralia. The anterior dorsal ribs have a plano-convex cross-section, whereas the more posterior dorsal ribs have an oval cross-section and are only half as wide anteroposteriorly near their ventral ends. Ribs interpreted here as representing the more anterior region have two distinct rib heads with a capitulum that is round to slightly oval in cross-section and a tuberculum that is strongly flattened proximally. The anterior dorsal rib-shafts are triangular in cross-section, a result of the presence of a reduced anteroventral flange and a rounded capitulum extending down the shaft.

**Sacral Rib**—A fragment of a right second sacral rib is preserved (Fig. 5A) (Weinbaum, pers. comm.). The wing-like piece is about 8 cm long. The original margin of the bone is represented anteriorly by a broader and anterolaterally by a narrow edge. The dorsal surface of the fragment bears a distinct medio-lateral ridge, which increases in anteroposterior width medially. Its ventral side is concave.

**Osteoderms**—Three distinct types of osteoderm can be distinguished: (1) elongated, paired cervical osteoderms; (2) box-like dorsal osteoderms developed as dorsal paramedian osteoderms; and (3) much smaller, slightly imbricated osteoderms.

A series of six consecutive left and fragments of several additional cervical paramedian osteoderms was found in association with a cervical vertebra. The elements are characterized by a nearly horizontal, sculptured dorsal surface and a strongly dorsolaterally inclined lateral surface (Fig. 6A). Anterior lappets (extending from the anterior edge of the lateral part of the osteoderms) are present on all cervical osteoderms. The posterior lappets of the osteoderm are shorter. The paired left and right members are in close contact, but do not form a midline sutural contact. The long, paired cervical osteoderms in *P. alisonae* are similar to the cervical osteoderms in *Rauisuchus* (Huene, 1942:pl. 27, fig. 12–15), and *Ticinosuchus* (PIMUZ T2817). On the shorter dorsal osteoderms a lateral ridge separates a nearly horizontal dorsal surface from a nearly vertical lateral surface (Fig. 6B–D). The anterior lappets are longer than the posterior lappets, and both are relatively shorter than those in the cervical region. The paired plates interdigitate slightly along the sagittal plane, to form a rigid, box-like structure over the anterior dorsal region (Fig. 6B). Nearly identical paramedian osteoderms are also present in *Rauisuchus* (Huene, 1942:pl. 27, fig. 10), and the osteoderms in the dorsal region of *Ticinosuchus* (Krebs, 1965:fig. 64), *Fasolasuchus* (Bonaparte, 1981:fig. 20B), and *Tikisuchus* (Chatterjee and Majumdar, 1987) are also similar. The cervical and dorsal paramedian osteoderms overlap, with the posterior end covering about one-third of the anterior end of the osteoderm behind it. At least in the cervical region of the body, approximately one pair of paramedian osteoderms is present for each vertebral segment. However, dorsal osteoderms are generally shorter anteroposteriorly than the cervical ones so that this one-



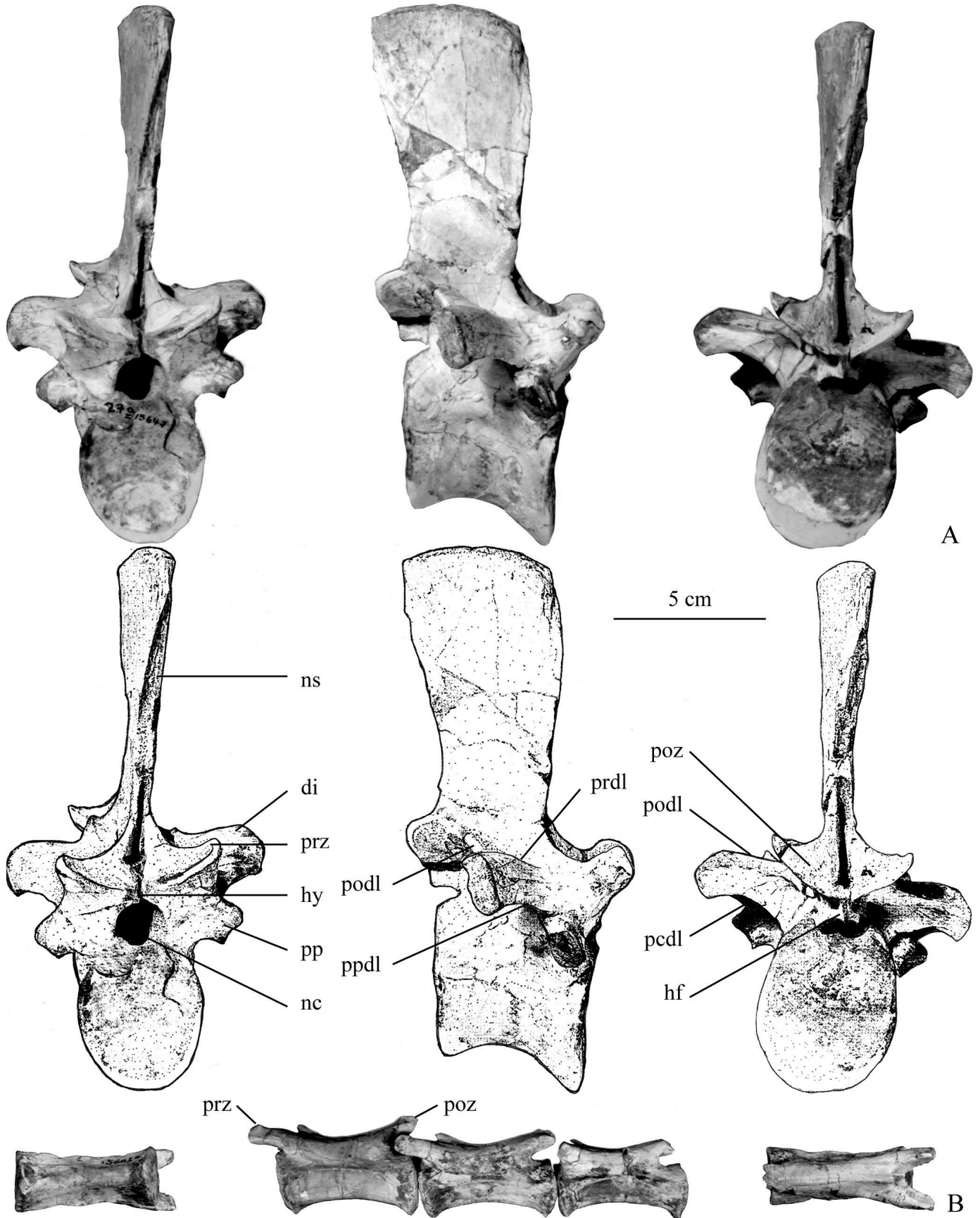


FIGURE 4. *Postosuchus alisonae*, UNC 15575 (holotype), dorsal and caudal vertebrae. **A**, dorsal vertebra in anterior, right lateral, and posterior view; **B**, caudal vertebrae in ventral, left lateral, and dorsal view.

