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POSTOSUCHUS, A NEW THECODONTIAN REPTILE FROM THE TRIASSIC OF TEXAS AND THE ORIGIN OF TYRANNOSAURS

By S. Chatterjee
The Museum, Texas Tech University, Lubbock, Texas 79409, *U.S.A.*

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CONTENTS

Postosuchus kirkpatricki (n.g., n.sp.) is a large, gracile, carnivorous thecodontian from the late Triassic Dockum Group of Texas. The species is characterized by its erect and facultative bipedal gait, highly advanced pelvis with slightly open acetabulum and footed pubis. The teeth are large, highly serrated, deeply set in sockets, and show a wave-like replacement pattern. Some flexibility in the palate and the lower jaw permitted the animal to swallow large chunks of flesh.

Postosuchus was the arch predator of its time, and lived in the interfluves or upland regions along with aetosaurs, coelurosaurs, and ictidosaurs. The quarry's thanatocoenose probably reflects autochthonous burials of a Dockum community, perhaps in consequence of a catastrophic event such as a flash flood.

Although *Postosuchus* exhibits many carnosaurian traits, its ankle joint is of 'crocodile-normal' pattern, which suggests its pseudosuchian affinity. All Triassic reptiles previously thought to be carnosaurs are considered herein as advanced thecodontians; true carnosaurs probably appeared in post-Triassic time. *Postosuchus* is grouped with *Poposaurus*, *Teratosaurus*, *Arizonasaurus* and the unnamed 'Warwick archosaur' in the family Poposauridae. The Poposauridae and Rauisuchidae are placed in the infraorder Rauisuchia. Tyrannosaurs probably evolved from poposaurids, as indicated by the correlation between skull, pelvis and ankle structure.

1. Introduction

The late Triassic Dockum Group, extending from eastern and southeastern New Mexico to West Texas, is one of the spectacular continental red bed sequences in the United States. Mile after mile, the panoramic exposures of the red beds crop out in the valleys of the Canadian river and along the eastern escarpment of the Southern High Plains, where there is little vegetation to cover the outcrops which are thus ideal for fossil exploration. Because of their lack of economic importance, the deposits have not been studied intensively. They do, however, offer important areas of interest in the field of stratigraphy, sedimentation and vertebrate palaeontology. The first important work dealing with the vertebrate fossils of the Dockum Group was published in 1893 by Cope who recognized the remains of both amphibians and reptiles. Since that time a series of distinguished palaeontologists made major contributions to the study of vertebrates from these sediments. The best-known tetrapod fauna, collected during the past century, includes parasuchids (phytosaurs), stagonolepidids (aetosaurs), metoposaurs, and trilophosaurs.

In the summer of 1980 an expedition from the Texas Tech University discovered a rich fossiliferous site near Post, Garza County, West Texas (figure 1). Skeletons representing at least three young, and one adult of a new thecodontian reptile were unearthed from a red mudstone facies of the Dockum Group. In the following three summers, further excavation in the same quarry yielded skeletons of eight more individuals of the same animal; seven small and one of intermediate size. The large number of well-preserved specimens permits a detailed analysis of the anatomy of this unusual reptile. In addition to the new thecodontian, the Post quarry has produced a varied tetrapod fauna including new representatives of taxa hitherto unknown from the Triassic of North America. These are the earliest lizard, an ictidosaur, and a unknown amphibian (Chatterjee 1983). Parasuchid, metoposaurid and stagonolepidid remains are also found along with these vertebrates. Such a rich occurrence is very rare in the Dockum. The new quarry at Post is dominated by terrestrial vertebrates, and offers a glimpse of late Triassic palaeocommunities.

The new thecodontian, *Postosuchus kirkpatricki*, n.g., n.sp., is comparable to *Poposaurus gracilis* from the late Triassic Popo Agie member of the Chugwater Formation of Wyoming (Mehl 1915). *Poposaurus*, although incompletely known, displays an interesting mosaic of advanced pseudosuchian and theropod features in the pelvis. For example, the pubis is remarkable in that it has a massive 'foot' at the distal end as suggested by Walker (1969) and confirmed by Galton (1977). The footed pubis is recorded in two Triassic saurischian genera, *Herrerasaurus* and *Staurikosaurus*, in Jurassic and Cretaceous theropods, and in *Archaeopteryx*. The acetabulum of *Poposaurus* contains an incipient perforation at the ilio-ischiadic junction. However, the systematics of *Poposaurus*, until now, have been highly confusing, owing to lack of diagnostic material; comparison with *Postosuchus* establishes its affinity. *Postosuchus* shows various carnosaurian traits in the skull, vertebrae, pelvis and hind limb, but the retention of the sigmoidal

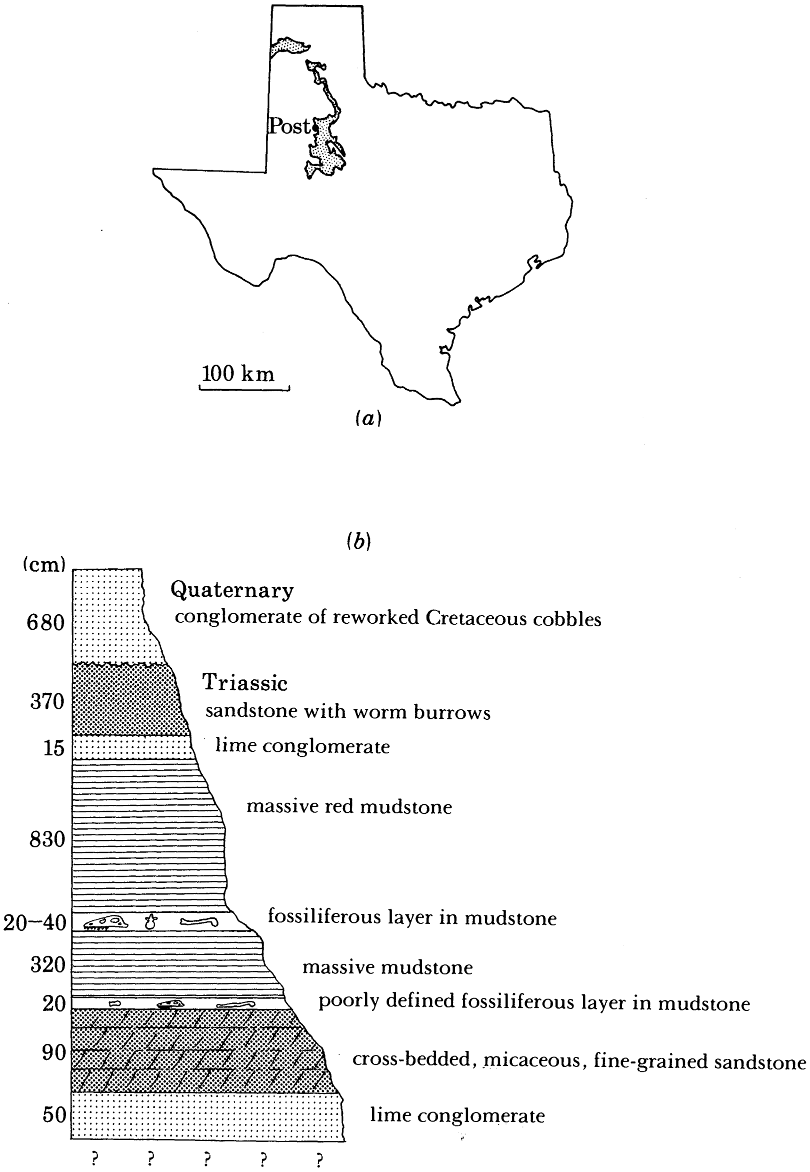

FIGURE 1. (*a*) Locality map; area of outcrop of the Dockum Group in Texas, stippled. (*b*) Geological section of the lithology of Quarry at Post. Most of the vertebrate fossils came from the upper fossiliferous layer.

femur and the crocodiloid ankle joint indicates its thecodontian affiliation. *Postosuchus* was one of the most advanced and interesting of all thecodontians, and stands in special relation to the ancestry of one group of carnosaurian dinosaurs, the Tyrannosauridae.

2. GEOLOGICAL SETTING

The late Triassic Dockum Group lies unconformably over the Permian red beds and is capped by Cretaceous, Tertiary or Quaternary sediments, or all three, which form the low plateau of the Llano Estacado (Staked Plains) of the southwestern United States. It is composed of 70–700 m of varied terrigenous clastics and was probably deposited in a fluvial–deltaic–lacustrine basin. The Dockum basins were completely enclosed by structurally high regions which might serve as the provenances of the sediments. These were the Palaeozoic remnants of the Amarillo Uplift, Bravo Dome and Matador Arch in the north, the Central Basin Platform in the west and the rejuvenated Ouchita Uplift in the south and east (McGowen *et al.* 1979). The coarse unit is composed of grey, cross-bedded sandstone, conglomerate and green lime-pellet rocks. The massive elements are often lenticular, grading laterally into a shallow mudstone, or vice versa. The coarse fractions of the rocks, which were mainly transported by tractive currents, possibly constituted the point bars and channel bars of the Dockum river system. The finer fractions (clay and silt) were probably deposited from suspension in the interchannel flood plains area. Consistent with such a fluvial interpretation, none of the various beds can be traced extensively which has led to much confusion in the subdivision of the Dockum Group. The lithological sequence present in one area is absent in another. As a result, the various subdivision schemes should only be applied locally (Dunay 1972).

The Dockum Group was named for the Dockum site in Dickens County, Texas, from which it was first described. Gould (1907) recognized two units within the Dockum Group. The basal unit, the Tecovas Formation, consists of variegated shales overlain by magenta shales and locally intercalated with massive white fine-grained sandstone. The upper unit, the Trujillo Formation is composed of a varying number of sandstones and conglomerate horizons, interbedded with red or grey shales. In the Palo Duro Canyon, this entire sequence is well exposed. This is not so in other areas. Although this subdivision is locally useful, it is difficult to apply these formational names to other regions of the Dockum until detailed lithological mapping is completed.

Gregory (1956, 1962) recognized four distinct biostratigraphic zones within the Dockum Group primarily based on the occurrence of primitive or advanced parasuchid genera. The apparent clarity of this scheme is marred by the overlap of primitive and advanced parasuchid genera in Crosby County (Chatterjee 1978*a*). In Garza County, from where the *Postosuchus* fossils were collected, an anomalous situation is seen between the lithological subdivisions and biostratigraphic zones of the Dockum Group. The sediments are predominantly red mudstone with subordinate fine-grained sandstone, as seen in the Tecovas Formation of the lower Dockum Group. However the parasuchid found along with *Postosuchus* is the advanced genus *Nicrosaurus*. It seems that these Dockum horizons cannot be taken as indicators of specific subdivisions of the late Triassic on the basis of parasuchid remains alone. Systematic mapping of the different rock units, and the careful collecting of the vertebrate fossil assemblages may help in resolving the long-standing confusion about Dockum stratigraphy.

3. Material and methods

The material of *Postosuchus* now known from Garza County of west Texas comprises 12 individuals (T.T.U. P 9000–9011). The bones were embedded in a clay matrix, mechanical preparation was done with pin-vice, ice-pick and brush. Acetone was often used to soften the clay so that the bones could be freed from the matrix. 'Glyptal' was found very effective to strengthen the bone during preparation.

The following abbreviations of institutional names precede the specimen numbers referred to in the text and identify the place of storage of the specimens: T.T.U., Texas Tech University;

T.M.M., Texas Memorial Museum, University of Texas; U.M., University of Michigan; F.M.N.H., Field Museum of Natural History, Chicago.

(i) T.T.U. P 9000: *Postosuchus kirkpatricki*, n.g., n.sp., holotype; well-preserved skull and partial postcranial skeleton of an adult individual; estimated skull length 550 mm; Garza County, Texas.

(ii) T.T.U. P 9001: *Postosuchus kirkpatricki*, n.g., n.sp., paratype; complete postcranial skeleton without skull of a young individual, about half the size of the adult one; Garza County, Texas.

(iii) T.T.U. P 9002: *Postosuchus kirkpatricki*, n.g., n.sp., paratype; nearly complete skeleton of an intermediate-sized individual; estimated skull length 450 mm; Garza County, Texas.

(iv) T.T.U. P 9003–9011: *Postosuchus kirkpatricki*, n.g., n.sp., paratype; nine incomplete postcranial skeletons of young individuals of similar size and proportions; Garza County, Texas.

(v) U.M. 7473: braincase; Case (1922, plate 13D–F) described this as *Coelophysis* sp. from the Dockum Group of Texas, but it definitely belongs to *Postosuchus*.

(vi) U.M. 23127: right side of a pelvis with a footed pubis, described by Case (1943) as a new parasuchid from the Dockum Group of Texas, but it is assigned to *Postosuchus*.

(vii) T.M.M. 31025-12: right ilium of an adult *Postosuchus* from the Dockum Group of Texas.

To illustrate the distribution of size range among large, intermediate and small individuals the main measurements of *Postosuchus* are given in table 1.

4. Systematic palaeontology

Class Reptilia
Subclass Archosauria
Order Thecodontia
Suborder Pseudosuchia
Infraorder Rauishuchia
Family Poposauridae Nopsca, 1928
Genus *Postosuchus*, new genus

Generic definition. Large gracile, predaceous pseudosuchian with erect and facultatively bipedal gait, up to 4 m in length. Skull large, narrow and deep with subnarial and antorbital fenestrae; interdental plates on the lingual alveolar margin; teeth highly serrate, recurved; braincase deep with ossified laterosphenoid; prominent dorso-lateral crest over the orbit; skull roof akinetic but palate flexible, and intramandibular kinesis present; lateral mandibular fenestrae 2. Cervicals elongate, dorsals short with accessory articulations, sacrals 4, co-ossified, caudals slender. Pelvis advanced; acetabulum deep with short anterior but long posterior processes; subvertical buttress above acetabulum; small perforation at the ilio–ichiadic contact; ischium and pubis long with strong median symphysis; ischium rod-like and slender, pubis with greatly expanded distal end. Femur sigmoidal; tibia with distal notch for ascending process of astragalus; ankle joint 'crocodile-normal'; pes symmetrical, digitigrade.

Type species. *Postosuchus kirkpatricki*, new species.

Horizon. Dockum Group, late Triassic.

Derivation of name. The generic name refers to the town of Post, near which the type material was discovered; the specific name is given in honour of Mr and Mrs Jack Kirkpatrick for their help and hospitality during my field work.

TABLE 1. MAIN MEASUREMENTS OF *POSTOSUCHUS*

	T.T.U. P 9001 (small)	T.T.U. P 9002 (intermediate)	T.T.U. P 9000 (large)
skull length	—	450	550
skull width	—	180	210
skull height	—	150	214
total length of the lower jaw		480 (e.)	600
height of the lower jaw	—	128	160
presacral column length	807	1180 (e.)	—
sacral length	117	170 (e.)	—
caudal length	816	1200 (e.)	—
total length of the vertebral column	1740	2550 (e.)	—
scapulocoracoid height	140	292	400
scapula, length of the dorsal edge	60	93	146
coracoid length, ventral edge	80	140	180
humerus length	152	225	265
humerus, least diameter of the shaft	10	20	29
humerus, greatest proximal width	28	82	100
humerus, greatest distal width	18	48	70
radius length	—	205	230
radius, least diameter of the shaft	—	13	14
radius, greatest proximal width	—	26	34
radius, greatest distal width	—	20	30
ulna length	—	230	257
ulna, least diameter of the shaft	—	16	18
ulna, greatest proximal width	—	35	46
ulna, greatest distal width	—	26	36
radiale length (proximo-distal)	—	25	—
radiale, transverse width	—	34	—
radiale, antero-posterior width	—	24	—
ulnare length (proximo-distal)	—	22	—
ulnare, transverse width	—	12	—
ulnare, antero-posterior width	—	17	—
metacarpal I length	—	31	—
metacarpal II length	—	40	—
metacarpal III length	—	40	—
metacarpal IV length	—	37	—
metacarpal V length	—	25	—
manus length, including carpus		105	—
ilium, crest length	125	214 (e.)	380
ilium height	90	115	180
ilium, across acetabulum	53	80	120
ischium height	150	230	330
ischium, width of proximal expansion	25	72	100
ischium, width of the distal expansion	11	30	50
pubis height	200	—	—
pubis, width of proximal expansion	30	—	—
pubis, width of distal expansion	84	—	—
femur length	231	383	505
femur, least diameter of the shaft	21	42	57
femur, greatest proximal width	45	77	95
femur, greatest distal width	30	76	93
tibia length	198	286	—
tibia, least diameter of the shaft	12	28	—
tibia, greatest proximal width	35	60	82
tibia, greatest distal width	25	48	—

TABLE 1. (*cont.*)

	T.T.U. P 9001 (small)	T.T.U. P 9002 (intermediate)	T.T.U. P 9000 (large)
fibula length	201	274	—
fibula, least diameter of the shaft	10	20	—
fibula, proximal transverse width	12	26	32
fibula, distal transverse width	8	18	24
astragalus length (proximo-distal)	32	56	100
astragalus, transverse width	33	56	110
astragalus, antero-posterior width	20	35	52
calcaneum length (proximo-distal)	20	40	70
calcaneum, transverse width	22	50	75
calcaneum, antero-posterior width	44	80	140
metatarsal I length	66	—	—
metatarsal II length	83	—	—
metatarsal III length	85	126	—
metatarsal IV length	61	110	—
metatarsal V length	41	77	—
pes length, including tarsus	180	270 (e.)	—
estimated total length	2000	3000	4000

(e.), Estimated.
All measurements in millimetres.

Specific definition. Same as for genus.

Holotype. T.T.U. P 9000, skull and partial postcranial material of an adult individual.

Paratype. T.T.U. P 9001–9011, additional material of 11 individuals.

Locality. Miller's Ranch, near Post, Garza County, West Texas.

All the poposaurid material from the Dockum Group is considered here as *Postosuchus kirkpatricki*. Rank and nomenclature are discussed in §11.

5. DESCRIPTION OF *POSTOSUCHUS*

Skull

Skull bones of two individuals (T.T.U. 9000 and 9002) were found disarticulated (figures 3 and 4), but they show fine detail, and are excellently preserved and permit a comprehensive description and restoration. The skull is extremely narrow in front, wide and deep behind, and is massively built with bony dermal excrescences, foreshadowing the structure of many tyrannosaurs. The holotype specimen is 55 cm long, 21 cm broad, and 21.4 cm deep.

Dermal roof bones

See figures 2–5. Each *premaxilla* forks postero-dorsally to encircle the external naris, the anterior fork meets the nasal, the posterior fork is wedged between the nasal and maxilla. The external naris is oval in outline, large, subterminal, and high up on the snout. Below the naris, the main body of the premaxilla is rectangular, longer than its depth. Posteriorly its articulation with the maxilla is loose, and is interrupted by the small subnarial fenestra. The median symphyseal facet is triangular and smooth. Below and behind the symphysis is a deep excavation which continues up to the adjoining maxilla. There are four alveoli, bordered internally by fused interdental plates. The anterior alveolus is very small.

The *maxillae* are nearly hidden in dorsal aspect, but well exposed in lateral view. Each bone is a triradiate vertical plate, deeply emarginated posteriorly by the large and elongate antorbital fenestra. The anterior margin curves postero-dorsally to receive the premaxilla and nasal above, and the lacrimal below. The ventral border is undulating, and forms the alveolar margin. Posteriorly, it meets the jugal by a strong and serrate suture. A rugose ridge runs horizontally along the length of the maxialla and jugal below the antorbital fenestra. Ventral to this ridge, there is a row of foramina that transmit nerves and blood vessels to the skin.

In médial view, the maxilla shows various vacuities and sinuses associated with olfaction. Behind the premaxillary excavation, discussed earlier, there is a similar excavation in the maxilla, just above the subnarial fenestra. Since this conjoined chamber is located postero-ventral to the naris, it might have served an area for Jacobson's organ (figure 3*b*). Anterior to the antorbital fenestra, there is another triangular depression that probably accommodated the vestibule. In the lingual wall of the alveoli, the fused interdental plates decrease in height posteriorly. They are bordered dorsally by a shallow horizontal groove, pierced with a row of pits at regular intervals. There are 13 alveoli in the maxilla.

The *nasals* are extremely long and narrow bones and take up about half the length of the skull roof. Anteriorly each bone is bifid to enclose the naris in conjunction with the premaxilla. There is a sharp 90° angulation between the dorsal and lateral surface of the nasal with a rugose and longitudinal ridge in between. The lateral surface rides over the maxilla and contracts in depth posteriorly and finally fades out. Behind the maxillary contact, the dorsal surface tapers

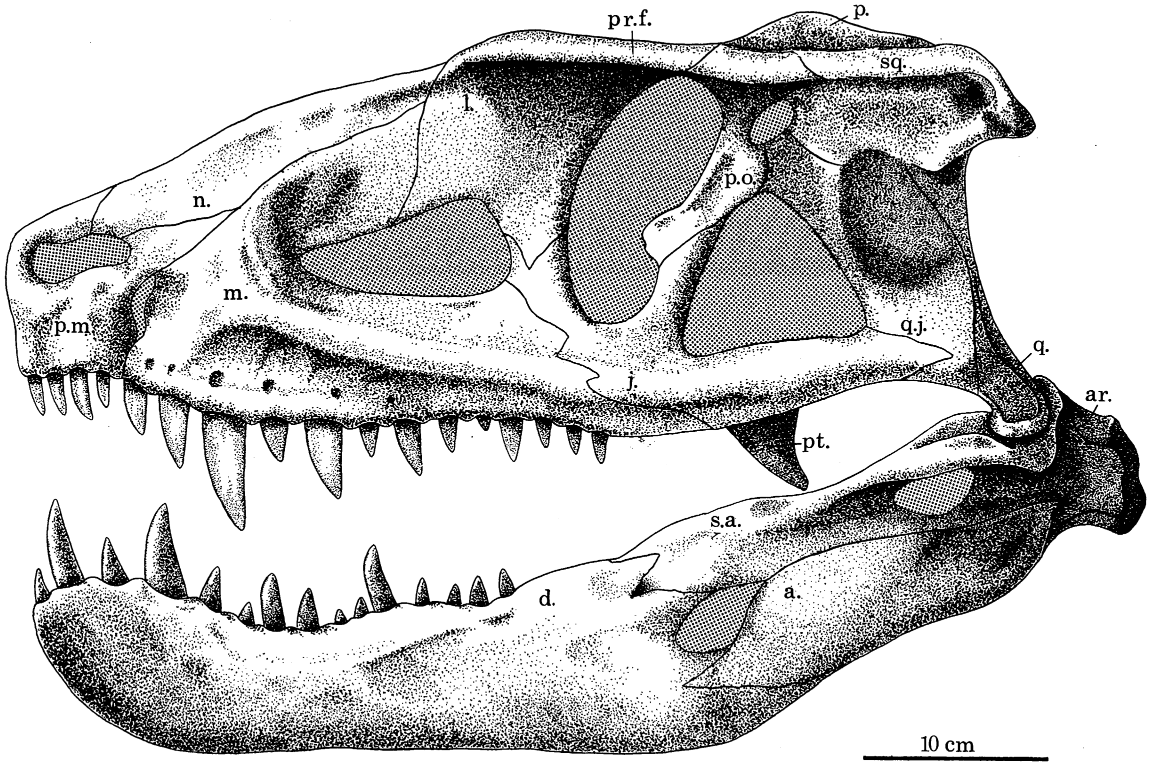

FIGURE 2. *Postosuchus kirkpatricki*, n.sp. Composite restoration of the skull in lateral view. Magn. × 0.25. Abbreviations: a., angular; ar., articular; d., dentary; j., jugal; l., lacrimal; m., maxilla; n., nasal; p., parietal; p.m., premaxilla; p.o., postorbital; pr.f., prefrontal; pt., pterygoid; q., quadrate; q.j., quadratojugal; s.a., surangular; sq., squamosal.

at its end and fits into a shelf of the lacrimal at the postero-lateral edge. The posterior apex is inserted into the frontal.