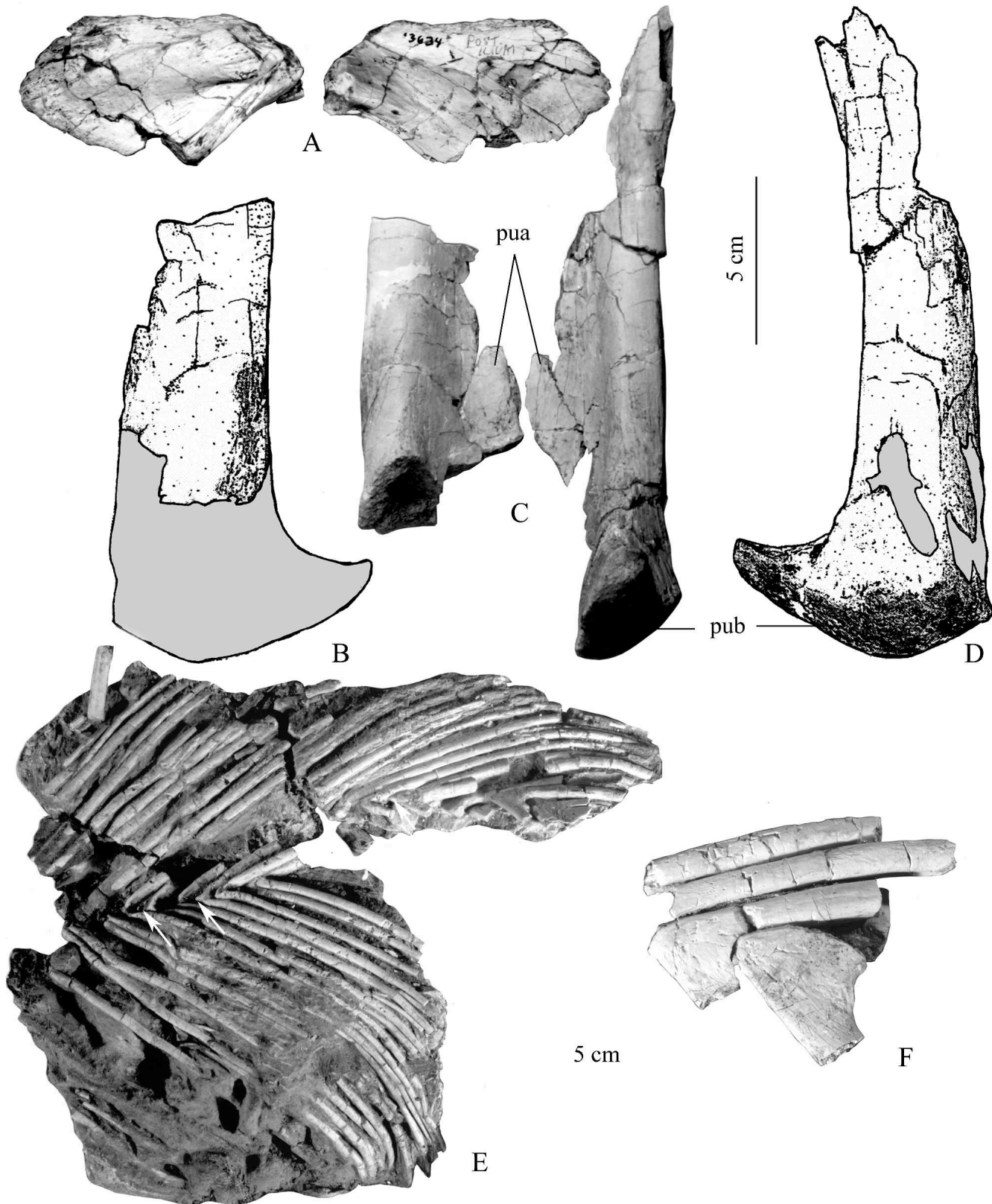


FIGURE 5. *Postosuchus alisonae*, UNC 15575 (holotype), pelvic girdle, sacral rib and gastralia. **A**, right, second sacral rib in dorsal and ventral view; **B**, left pubis in lateral view; **C**, pubes in posterior view; **D**, right pubis in lateral view; **E**, gastral basket; **F**, close-up of gastralia fusion along midline. Arrow indicates anterior process at midline fusion.

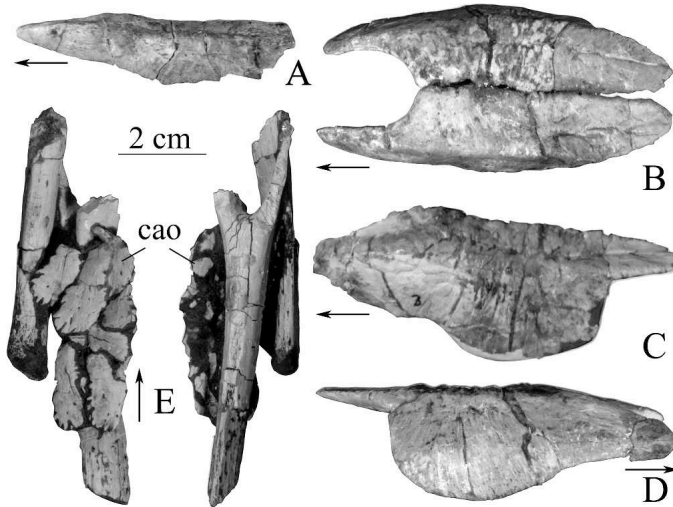


FIGURE 6. *Postosuchus alisonae*, UNC 15575 (holotype), osteoderms and chevron bones. **A**, cervicals osteoderm in lateral view; **B**, dorsal osteoderms in lateral; **C**, dorsolateral; and **D**, dorsal view; **E**, chevron bones in anterior and posterior view with small ventral or dorsal caudal osteoderms. Arrow indicates anterior direction.

to-one relationship may not hold throughout the presacral vertebral column. Cervical and dorsal osteoderms are finely ornamented dorsally with radiating ridges and pits. The dorsal segment of the paired cervical and dorsal osteoderms ranges from 1.2 to 1.7 cm in transverse width. A set of small, unpaired, and slightly imbricated osteoderms was found overlying a pair of chevron bones from the proximal region of the tail (Fig. 6E). These osteoderms are elongate, with some being three times longer than wide. Posteriorly, the plates are more mediolaterally expanded than anteriorly and, except for small pits, the dorsal surface is smooth and the edges are finely grooved. In *Batrachotomus* (SMNS 84027), the small osteoderms also have finely grooved edges but are more rounded and there is a midline ridge on the dorsal surface. In *Ticinosuchus*, small osteoderms cover the tail ventrally (Krebs, 1965). They are pointed anteriorly, slightly waisted, and concave posteriorly. Several small osteoderms with anterolateral processes and medial sutures formed two paramedian rows along the tail of *Teratosaurus silesiacus* (Sulej, 2005) but only a single row in *Saurosuchus* (Sill, 1974) and *Fasolasuchus* (Bonaparte, 1981). It is not clear whether the small osteoderms in the present specimen covered the tail ventrally or whether they were displaced and were, in fact, placed above the neural spines in life or somewhere else on the body.

**Chevron Bones**—Four partial chevron bones have been recovered. They are Y-shaped in anterior and posterior view (Fig. 6E). The distal process is rod-shaped proximally, but becomes increasingly mediolaterally flattened more distally. Proximally, the bone forks into two mediolaterally flattened limbs. The hemal canal appears to be deep and narrow. One of the chevron bones is much more massive than the other two, implying that it was located more anteriorly.

**Gastralia**—Virtually the entire gastralia basket is preserved. It covers the ventral surface of the trunk between the mid-dorsal region and the pubes. Over 30 rows of closely spaced, rod-shaped gastralia rods are present, with the rods more closely spaced posteriorly than anteriorly (Fig. 5E, F). Left and right gastralia segments are fused along the midline, meeting at an angle of about 25°. The more anterior gastralia rods are dorsoventrally thickened near the sagittal plane, whereas, more posteriorly along the series, the rods are anteroposteriorly expanded and dorsoventrally flattened near the sagittal plane. Posteriorly, two

or occasionally three consecutive flattened rods may be fused together on one side, usually in an asymmetric pattern (Fig. 5F). Slightly lateral to the area of fusion of the posterior gastralia rods, where they become distinct, the rods have a figure-eight cross-section and are distinctly imbricated. At the point of the midline fusion a short anterior process may be developed (Fig. 5E). Each set of paramedian gastralia rods is accompanied by much more slender rods on either side of the body, starting about one third the way back from the midline. These additional rods are in close contact with the paramedian rods for a short distance at their base but lose their contact farther distally and float between two paramedian rods.

The gastralia in *Ticinosuchus* (Krebs, 1965:fig. 62) and *Prestosuchus chiniquensis* (Huene, 1942:pl. 19, fig. 1) resemble those in *P. alisonae* except for the imbrication and more extensive fusion of adjacent gastralia rods posteriorly in the latter.

### Pectoral Girdle and Forelimb

**Scapula and Coracoid**—UNC 15575 preserves a complete right coracoid and attached right proximal end of the scapula, the glenoid region of the left coracoid, and an incomplete scapular blade. The scapula and coracoid are firmly attached to each other, although the suture is still visible. The coracoid is subrectangular in lateral view and more than twice as tall as long, resembling the coracoid in *P. kirkpatricki* (TTUP 9002) but differing from the rounded coracoid in *Batrachotomus* (Gebauer, 2004:fig. 13B), *Ticinosuchus* (PIMUZ T2817), *Arizonasaurus* (Nesbitt, 2003), and *Yarasuchus* (Sen, 2005). Anteriorly, the coracoid is thin and plate-like but it becomes greatly thickened posteriorly where it forms part of the glenoid fossa (Fig. 7A). A large coracoid foramen serves for the passage of the supracoracoid nerve extending posteromedially through the coracoid. The coracoid comprises a larger portion of the glenoid than the scapula. The concave surfaces of the scapula and coracoid forming the glenoid cavity meet at nearly a right angle. The glenoid surface faces ventrolaterally. As in *Batrachotomus* (Gebauer, 2004:fig. 13B) and *P. kirkpatricki* (TTUP 9002), the postglenoid process is slightly elongate and separated from the glenoid by a deep notch. In contrast, a short, rounded postglenoid process is present in *Arizonasaurus* (Nesbitt, 2005a) and *Prestosuchus chiniquensis* (Huene, 1942). The scapula is massive where it forms the posterior part of the glenoid cavity (Fig. 7A). Posterior to the glenoid, the scapular blade is generally thin but becomes slightly thicker toward its rounded posterior edge than along its anterior border. As a result, the shaft is triangular in cross-section. The preserved part of the scapular blade is slender and bowed along its long axis so that its lateral surface is convex and the medial surface concave (Fig. 7B). The scapular blade in *Prestosuchus chiniquensis* (Huene, 1942:pl. 19, fig. 2) and *Rauisuchus* (Huene, 1942:pl. 29, fig. 1) progressively decreases in width towards the middle of the scapular blade whereas in *P. alisonae*, *Batrachotomus* (Gebauer, 2004:fig. 13B), and *P. kirkpatricki* (TTUP 9002) it immediately narrows just posterior to the glenoid fossa, resulting in a more constricted mid-shaft.

The scapulocoracoid are strikingly similar to that in *P. kirkpatricki* (TTUP 9002). However, the scapulocoracoid in *P. alisonae* is much more massive near the glenoid fossa, despite the fact that the corresponding bones in *P. kirkpatricki* (TTUP 9002) are larger.

**Clavicle and Interclavicle**—The interclavicle was found attached but not fused to the anterior part of the left coracoid (Fig. 7A). It is thin and blade-like, convex along its length, and slightly tapering toward either end. It forms essentially a single median structure between the coracoids. Its anterior surface bears fine longitudinal striations. An almost complete right clavicle is preserved (Fig. 7C). It is rod-like except for its somewhat inflated proximal articular end, which meets its counterpart and the in-

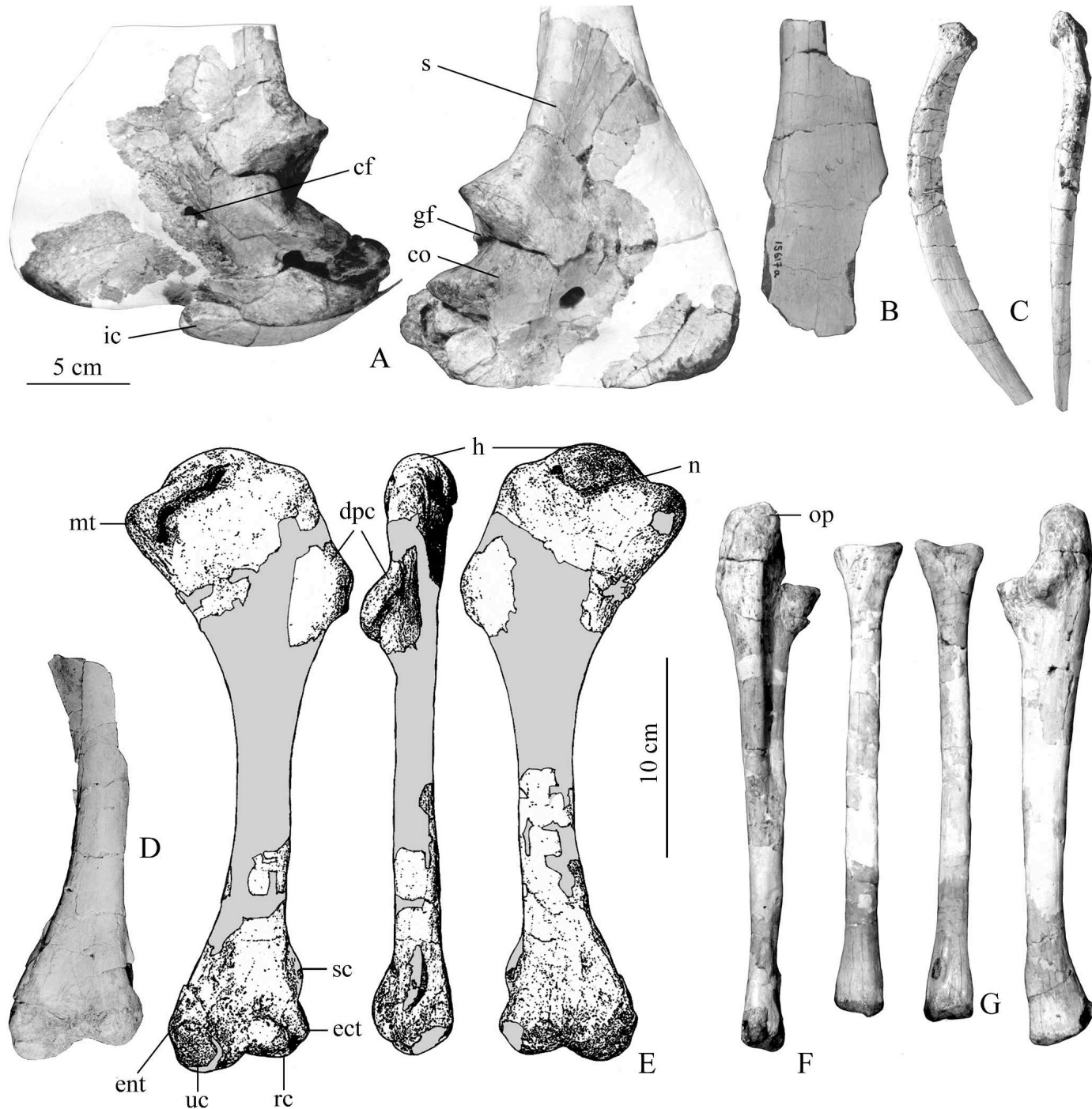


FIGURE 7. *Postosuchus alisonae*, UNC 15575 (holotype), shoulder girdle and forelimb. **A**, left scapulocoracoid with interclavicle in lateral and medial view; **B**, partial scapular blade; **C**, clavicle in lateral and dorsal view; **D**, right humerus in posterior view; **E**, left humerus in anterior, lateral, and posterior view; **F**, ulna in medial and lateral view; **G**, radius in anterior and posterior view.

terclavicle. Dermal elements of the pectoral girdle have also been reported for *Prestosuchus chiniquensis* (Huene, 1942), *Procerosuchus* (Huene, 1942), and *Ticinosuchus* (Krebs, 1965).