The *frontals* are relatively short, wide and heavy, paired bones, each receiving the prefrontal antero-ventrally, and underlapping the nasal forward. Posteriorly, they firmly suture with the parietals. The frontal does not enter into either the orbital margin or supratemporal fenestra. The undersurface is hollowed out for the passage of the olfactory tract.

The *parietals* form, by their union, a sagittal crest. Each bone is an L-shaped structure, bordering the supratemporal fenestra laterally. The lower leg of the L curves postero-laterally as a vertical plate to join the squamosal. The upper leg of the L meets the frontal and postfrontal by serrate sutures. Ventrally the parietals firmly lap the dorso-lateral edge of the supraoccipital.

The *lachrymal* is an extensive thick plate forming a deep shelf around the postero-dorsal part of the antorbital fenestra. The shelf is pierced by a lachrymal duct passing from the orbital cavity to the antorbital fenestra. Above the shelf, the dorsal border forms a thick, rugose, overhanging crest. The tapered anterior process contacts the maxilla and nasal. Medially it has extensive articulation with the nasal and frontal. Posteriorly, there is a distinct facet for the reception of the prefrontal: the two elements form the entire antero-dorsal border of the orbit, excluding the frontal from its formation. A strong descending process of the lachrymal joins firmly with the jugal to form the preorbital bar.

The *prefrontal* is a large triangular plate forming an overhanging ledge to the orbit. Its lateral free edge is highly rugose. The bone is firmly fixed against the lachrymal, frontal, postfrontal, and postorbital.

The *postfrontal* is a small bone occupying the position between the parietal and postorbital.

The *postorbital* is a T-shaped bone in side view, the cross-bar lies between the prefrontal and squamosal. The ventral bar curves forward with an anterior projection into the orbit, as seen in tyrannosaurs, and overlaps the ascending process of the jugal. Posteriorly it makes contacts with the quadratojugal and squamosal above the infratemporal fenestra.

The *jugal* is a large, three-pronged bone, radiating anteriorly, dorsally and posteriorly. The anterior prong receives the maxilla in front and the lachrymal above. The dorsal branch joins with the postorbital to form a bar between the orbit and the infratemporal fenestra. Internally, directly below the postorbital bar, there are two distinct facets on the jugal for the reception of the ectopterygoid (figure 3*b*). The posterior branch extends almost to the level of the jaw joint and intimately embraces the quadratojugal.

The *quadratojugal* is very extensive in side view. Posteriorly it joins the quadrate by a vertical suture. The bone is expanded dorsally and abuts against the squamosal. Here the lateral wall is deeply hollowed out probably to support the anterior edge of the tympanum. Anteriorly the bone makes such a pronounced forward projection across the infratemporal fenestra that is divides it into two separate openings, and touches the portorbital on the other side. This kind of forward projection of the quadratojugal is known in tyrannosaurs: it may afford additional area for the origin of m. adductor mandibulae externus superficialis et medialis (Walker, A. D., 1964). Below the infratemporal fenestra, the quadratojugal firmly articulates with the jugal.

The *squamosal* is a complex bone showing five projections in different directions. Two projections on the dorsal surface border the supratemporal fenestra and meet the parietal and postorbital at two ends. Behind these, there is a hook-like ventral projection which has a cup-shaped depression for the reception of the quadrate head. A ventro-lateral projection, seen

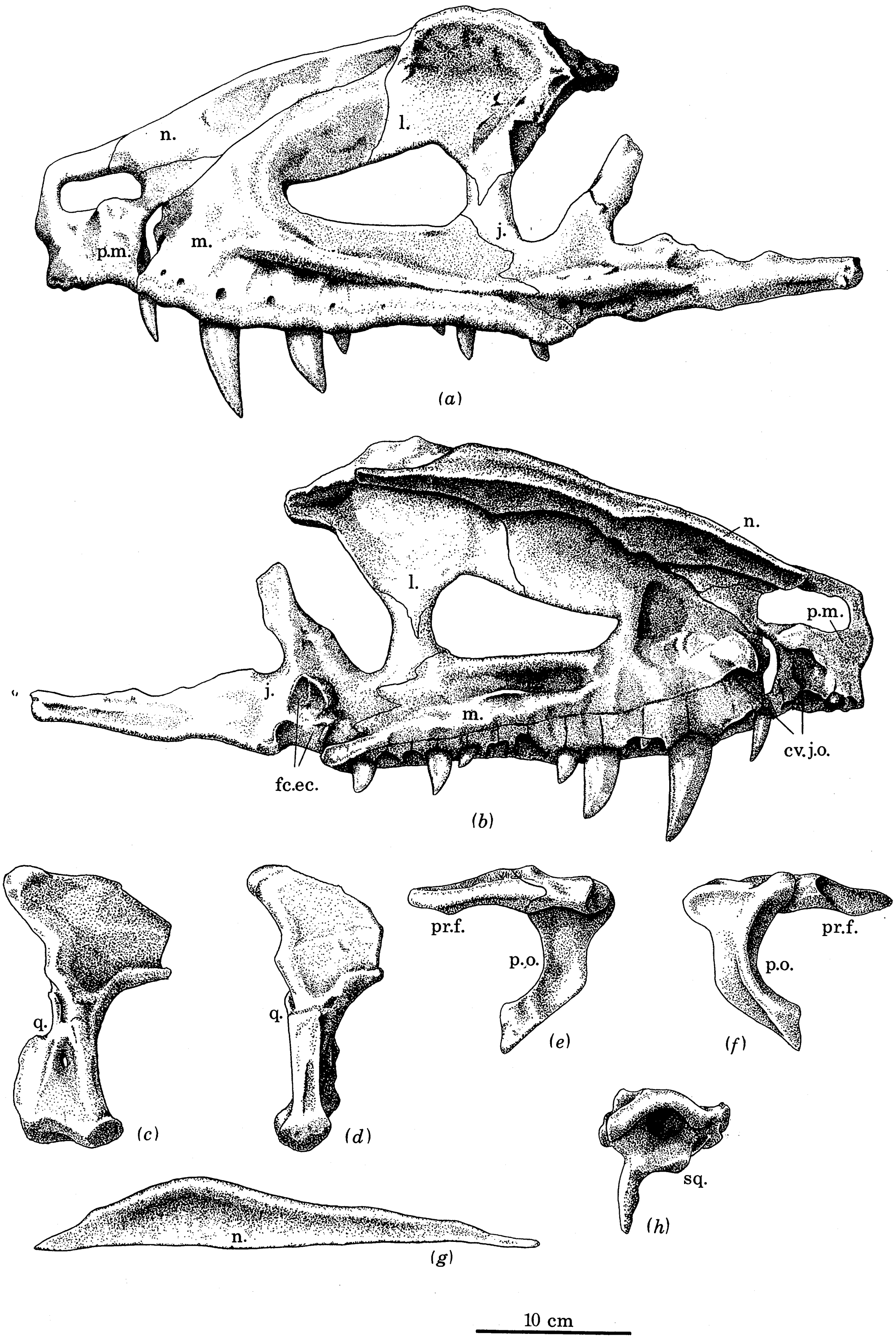

FIGURE 3. *Postosuchus kirkpatricki*, n.sp. Isolated skull fragments, left side, specimen T.T.U. P 9000, holotype (magn. × 0.25). (*a*) and (*b*) Lateral and medial views of the partial skull. Abbreviations: p.m., premaxilla; m., maxilla; n., nasal; l., lacrimal; j., jugal; cv.j.o., cavity for Jacobson's organ; fc.ec., facets for ectopterygoid. (*c*) and (*d*) Posterior and medial views of the quadrate; (*e*) and (*f*) lateral and medial views of the conjoined prefrontal–postorbital; (*g*) dorsal view of nasal; (*h*) squamosal, lateral view.

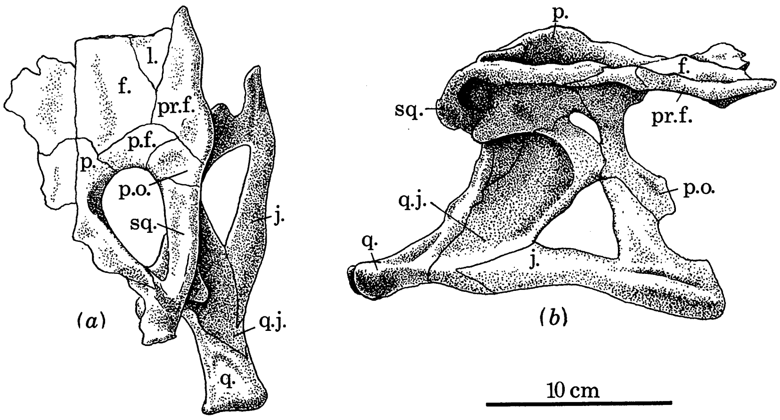

FIGURE 4. *Postosuchus kirkpatricki*, n.sp. Isolated skull fragments, specimen T.T.U. P 9002 (magn. × 0.25). (*a*) and (*b*) Dorsal and lateral views of the posterior half of the skull, mainly right side. Abbreviations: f., frontal; j., jugal; l., lacrimal; p., parietal; p.f., postfrontal; p.o., postorbital; pr.f., prefrontal; q., quadrate; q.j., quadratojugal; sq., squamosal.

in side view, is inserted between the quadrate and the quadratojugal. Above this a strong lateral projection overhangs the quadratojugal.

Palatal complex

See figures 5 and 6. The palate is narrow, deeply vaulted and lacks teeth. It is interrupted by the internal nares in front and palatal fenestra behind. The internal nares are placed far behind the external nares.

The *vomers* are represented by fragile elongate bones. Anteriorly they insert into the premaxillae. Laterally they are bordered by the maxillae.

The *palatines* are small and articulate with the pterygoid posteriorly. Each bone takes part in the formation of choana and palatal fenestra.

The *pterygoid* is an extremely long and tripartite bone, differentiating into a medial palatal ramus, a thick postero-dorsal quadrate ramus, and narrow postero-ventral process for the ectopterygoid. The palatal ramus extends forward as a long vertical plate to meet its antimere briefly; the palatal vacuity is narrow. Behind this contact, the quadrate ramus rises upward and backward, and sits loosely on a shelf of the quadrate. There is a deep pocket at the root of the quadrate ramus for the reception of the basipterygoid process. The postero-ventral branch tapers to its end and makes an extensive but loose contact with the ectopteryoid laterally.

The *ectopterygoid* is a stout, rib-like structure with two articulating facets for the jugal. A groove of unknown function runs horizontally between the two facets (figure 6*c*). This feature is described as 'carnosaurian' by Ostrom (1969). The shaft is triangular in cross-section. It forms a lateral support for the palate, curving posteriorly to lap the undersurface of the pterygoid. The unions of the ectopterygoid with the jugal and pterygoid seem to be loose permitting some kinesis.

The *quadrate* is very tall, and distinctive in that the head is twisted and curved dorso-laterally in relation to the ventral expansion. The head has a spherical knob which fits firmly into a socket of the squamosal. A longitudinal groove runs vertically from the head in lateral aspect. The posterior surface is concave in side view, providing the frame for the eardrum. The lower

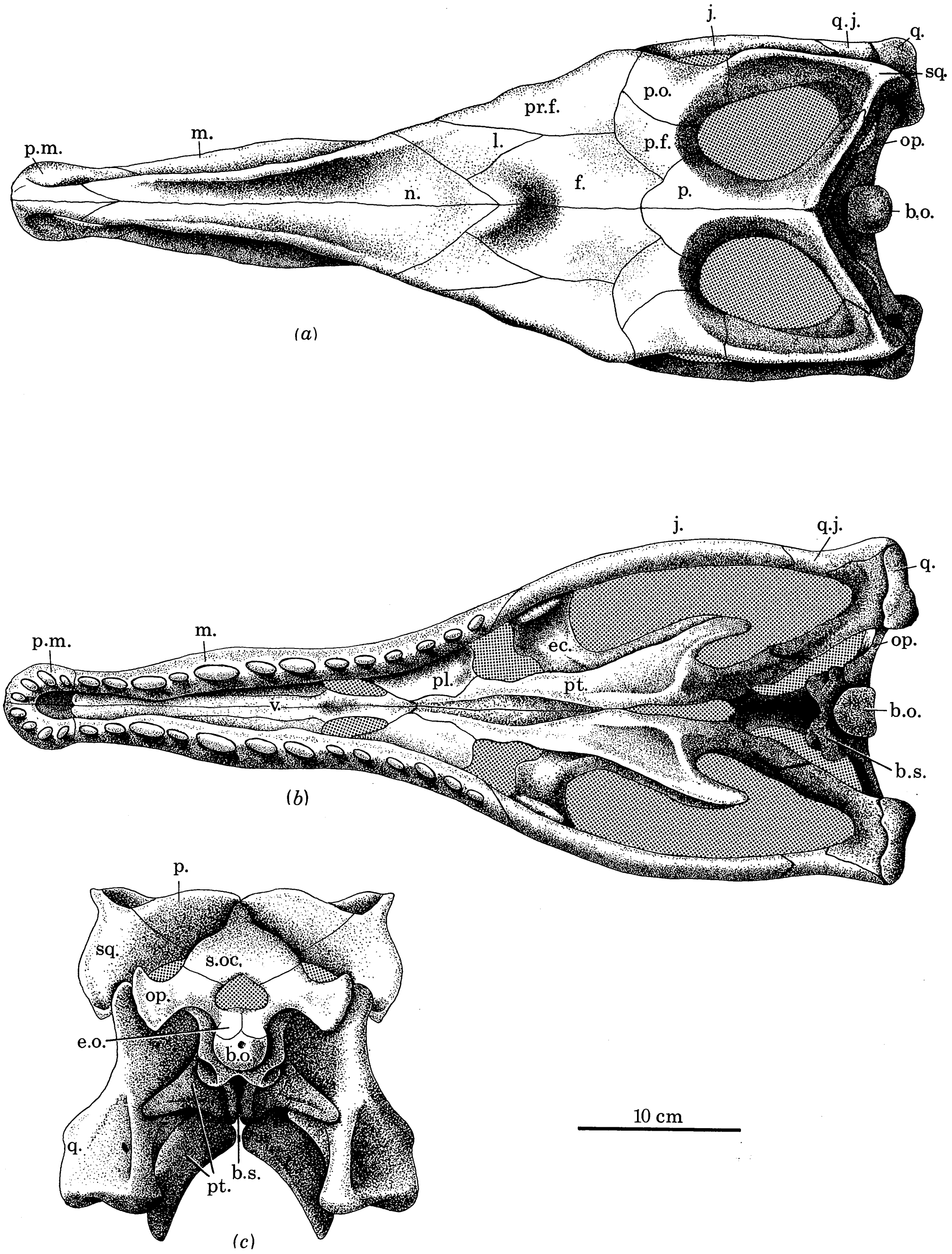

FIGURE 5. *Postosuchus kirkpatricki*, n.sp. Composite restoration of the skull (magn. × 0.25). (*a*) Dorsal view; (*b*) ventral view; (*c*) occipital view. Abbreviations: b.o., basioccipital; b.s., basisphenoid; ec., ectopterygoid; e.o., exocipital; f., frontal; j., jugal; l., lacrimal; m., maxilla; n., nasal; op., opisthotic; p., parietal; p.f., postfrontal; pl., palatine; p.m., premaxilla; p.o., postorbital; pr.f., prefrontal; pt., pterygoid; q., quadrate; q.j., quadratojugal; s.oc., supraoccipital; sq., squamosal; v., vomer.

half of the lateral process is braced strongly by the quadratojugal, prohibiting any movement. The quadrate–quadrotojugal suture is interrupted by a small foramen. Ventrally there are two condyles which fit into the articular of the lower jaw.

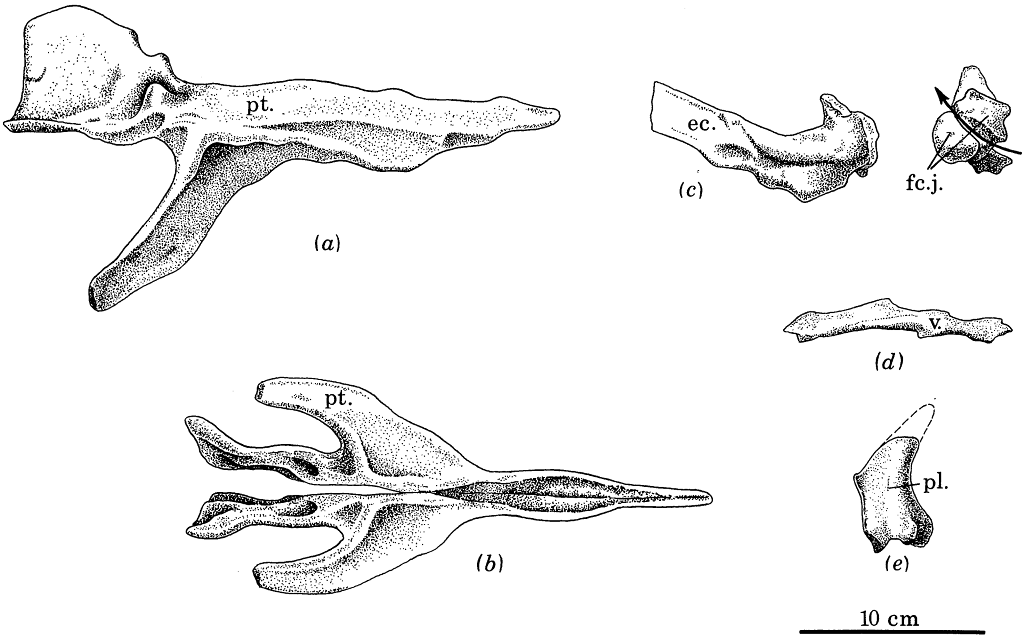

FIGURE 6. *Postosuchus kirkpatricki*, n.sp. Isolated skull fragments of the palate, left side (magn. ×0.25). (*a*) and (*b*) Pterygoid in medial and ventral views; (*c*) ectopterygoid in dorsal and lateral views; fc.j., facets for jugal; arrow indicates the ectopterygoid groove; (*d*) vomer, dorsal view; (*e*) palatine, dorsal view.

Braincase

See figure 7. Two well-preserved specimens (T.T.U. 9000 and 9002) display the detailed morphological features of the braincase. Also, Case (1922, plate 13D–F) described an isolated braincase from the Dockum Group of Crosby County, Texas, as very reminiscent of a primitive theropod dinosaur. Since the only dinosaur known from the late Triassic of the southwest United States at that time was *Coelophysis*, Case provisionally placed this braincase in that genus. However Case's specimen (U.M. 7473) shows very little resemblance to *Coelophysis*, but corresponds so well with *Postosuchus kirkpatricki* that there is little doubt of its taxonomic affinity.

The braincase, in posterior view, is very deep with a plate-like occiput occupying a nearly vertical position. The occipital condyle, formed mainly by the basioccipital, is single and hemispherical with an extremely short neck. Below the level of the condyle, the basioccipital is differentiated into a pair of knobs which are closely apposed to the lateral tubera of the *basisphenoid*. The ventral suture between these two elements is deeply grooved and is pierced by a single median and two lateral pits indicating residual areas of cartilage. Anterior to the tubera, the basisphenoid descends as a confluent median structure which is V-shaped in cross-section, but diverges terminally to form the basipterygoid processes. Each process shows a distinct ventro-lateral facet for articulation with the pterygoid.