**Humerus**—The left humerus of UNC 15575 is represented by its proximal and distal ends, and the right element by its distal end and a large portion of the mid-shaft. The humerus is expanded at both ends. Its shaft is nearly circular in cross-section from mid-shaft to the distal end, but becomes dorsoventrally flattened toward the proximal end (Fig. 7D-E). The proximal

and distal articular ends of the humerus are arranged so that the distal end is slightly offset ventrally from the plane of the proximal end. The distal expansion is about half as wide as the proximal one and is divided into two rounded convexities, which form the lateral (radial) and medial (ulnar) condyle, respectively. The two condyles are more or less equal in size and separated from each other by a shallow trochlea. A well-defined longitudinal supinator ridge extends just dorsal and lateral to the radial condyle (Fig. 7E). A longitudinal depression adjacent to that ridge

provides passage for the radial nerve and associated vessels. Epicondylar rugosities are well developed on both lateral and medial sides of the distal end of the humerus. The proximal part of the humerus curves medially. The humeral head is separated by a well-defined notch from the medial tuberosity. It is well rounded anteroposteriorly and also ventromedially and terminates in a knob-like process ventromedially. There is a deep notch just ventral to this process. An equally deep notch is present in *P. kirkpatricki* (TTUP 9002), but is very shallow in *Batrachotomus* (Gebauer, 2004:fig. 12B). As in *Batrachotomus* (Gebauer, 2004:fig. 12B), *P. kirkpatricki* (TTUP 9000) (Long and Murry, 1995:fig. 132A–D), and possibly *Ticinosuchus* (Krebs 1965:fig. 38A–B), the deltopectoral crest is fairly distinct, triangular, and extends for one-fourth of the length of the shaft.

Overall, the fragmentary left humerus of *Prestosuchus chiniquensis* (Huene, 1942:fig. 35–36) and the humerus of *P. kirkpatricki* (TTUP 9002) most closely resemble that of *P. alisonae* in their general structure and development of the articular condyles.

**Ulna**—The right ulna only lacks its distal end. The left ulna has completely preserved proximal and distal ends but is missing portions of the shaft. The ulnar shaft is almost columnar about one-third from its distal end, and becomes flattened dorsoventrally towards the articular ends (Fig. 7F). A distinct olecranon process for the attachment of the triceps muscle is developed on the proximal end. An equally pronounced olecranon process is present in *P. kirkpatricki* (TTUP 9002). In contrast, *Batrachotomus* (SMNS 80275) and *Ticinosuchus* (PIMUZ T2817) have a much shorter olecranon process, whereas *Fasolasuchus* (Bonaparte, 1981:fig. 19) has a large olecranon process associated with its more massive ulna. Medially, a flat articular surface contacted the humerus. Together with the proximal articular surface of the radius, the articular surface forms a continuous surface for the trochlear condyle of the humerus. Starting just distal to the olecranon process, a longitudinal depression extends half way down the shaft along the dorsal aspect of the ulna. The distal end of the ulna is relatively flat dorsoventrally and tapers slightly. The length of the ulna is 92% of that of the humerus.

**Radius**—The right radius only lacks its proximal end and a few small pieces from its shaft. The left bone preserves the proximal and distal ends, but its shaft is missing a 2 cm long segment near the distal end. In outline, the radius is a relatively simple, slender bone with a dorsoventrally flattened shaft at mid-diaphysis and expanded proximal and distal ends (Fig. 7G). Its reconstructed length is 81% the length of the humerus. The distal end of the radius is only slightly expanded anteroposteriorly, and its articular surface is slightly convex and nearly round in distal view, except for a small medial groove for articulation with the ulna. The proximal articular surface is slightly concave, elliptical in outline, and more expanded than the distal end. The long axes of the proximal and distal articular surfaces of the radius extend more or less parallel to each other.

**Manus**—The manus is very small relative to the size of the forelimb, and its length is only one-third the length of the pes (Fig. 8A–G). A comparison of manual and pedal length, based on the McIII/MtIII ratio, shows that *P. alisonae* and *P. kirkpatricki* (TTUP 9002) with a ratio of 0.31 and 0.32, respectively, have proportionately shorter hands than *Ticinosuchus* (0.41; Krebs, 1965). The manus is partially known in *Ticinosuchus* and *P. kirkpatricki* from Ghost Ranch (CM 73372). A few disassociated manual bones associated with *P. kirkpatricki* (TTUP 9002) are comparable in size and shape with the manual elements in *P. alisonae*. In *Ticinosuchus* and *P. alisonae*, the metacarpals are tightly imbricated and the ungual phalanx of manual digit I is large and strongly recurved.

Five bones are present in the right carpus, but none is preserved for the left. Three articulated carpals, two of which are fused together, comprise an arch, curving in the same manner as

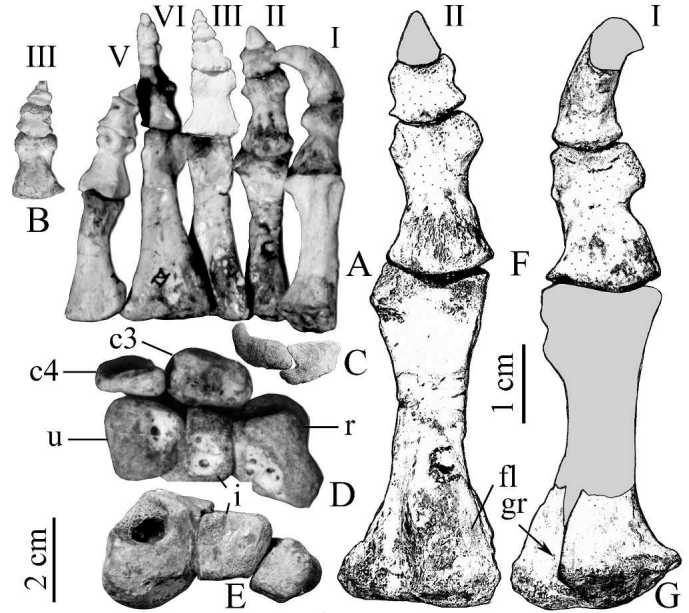


FIGURE 8. *Postosuchus alisonae*, UNC 15575 (holotype), carpus and manus. A, right manual phalanges in ventral view; B, phalanges 1 to 3 of left manual digit III; C, metacarpals I and II in proximal view; D, right carpus in ventral view; E, right radiale, intermedium, and ulnare in distal view; right manual digits F, I and G, II in ventral view.

the metacarpals (Fig. 8D, E). These three carpals represent the radiale, intermedium, and ulnare. The radiale is larger than the ulnare. Two additional right carpals represent distal carpals 3 and 4. The surfaces of all carpals have ligamentous attachment marks on their dorsal and ventral surfaces. Identical proximal and distal carpal elements are known for *P. kirkpatricki* (TTUP 9002). These were previously arranged in a semilunate fashion (Chatterjee, 1985), but this reconstruction has now been invalidated by the discovery of the articulated manus of UNC 15575. Four articulated, dorsoventrally compressed left carpals are also present in *P. kirkpatricki* (CM 73372) from Ghost Ranch. The elements are, however, distorted and comparisons with other 'rauisuchian' specimens are limited. It appears that the ulnare is missing in the Carnegie specimen.