Dorsally, the *basioccipital* is capped by the conjoined exoccipitals which form the floor and the lateral wall of the foramen magnum. The latter is oval in outline with a transverse width

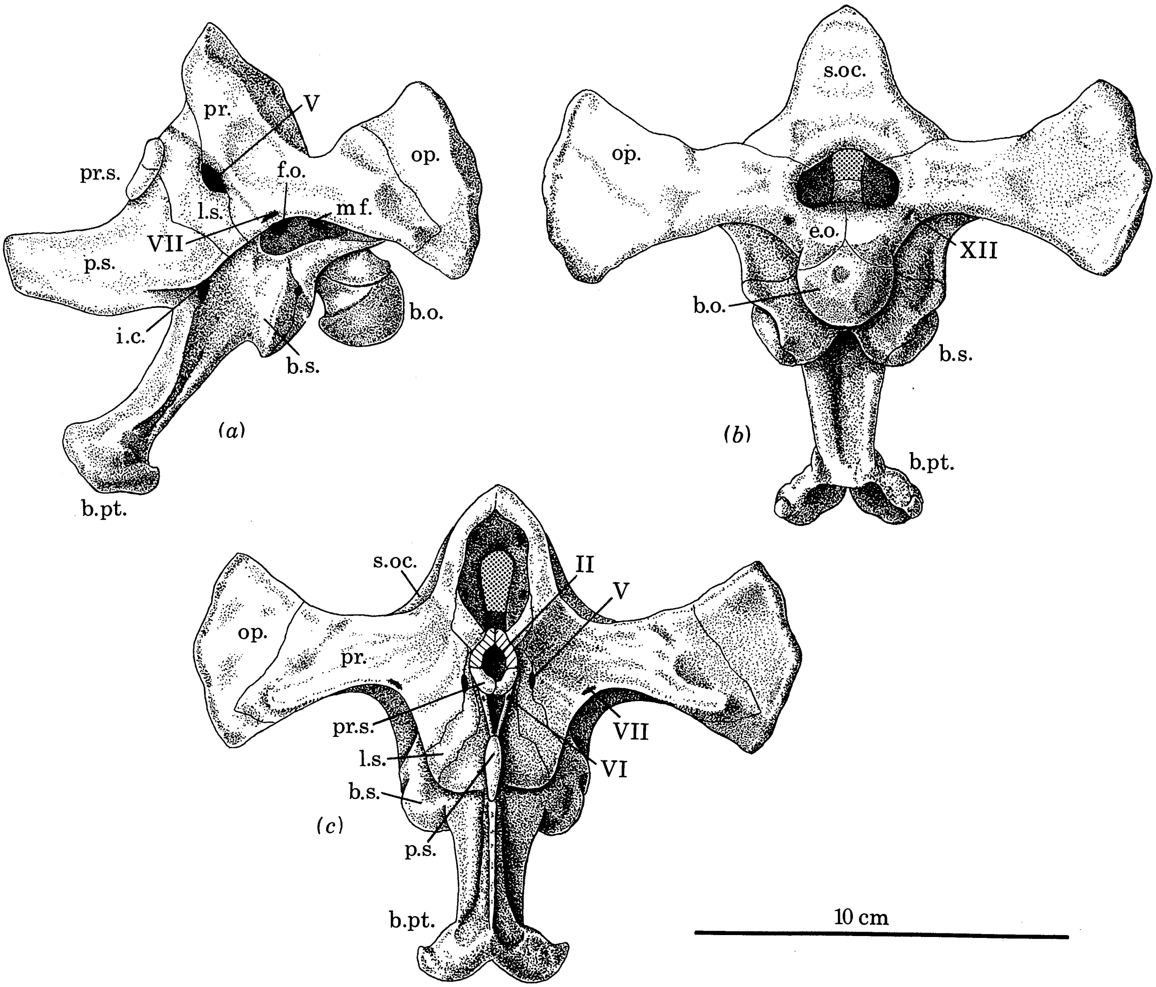

FIGURE 7. *Postosuchus kirkpatricki*, n.sp. (magn. × 0.5). Composite restoration of the braincase. (*a*) Left lateral view; (*b*) posterior view; (*c*) anterior view. Abbreviations: b.o., basioccipital; b.s., basisphenoid; b.pt., basipterygoid process; e.o., exoccipital; eu., eustachian fossa; f.o., fenestra ovalis; i.c., foramen for internal carotid; l.s., laterosphenoid; m.f., metotic foramen; op., opisthotic; pr., prootic; pr.s., presphenoid; p.s., parasphenoid; s.oc., supraoccipital; foramina for cranial nerves in Roman numerals.

equal to that of the condyle. Ventrolateral to the foramen magnum, each *exoccipital* shows a foramen for the hypoglossal (XII) nerve. The suture between the exoccipital and opisthotic is not visible in any specimens. The *opisthotics* are wing-like structures, extending backward and outward as powerful paroccipital processes which abut against the squamosal and quadrate head. Anteriorly it is sheathed by the pro-otics. The *supraoccipital* is a flat bone on its dorsal aspect, and slants upward and forward as a narrow process. Laterally it shows a rugose articular facet for the parietal.

In lateral view, the *basisphenoid* extends forward as a narrow median blade, the cultriform process, which is sheathed externally by the parasphenoid. Dorsally the blade is excavated into a large pituitary fossa or sella turcica. The posterior wall of the fossa, the dorsum sellae, is pierced laterally by a pair of openings for the abducens (VI) nerve. Above the sella turcica, the crescentic presphenoids, in conjunction with the laterosphenoids, enclose a large fissure for the optic (II) nerve. Ventrally, a deep horizontal groove on either side of the cultriform process continues backward close to the mouth of the metotic foramen. The anterior end of the groove communicates by a small foramen to the pituitary fossa and indicates the course of the internal carotid artery. Dorso-laterally, the suture of basioccipital–basisphenoid is excavated into a pair of pockets: the cochlear process for the reception of the elongated lagenae.

Behind the cultriform process, the *laterosphenoid* is wedged between parasphenoid and pro-otic. The bone is incompletely preserved in the front, so its relation with the skull roof is not clear, and the foramina for the oculomotor (III) and trochlearis (IV) could not be located. Posteriorly the laterosphenoid is bounded by the pro-otic, but is partly separated by a large foramen for the trigeminal (V) nerve. A narrow longitudinal groove running upward from the trigeminal foramen indicates the course of the opthalmic branch of the fifth nerve.

Each *pro-otic* tapers backward and upward to overlap the anterior part of the opisthotic; together they form the tympanic groove which leads into the fenestra ovalis for the reception of the stapes. A large opening posterior to it is the metotic foramen, transmitting nerves IX–XI, and the posterior branch of the jugular vein. Anterior to it is a slit-like aperture indicating the outlet for the facialis (VII) nerve.

Lower jaw

See figures 8 and 9. The lower jaw consists of seven elements: the dentary, splenial, coronoid, angular, surangular, prearticular and articular, most of which were found disarticulated. The jaw is strongly built, with a pronounced retroarticular process, but no projection in the coronoid region. Two external fenestrae are developed in the lateral wall of the mandible. The symphyseal union is weak, probably held in life by a ligament.

The *dentary* is the most massive element in the lower jaw, occupying three-quarters of the total length. It is narrow in the front but deep behind. Anteriorly the inner surface lacks a symphyseal facet. The dental margin curves upward and supports 15 alveoli. The lingual border of the alveoli was formed by the fused interdental plates. Below this, the inner surface is traversed by a longitudinal Meckelian canal which tapers forward and contains a few small foramina. The canal carried the chorda tympani nerve, the internal mandibular nerve and artery, and anteriorly, the mandibular vein (O'Donoghue 1920). Along the ventral border, the dentary shows a flange for the attachment of the splenial. Posteriorly the dentary joins with the surangular and angular laterally, and prearticular and coronoid medially in a flexible contact.

The *splenial* is a thin subtriangular plate with tapering ends forming part of the floor and much of the inner wall of the Meckelian canal. The ventral margin has a longitudinal groove for union with the dentary. At mid-length, a small foramen indicates the outlet for the mandibular ramus of the fifth nerve. Posteriorly, together with the dentary, the splenial has a slot for the reception of the angular.

The *coronoid* is a small triradiate bone forming the anterior rim of the adductor fossa. It lies behind the dentary and between the surangular and prearticular.

The *angular* bridges the gap between the dentary and prearticular. It lies below the surangular, forming a large external mandibular fenestra. Internally, the bone is trough-like, forming the floor of the adductor fossa and the posterior part of the Meckelian canal. Below the trough a strong ventro-medial facet fits against a similar facet of the prearticular. Behind the facet, the bone curves upward to a tapering end, and covers the lateral and lower surfaces of the surangular.

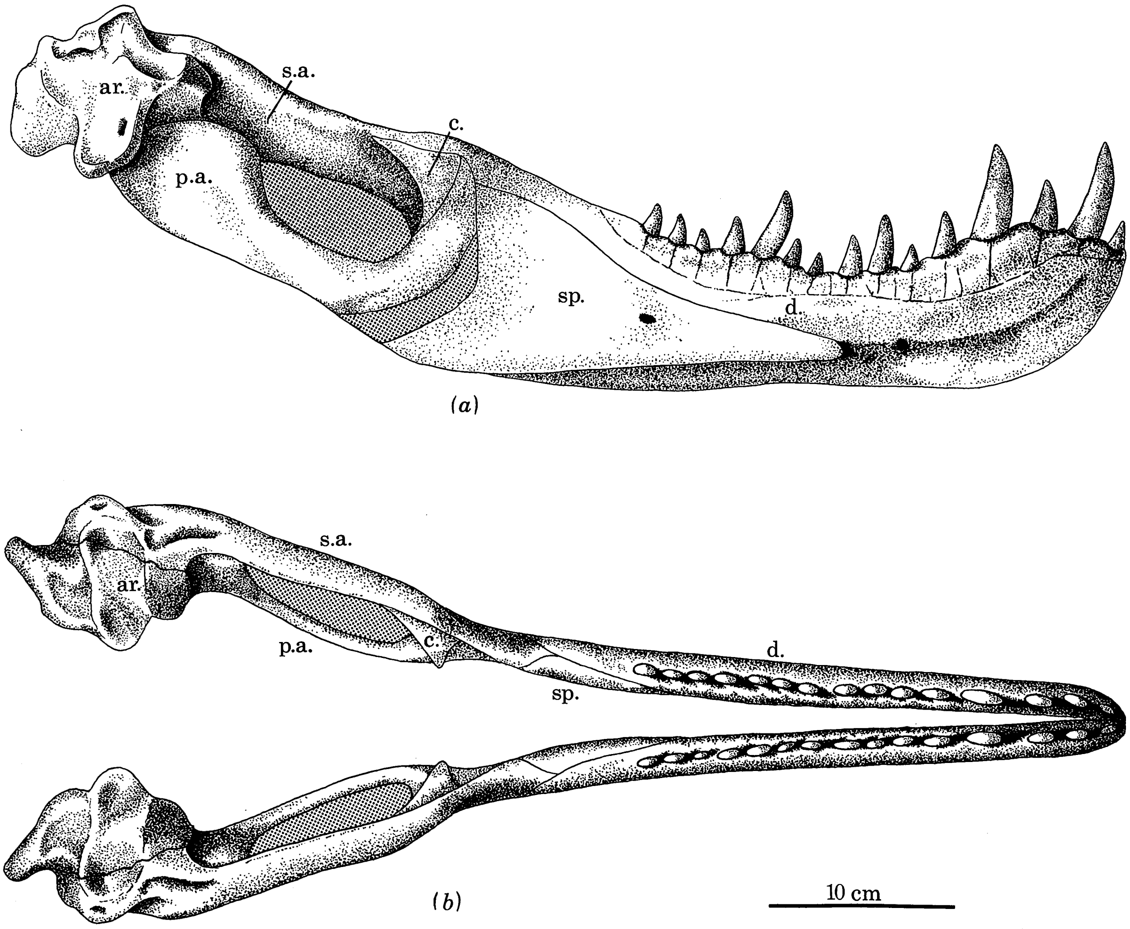

FIGURE 8. *Postosuchus kirkpatricki*, n.sp. (magn. ×0.25). Composite restoration of the lower jaw. (*a*) Medial view; (*b*) dorsal view. Abbreviations: ar., articular; c., coronoid; d., dentary; p.a., prearticular; s.a., surangular; sp., splenial.

The *surangular* is a long bone forming the upper limit of the mandibular fenestra. Anteriorly the bone becomes thin and shows a deep internal groove which fits into the posterodorsal end of the dentary. From this groove a foramen emerges obliquely on to the outer surface. Above this groove a strong facet near the coronoid contact indicates the insertion point of the mandibular adductor tendon. Posteriorly the bone coats the whole lateral surface of the articular and takes a joint role in the formation of the glenoid fossa. A longitudinal ridge is seen on the lateral surface almost throughout its length, passing above the surangular foramen (= posterior mandibular fenestra), but dies out behind the glenoid. A small foramen lies here between the glenoid and the ridge. Behind the surangular foramen, the bone projects ventrally as a thin blade which laps against the inner surface of the angular.

The *prearticular* extends forward as a narrow process and slips between the dentary and splenial. It receives the coronid above the splenial. The dorsal margin is highly curved and forms the lower margin of the adductor fossa. Ventrally, it has a broad contact with the angular. A thin posterior process wraps the medial and lower surfaces of the articular.

The *articular* is a short, compact bone which is broadest at the glenoid fossa. The conjoined glenoid with the surangular is saddle-shaped to receive the double condyles of the quadrate.

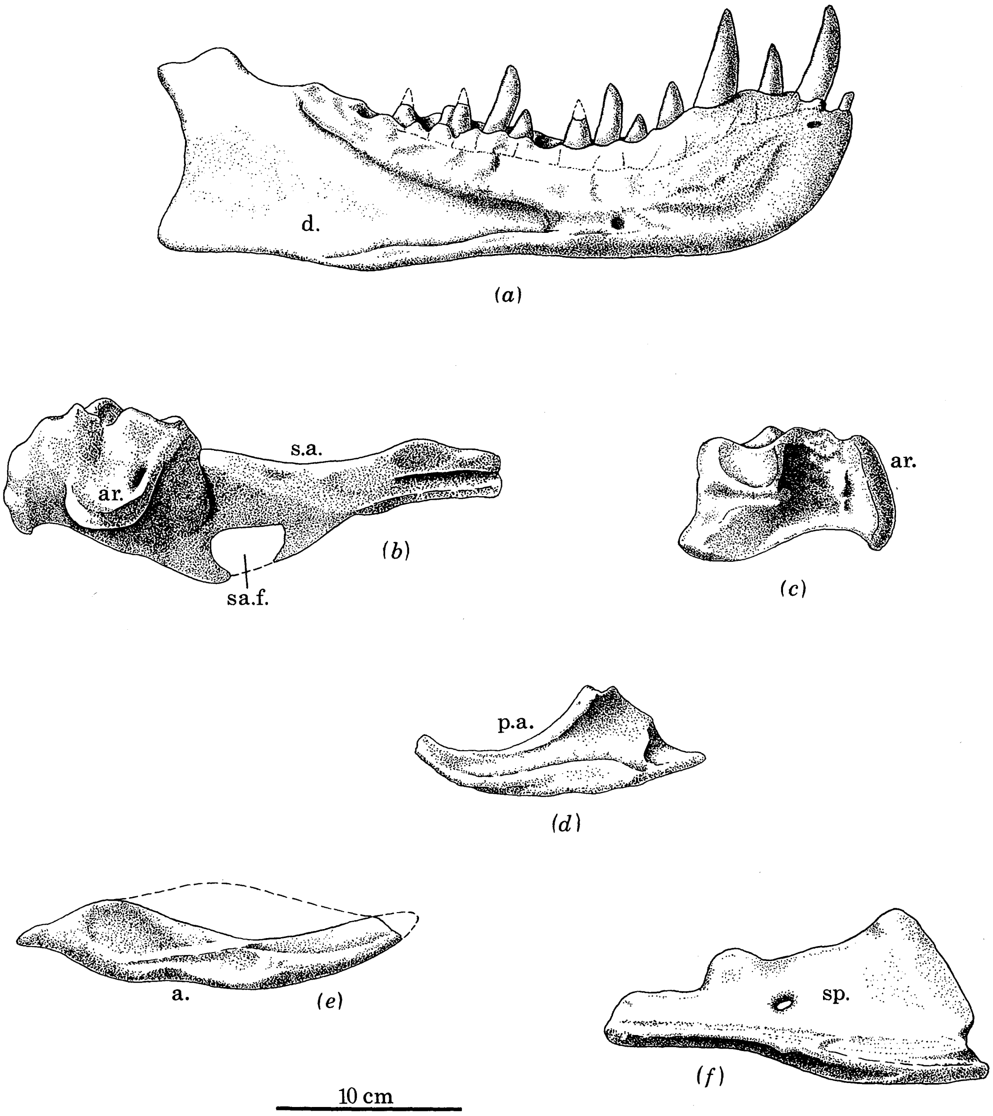

FIGURE 9. *Postosuchus kirkpatricki*, n.sp. Isolated fragments of the lower jaw, left side, holotype: specimen: T.T.U. P 9000. (*a*) Dentary in medial view showing Meckelian canal; (*b*) medial view of the conjoined articular-surangular; s.a.f., surangular foramen; (*c*) lateral view of articular; (*d*) lateral view of the prearticular; (*e*) medial view of the angular; (*f*) lateral view of the splenial.

The close articulation of the quadrate with the glenoid indicates a strictly orthal motion of the jaw. From the glenoid, a tongue-like process extends mesially above the prearticular, and is pierced by a foramen for the chorda tympani nerve. Behind the glenoid, two narrow transverse grooves can be seen. The retroarticular process bears a rugose, hook-like extremity for the insertion of the M. depressor manidibulae. Laterally the articular is firmly joined with the surangular by a broad surface, but the union is loose in juvenile specimens (figure 9*c*). The ventral margin has a sharp, blade-like flange. The anterior tip of the articular forms a roughened surface for the attachment of the Meckel's cartilage.

Dentition

See figures 10 and 11. The marginal teeth are borne in a linear series on the premaxilla and maxilla above, and on the dentary below. The dental formula is premaxillary teeth 4, maxillary teeth 13, and dentary teeth 15. The count compares well with that of tyrannosaurs (table 2). The teeth are large, recurved, and sharply tapered with serrated anterior and posterior edges. The premaxillary teeth were found dissociated from, but in close proximity to, the corresponding bone. They are more slender and conical than the maxillary and dentary teeth, with a higher density of serrations. The maxillary and dentary teeth are highly compressed labio-lingually, with their crowns tilted backward and inward. Some of the anterior teeth of the maxilla and the dentary are developed as large, curved sabres for cutting flesh. The highest tooth in this region is 5.8 cm in the holotype. Density of serrations per 5 mm is 12 in a fully erupted tooth, and the count is the same in anterior and posterior edges (table 3). In cross-section, each crown at the base is bi-convex with its long axis in the anterio-posterior direction. Below the crown, the root is slightly constricted and lacks the sharp anterior and posterior edges. Each tooth has a long cylindrical root, almost twice as long as the crown, and is set in a well-formed socket to form the thecodont type of implantation. In vertical section, each tooth shows an enamel-capped crown, a long dentinal root, and axial pulp cavity. The enamel capping of the crown is extremely thin (figure 10).

TABLE 2. COMPARISON OF TOOTH COUNTS OF *POSTOSUCHUS* WITH SOME THEROPODS

(The last five taxa are tyrannosaurs.)

genus	number of premaxillary teeth	number of maxillary teeth
Megalosaurus	5 (4+)	15–18
Allosaurus	5	15–17
Eusteptospondylus	4	9+
Ceratosaurus	3	16
Dryptosaurus	—	12
Deinonychus	4	15
Dromaeosaurus	4	9
Postosuchus	4	13
Indosuchus	4	14
Albertosaurus	4	13–15
Daspletosaurus	4	14–15
Tyrannosaurus	4	12
Tarbosaurus	4	12

Replacement activity is clear in the jaws; empty alveoli and teeth in all stages of eruption are encountered. However no lingual pit on the alveolus or at the tooth base is seen. Instead, a series of pits are found along the longitudinal groove bordering the interdental plates, a condition seen in carnosaur jaws. Each pit corresponds to one alveolus. Chatterjee (1978*b*) interpreted this groove as the site for the dental lamina. Each pit forms a 'window' for the corresponding alveolus through which tooth germ migrates from the longitudinal groove to the inner base of the old tooth. Several radiographs of the jaws fail to show the presence of replacing teeth, probably due to interference of the infilling minerals, causing too great a scattering radiation or lack of contrast. However, serial transverse sections through the right dentary reveal the details of the replacement cycle (figure 10). The first indication of

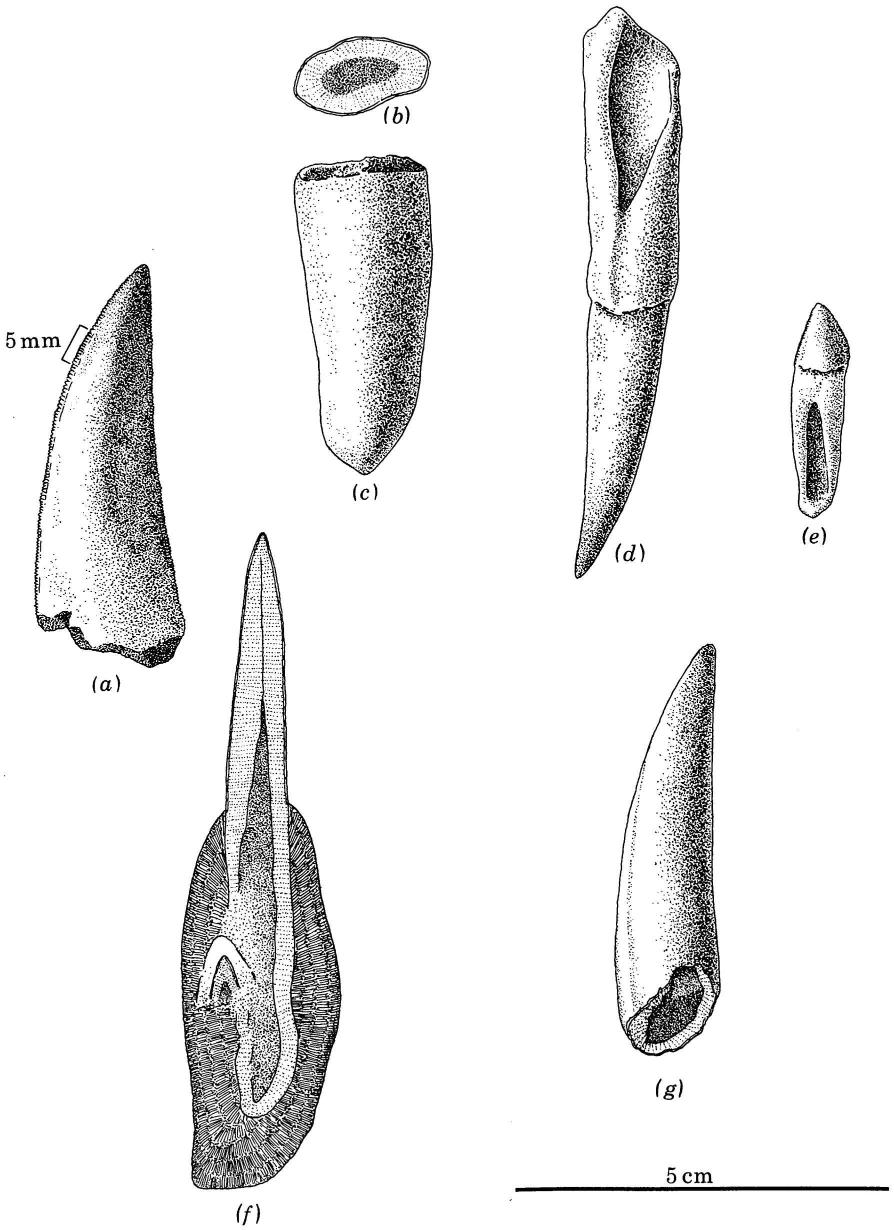

FIGURE 10. *Postosuchus kirkpatricki*, n.sp. Dentition. (*a*)–(*e*) Different tooth structures showing crown, carinae, root and pulp cavity; (*f*) transverse section of the right dentary, showing replacing tooth lingual to the old tooth; (*g*) premaxillary tooth showing hollow pulp cavity.

replacement activity is the appearance of a small calcified tooth germ in a shallow pocket in the alveolus lingual to the functional tooth. Unlike crocodiles, the replacement tooth did not enter its predecessor's pulp cavity at an early stage but seems to have been associated with a progressive lingual resorption of the old tooth. The replacing tooth undergoes considerable growth, with further resorption of the old tooth, and finally enters into the pulp cavity of its predecessor to grow directly beneath it. Eventually the old tooth is lost, and the new tooth takes its position, growing to quite considerable size in the socket and ready for eruption.