Of the right metacarpus, metacarpals II–V and the proximal portion of metacarpal I are preserved (Fig. 8A). The left metacarpus is documented by the proximal portions of metacarpals II–IV and the distal end of metacarpal II. The metacarpals of both hands were found largely in articulation. Their proximal ends are imbricated. The tightly conjoined metacarpals form a strong arch, the palmar side forming a concave ventral surface. Metacarpals I–II have a tongue-and-groove articulation so that metacarpal I proximally surrounds metacarpal II on the dorsal and ventral side (Fig. 8C, F, G). The groove on metacarpal I is very deep, measuring almost a third the mediolateral length of the proximal articular surface. The entire preserved segment of metacarpal I is grooved and the contact between metacarpals I and II extended close to mid-shaft length of metacarpal II. In *P. kirkpatricki* (TTUP 9002; CM 73372) a very small flange of different structure is present medially on the proximal end of metacarpal I. The proximal articular surface of metacarpal II in *P. alisonae* is slightly laterally rotated along the long axis of the shaft relative to the distal articular surface by approximately 45°. This rotation caused articulation with metacarpal I to be rotated ventrally with respect to other elements of the manus. The proximal articular surface in metacarpal I associated with *P. kirkpatricki* (TTUP 9002) is even more laterally twisted (70°) relative to

the distal articular surface but proximal and distal articular surfaces are almost parallel to each other in CM 73372. Other than this asymmetry, the metacarpals of the present specimen are similar in shape, with expanded proximal and distal ends and a shaft that is narrowest near the distal end. Metacarpal III has a narrower shaft than the other metacarpals. The distal ends of the metacarpals are generally about half as wide as their proximal ends. However, metacarpal V does not show as much difference between its proximal and distal widths and its shaft is less constricted. The proximal articular surfaces of the metacarpals vary from slightly convex to flat in metacarpals II–V to slightly concave in metacarpal I (inferred from the convex proximal articular surface of manual phalanx I-1). The metacarpals are much longer than the immediately adjoining phalanges and, where preserved, are also longer than the combined lengths of all phalanges of any particular digit. The metacarpals in the right manus increase in length from the second to the fourth. Metacarpal V is about 25% shorter than metacarpals II–IV.

Eight phalanges from the right manus and four from the left are preserved in UNC 15575 (Fig. 8A, B). Some phalanges were found articulated or nearly articulated. The right manus preserves phalanx I-1 and a mediolaterally compressed, strongly recurved unguis phalanx (I-2), phalanges II-1 and II-2, III-3 and III-4 (the latter being a minute, dorsoventrally flattened, hoof-like unguis) and phalanges IV-1 and IV-2. The left manus is represented by an articulated digit III with phalanges III-1, 2, and 3 and a hoof-like unguis (III-4). All non-terminal phalanges are similar in shape. They have two distal articular condyles extending onto the ventral side, and are less expanded distally than proximally. The more distal non-terminal phalanges decrease in length/width ratio and finally become shorter than wide. The unguis phalanx of digit I is slightly mediolaterally compressed, strongly curved, and bilaterally symmetrical as in *P. kirkpatricki* (manual phalanges associated with TTUP 9002). As in *P. kirkpatricki* (TTUP 9002), the unguis of digit III is short and conical. In comparison, the unguis of manual digit III in *Ticinosuchus* (PIMUZ T2817) is proportionately longer than in *P. alisonae* and *P. kirkpatricki* (TTUP 9002).

The preservational loss of some distal phalanges makes it difficult to reconstruct the manual phalangeal formula of *P. alisonae* with confidence. The distal articular surfaces on the distal most preserved phalanges II-2 and IV-2 indicate the presence of at least one more phalanx in both digits II and IV. Currently only three known 'rauisuchian' specimens, the holotype of *Ticinosuchus ferox* and two specimens of *P. kirkpatricki* (TTUP 9002; CM 73372) preserve a partial manus. *Ticinosuchus* has at least two and at least four phalanges in manual digits II and IV, respectively; both digits lack the unguis phalanx (Krebs, 1965). The incomplete manual digit IV in *P. kirkpatricki* (CM 73372) preserves only phalanx IV-1. The manus of *Ticinosuchus* preserves a complete manual digit III comprising four phalanges (Krebs, 1965). A possible manual phalangeal formula for 'rauisuchian' archosaurs is 2-3?-4-5?-3. The manual elements of presently known taxa do not indicate variation in phalangeal counts in 'rauisuchians'.

### Pelvic Girdle and Limbs

The pelvic girdle of UNC 15575 is only documented by the distal portions of both pubes. The distal portions of the left and right hind limbs of UNC 15575 were recovered fully articulated, with only slight displacement of some of the more distal phalanges of the pedes. The tibia and fibula were tightly attached to the astragalus and calcaneum, respectively.

**Pubis**—The right pubis, the more complete of the two, comprises the distal two thirds of the shaft and terminates distally in a boot (Fig. 5C, D). Approximately one third of the distal portion of the left pubic shaft is preserved, but the distal boot is

broken off (Fig. 5B, C). The pubes are slender and long, and have rod-like shafts. The pubic apron is represented by flat, possibly long crests on the anteromedial faces of both shafts that contact each other along a median symphysis. As in *Batrachotomus* (Gebauer, 2004:fig. 14B) and the pubis of a pelvis illustrated by Case (1943) and later referred to *P. kirkpatricki* (Chatterjee 1985, Long and Murry 1995), the pubic boot is well developed. The pubic boots in *Poposaurus*, *Arizonasaurus*, and *Bromsgroveia* are narrow and small, whereas in *Chatterjeea* the pubic boot is long anteroposteriorly (Long and Murry, 1995). The pubic boot of *P. alisonae* is mediolaterally thickened, and, in lateral view, it has a semicircular base with the posterior tip slightly turned upwards. In comparison, the pubic boot is flat along its ventral side in *Arizonasaurus* (Nesbitt, 2005a). There is no indication that the pubic boots were fused to each other. Where the pubic boot grades into the shaft, it is swollen medially. The foot forms an angle of 62° with the long axis of the shaft.

**Tibia**—The left tibia is complete except for a small piece on the anterior part of the proximal end. The right element lacks its proximal end. The tibia is rather slender, with a columnar shaft that reaches its minimum width just above mid-length (Fig. 9A, B). The long axes of its proximal and distal ends of the tibia are slightly set at an angle to each other, giving the tibia a twisted appearance. The distal articular end is slightly expanded and the well developed posterior condyle extends below the anterior condyle as in *P. kirkpatricki* (TTUP 9002). The distal articular surface is concave to straight anteriorly but convex posteriorly. The proximal articular end of the tibia is more massive and much more expanded anteroposteriorly than the distal end. Its articular surface is poorly ossified, perhaps reflecting immaturity of the animal. Its cnemial crest extends distally for about one fourth of the length of the tibia before merging with the shaft. In posterior view, the proximal and distal ends of the tibia gently curve medially away from the fibula. A 3 cm long, oval depression is situated distal to the proximal end on the posteromedial aspect of the tibia. This depression represents the attachment area for *M. extensor iliobialis* (posterior) or *flexor tibialis externus*. Another muscle insertion scar is located just below and anterolateral to the proximal end and does not make direct contact with the fibula.

The tibia in *P. alisonae* is practically identical in relative length, width, and articular expansion with that of *P. kirkpatricki* (TTUP 9002) (the tibia/humerus ratio is 1 in *P. alisonae* and *P. kirkpatricki*). *Hoplitosuchus* (Huene, 1942:pl. 28, fig. 2A, B) and *Prestosuchus chiniquensis* (Huene 1942) have considerably more massive and stout tibiae, and *Chatterjeea* (Long and Murry, 1995) has a much longer and more slender tibia compared to *P. alisonae*.

**Fibula**—Both fibulae are complete. Viewed in the mediolateral plane, the fibula is sigmoidal, with its convexity facing the proximal half of the tibia (Fig. 9A, B). With the exception of the iliofibularis trochanter, the width of the shaft is more or less constant along its length and D-shaped in cross-section. The proximal end is mediolaterally flattened, anteroposteriorly expanded, and has a flat to slightly convex articular surface that slopes to the side where it contacts the tibia. The posterior lip on the proximal extremity is moderately developed. The distal end is oval and concave in distal view and slightly more massive than the proximal end. The anterolateral surface of the shaft bears a fairly pronounced, 4 cm long insertion scar for *M. iliofibularis*. On the posteromedial side of the fibula, starting just below the proximal end, a deep groove extends half way down the shaft. The fibula and tibia are equal in length.