The lingual border of the alveoli, under the gum, is formed by a series of overlapping interdental plates. Although the number of the plates is equal to the number of the alveoli, each plate occupies an interdental position so that the suture between them lies at the middle of the alveolus (figure 8*a*). The origin and function of these plates are obscure. They are not separate ossifications, merely expansion of the interalveolar septa. These plates are present only in large reptiles such as carnosaurs, rauisuchians, aetosaurs and sphenosuchids which had long roots set in the alveoli, and may be related to a supporting function for large teeth in the lingual margin.

In most reptiles, the teeth are being continuously replaced throughout life in a definite sequence, and not randomly. Edmund (1960) has shown that teeth in reptiles are replaced in waves that sweep from the back to the front of the jaw through alternate positions. That is, the odd-numbered teeth are replaced as a series, more or less independent of the series formed by the even-numbered teeth. Alternation in replacement allows a maximum number of teeth to function at the same time. A more irregular pattern of replacement could result in simultaneous loss of numbers of adjacent teeth, with consequent impairment of function. Under the alternating system, at least every other tooth is always present throughout the jaw (Romer 1956; Osborn 1971).

TABLE 3. COMPARISON OF DENTAL SERRATION COUNTS OF *POSTOSUCHUS* WITH SOME THEROPODS

(The last three taxa are tyrannosaurs.)

genus	dental serrations per five millimetres
Coelophysis	34–36
Allosaurus	10–12
Ceratosaurus	10
Deinonychus	16–18 (anterior)
Dromaeosaurus	16
Postosuchus	12
Indosuchus	12
Albertosaurus	9–12
Tyrannosaurus	7–9

To determine the sequence in which reptilian teeth are replaced, the ideal condition would be to use live animals. By periodic examination of teeth, a dynamic picture of development and replacement can be reconstructed. In fossil forms, the dental pattern represents a 'still picture' of the continuous replacement process at a particular time, the moment of animal's death. Even then, the pattern of tooth replacement is clearly evident in many fossil forms (Edmund 1960).

In the *Postosuchus* jaws, a series of small overlapping waves, succeeding each other like shingles of roof, can be observed, following Edmund's method of analysis in the alternate numbered series (figure 11*a*). For example, in the upper jaw, teeth 7 and 5 decline in size towards the front. This indicates that tooth 7 is older than tooth 5. Clearly the wave of replacement is progressing forward. The wave length is about two dental spaces. When the different waves between the odd and even, and between the upper and lower jaws are separated, analysed, and plotted in a graph, an interesting picture emerges. An alternate replacement pattern can be seen not only between odd and even series, but also between opposing upper and lower series. If the upper tooth is fully erupted, the lower matching tooth would be small or empty, and vice versa. For a carnivorous reptile such as *Postosuchus*, in which the teeth were used for seizure of prey and stabbing, slashing and cutting of flesh, alternation between odd and even, and between upper and lower series guarantees that at least every other tooth between opposing pairs is always present throughout the jaw.

When all the waves are combined in a graph, a continuous wave, mathematically comparable to a sine wave, sweeps from back to the front through upper and lower jaws (figure 11*b*). The neighbouring teeth in two alternate series may represent opposite phases of the sine waves.

No doubt, this is a very simplistic visual analysis. I have no data about the size of the unerupted teeth in the empty alveoli. Also there is one departure in the forward moving wave of replacement: between teeth 9 and 7 in the upper jaw, tooth 7 seems to be longer than tooth 9.

In explaining the origin of the pattern of succession of reptilian teeth, Edmund (1960) suggested that a stimulus, perhaps of a chemical nature, is initiated at the front of the jaw and passes backward at a regular speed. Whenever the stimulus encounters a tooth position, it initiates the development of a new tooth. The row of teeth developed in response to this stimulus constitutes a Zahnreihe. Throughout life Zahnreihe after Zahnreihe is produced, each following the next posteriorly along the jaw. Edmund has documented, if the timing is a certain interval, this sequence of tooth development may lead to the appearance of wave of replacement of alternate teeth from back to the front of the jaw.

Osborn (1971, 1974, 1977) rejected the Zahnreihe theory, and offered a different model to explain the alternate tooth replacement phenomenon. He observed that embryo reptile teeth are initiated in alternating sequences from back to the front of the jaw. Whenever a tooth is initiated, it is surrounded by a region in which the development of a new tooth is temporarily inhibited. With such restriction no two adjacent teeth could be at a close stage of development. Without inhibition, Osborn argued, one massive fused tooth would be produced all along the jaw. Osborn thus regarded alternation as the outcome of such an inhibition system of tooth development.

In reptiles, the teeth are continuously replaced throughout life irrespective of wear or injury. Osborn suggested that the tooth replacement process is a mechanism to accommodate the progressively larger teeth during the growth of the animal. To accommodate larger teeth, the size of the alveoli and the space between two teeth have to be increased. This is accomplished by suppression of a few alveoli, and the gradual addition of new teeth at the back.

The vertebral column

See figures 12 and 13. The juvenile specimen (T.T.U. P 9001) has a fairly continuous series of vertebrae, but because most of these lack neural arches, the detailed description of the vertebrae is based on the somewhat larger individual (T.T.U. P 9002). Only a few isolated vertebrae are found with the holotype (T.T.U. P 9000). There seem to be 8 cervicals, 16 dorsals, 4 sacrals, and more than 30 caudals. The centra are weakly amphicoelous throughout the column.

Cervicals

The atlas intercentrum and neural arch structures are found articulated into a ring-like structure. Anteriorly they form a cup-shaped depression for the reception of the spherical occipital condyle. Above this joint, two arches enclose a large neural canal which is as big as the foramen magnum. A stout postzygapophyseal process extends postero-dorsally with a

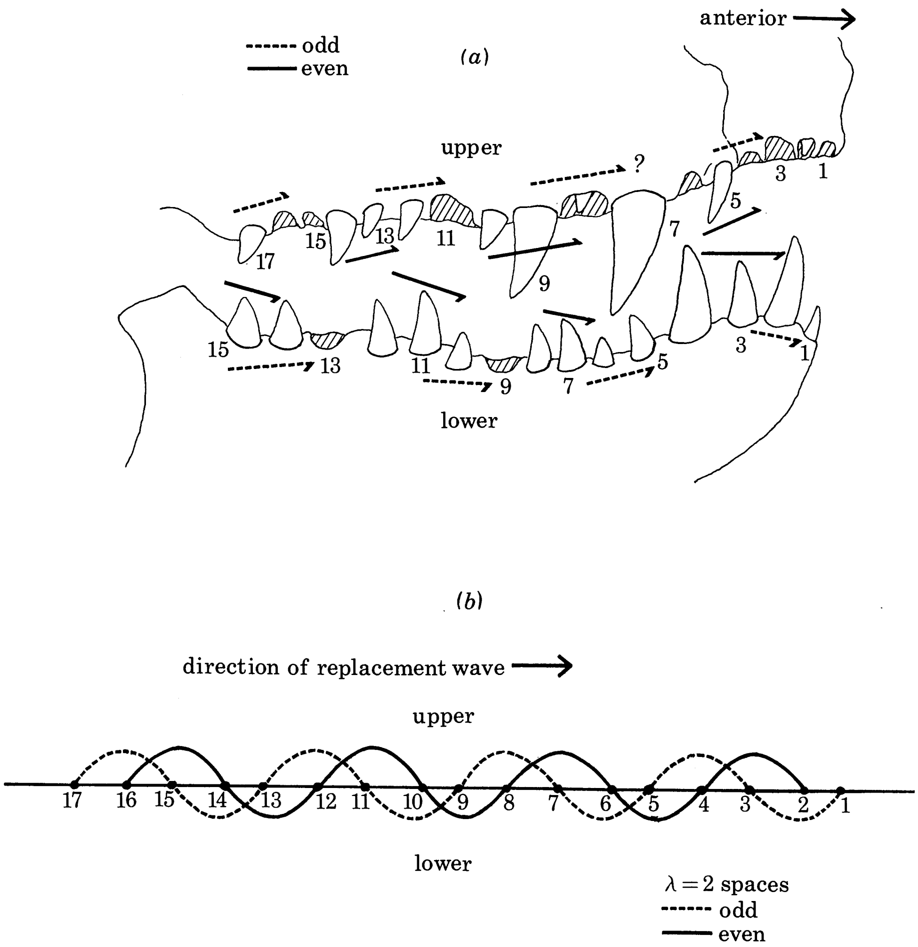

FIGURE 11. *Postosuchus kirkpatricki*, n.sp. Dentition. (*a*) Medial view of the skull and lower jaw showing the wave-like tooth-replacement pattern. (*b*) Graphic analysis of the replacement wave of combined jaws.

prominent oval articular facet on the inner surface. The ventral surface of the atlas intercentrum is flat, and is marked by paired, laterally placed parapophyses.

The three components of the axis, odontoid, intercentrum and the axis proper, are fused together. The axis intercentrum is a small crescent lying ventral to the convex odontoid process. Intercentra are absent posterior to the axis. The axis centrum is very elongate, like the following cervicals, but has a distinctive neural spine, which is very low and as long as its centrum. In the following cervicals, there is a gradual rise and development of the neural spine. The centra are about three times as long as they are wide. In end view, the centrum is small and elliptical in outline with the long axis transverse. The parapophysis lies low down at the anterior rim of the centrum. The diapophysis is weak and slightly overhanging. The zygapophyses are extended antero-posteriorly beyond the ends of their respective centra. The high degree of tilt of the zygapophyseal facets may have restricted the lateral bending, but permitted great vertical flexure of the neck. The last cervical is transitional: its centrum becomes shorter with the development of a ventral keel, and the parapophysis rises close to the neural arch.

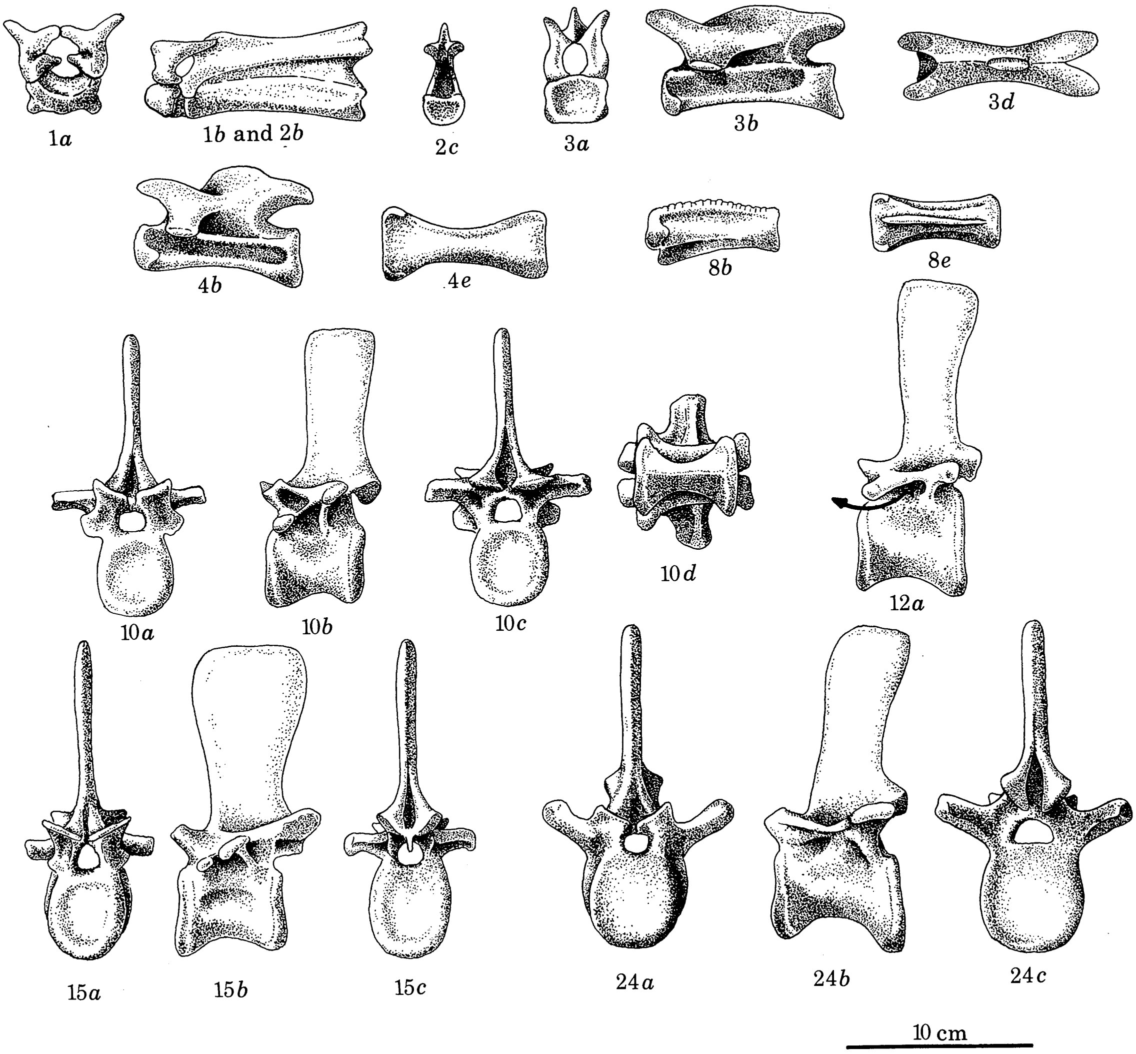

FIGURE 12. *Postosuchus kirkpatricki*, n.sp. Presacral vertebrae as numbered. Composite restoration (magn. ×0.25). 1–8, cervical; 9–24, dorsals. (*a*) Anterior; (*b*) lateral; (*c*) posterior; (*d*) dorsal; (*e*) ventral.

Dorsals

The dorsals are shorter, about two-thirds of the length of the anterior cervicals. The central faces are enlarged with a circular or oval rim. The first three anterior dorsals have ventral keels on the centra, but the keel fades away in the posterior series. Each centrum is constricted at the middle, and is uniformly spool-shaped. The neural spines of the dorsal vertebrae are robust, rectangular blades. They progressively become narrower but taller toward the rear. The parapophyses gradually migrate onto the transverse process, and finally the two rib facets become confluent in the posterior dorsals, and lose their separate identities. The zygapophyses are short, more horizontally placed allowing greater degree of lateral bending. In the mid-dorsal region, accessory articulation between the arches, hyposphenes and hypantra, are encountered.

The presacral series show some reduction of ossification. Although there is no pleurocoel, the lateral surface of the centrum is deeply hollowed out. Further dorsally in the region of zygapophyses, transverse processes, and spine base, the bone is deeply excavated with numerous hollows and grooves between which are lamellar structures to provide strength. In the fourth dorsal, there is a slit-like opening below the transverse process which connects with the neural canal. This might indicate an outlet for a branch of a pectoral ganglion or a brachial plexus (figure 12, 12*a*).

Sacrals

The sacrum contains four co-ossified centra in specimen T.T.U. P 9001, all lacking neural arches. A massive sacral vertebra is found intact in a larger individual (T.T.U. P 9002), without any sign of co-ossification. Fusion of centra is generally considered as age character (Romer 1956). However this reverse trend of sacral fusion with smaller size is also known in *Allosaurus*, and may be attributed to sexual dimorphism (Madsen 1976). Other differences in the architecture of the centra between small and large individuals is noticed. In the former, the centra are dorso-ventrally compressed, so that in end view they are elliptical with the long axis transverse. In the latter, the centra are circular or oval with the long axis vertical.

The details of sacral structures are based on the isolated specimen (T.T.U. P 9002). This specimen has distinctive, wing-like ribs for major articulation with the ilium. The articular facet is semicircular, facing ventro-laterally. Each rib attaches to the posterior half of the centrum, and the neural arch. Distally, the tubercular and capitular areas of the ribs are separated by a deep cleft. The prezygapophyses are moderately tilted and wide apart from each other forming a semicircular arc, so that the last dorsal can rotate considerably. The postzygapophyses are closely spaced, and the neural spine is tall and massive (figure 13).

Caudals

There are about 30 caudals preserved in specimen T.T.U. P 9001, but the total count must be higher. The caudal centra vary little in length from the dorsals, but become progressively more slender and delicate posteriorly. In the anterior caudals, both the neural spines and the fused ribs (pleurapophyses) are moderately developed. There is a gradual decline of the height of the neural spines, passing backward, and in the mid-caudal region, the spines do not rise above the zygapophyses. Likewise, the pleurapophyses became progressively smaller backwardly, and finally disappear. In the juvenile specimen (except for the first three caudals) the neural arches are firmly fused with the centra. Chevron facets occur from the third caudal backwards. The chevrons are Y-shaped in anterior view, enclosing a large haemal canal at the confluence of the centrum.

Ribs

Ribs are found disarticulated. Their collection and preparation are difficult because of a large number of cracks in these delicate bones. The regional identification is tentative, based on spacing, shapes and relative positions of the rib facets.

Cervical ribs are short and dichocephalous. The lower capitular head curves strongly inward and downward from the shaft. It is nearly round in section and slightly flares at its end. The tuberculum is short and compressed, oval in section. Just below the head, a strong ridge projects onto the anterior surface.

The thoracic ribs are longer and highly curved. Passing backwards, the capitulum gradually approaches the tuberculum, and ultimately the two articular areas become confluent. The sacral and caudal ribs are immovably attached to the vertebrae.

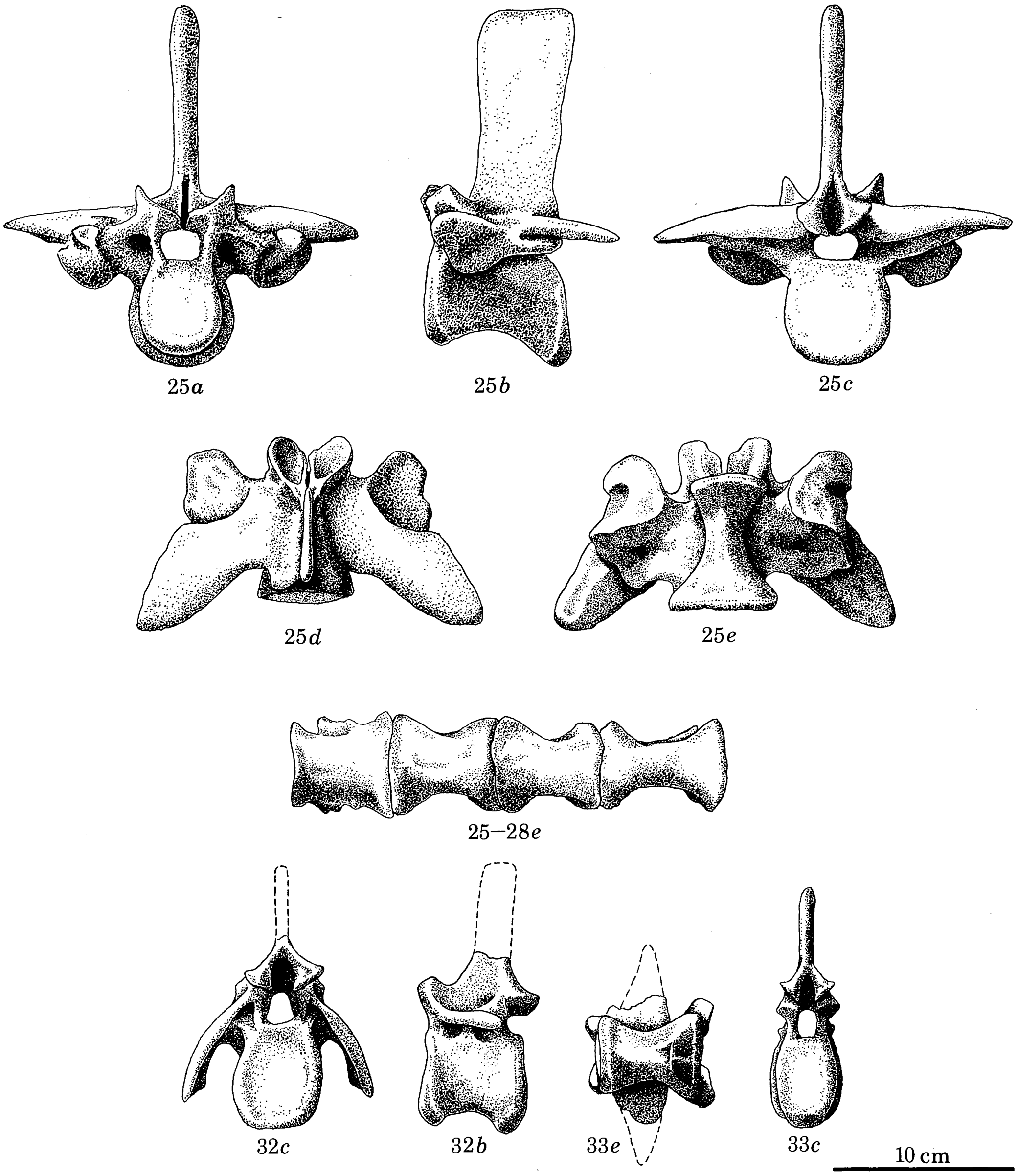

Figure 13. *Postosuchus kirkpatricki*, n.sp. Sacral and caudal vertebrae, as numbered. Composite restoration (magn. ×0.25): 25–28, sacrals; 32–33, caudal; (*a*) anterior; (*b*) lateral; (*c*) posterior; (*d*) dorsal; (*e*) ventral.

Scutes

A large number of spinous scutes similar to those of *Typothorax* and *Desmatosuchus* have been found along with *Postosuchus* skeletons. Because several aetosaur skeletons have been recovered from this quarry, there is no doubt that aetosaur scutes were somehow intermixed with *Postosuchus* skeletons. However a few scutes without spines tend to form pairs, as in *Ornithosuchus* Walker, A. D., 1964), and may belong to *Postosuchus*. Because the scutes and vertebrae were never found articulated, their presence in *Postosuchus* is not certain.

Shoulder girdle

See figure 14. The scapula and coracoid are not tightly sutured to one another, and were found separated in all specimens. The *scapula* is tall and slender with a narrow waist and expanded ends. The anterior margin is a thin, curved blade throughout its length. The lower half of the posterior margin is highly thickened and bears terminally the well-defined upper margin of the glenoid cavity, which faces posteriorly. At its lower end, the scapula is highly expanded where it meets the coracoid in a long, horizontal suture.

The *coracoid* is a short, quadrangular plate, thickened postero-ventrally to bear the lower part of the glenoid. Anterior to the glenoid, lies a small coracoid foramen, entirely within the coracoid. The lower edge of the bone is highly truncated and rugose, with a pronounced postglenoid projection toward the rear.

The *clavicles* and *interclavicle* are apparently absent in *Postosuchus*.

The fore-limb

See figure 14. The fore-limb is much shorter than the hind, the humerus being 52% of the length of the femur. The *humerus* has an expanded proximal end with an oval convex head for fitting into the glenoid. From the head, a prominent internal tuberosity extends medially as a short rugose process. On the lateral edge, below the level of the internal tuberosity, the deltopectoral crest projects anteriorly to bound a large trochanteric fossa. Below the crest, the shaft is straight and cylindrical, and is somewhat compressed antero-posteriorly. Distally, the humerus is expanded transversely, but the distal expansion would be half the size of the proximal one. The distal end is divided into two distinct condyles, the lateral radial condyle being larger than the medial ulnare condyle. Above the radial condyle, a deep longitudinal groove on the lateral edge indicates the passage for the radial nerve and blood vessel.

The *radius* is less robust than the ulna. The bone is equally expanded at either end, but slim in the shaft. The proximal articular surface has a concavity for rolling over the capitellum of the humerus. At its proximo-lateral corner, the radius is apposed to a rugose surface of the ulna, just below the sigmoid notch. The articular surfaces of the two bones are essentially continuous. The shaft of the radius is extremely long and narrow. The distal end is slightly convex and oval in outline.

The *ulna* is as long as the humerus. It has a highly developed olecranon process for the attachment of the triceps muscles. The proximal articular area bears an asymmetric ridge which fits into the intercondylar groove of the humerus, to allow the hinge movement. Below the head, the bone gradually contracts its width and then flares slightly at the distal end for articulation with the carpus.

The *carpus* is represented by two large proximal elements, namely radiale and ulnare, and a solitary distal carpal bone. The radiale is about twice the size of the ulnare. Its proximal surface is saddle-shaped, with an asymmetric pulley-like groove which affords a rolling movement of the carpus over the distal end of the radius, indicating high degree of flexibility. The distal surface shows two distinct concavities for metacarpals I and II, their fittings must be very close and exact.

The ulnare is a small triangular bone. The proximal surface is slightly faceted for the reception of the ulna; its distal surface is convex. Laterally it has a loose contact with the radiale. A disc-like element probably represents the fourth distal carpal bone.

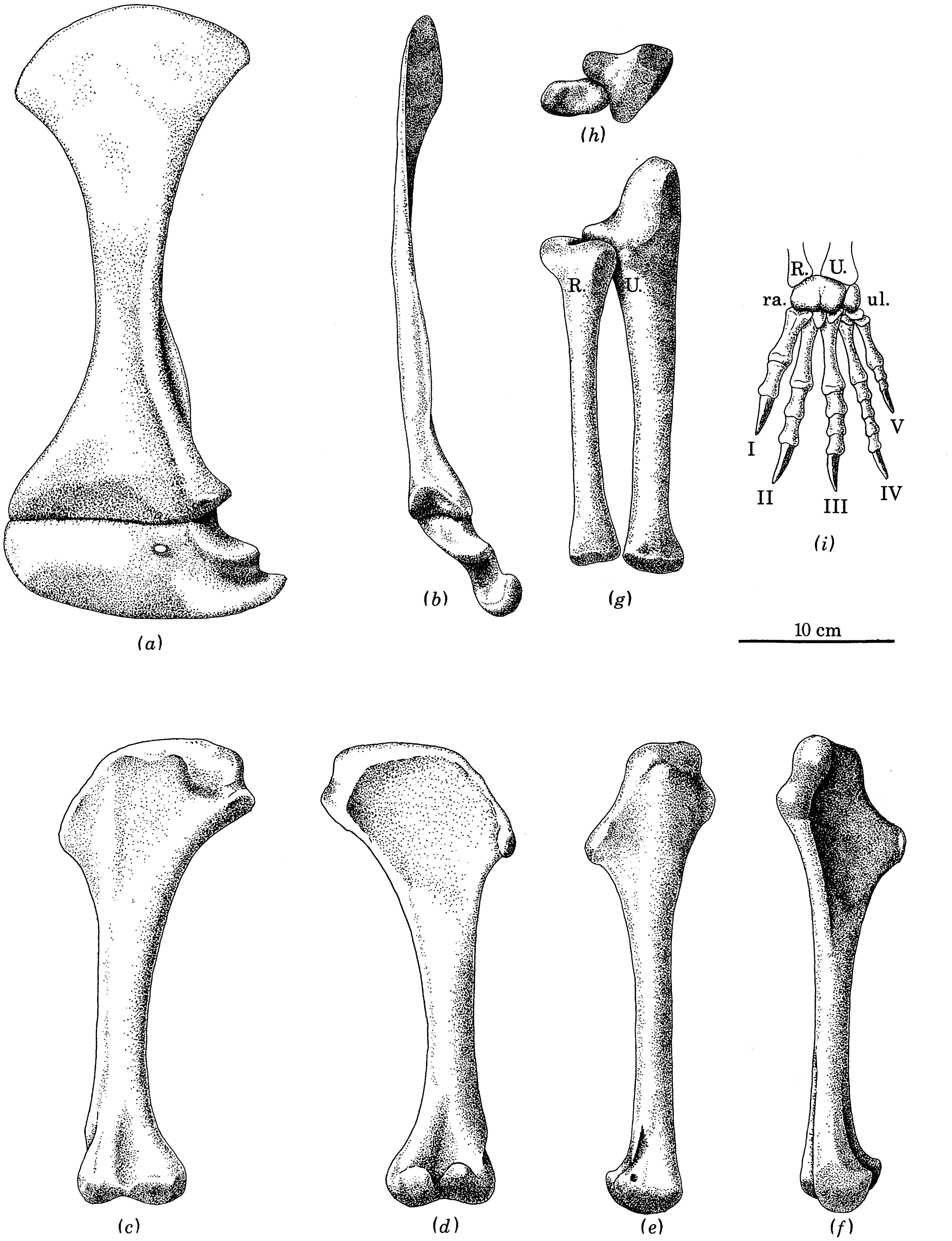

FIGURE 14. *Postosuchus kirkpatricki*, n.sp. Shoulder girdle and fore limb (magn. ×0.25). (*a*) and (*b*) Lateral and posterior views of scapulocoracoid. (*c*)–(*e*) and (*f*) Posterior, anterior, lateral and medial views of humerus; (*g*) and (*h*) anterior and proximal views of radius-ulna; (*i*) restoration of manus, dorsal view. Abbreviations: R., radius; U., ulna; ra., radiale; ul., ulnare; I–V: number of digits.

The *manus* is much smaller than the pes, the probably phalangeal formula being 2, 3, 4, 5, 3. Metacarpal I is short and stout; its phalanges are big, and the claw is much larger, sharper, and more recurved than those of other digits. The specialization of the thumb reflects its possible use as an offensive weapon. Metacarpal II has a roughened projection on the proximo-lateral corner. It is equal in length to metacarpals III and IV, but more robust. The third toe is the longest in the series. Metacarpal V would be as long as I, but is slimmer. Its phalanges are highly reduced. All digits terminate in a short, laterally compressed claw.

Pelvic girdle

See figures 15 and 16. The pelvis of *Postosuchus* is very distinctive, specialized, and carnosaur-like in construction. Elements available are a complete pelvis of T.T.U. 9001, the left ilium and paired ischia of T.T.U. 9002, and the paired ischia of T.T.U. 9000. Other specimens of *Postosuchus* providing supplementary information are a right ilium (T.M.M. 31025-12), and paired ilia and pubes (U.M. 7244), the former matching the size of the holotype. The most notable feature is the variation in the architecture of the iliac blade among different individuals which may be attributed to growth or sexual dimorphism rather than to specific differences. In a small specimen, the iliac blade is very thin and slightly arched, whereas in the intermediate and large individuals, it is thick, low and straight-edged.

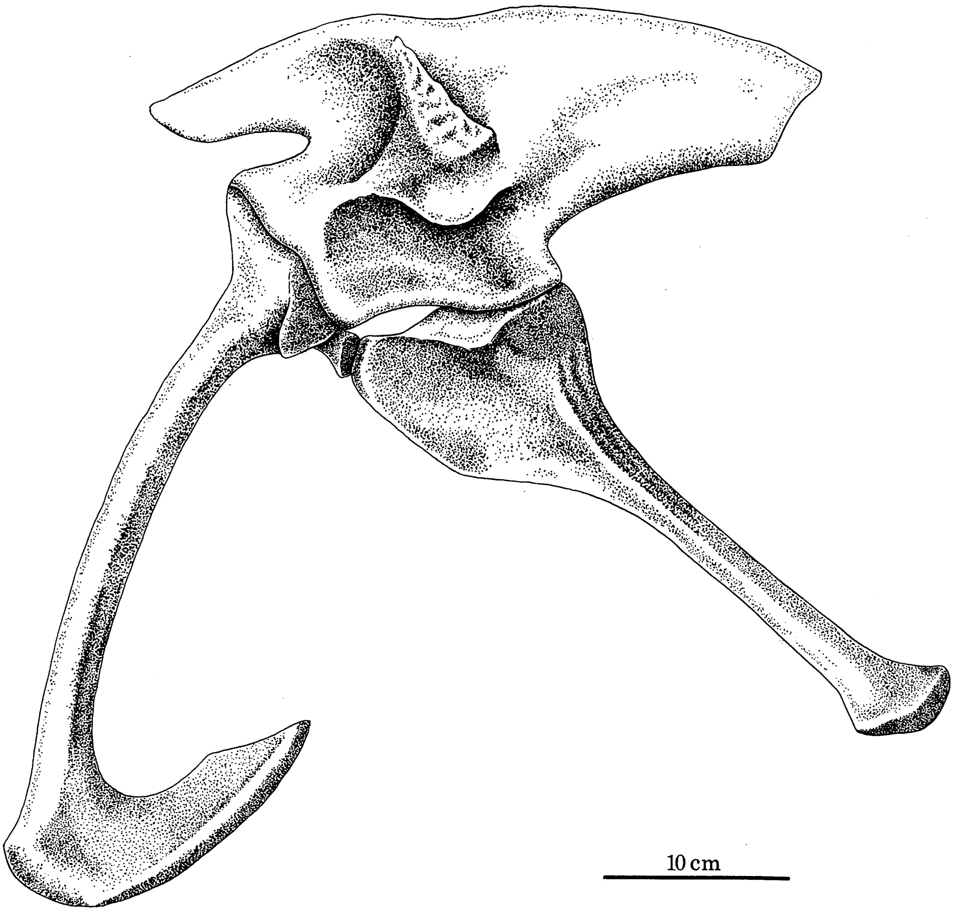

FIGURE 15. *Postosuchus kirkpatricki*, n.sp. Composite restoration of the pelvis, lateral view. Magn. × 0.25.

The *ilium* has a deep acetabular socket dorsally and anteriorly with an overhanging supraacetabular crest to receive the upward thrust of the femur. However the acetabulum becomes shallow posteriorly without any margin. A strong ridge curves antero-dorsally from the supraacetabular crest to the tip of the preacetabular process and bounds a deep fossa anteriorly. The ridge bears a large subvertical rugose buttress, probably to accommodate the ilio-tibialis 2 muscle. The preacetabular process is in the form of a short, forwardly projecting spine. The postacetabular process is greatly elongated and terminates in a sharp point. Elongation of this process must have improved the action of femoral retractors. From the dorsal edge of the acetabulum, a faint ridge rises upward and backward along the contour of the postacetabular process. Between these two ridges, the iliac blade is depressed on its outer surface for accommodation of the ilio-femoralis muscle.

Internally, above the level of the acetabulum, the ilium shows deep indentations for attachment of four sacral ribs. Ventrally, the pubic peduncle is quite massive and subtriangular in cross-section. The ischiadic peduncle is much shorter and narrower. A small triangular acetabular perforation is developed between ilium and ischium. Among theocodontians, acetabular perforation is recorded in *Poposaurus* (Mehl 1915; Galton 1977), *Ornithosuchus* (Walker, A. D., 1964), *Riojasuchus* (Bonaparte 1971), and *Lagosuchus* (Bonaparte 1975).

The *ischium* is long, rod-like, with a highly expanded proximal head. The postero-dorsal region of the head is appreciably thickened and is differentiated into two distinct surfaces, the inner surface and the outer acetabular lip. Farther anteriorly, the ischium shows a facet for union with the pubis. Below the head, the bone rapidly contracts its antero-posterior width, but is slightly enlarged at its distal tip. The shaft is slim and bears a longitudinal ridge at its outer surface. The ischia are fused all along their length, the median symphysis created a deep channel on the posterior midline, and a corresponding ridge on the anterior surface.

The *pubis* resembles that of carnosaurs in many respects. It is an L-shaped bone, longer than the ischium, with a narrow curved shaft, and greatly expanded distal end. Proximally the bone is forked, the posterior branch articulates with the ischium, the anterior one with the ilium. The union with the ilium is extensive. The acetabular lip is small and semi-oval in outline. Between the iliac and ischial articular processes lies an open notch for the obturator foramen. Below the ischiadic contact, the pubis has a transverse apron bearing the facet for the median symphysis. Below the symphysis, the two bones part again distally leaving a narrow median gap, but re-unite at the distal end.

The distal end is expanded into an elongate hook which is wide in front but narrow behind. The hook points upward and backward toward the tail. There is a great deal of speculation about the function of the hook in carnosaurs. Usually in reptiles, the distal end of pubis serves for the origin of abdominal muscles. Romer (1923) believed that a branch of puboischio-femoralis externus (p.i.f.e. II) could have originated from this hook. Van Heerden (1978) argued that in *Herrerasaurus*, the hook served as origin for a femoral adductor. Marsh (1896) speculated that this hook acted as a 'rocker' to support the great weight of the body while the animal was sitting or lying on the belly, and to prevent it from crushing the viscera.

The hind-limb

See figures 17–19. The hind-limb bones are thin-walled, with a hollow marrow cavity, and often show the effect of crushing. The *femur* is relatively long and slender, and shows a primitive sigmoidal shaft with specializations at both ends. The proximal and distal expansions are

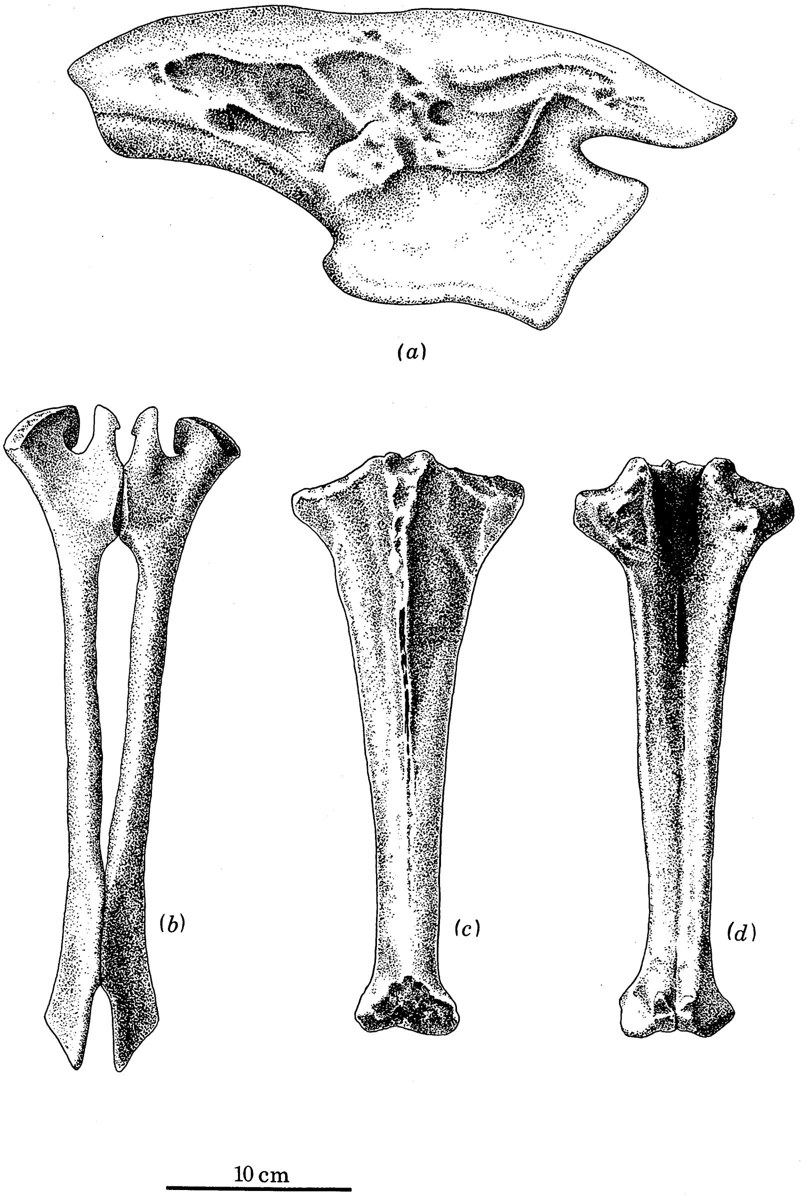

FIGURE 16. *Postosuchus kirkpatricki*, n.sp. Disarticulated elements of the pelvis (magn. × 0.25). (*a*) Medial view of the ilium showing the indentations for sacral ribs; (*b*) conjoined pubes in anterior view; (*c*) and (*d*) anterior and posterior views of conjoined ischia.

twisted about 45° in relation to one another. Proximally the curved articular area is thickened, the thickening increasing toward the medial border in the form of an inturned head which is set off at angle from the shaft. However the articular surface does not face directly to the acetabulum, but more dorsally toward the supraacetabular crest. On the lateral edge of the head, there is an incipient greater trochanter, but the lesser trochanter is absent.

The fourth trochanter on the ventral surface of the shaft is weak, appearing in the form of a ridge one-third way down of the head. It marks the insertions of the powerful caudi-femoralis muscles. The shaft is flattened antero-posteriorly with a gentle sigmoid flexure. Distally the termination flares out into two condyles, similar in general construction to those of theropods. The outer condyle is compressed and swings up to terminate in a hook. External to this condyle is a deep groove joint in which the fibula slid. The inner condyle is moderately developed. Between the two condyles, a longitudinal intercondylar groove accommodated the tendon of the quadriceps femoris muscle.

The *tibia* is about three-quarters of the length of the femur. Viewed proximally, the outline is roughly triangular, the apex being directed laterally, and the weak cnemial crest directly forward. Behind the apex is a shallow concavity for the reception of the fibula. The shaft of the tibia is arched laterally toward the fibula in such a manner that the two bones are closely apposed for most of their length.

The nature of the distal expansion of the tibia and its articulation with the astragalus is very interesting. Usually in thecodontians the greater diameter of the distal end-surface runs more or less antero-posteriorly, whereas in dinosaurs it runs approximately latero-medially (Bonaparte 1969). *Postosuchus* appears to represent a transitional stage in which the greater diameter of the distal end is oblique, rotated about 60° from the antero-posterior direction. Moreover, its distal end is specialized, where the antero-lateral corner is notched to receive the central ascending process of the astragalus, a condition seen in the sauropodomorph ankle (Charig *et al.* 1965).

The *fibula* is much more slender than the tibia. Both the proximal and distal ends are expanded in the antero-posterior direction, linking a sigmoidal shaft. The proximal end is ovoid in outline, with a down-turned lip for adjoining the tibial head. Together they receive the double condyles of the femur. The distal end is a narrow, elongate surface for articulation with two facets formed by the combined astragalus and calcaneum. Its union with the astragalus is firm, but the calcaneum could rotate freely on its distal end.

The *tarsus* consists of two large and stout proximal elements, the astragalus and calcaneum, and two smaller distal tarsals identified as the third and fourth. Morphologically, the astragalus and calcaneum are very similar to those of extant crocodilians except for the tibial articular facet. Proximally the astragalus is highly arched to support the tibia medially and the fibula laterally. Contrary to the crocodilian condition, the tibial facet of *Postosuchus* sweeps from the highest point of the arch not only medially, but also postero-dorsally, and changes its surface contour from convexity to concavity. The postero-distal concavity is so low that the distal end of the tibia, when in articulation with the astragalus, is partly concealed in anterior view. The way the anterior wall of the tibial facet rises suggests the initiation of the ascending process of the astragalus, so prominent in later carnosaurs, for locking against the tibia.

The fibular facet on the astragalus is rhomboidal in outline and is depressed diagonally for contacting the fibula. The anterior and distal surfaces of the astragalus are strongly convex for articulations with the first two metatarsals and the third distal tarsal. Laterally the bone is protruded as a peg which fits into a corresponding socket of the calcaneum. Above the peg, a deep notch in the lateral edge of the astragalus forms an additional articulation with the calcaneum.