A moderately developed posterior lip on the proximal end is also present in *Chatterjeea* (Long and Murry, 1995), *P. kirkpatricki* (TTUP 9002) and *Batrachotomus* (SMNS 80277) but is more pronounced in *Fasolasuchus* (Bonaparte, 1981) and absent in *Prestosuchus chiniquensis* (BSP 34B) and *Rauisuchus* (Huene, 1942:pl. 27, fig. 8). The insertion for *M. iliofibularis* is well-

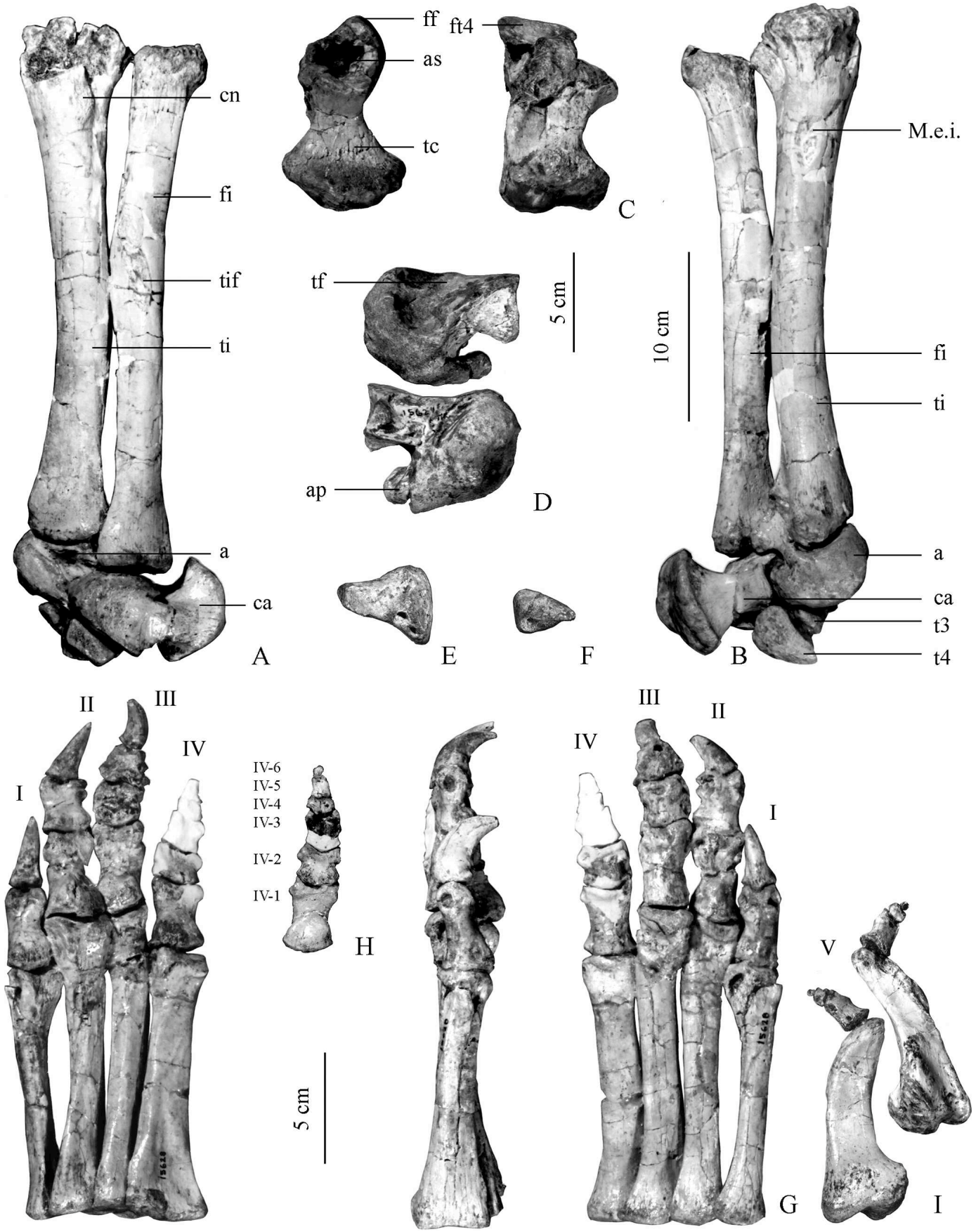


FIGURE 9. *Postosuchus alisonae*, UNC 15575 (holotype), hindlimb. Left tibia, fibula, and tarsus in **A**, anterolateral, and **B**, posteromedial view; **C**, right calcaneum in posteromedial and anteroventral view; **D**, right astragalus in posterior and anterior view; **E**, right tarsal 4; **F**, right tarsal 3; **G**, left pes in ventral, medial, and dorsal view; **H**, right pedal phalanges IV-1 to IV-6; **I**, right and left pedal digit V.

developed as in *Batrachotomus* (SMNS 80277) and *Ticinosuchus* (Krebs, 1965:fig. 52B), and less well-developed or absent in *Chatterjeea* (Long and Murry, 1995). A strongly pronounced iliofibularis trochanter is present in *Fasolasuchus* (Bonaparte, 1981:fig. 16), *Procerosuchus* (Huene, 1942), *Arganasuchus* Jalil and Peyer, 2007, and a fibula (PVL 2557) referred to *Saurosuchus* (Sill, 1974:fig. 2C). In *Prestosuchus chiniquensis* and *Rauisuchus*, the insertion for M. iliofibularis appears to form two distinct bumps (Huene, 1942).

**Pes**—The pes is relatively large compared to the manus, with the length of metatarsal III equivalent to about 48% of tibia length. It is plantigrade and has a pronounced calcaneal tuber. The pes is nearly bilaterally symmetrical, with digit IV slightly shorter than digit III and digit V reduced. All elements of the left and right pes are preserved with the exception of four distal phalanges on digit IV of the left pes, and three phalanges on digit V of the right pes.

Four tarsals are preserved for each pes: astragalus, calcaneum, and distal tarsals 3 and 4 (Fig. 9C–H). Distal tarsal 3 contacts the base of metatarsal III, and distal tarsal 4 contacts the base of metatarsal IV. Metatarsals I and II articulate with the astragalus whereas metatarsal V articulates with tarsal 4. Distal tarsals 3 and 4 bear circular ligament-attachment scars on their anterior and posterior surfaces. Distal tarsal 3 is triangular and wedge-shaped and about one third of the size of tarsal 4. Distal tarsal 4 is more complex, with several articular surfaces.

The right astragalus and calcaneum are somewhat distorted, but the left elements are well preserved. The astragalus and calcaneum are of the ‘crocodile-normal’ type, with a peg on the astragalus fitting into a socket on the calcaneum. The astragalus articulates tightly with the tibia. The dorsal process of the astragalus is moderately well developed (Fig. 9D).

The calcaneum has a prominent tuber calcanei, which is longer than broad (Fig. 9C). The lateral side of the tuber is convex, and its medial side is concave. A pronounced median groove extends the dorsoventral length of the distal surface of the calcaneal tuber.

The dorsal process of the astragalus is similar to that in *Fasolasuchus* (Bonaparte, 1981:fig. 17), *P. kirkpatricki* (TTUP 9002), *Chatterjeea* (Long and Murry, 1995:fig. 170A–C), and *Poposaurus* (Long and Murry, 1995). A similar process is also found on the astragalus (PVL 2557) referred to *Saurosuchus* (Sill, 1974:pl. 4A). *Tikisuchus* (Chatterjee and Majumdar, 1987) has a tall dorsal process on the astragalus, whereas the reconstruction of that bone in *Ticinosuchus* (Krebs, 1965:fig. 56) only shows a weakly developed dorsal process. The calcaneal tuber is longer than wide in *P. alisonae*, *Poposaurus* (Long and Murry, 1995), *P. kirkpatricki* (TTUP 9002), and *Chatterjeea* (Long and Murry, 1995), and the calcaneum (PVL 2557) referred to *Saurosuchus* (Sill, 1974:pl. 4A), but wider than long in *Fasolasuchus* (Bonaparte, 1981:fig. 18). A calcaneal tuber with a convex lateral and concave medial side is also present in *P. kirkpatricki* (TTUP 9002) and *Chatterjeea* (Long and Murry, 1995:fig. 170A–C). *Poposaurus* (Long and Murry, 1995:fig. 156A–F), and *Fasolasuchus* (Bonaparte, 1981:fig. 18) have a calcaneal tuber that is concave laterally and medially. *Chatterjeea*, *Ticinosuchus*, *Prestosuchus chiniquensis*, and *Batrachotomus* lack a dorsoventral groove on the distal end of the calcaneal tuber (Long and Murry, 1995).