The calcaneum has a deep socket for the reception of the astragalus. It shows four characteristic areas: a proximal rolling convex surface for sliding on the fibula and astragalus, a distal flat surface for contacting the fourth distal tarsal, a medially directed flange that underlies the astragalar peg, and a posteriorly directed tuber. The medial half of the proximal convex surface is overlapped by the lateral notch of the astragalus; the lateral half in

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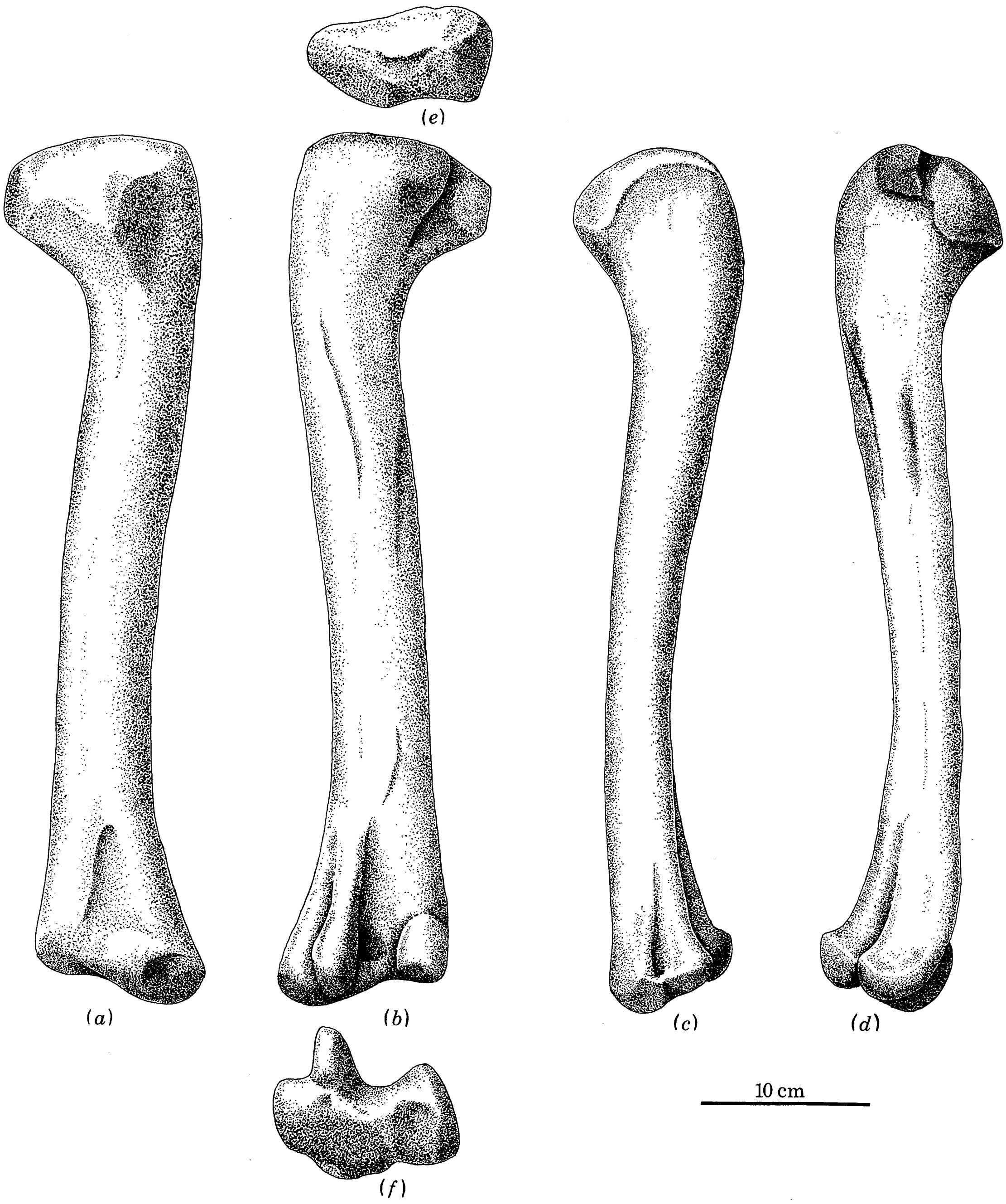

FIGURE 17. *Postosuchus kirkpatricki*, n.sp. Femur (magn. × 0.25). (*a*)–(*f*) Anterior, posterior, lateral, medial, proximal, and distal views.

conjunction with the astragalus supports the fibula. The calcaneal tuber has a pulley-like groove on its posterior surface in which lay tendons of the long pedal flexors.

Of the two distal tarsals, the lateral one is larger, and it articulates with the fifth, fourth and third metatarsals, and the calcaneum. The medial one is wedged between the second metatarsal and astragalus.

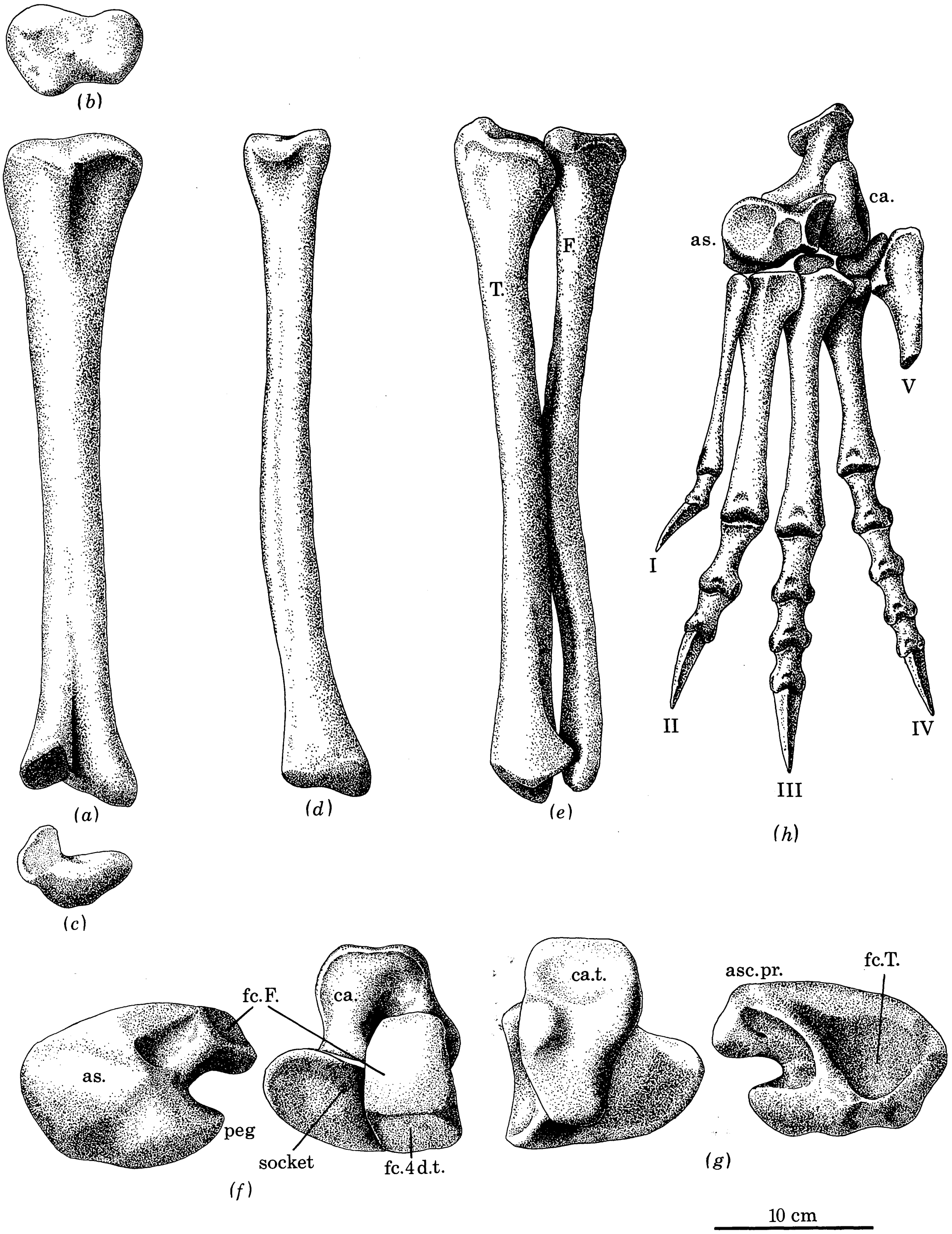

FIGURE 18. *Postosuchus kirkpatricki*, n.sp. Hind limb, composite restoration, magn. ×0.25. (*a*)–(*c*) Lateral, proximal and distal views of tibia; (*d*) medial view of fibula; (*e*) anterior view of the tibia-fibula; (*f*) and (*g*) anterior and posterior views of astragalus and calcaneum; (*h*) dorsal view of pes. Abbreviations: as., astragalus; asc., ascending process of the astragalus; ca., calcaneum; ca.t., calcaneal tuber; F., Fibula; fc.F., facets for fibula; fc.T., facet for tibia; fc. 4 d.t., facet for fourth distal tarsal; I–V: digits.

The structure of the *pes* is very distinctive, and shows antecedent stages in the development of a theropod-like foot. The pes is well represented in T.T.U. 9001 and 9002. The phalangeal formula is 2–3–4–5–0. Digit V is represented only by a metatarsal spur. The hallux is much more slender and much shorter than the remaining toes. The three central toes are moderately elongated in digitigrade fashion, with III longer and stronger than its neighbours, whereas the toes I and V failed to reach the ground. Each metatarsal is well expanded at its proximal and distal ends, except the fifth which is hooked. Its upper end turns sharply inward toward the fourth distal tarsal. The claws are slightly recurved, and compressed sideways. The medial surface of each claw is convex and smooth, the lateral surface bears a longitudinal ridge almost the entire length.

6. STANCE AND GAIT

Postosuchus, as restored from the available skeletal remains, is a large gracile carnivore with a narrow but robust skull supported on an elongated neck. The trunk is short, the sacrals co-ossified, and the tail long (table 4). In proportions of the different segments of the skeleton, *Postosuchus* was not far from the bipedal theropods (table 5). Usually in bipedal reptiles, the forelimbs are considerably reduced compared with the hindlimbs, and the trunk region is short (Ewer 1965). *Postosuchus* exhibits both of these bipedal attributes. With the forelimb 64 % of the length of the hind, *Postosuchus* is in the same group as the theropod *Ornitholestes*. Like tyrannosaurs, the manus is highly reduced, about 39 % of the length of the pes. It appears that the short forelimbs of *Postosuchus* were probably used during slow locomotion, and the animal was a facultative biped.

Both Bakker (1971) and Charig (1972) recognized three grades of locomotion in archosaurs that are essentially walkers or runners: 'sprawling' grade, 'semi-improved' and 'fully improved'. The major structural changes from thecodontians to dinosaur are clearly visible in the pelvis and the hindlimbs from 'semi-improved' to 'fully improved' condition with the acquisition of vertical limb posture. Charig (1972) listed several modifications of the anatomical characters to be found in the fully improved condition, such as in dinosaurs. These are the following: (i) fenestration of acetabulum; (ii) increase of the number of sacral vertebrae, 3–11; (iii) pubis and ischium elongated and rod-like; (iv) femur with straight shaft and strongly inturned head; fourth trochanter often strongly developed; (v) tibia twisted; (vi) mesotarsal ankle joint; absence of calcaneal tuber; (vii) pes digitigrade, showing bilateral symmetry; (viii) metatarsals I and V reduced or absent.

It is interesting to note that most of the dinosaurian hallmarks appeared in *Postosuchus* except for (iv) and (vi) in the above list. Although the femur of *Postosuchus* is sigmoidal its articulation with the acetabulum is highly specialized. The acetabulum has a strong, horizontally projecting supraacetabular crest to receive the upward thrust of the femur. The articular head of the femur is expanded antero-posteriorly in such a fashion that it can swing backward and forward in vertical posture against the ventral surface of the supraacetabular crest without knocking the pubis or ischium. Thus the transfer of the body mass of the animal to the femur was transmitted through the roof of the acetabulum. The femur fits so nicely into the acetabulum in vertical pose that this seems to be the habitual position. This is an attempt to achieve an erect stance by modification of the acetabulum rather than the femur (figure 19).

Bonaparte (1981) concluded that *Fasolasuchus*, an advanced rauisuchid from the Los

Table 4. Body proportions and indices of *Postosuchus*

(1)	$100\times\dfrac{\text{skull width}}{\text{skull length}}$	38
(2)	$100\times\dfrac{\text{skull length}}{\text{length of presacral column}}$	39
(3)	$100\times\dfrac{\text{length of cervicals}}{\text{length of dorsals}}$	60
(4)	$100\times\dfrac{\text{length of (humerus + radius)}}{\text{length of (femur + tibia)}}$	64
(5)	$100\times\dfrac{\text{length of (humerus + radius + manus)}}{\text{length of (femur + tibia + pes)}}$	57
(6)	$100\times\dfrac{\text{length of (femur + tibia)}}{\text{length of trunk}}$	88
(7)	$100\times\dfrac{\text{length of humerus}}{\text{length of femur}}$	52
(8)	$100\times\dfrac{\text{length of radius}}{\text{length of humerus}}$	91
(9)	$100\times\dfrac{\text{length of tibia}}{\text{length of femur}}$	75
(10)	$100\times\dfrac{\text{length of manus}}{\text{length of pes}}$	39
(11)	$100\times\dfrac{\text{length of metatarsal III}}{\text{length of tibia}}$	44
(12)	slenderness index $= 100\times\dfrac{\text{least diameter of the shaft}}{\text{length of the limb}}$	
	(*a*) humerus	9
	(*b*) radius	6
	(*c*) femus	11
	(*d*) tibia	10

Table 5. Selected anatomical indices in some theropods and *Postosuchus*

		Postosuchus	*Allosaurus*	*Albertosaurus*	*Tyrannosaurus*	*Ornitholestes*	*Coelophysis*
(1)	$100\times\dfrac{\text{skull width}}{\text{skull length}}$	38	47	40	47	35	32
(2)	$100\times\dfrac{\text{fore limb}}{\text{hind limb}}$	64	42	26	—	66	45
(3)	$100\times\dfrac{\text{radius}}{\text{humerus}}$	91	71	48	—	71	67
(4)	$100\times\dfrac{\text{tibia}}{\text{femur}}$	75	82	95	80	81	100
(5)	$100\times\dfrac{\text{manus}}{\text{pes}}$	39	70	28	20	70	52
(6)	$100\times\dfrac{\text{metatarsus}}{\text{tibia}}$	44	51	60	60	73	56

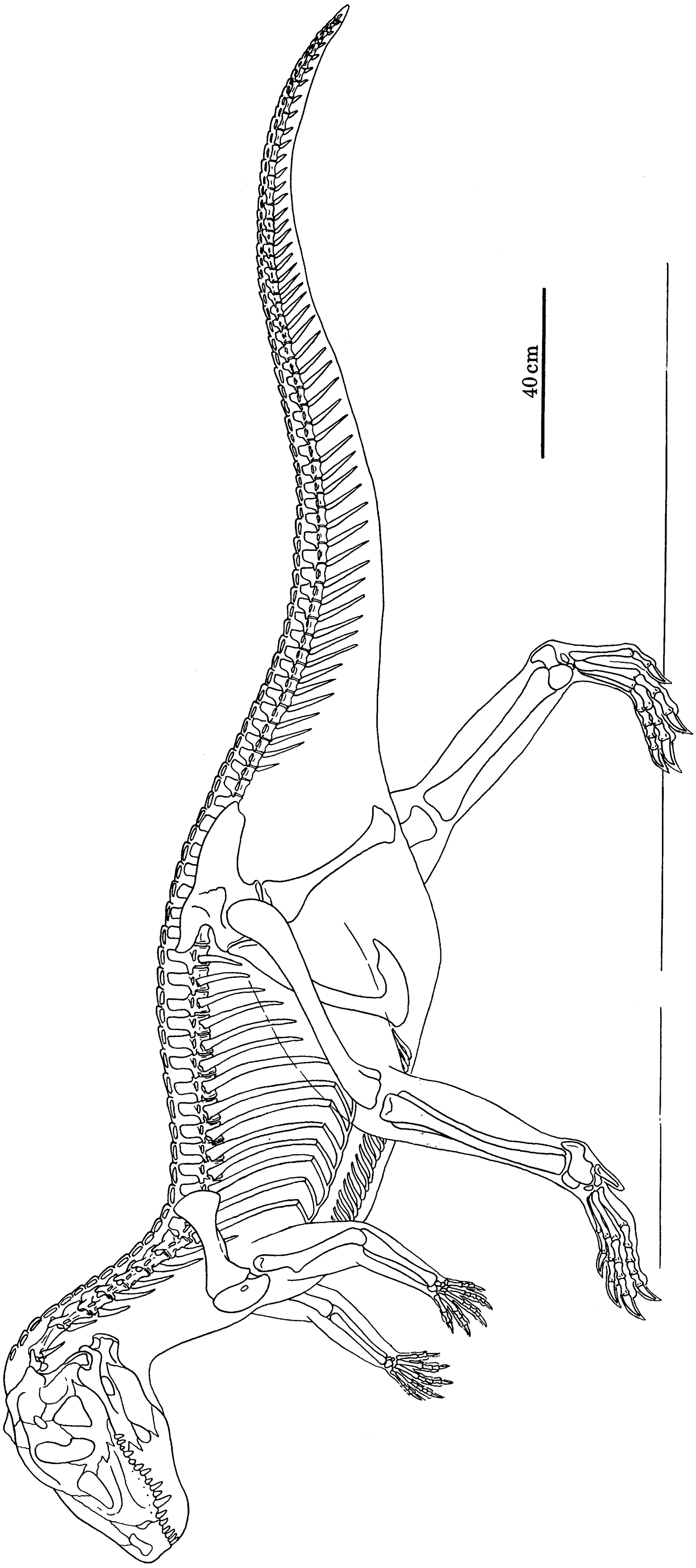

FIGURE 19. *Postosuchus kirkpatricki*, n.sp. Skeletal restoration.

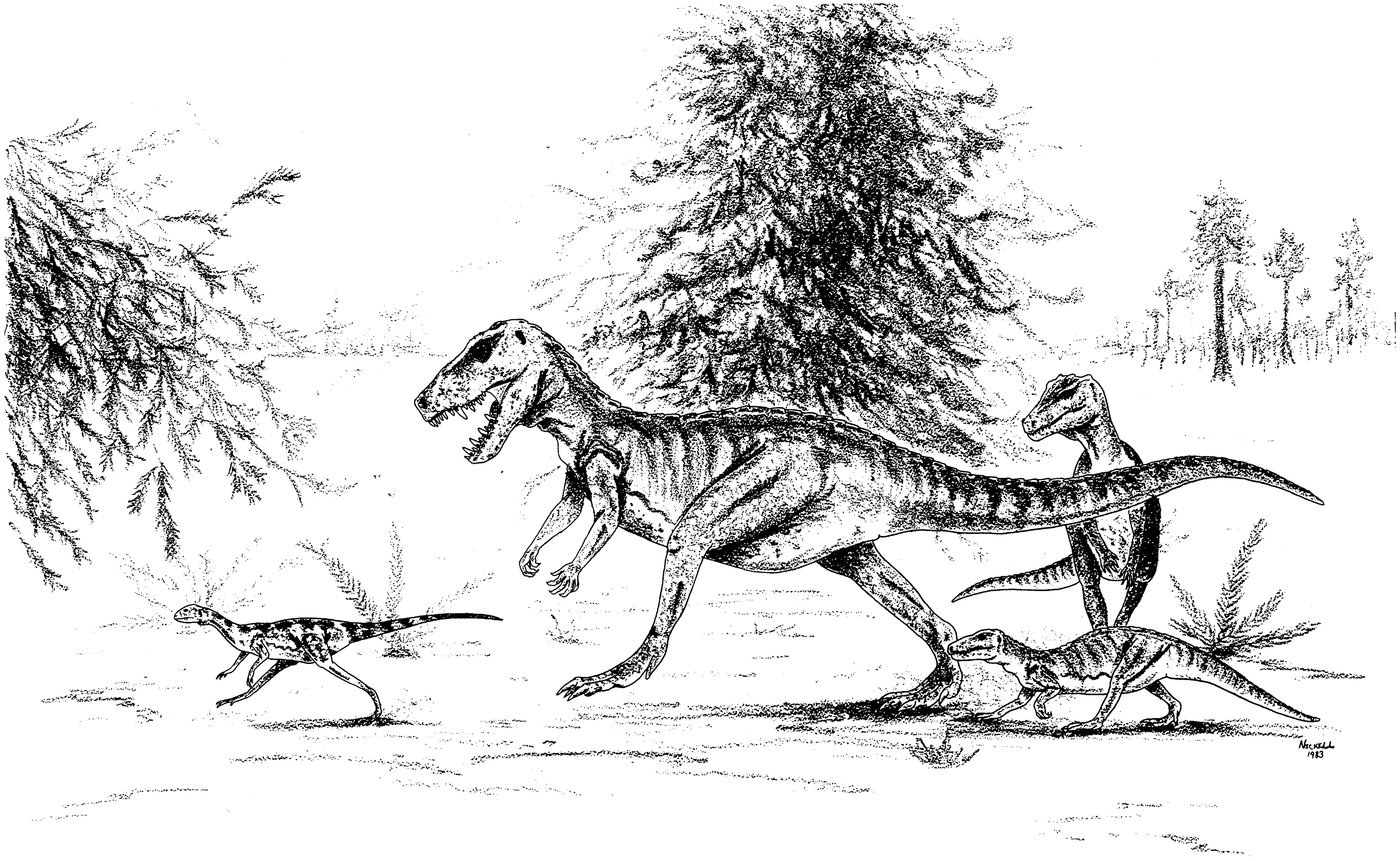

FIGURE 20. *Postosuchus kirkpatricki*, n.sp. Life restoration.

Colorados Formation of Argentina, could attain vertical limb posture through the inclination of the ilium into a subhorizontal position, retaining a rather primitive type of sigmoidal femur. This is quite different from the condition seen in *Postosuchus* and dinosaurs in which the ilium remained essentially vertical, and the acetabulum is more laterally projected and fenestrated. It seems that alternative anatomical features were developed by advanced thecodontians to reach a vertical posture. This contention contrasts with the popular idea that thecodontians were incapable of adopting a vertical limb posture (Charig 1972).

Figure 20 shows the life restoration of a group of animals using both quadrupedal and bipedal gait. Adult *Postosuchus* would be about 2 m high at the head as standing, reaching somewhat 4 m from snout to tail tip, and live mass of the animal may have ranged from 250 to 300 kg.

7. Palaeoecology

The Upper Triassic Dockum Group, exposed over a huge area of the eastern and southeastern New Mexico to West Texas, is one of the spectacular red bed sequences in the United States. The sediments are poorly sorted continental clastics accumulated in a mosaic of fluvial, lacustrine and flood plain environments (McGowen *et al.* 1979). The source areas were probably nearby topographic areas such as Llano Uplift, the Bench Arch, and the Wichita and Arbuckle Mountains (Kiatta 1960). Volumetrically, the dominant lithology is the red mudstone, usually structureless and unlithified, intercalated with lenses of cross-bedded sandstones, conglomerates, and lime-pellet rocks.

Red beds have been studied in great detail to use them as palaeoclimatic, palaeomagnetic, and geochemical indicators. The pigmentation of the red bed is due to ferric oxide in the form of finely disseminated haematite in the clay, but their origin has been debated. Krynine (1949) believed that red beds could form by direct derivation of haematite from tropical lateritic soil. On the other hand, Van Houten (1964) suggested that the haematite could form diagenetically by *in situ* dehydration of yellow or brown hydroxides from deeply weathered soils. This indicates that many ancient red sediments could have been originally yellow and the red colour could have developed diagenetically by limonite dehydration even during shallow burial at low temperatures (Walker, T. R., 1967). In modern alluvium, regardless of climate or colour of the soils, source areas generally deliver brown sediments; there is a paucity of red pigments in these modern soils. On the other hand, in ancient sediments, the reverse is the case. T. R. Walker (1974) thus concluded that the modern brown muddy matrix that contained amorphous to poorly crystalline ferric oxide may become red after deposition on further ageing by intrastratal solution. The site of deposition must have had an oxidizing environment to retain the red coloration.

The continental red beds occur in two different associations (Van Houten 1961): (i) an arid climate association with well-sorted sediments and evaporites; (ii) a moist climate association with poorly sorted sediments and coal.

These two red bed associations are well documented in Texas. The Permian Wichita and Clear Fork Groups which were deposited under arid conditions in restricted, shallow, hypersaline waterbodies, tidal flats, and sabkhas, are in marked contrast to the overlying Dockum Group that was accumulated in fluvial, deltaic and lacustrine environments. Thus the red beds *per se* do not provide any specific clue to the climate of source area or at the place of deposition (Walker, T. R., 1974). Criteria such as associated flora, fauna, aeolian sands, evaporites, calcretes, or coal measures provide the most reliable evidence about the palaeoclimate.

Although there is no detailed work on the Dockum lithology, the lime pellet rocks (calcretes) indicate an alkaline oxidizing environment in a tropical to subtropical climate with ample rainfall but a distinct dry season (Robinson 1964). Palaeomagnetic studies on the adjacent areas of Chinle indicate a latitude of 16–18° N (Irving 1964), which would seem to substantiate this. In addition, alteration of feldspar in the Dockum sandstone suggests that the palaeoclimate was moist.

Plant fossils are good indicators of past climates. Unfortunately the flora is poorly documented in the Dockum sediments. So far nine genera of plant fossils, including remains of three ferns, five gymnosperms, and one possible cycad have been recorded (table 6). The rarity of plant fossils in the red beds is due to the oxidizing environment which destroyed most of their remains. I have encountered beautiful leaf impressions, petrified wood, lignite layers along with conchostracans in green mudstone, which may indicate reducing pond deposits.

TABLE 6. THE DOCKUM FLORA

(After Ash 1972, 1976.)

groups	genera
Ferns	*Cynepteris* *Phelopteris* *Clathropteris*
Gymnosperms	*Pelourdea* *Araucarioxylon* *Woodworthia* *Otozamites* *Dinophyton*
Cycads	*Sanmiguelia*

Ash (1972) concluded from the remains of the Dockum flora that the climate was moist and warm. He argued that the living relatives of the Dockum ferns and gymnosperms now mostly inhabit humid tropical areas, and the large specimens of *Araucarioxylon* suggest an abundant water supply. The pollen assemblages demonstrate that a moderately diverse flora was present in the Dockum environments and the climate was moist (Dunay 1972). Gottesfield (1972) recognized three distinct plant communities in the contemporaneous Chinle Formation of nearby areas which has a similar but more diverse flora. These are: (i) flood plain swamp community of ferns and cycads; (ii) lowland closed canopy forest of *Araucarioxylon*; (iii) upland gymnospermous community. It seems reasonable to assume that similar vegetation communities prevailed in the Dockum landscape. Certainly there should have been a considerable amount and variety of plants available to support the Dockum herbivores.

The Dockum assemblage of fossil animals give some clue about the past environment. That the area was well watered, at least seasonally, is suggested by the locally abundant unionids, conchostracans, fish, metoposaurs, and parasuchids. Within the Dockum ecosystems, three principal habitat subzones for the vertebrates have been differentiated: (i) aquatic: rivers, lakes and ponds; (ii) lowland: margins of rivers, lakes and ponds; (iii) upland: divides between two streams; interfluves.

In general, the aquatic members have dominated the collections for several decades, but the terrestrial components are less well known. The rarity of poposaurs and coelurosaurs and other strictly terrestrial animals suggests that they inhabited higher terrain away from the streams and ponds in which the deposits and fossils were accumulating. A list of the Dockum vertebrates, known to date, with their probable habitats, is shown in table 7.

TABLE 7. THE DOCKUM VERTEBRATE FAUNA

groups	genera	habitats
I. Fish		
Chondrichthyes:		
Xenacanthid:	*Xenacanthus*	aquatic
Hybodontid:	*Lonchidion*	aquatic
Osteichthyes:		
Redfieldiids:	*Cionichthys*	aquatic
	Lasalichthys	aquatic
	Synorichthys	aquatic
Coelacanths:	*Chinlea*	aquatic
Dipnoans:	*Ceratodus*	aquatic
II. Amphibians		
Metoposaurs:	*Metoposaurus*	aquatic
Labyrinthodonts	*Latiscopus*	lowland
III. Reptiles		
Lepidosaurs:		
Rhynchosaurs:	aff. *Paradapedon*	lowland
Protorosaurs	*Malerisaurus*	lowland
Trilophosaurs:	*Trilophosaurus*	lowland
Lizard:	unnamed	lowland
Archosaurs:		
Parasuchids:	*Parasuchus*	aquatic
	Angistorhinus	aquatic
	Nicrosaurus	aquatic
	Rutiodon	aquatic
Stagonolepidids:	*Typothorax*	upland
	Desmatosuchus	upland
Poposaurs:	*Postosuchus*	upland
Coelurosaurs:	*Coelophysis*	upland
	Spinosuchus	upland
Cynodonts:		
Ictidosaurs:	*Pachygenelus*	upland

The fish, metoposaurs, and parasuchids show marked aquatic adaptations. The labyrinthodonts, rhynchosaurs, protorosaurs, trilophosaurs, and the lizards probably lived near the flood plains of river valleys and the margins of the lakes. In this flood plain community, parasuchids would be the arch predators. I found remains of rhynchosaurs and protorosaurs in their stomach contents (Chatterjee 1980). On the other hand, aetosaurs, coelurosaurs, poposaurs, and ictidosaurs were probably upland fauna.

The three palaeocommunities would blend gradually into one another. These were blurred boundaries where the tetrapods could move back and forth for food, protection or escape from their enemies. The constantly shifting channels, islands and pointbars in the floodplains of the rivers provided continuous new ground for the initiation of succession. The intermixing of communities could make the border areas particularly interesting. Elder (1978) and Murry (1982) elaborately discussed the ecosystems of the Dockum palaeocommunities. The aquatic food chain, outlined by them, is excellent, but the ecological relations of the terrestrial vertebrates need modifications as new taxa have been discovered since then.

Beginning with the eating of plants, the food chain of the terrestrial fauna moved through a series of ever-larger carnivorous animals. Each took its turn in the double role of predator and prey, until the food chain ended with *Postosuchus*. It is assumed that the base of the terrestrial ecosystems was formed by a variety of ferns and gymnosperms consumed by the Dockum herbivores such as *Trilophosaurus*, *Typothorax* and *Desmatosuchus*. *Trilophosaurus* lacked any offensive or defensive structures, but *Typothorax* and *Desmatosuchus* were covered by an armour of heavy plates as a protection against attack from predators. Rhynchosaurs probably relied heavily on freshwater mussels such as unionids, abundant in the Dockum ecology (Chatterjee 1974). In the role of secondary consumer, or lowest level of carnivores, were small-sized tetrapods such as *Latiscopus*, ictidosaurs, iguanid lizards, and *Malerisaurus* which probably consumed terrestrial arthropods and molluscs as their primary diet (Chatterjee 1980).

Coelophysis was a very agile bipedal carnivore, obviously able to run down its prey in swift pursuit. It played a secondary role as predator, but had potential enemies, such as *Postosuchus*, from which it could protect itself by hiding, or by rapid escape into the forested uplands. There are indications that *Coelophysis* was occasionally cannibalistic when other food became scarce (Colbert 1972). Cannibalism is actually more widespread than was once believed, and often serves importantly as a regulator of population growth (Cott 1961; Auffenberg 1981).

Postosuchus was the largest member of the terrestrial community. Its highly predatory dentition, wide gape, bipedal and erect posture, swift movement: all these features indicate that *Postosuchus* was an ultimate consumer, occupying the apex of the Dockum food pyramid. They probably ate anything they could catch (figure 21).

Details of the food web are difficult to establish. An organism may feed on several levels at the same time, or it may feed on several levels through time, shifting its preferences with individual age, season and changing availability. Analysis of community structures by reconstruction of the food web is difficult for modern communities and quickly leads to complex flow charts. It is even more difficult for fossil communities because much of the necessary information is not preserved. Consequently, analysis of trophic structure of fossil communities is best approached through attributes that are more easily described.

8. Taphonomy of the quarry

The enormous area of the Dockum exposures is completely barren except for some localized concentrations of fossil bones. Previous collections of the Dockum vertebrates for the past 80 years were made essentially from the Potter, Crosby, and Howard counties, where the aquatic and semi-aquatic elements have predominated. The new quarry at Post in the Garza county is distinctive in two ways. First, terrestrial forms are abundant, and many of them represent new taxa. From a 90 m^2 patch of ground, the remains of 12 *Postosuchus*, 5 aetosaurs, 2 lizards, 1 labyrinthodont, 1 protorosaur, 1 ictidosaur, 2 parasuchids, 1 metoposaur, and various unknown microvertebrates were recovered, while there are many more bones still to be exposed. Second, the quarry assemblage is highly unbalanced, as the relative numbers of carnivores exceed those of herbivores (table 8). Obviously this is not a true reflection of the vertebrate community structure existing in the area during that time.

The bones in the quarry are a diverse mixture of massive and delicate elements which are found entirely in the mudstone, associated but disarticulated. Skull bones of *Postosuchus*, ictidosaur, and lizard are disarticulated, with low dispersion, whereas parasuchids, aetosaurs, metoposaurs, and labyrinthodonts show intact skulls. In *Postosuchus*, loss of some skeletal

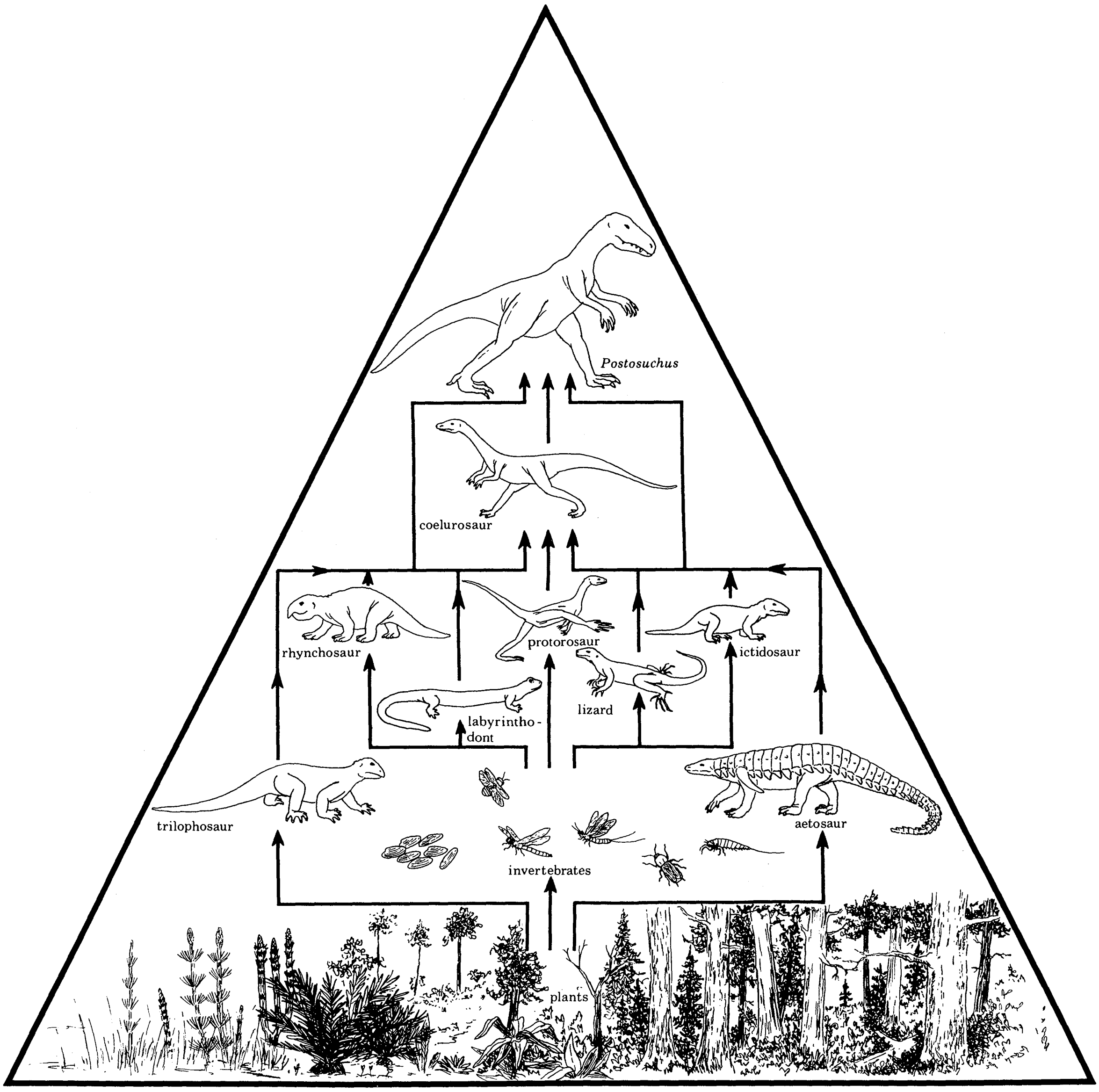

FIGURE 21. Food chain of the terrestrial components of the Dockum palaeocommunities.

TABLE 8. ANALYSIS OF QUARRY POPULATION

major group	number of individuals	percentage population	habitat	habitat percentage
Postosuchus	12	48	upland	72
aetosaurs	5	20	upland	
ictidosaur	1	4	upland	
lizard	2	8	lowland	16
labyrinthodont	1	4	lowland	
protorosaur	1	4	lowland	
parasuchids	2	8	aquatic	12
metoposaur	1	4	aquatic	

elements in relation to size is observed. In all juvenile specimens, the skull is absent, though the postcranial skeleton is beautifully preserved. In the sub-adult specimen, the skeleton is fairly complete except for the neck region. In the adult specimen, skull, limbs and girdles are well represented, but the vertebral column is missing (figure 22). In the adult and sub-adult specimens, teeth are found intact in the alveoli of the jaws. The missing parts among different individuals indicate some sort of *post mortem* disturbance. Each individual retained some degree of polarity in the preserved parts so that the skull and the hind limbs are always in the opposite direction.

Although the mudstone in the Dockum Group is usually structureless, trough-shaped cross-beddings were encountered during opening up a quarry face. Also the newly exposed bedding or cross-bedding surface is often highly glazed, and shows kuten or slickensides, indicating small scale faultings. These structures are usually obliterated after a rain. The palaeocurrent azimuth is 30°→108°. The bones of *Postosuchus* show some preferred directions. A rose diagram of orientations of 110 elongated bones was prepared (figure 22), which indicates that individual carcasses, or their long bones, were aligned in response to the current direction. Most of the bones were oriented by sliding their long axes parallel to the current. This is consistent with stream table experiments with recent animals (Voorhies 1969; Hanson 1980). However the current was apparently not competent enough to disturb the association of the individual skeletons. The transport of bones must be short or negligible, both temporally and spatially because of the following reasons: (i) lack of abrasion or mechanical fragmentation of bones; (ii) presence of delicate bones of the skull and the pelvis, and the intact teeth in the alveoli; (iii) partial association of skeletons; and (iv) presence of articulated and closed unionid shells. Since there is no sign of scavenging, such as tooth marks, depressed fractures, perforation or cracking in the bone, the cause of post-mortem damage may be attributed to the flowing current. In case of floating dead, disarticulation is usually rapid, and the dispersal of dismembered parts of the bodies by water is considerable, as they fell from the carcass.

The bones of the different individuals occur in a single bone bed which is about 30 cm thick, with an exposed area of 90 m^2, and was probably deposited rapidly during a single flood. The presence of cross-bedding, unstable vertical positions of many bones, and the poorly sorted nature of the enclosing matrix, all point toward rapid deposition.

How did so many diverse animals die in one place? It has become clear in recent years that catastrophic death of large animals is not as unusual a phenomenon as had often been supposed. In modern ecosystems, both drought and flood may lead to massive mortality. The population of the Nairobi National Park was halved in 1961 owing to drought and floods (Foster & Coe 1968). At such times a large number of entire skeletons could become fossilized if they were buried. In Post Quarry, evidence of subaerial exposures or drought (such as mudcracks, rain prints, aeolian deposits) is not found. The nature of the unbalanced assemblage of the fauna, as well as the presence of several juvenile specimens of *Postosuchus*, indicate that death was due to a catastrophic rather than an attritional event. I interpret the quarry's mass mortality as the consequence of a single event such as flash flood in the interfluve areas. It has been observed that terrestrial forms especially mammalian herbivores, may form tightly packed death assemblages when caught by flooding (Voorhies 1969). In India and Bangladesh, torrential floods during the monsoon are responsible for large scale mortality among wild and domestic animals as well as human populations.

There seemed to be a brief time gap, perhaps a week, between the two events: mass mortality

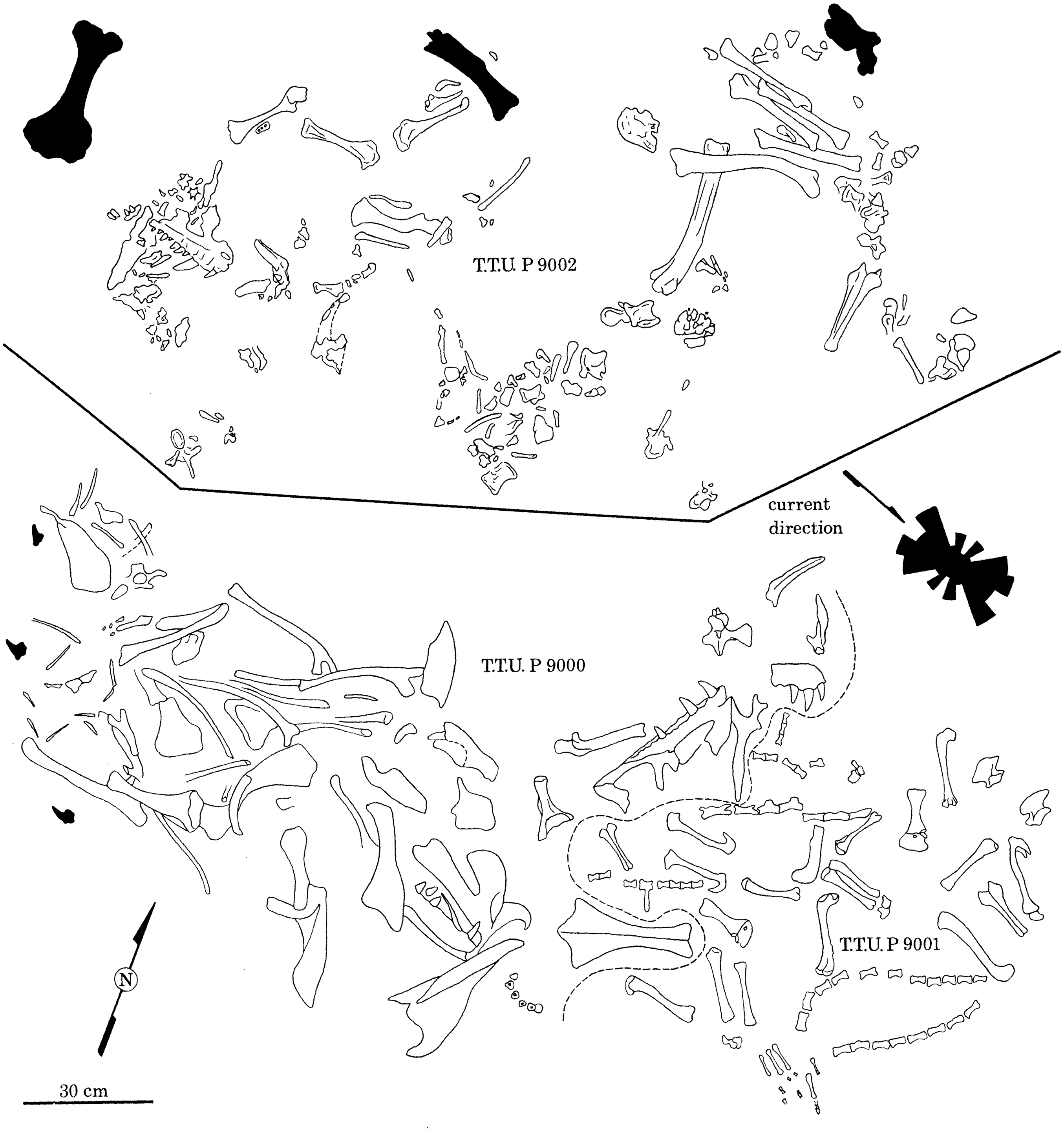

FIGURE 22. Orientation of bones of *Postosuchus* in the Post Quarry; isolated bones of aetosaur are shown black. Rose diagrams of the long bones of *Postosuchus* correspond well with the current direction. Only three individuals, small (T.T.U. P 9001), medium (T.T.U. P 9002), and the large (T.T.U. P 9000) are shown here.

and mass burial. The flood which caused the death cannot have been the same flood which deposited the bones, because the remains have had time to become disarticulated and reoriented in response to the flowing current, where some of the elements in this process were removed by hydraulic winnowing. The quarry's thanatocoenose probably reflects autochthonous burials in which sorting occurred *in situ* rather than in transit (Voorhies 1969). The carcasses were partly submerged in the soft mud and partly exposed to moving water. When the current waned sufficiently the skeletons were quickly buried by mud. Mud not only helped protect carcasses from scavengers and tramplers, but it also served to bind bones to the substrate and to inhibit further transport from the death site.