The metatarsals increase in size from the first to the third, with metatarsal III being the longest (Fig. 8G–I). Metatarsal IV is longer than metatarsal I but shorter than metatarsal II. There is a slight reduction in length of metatarsal V, which is slightly more than half as long as metatarsal III. Metatarsals I–IV are similar in being expanded proximally and distally and having a narrow shaft with its minimum width about two-thirds from the proximal end. Metatarsals I–IV imbricate so that metatarsal I overlies half of metatarsal II, and so forth. Metatarsal V tapers to

a distal point (Fig. 8I). Its mediolaterally compressed distal portion and a slight dorsal curvature give it a hooked appearance.

In *Chatterjeea*, *P. kirkpatricki* (TTUP 9002), *Prestosuchus chiniquensis*, *Ticinosuchus*, and *Tikisuchus*, the metatarsals are proximally imbricated. Except for *Prestosuchus chiniquensis* (Huene, 1942), where metatarsals III and IV are of equal length, metatarsal III is generally the longest metatarsal. Metatarsal V is massive and hook-shaped in most ‘rauisuchian’ taxa. *Ticinosuchus*, however, has a longer, more slender metatarsal V (PIMUZ T2817), and *Chatterjeea* has a rather short one that is less than one half of metatarsal III (Long and Murry, 1995).

The phalangeal formula of the pes in the present specimen is 2-3-4-6-3. The right pes preserves all phalanges with the exception of phalanges 1–2 in digit V the left pes is missing phalanges 3–6 of digit IV. The fourth digit is unusual for a ‘rauisuchian’ in having six rather than five phalanges, possibly a developmental abnormality (Fig. 9H). There are three phalanges on digit V, the unguis being very small (Fig. 8I). The combined phalanges in all digits are shorter than the corresponding metatarsals. Digit I on the right pes has a large, mediolaterally compressed unguis that is longer than the first phalanx. Pedal digit II also has a large unguis, and digit III has a somewhat shorter unguis. The unguis on pedal digit IV was nearly identical in size and shape to that on digit V, but was unfortunately lost after preparation.

Three phalanges for pedal digit V were also reported for *Ticinosuchus* (Krebs, 1965). Digit V of the pes (PVL 2557) referred to *Saurosuchus* (Sill, 1974) is incompletely preserved with only a single phalanx, but the articular face of the phalanx present in *Saurosuchus* clearly indicates the original presence of additional phalanges. The phalanges of pedal digit V in *P. kirkpatricki* (TTUP 9002), *Prestosuchus chiniquensis*, and *Chatterjeea* remain unknown. *P. kirkpatricki* has often been coded as having no phalanges on pedal digit V (e.g., Chatterjee, 1985; Parrish, 1991; Parrish 1993). In *Chatterjeea* (Long and Murry, 1995:fig. 170), the pedal unguis are proportionately large and mediolaterally more compressed than in *Ticinosuchus* (Krebs, 1965), *Prestosuchus chiniquensis* (Huene, 1942), *Saurosuchus* (Sill, 1974), and *P. alisonae*.

## DISCUSSION

### Rauisuchian Relationships

A detailed assessment of the phylogenetic position of *P. alisonae* (Fig. 10) is not yet possible because there exists as yet no comprehensive analysis of the interrelationships of the known ‘rauisuchian’ taxa despite a number of recent studies on ‘rauisuchians’ (Bonaparte, 1981, 1984; Chatterjee, 1985; Galton, 1985; Kalandadze and Sennikov, 1985; Chatterjee and Majumdar, 1987; Sennikov, 1988, 1990; Parrish, 1993; Long and Murry, 1995; Alcober and Parrish, 1997; Gower, 1999, 2000, 2002; Gower and Nesbitt, 2006; Nesbitt 2003, 2005a, 2005b, 2006; Nesbitt and Norell, 2006; Gebauer, 2004; Sen, 2005; Sulej, 2005). At this point it is important to provide detailed anatomical descriptions for all valid taxa before attempting to conduct a major phylogenetic analysis of ‘rauisuchians’ (Gower, 2000). The problem of comparative data for ‘rauisuchians’ is further complicated by the fact that our understanding of Texas *P. kirkpatricki* is based in a large part on non-type specimens from coeval strata in a neighboring state, and by the reassignment of much of the original Texas material to other ‘rauisuchian’ genera. The present discussion is therefore limited to an assessment of *P. alisonae* in relation to the Texas and New Mexico specimens of *P. kirkpatricki*.

The well-preserved holotype of *P. alisonae* described here includes a number of bones previously unknown for ‘rauisuchians’ and *Postosuchus* in particular. This new information has made possible an emended generic diagnosis and more extensive comparisons of *Postosuchus* with other well known ‘rauisuchian’



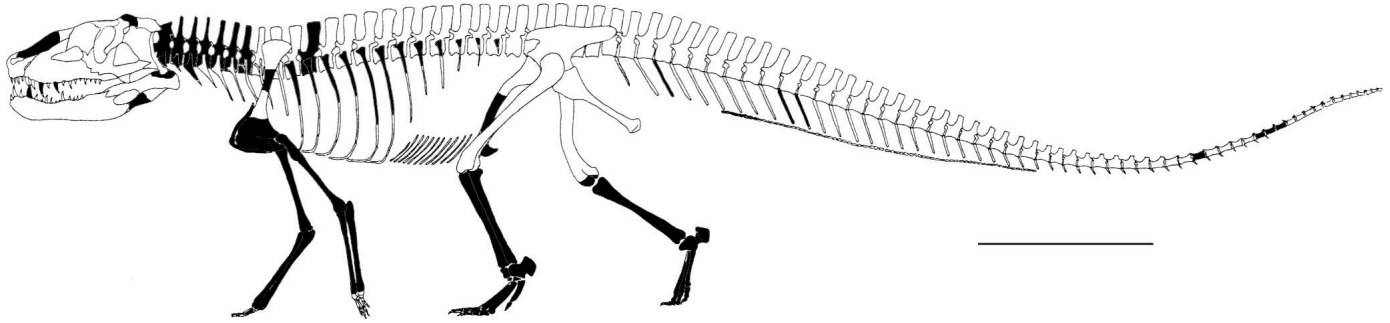


FIGURE 10. Skeletal reconstruction of *Postosuchus alisonae* based on the preserved elements of UNC 15575 (holotype). Preserved bones are shown in black. The reconstruction of the skull and pelvic bones are based on *Postosuchus kirkpatricki* (TTUP 9002). Scale bar equals 50 cm.

taxa. UNC 15575 can be referred to *Postosuchus* (Chatterjee, 1985) based on the presence of: a rugose dorsolateral ridge formed by the nasal, frontal, postorbital, and squamosal bones; sculptured frontals without a median crest; axis with two ventral keels and an anteriorly convex centrum; postaxial cervical centra with strongly developed single ventral keels that are anteriorly and/or posteriorly developed into hypapophyses; short, keeled cervical ribs on anterior cervical vertebrae; heart-shaped cervical neural 'spine tables'; subrectangular and relatively short coracoid; scapula narrowing immediately posterior to glenoid fossa and grading into thin scapular blade; deep notch ventral to medioventrally developed process of humeral head; well developed olecranon process; short manus; dorsoventrally compressed, short, blunt unguals on manual digits III and IV; a mediolaterally broad, well developed pubic boot; and a pronounced posterior lip on the proximal portion of fibula. All presently known specimens of *Postosuchus* have relatively slender limb-bone shafts compared with other 'rauisuchian' archosaurs. On the other hand *P. alisonae* clearly differs from the present, composite hypodigm of *P. kirkpatricki* in having a well-developed proximal flange on metacarpal II, inserting deeply into a proximally grooved metacarpal I. The morphologies are too regularly developed, on both the left and right sides, to be teratological, and the unique articulation of these digits points to a biomechanical adaptation which likely transcends sexual dimorphism. Certain other observed differences between *P. alisonae* and *P. kirkpatricki* are less striking and may be developmentally related such as a prearticular with a less strongly curved ventral adductor fossa margin, a retroarticular process that is dorsoventrally less expanded, and the proportionately more robust supraglenoid buttress of the scapulocoracoid. The presence of six phalanges on pedal digit IV in *P. alisonae* is unique among 'rauisuchians' but comparable material is unavailable for *P. kirkpatricki*. *P. alisonae* has three phalanges on pedal digit five whereas *P. kirkpatricki* has previously been believed to have none (Chatterjee, 1985; Parrish, 1991; Parrish, 1993). In this case, the presence of a rough, articular surface indicates the former presence of at least one additional phalanx on pedal digit V in *P. kirkpatricki*.

One of the most distinctive morphological features on the ilium of 'rauisuchians' is the presence of a buttress on the lateral side of the bone above the supraacetabular rim, which, in some taxa, extends anterodorsally onto the preacetabular process of the ilium (Gower, 2000). Another ridge, originating dorsal to the acetabular rim and extending onto the postacetabular wing of the ilium, is present in *Poposaurus* (UCMP A269/25974), *Chatterjeea* (Long and Murry, 1995), *Arizonasaurus* (Nesbitt, 2005b), and *Sillosuchus* (Alcober and Parrish, 1997), but is absent in *P. kirkpatricki* (UMMP 7266 and CM 73372; Weinbaum, pers. comm.), *Lythrosuchus* (TMM 31025-12), *Fasolasuchus* (Bonaparte, 1981:fig. 2A), *Rauisuchus* (Huene, 1942:pl. 27, fig. 6), *Prestosuchus chiniquensis* (Huene 1942:pl. 19, fig. 4), *Broms-*

*groveia* (Galton and Walker 1996:fig. 1E), *Saurosuchus* (PVL 2557), and *Batrachotomus* (SMNS 80268-80273). This character has been used to unite *Poposaurus*, *Chatterjeea*, *Arizonasaurus*, and *Sillosuchus* in a clade (Nesbitt, 2005b) and to distinguish this group from *Postosuchus* and other 'rauisuchians'.

Nesbitt (2005a) proposed a 'Group X' that unites *Arizonasaurus*, *Bromsgroveia*, *Poposaurus*, *Chatterjeea*, and *Sillosuchus* based on 10 shared derived character-states. This group, as well as *Ctenosauriscus*, '*Hypselorhachis*', and *Lotosaurus*, might potentially be united in a clade called Ctenosauriscidae (Nesbitt, 2005a). *P. alisonae* is clearly distinguished from this group by the presence of osteoderms, presence of distally expanded neural spines, undivided parapophyses on the posterior cervical vertebrae and a mediolaterally thick, well-developed pubic boot and possibly the presence of highly sculptured frontal and a well-developed dorsolateral ridge formed by the nasal, frontal, postorbital, and squamosal. However, *Arizonasaurus* and *Lotosaurus* are the only taxa of Nesbitt's (2005a) 'Group X' that preserve comparable skull material. Other characters distinguishing *Postosuchus* from 'Group X' relate to characters of the pelvic region. The relationship of *Postosuchus* to other 'rauisuchian' archosaurs not included in 'Group X' (Nesbitt, 2005a) is more difficult to assess, and further research is needed to address their relations.

*Postosuchus* is more closely related to *Batrachotomus* than to other 'rauisuchian' archosaurs as is evident from the shared features discussed above. This close relationship was previously demonstrated in phylogenetic analyses of archosaurian braincases (Gower, 2002; Gower and Nesbitt, 2006). Gower (2002) and Gower and Nesbitt (2006) proposed a sister-group relationship between *Postosuchus* and *Tikisuchus* based on similarities in the structure of the braincase. The associated postcranial material of *Tikisuchus* has only been partially described and a more detailed comparison with *P. alisonae* is not possible at the present time. However, future research might further support a close relationship between *Postosuchus* and *Tikisuchus*.

### Morphological Implications

The cervical vertebrae in *P. alisonae* have prezygapophyses with steeply dorsomedially inclined articular surfaces and postzygapophyses with steeply inclined ventrolaterally articular facets. This nearly vertical arrangement of pre- and postzygapophyses on the cervical vertebrae was also reported in *Ticinosuchus* and must have allowed considerable dorsoventral but little side-to-side mobility of the neck (Krebs, 1965). The articular surfaces of the pre- and postzygapophyses on the dorsal vertebrae are only slightly inclined, allowing for considerable side-to-side movement of the more anterior portion of the back. The prezygapophyses on the mid-caudals are directed anteriorly and have steeply medially inclined articular facets, as on the cervical

vertebrae, indicating a decrease in lateral flexibility of the mid- and distal tail region.

In *P. alisonae*, the glenoid fossa was almost perpendicular to the long axis of the scapulocoracoid, implying that the humerus could not be moved far laterally as in typically sprawling reptiles and that the forelimbs moved fore-and-aft underneath the body. The humerus could be extended considerably posteriorly but only slightly forward (out of its vertical position) resulting in a total fore-and-aft movement of about 45°. *P. alisonae* had rather long forelimbs with a proportionally small manus, the latter only about 15% of the combined length of the radius and humerus, and a rather massive coracoid.

A complete carpus is presently only known for *Postosuchus* among 'rauisuchians'. Three of the five carpal elements are somewhat rectangular and are partially fused or tightly articulated to form an arch in the same manner as the metacarpus. The fourth and fifth distal carpals are somewhat quadrangular and discoidal, respectively. The carpal elements in *P. kirkpatricki* (CM 73372) and *P. alisonae* are virtually identical, and it can be assumed that the carpus included only five ossified elements. Contrary to a statement by Chatterjee (1985), the carpus of *P. kirkpatricki* does not include a semilunate carpal, which remains a unique feature of maniraptoran theropod dinosaurs.

The unique slot-and-groove articulation between metacarpals I and II in *P. alisonae* might have served to tightly join these bones at their proximal ends and thus strengthen the metacarpus. Considering that the manus was small and had a large claw only on its first digit, it was probably not used as the major means of subduing and dismembering prey. However, the robust forelimbs could have been used to hold prey while it was ripped apart with the powerful jaws. The massive pectoral girdle, extended arms, the tightly joined metacarpus indicate that the forelimbs were actively involved in locomotion. However, this does not falsify the hypothesis that *Postosuchus* may have been facultatively bipedal (Chatterjee, 1985).

#### ACKNOWLEDGMENTS

The holotype of *Postosuchus alisonae* was discovered by Brian Coffey and Marco Brewer, then students at the University of North Carolina at Chapel Hill, in 1994. We thank many students at UNC, Chapel Hill, most notably Samantha Harlow, for preparatory work. Staff at the Paläontologisches Museum of the Universität Zürich, Staatliches Museum für Naturkunde (Stuttgart), Natural History Museum (London), Muséum National d'Histoire Naturelle (Paris), Bayerische Staatssammlung für Paläontologie und historische Geologie (Munich), and the University of California Museum of Paleontology (Berkeley) kindly granted access to material in their care. This work was supported by the Martin Research Grant, GSA research grant, the Welles Fund from the University of California Museum of Paleontology, University of North Carolina Research Council, and the Office for Undergraduate Excellence in Teaching at the University of North Carolina. Reviewers Sterling Nesbitt, David Gower, and Jonathan Weinbaum, and editor Ross Damiani, are thanked for their helpful reviews of this paper.

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Submitted June 22, 2007; accepted November 14, 2007.