9. Habits of *Postosuchus*

Postosuchus was lightly built for its size, and had fully erect hind limbs on which a slender body, tapering to the narrow head and into the long tail, was balanced when the animal was in a hurry. Although it was capable of walking bipedally, a temporarily quadrupedal position would be advantageous during drinking, foraging or feeding. When seated, or stretched on the ground, the pubic 'foot' would receive some of the weight of the body. *Postosuchus* was the largest animal in the Dockum environment, the adult individual being about 4 m long. In consequence of the increase of size, various modifications are seen in the skeletal elements aimed at supporting the enormous load with bone economy, and thereby, perhaps reduction of the dead weight. The fore and hind limb bones were hollow. The vertebrae show excavations on the side of the centra and neural arches, but are reinforced by various lamellar structures. The sacro-iliac joint was lengthened, and greatly strengthened by fusion of the centra; accessory articulations (hyposphene–hypantrum) between dorsal vertebrae afforded greater strength to the backbone. The skull became disproportionately large to provide a large gape. Lightness was achieved by fenestration and development of various sinuses and cavities. The skull was essentially a series of bony arches and struts. Thus the strength and structure of the skeleton were maintained to cope with the large size, and the dead weight was considerably reduced.

With its sharp, dagger-like teeth, large gape and large orbit, the skull of *Postosuchus* is clearly that of a formidable carnivore. The teeth are highly serrated, compressed laterally, curved posteriorly, and have a sharp tip and broad base. They were highly adapted for cutting and shearing flesh. In lateral view, the dental margin of the upper tooth row is convex downward, whereas that of the lower is concave upward like a garden shear, affording additional grip to hold the food in position while slicing. Moreover the teeth are recurved and interdigitate when the jaws are closed. All these features are well suited for prehension.

The skull probably showed very little kinesis except for the pteryoids which had movable joints with the quadrates, ectopterygoids, braincase and palatines, allowing some medio-lateral as well as dorso-ventral motion between them to increase the depth of the oral cavity. In the lower jaw, the symphysis was weak, probably held in life by a ligament. There developed intramandibular kinesis between anterior and posterior segments of the lower jaw, the dentary and splenial forming the anterior moiety (Romer 1956; Frazzetta 1962). The movable mandibular tip in conjunction with intramandibular kinesis would allow outward bending of the middle part of each ramus with the result that large chunks of flesh could be manipulated and swallowed, aided by the movable palate (figure 23). This flexibility of the lower jaw would also reduce the biting forces to be carried by the elements of the skull (Gans 1961). This kind of intramandibular movement may also have been present in *Ornithosuchus*, *Ceratosaurus*, *Allosaurus*, *Albertosaurus* and *Tyrannosaurus* (Walker, A. D., 1964).

The frontal position of the large orbits, behind the narrow snout with a fairly large degree of stereoscopic vision indicates that *Postosuchus* had sharp eyes for good distance judgement. The eyes were protected from the glare by a supraorbital ridge. Internally adjacent to the naris, there is a large chamber that probably housed the Jacobson organ. The function of the Jacobson organ in reptiles is poorly understood. Since it is partly lined by olfactory epithelium, and is innervated by the olfactory nerve, it is considered to be an olfactory receptor. Good sight and good olfaction power of *Postosuchus* were of special significance for predation. The teeth were probably the major offensive weapon. Considerable degree of rotation was possible in the elbow and wrist joints. The sharp talon of the pollex could be used for impaling the prey while tearing at it with the teeth. Thus the front limbs were used for grasping, holding, piercing and manipulating the prey.

Although *Postosuchus* could run moderately well when occasion arose, it probably captured prey by stealth and surprise. The long neck and high position of the skull would allow the animal to scan a large terrain for food. If the prey was small, it could be seized and devoured whole. In the case of large prey, *Postosuchus*, towering over the opponent, could attack from above to grab the vulnerable neck. When the prey was killed, a sideward and backward jerk of the head

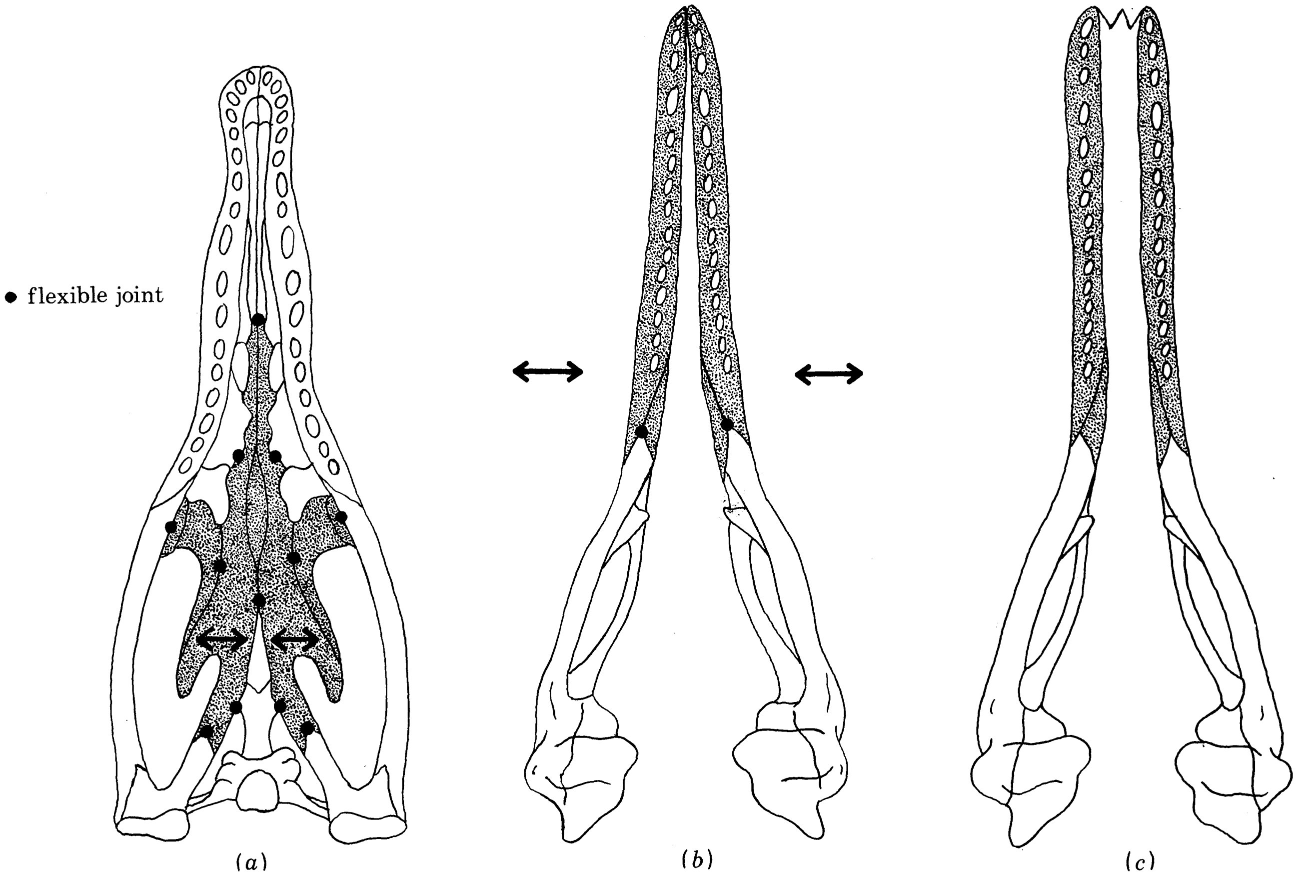

FIGURE 23. *Postosuchus kirkpatricki*, n.sp. (*a*) Palatal view of the skull showing flexible pterygoidal joints; (*b*) and (*c*) dorsal views of the lower jaw showing the intramandibular kinesis.

would produce a deep slice in the flesh. When a large piece of flesh had been ripped off, it could be easily gulped down with the aid of the movable jaw and the palate.

Postosuchus probably hunted in a pack. The association of 10 young, 1 sub-adult, and 1 adult skeletons in the Post quarry indicates some kind of group coordinated activities and seasonal reproduction. I suggest that many young individuals were protected in nesting areas by the parents until the young were large enough to move with the group or set off on their own. *Postosuchus* would probably feed on both live and dead animals. The diet must have been extremely varied with age, like modern crocodiles (Cott 1961), and komodo dragons (Auffenberg 1981), ranging from arthropods to various amphibians and reptiles available in the Dockum biota. Being the arch predator in its environment, adult *Postosuchus* had little to fear from any aggression, but various enemies could take a heavy toll of both eggs and defenceless young.

10. Relative growth

Relative growth denotes change of proportions as organisms increase in size. Relations between size and shape of organs and organisms have long been of interest to biologists. However, measurements of biological shape are not easy, as their mathematics are often very complex. Homoeomorphic forms are generally compared piecemeal, feature by feature, with occasional measurement of proportions. A pioneering attempt to compare biological shape was made by d'Arcy Thompson (1942) who succeeded in representing all kinds of apparently complex changes in morphology in terms of geometric distortion of a grid placed over an evolving or growing organism. Thompson's method of cartesian coordinate deformation was used by many palaeontologists to study the ontogeny or phylogeny of various extinct groups, including Colbert (1935) on Siwalik rhinoceroses, Lull & Gray (1949) on growth in ceratopsians, Langston (1953) on Permian amphibians, and Chatterjee (1974) on rhynchosaurs.

Thompson's deformation diagrams are visually impressive and give one instantly the sense and trend of transformation. Simpson *et al.* (1960) regarded it as a 'very interesting way of making similar comparisons in greater detail and taking into account areas and angles or directions as well as linear dimension'. But his method was criticized for its inherent subjectivity and its failure to yield quantitative information. Bookstein (1978) modified Thompson's method with 'bioorthogonal grids' whereas Todd *et al.* (1980) applied 'cardiodal-strain transformation' so that the shape could be analysed quantitatively. However these methods, though promising, are very complex to analyse without computer assistance. Others have used various proportions and ratios (Huxley, J. S., 1932; Dodson 1975) to study growth phenomena, but there is a debate on whether their use is appropriate (Atchley 1978).

In palaeontology growth study is indirect as it estimates individual growth from a mass sample of individuals in various growth stages. This is further hampered by the uncertainty of sex in fossil populations. Sexual differences in the skeletal anatomy of both living and fossil reptiles are generally poorly expressed and difficult to identify (Olson 1969).

Postosuchus, like any other growing animal, shows marked changes in form of skeletal elements from small to large individuals. Basically all the individuals of *Postosuchus*, fall into three size groups: small, intermediate, and large, and there is not much scope for rigorous biometric analysis. However morphological change in the different skeletal elements is clearly visible. This is shown here in figure 24. For example, there is a progressive decrease of humerus: femur

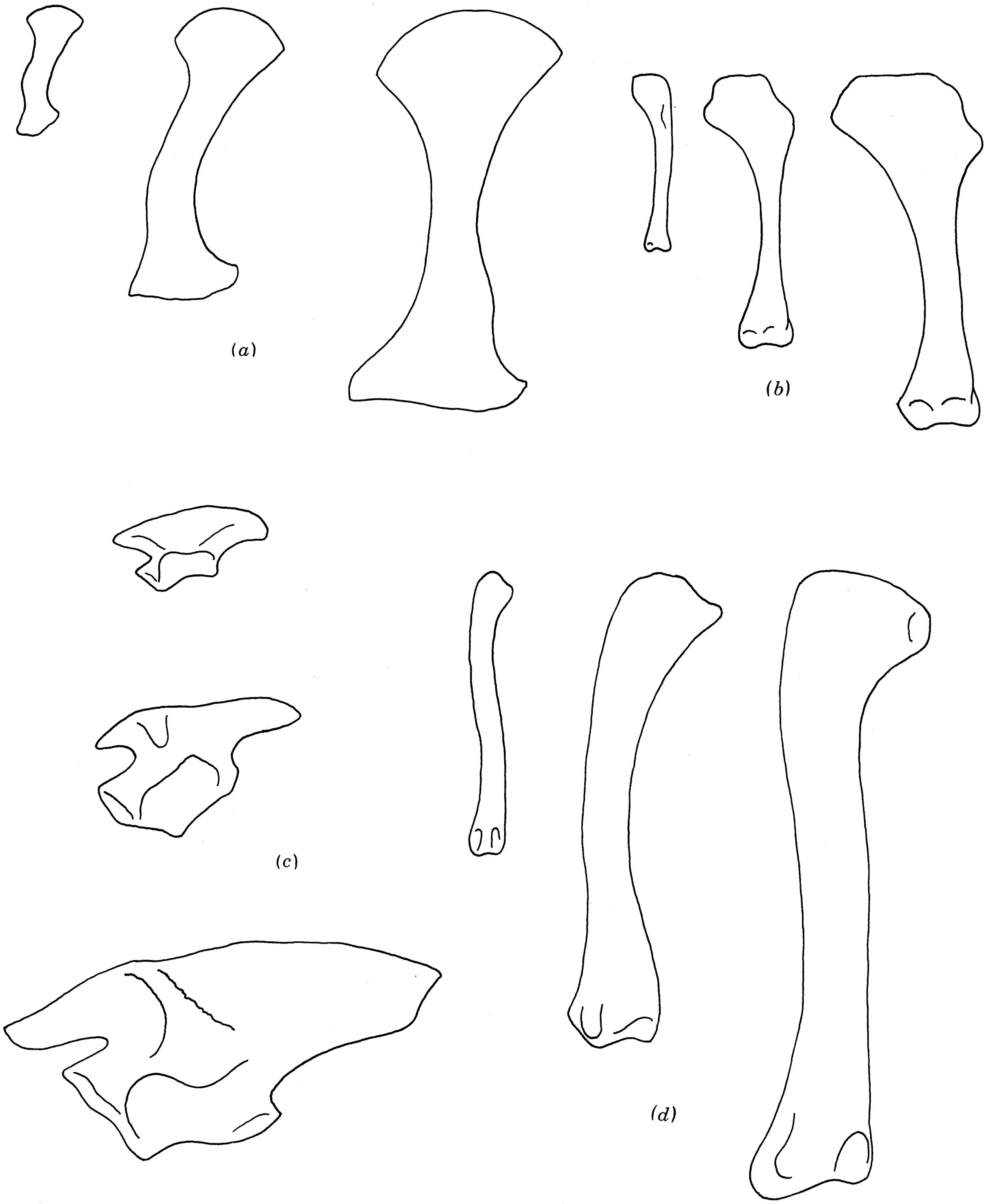

FIGURE 24. Relative growth of limb and girdles of *Postosuchus kirkpatricki*, n.sp., (*a*) scapula; (*b*) humerus; (*c*) ilium; (*d*) femur. For each element, small (T.T.U. P 9001), medium (T.T.U. P 9002), and large (T.T.U. P 9000) sizes are compared.

ratio from small to large individuals. The ratio is 66% (small), 59% (intermediate), and 52% (large). Alongside this, there is a gradual enlargement of the subvertical buttress of the ilium from small to large size. These morphological changes with growth may indicate locomotory specialization from young to adult form leading towards bipedal gait.

11. THE AFFINITIES OF *POSTOSUCHUS*

(*a*) *Summary of the essential characters of Postosuchus*

(i) Large, slenderly built, carnivorous thecodontian with erect and facultative bipedal gait; skull length 55 cm, total length estimated at 4 m.

(ii) Skull relatively large, narrow, deep with subnarial and antorbital fenestrae, the jaw with two lateral mandibular fenestrae; cavities and sinuses in the narial region. Lachrymal and prefrontal forming a rugose dorso-lateral crest over the orbit. Lower temporal opening divided by a forward projection of the quadratojugal–squamosal. Premaxilla, maxilla and dentary bordered lingually by interdental plates. Teeth large, highly serrate and recurved, deeply set in sockets. Dental formula: premaxillary teeth 4, maxillary teeth 13 and dentary teeth 15. Braincase deep with ossified laterosphenoid. Skull roof akinetic but palate flexible. Lateral mandibular fenestra and surangular foramen present; indication of intramandibular kinesis.

(iii) Centra weakly amphicoelous, spool-shaped, constricted in the middle, and showing lateral excavation; elongated cervicals, dorsals short, oblique lamina below the diapophysis; hyposphene–hypantrum articulation in mid-dorsals; sacrals 4, co-ossified, caudals slender.

(iv) Scapula tall and narrow, coracoid short and quadrangular. Clavicles and interclavicle probably lost.

(v) Pelvic girdle specialized and advanced; ilium with a short anterior process, a long posterior process and a prominent subvertical buttress above the acetabulum; acetabulum deep with overhanging supraacetabular crest allowing femur to move in vertical position; small perforation of acetabulum at the ilio-ischiadic contact; ischium and pubis elongate with strong median symphysis. Ischium rod-like and slender, pubis with prominent, hooked-back foot.

(vi) Fore-limbs much shorter and more slender than the hind, humerus a little more than half as long as femur. Limb bones hollow and thin-walled. Femur slightly sigmoidal with inturned head and well-developed distal condyles; fourth and greater trochanters weak; lesser trochanter absent. Tibia and fibula closely apposed; tibia with a ventral notch for ascending process of the astragalus. Ankle joint 'crocodile-normal'. Pes symmetrical, digitigrade, digit III longest, hallux slender, digit V lacking phalanges.

(vii) Paramedian dorsal scutes probably present.

(*b*) *Discussion of relationships of Postosuchus*

The skull and skeletal morphology of thecodontians is uniform, and many palaeontologists feel that the ankle joint may provide a key to the classification and phylogeny of these groups. Chatterjee (1982) classified thecodontians into four suborders on the basis of tarsal anatomy: Proterosuchia, Pseudosuchia, Ornithosuchia and Lagosuchia (see table 9). Since *Postosuchus* possesses a 'crocodile-normal' ankle joint, it should be assigned to the Suborder Pseudosuchia. Within the Pseudosuchia, three infraorders are recognized and defined as follows:

(I) Infraorder Parasuchia: long snouted carnivores, external nares posteriorly placed, primitive pelvis, ischium and pubis plate-like, heavily armoured.

(II) Infraorder Aetosauria: edentulous snout, possibly herbivorous, specialized and reduced lower temporal opening, primitive pelvis, ischium and pubis plate-like, heavily armoured.

(III) Infraorder Rauisuchia: highly carnivorous group, short-snouted; teeth highly serrate and recurved; subnarial and antorbital fenestrae present; pelvis advanced, ischium and pubis rod-like with long median symphysis; highly reduced dermal armour.

Table 9. Classification of Thecodontia

(After Chatterjee 1982.)

nature of ankle joint	Order Thecodontia Owen 1959
PM joint	(1) Suborder Proterosuchia
	Family Proterosuchidae Broom, 1906
	Family Erythrosuchidae Watson, 1917
CN joint	(2) Suborder Pseudosuchia
	(*a*) Infraorder Parasuchia
	Family Parasuchidae Lydekker, 1885
	(*b*) Infraorder Aetosauria
	Family Stagonolepididae Lydekker, 1887
	Family Scleromochliidae von Huene, 1914
	(*c*) Infraorder Rauisuchia
	Family Rauisuchidae von Huene, 1942
	Family Poposauridae Nopsca, 1928
CR joint	(3) Suborder Ornithosuchia
	Family Ornithosuchidae von Huene, 1908
	Family Euparkeriidae von Huene, 1920
AM joint	(4) Suborder Lagosuchia
	Family Lagosuchidae Bonaparte, 1975
unknown	Thecodontia incertae sedis
	Family Proterochampsidae Sill, 1967
	Family Doswelliidae Weems, 1980
	Family Longisquamidae Sharov, 1970

It is evident from the above diagnosis that *Postosuchus* belongs to the Infraorder Rauisuchia. The family Rauisuchidae includes eight well-established genera from the Middle and Late Triassic sediments of Brazil, Argentina and East Africa (Sill 1974; Dawley *et al.* 1979; Bonaparte 1981). The proportionately large skulls of rauisuchids and *Postosuchus* are closely allied in the development of subnarial and antorbital fenestrae, large highly serrated teeth and interdental plates. In the postcranial skeleton, ischium, femur and tarsus of the two groups are remarkably similar. However rauisuchids are heavily built and obligatory quadrapeds, whereas *Postosuchus* is gracile, and facultatively bipedal. The ilium and pubis of *Postosuchus* are highly distinctive. The ilium is vertical; there is a prominent subvertical buttress above the acetabulum, and the acetabulum shows a small perforation. The pubis is expanded distally into a hook. None of these features are found in the rauisuchids. Moreover the ilium of advanced species of rauisuchids was held in a subhorizontal position (Bonaparte 1981). The differences between these two groups may be attributed to differences in posture and locomotion, and indicate early phyletic separation. Thus *Postosuchus* cannot be accommodated in the existing Family Rauisuchidae.

Problems in the Family Poposauridae

A comparison of *Postosuchus* with a number of imperfectly known forms, principally from the Triassic sediments of the United States and Europe may be helpful to estimate its systematic position. *Postosuchus* shows clear affinities with *Poposaurus gracilis* which is from the Popo Agie

Member of the Chugwater Formation in Wyoming. *Poposaurus*, the sole genus of the family Poposauridae, is based on postcranial material including part of a pelvis, hind limbs and a few poorly preserved vertebrae (Mehl 1915). Because this material is not fully diagnostic, the systematics of *Poposaurus* have been highly confusing. It has been assigned to Saurischia (Hay 1930; Colbert 1961), Ornithischia (Nopsca 1928; von Huene 1956), and Thecodontia (Romer 1956; Galton 1977). In spite of the incompleteness of the material, the pelvis of *Poposaurus* is most readily comparable with that of *Postosuchus* (figure 25). The ilium shows short pre- and long post-acetabular processes, prominent subvertical buttress on the iliac blade, and slightly perforated acetabulum. The pubis is long and narrow, with recurved foot which projects ventrally beyond the symphysis (Walker, A. D., 1969; Galton 1977). However the pubic foot is not as extensive as that of *Postosuchus*. It seems that the *Postosuchus* pelvis can readily be derived from that of a *Poposaurus*. The preserved part of the femur, spool-shaped dorsal vertebrae, and co-ossified sacrals, collectively indicate strong morphological similarities with those of *Postosuchus*, and confirm Galton's assignment (1977) of the family Poposauridae to the Order Thecodontia.

Several specimens of pelvis materials, mainly ilia, from the Triassic of Texas, Arizona, and Germany have been referred to the Family Poposauridae by A. D. Walker (1969) and Galton (1977). Allocation of specimens on the basis of similarity of ilia is not always reliable. Moreover the ilia of *Postosuchus* show remarkable ontogenic variations (figure 24). In spite of this, I concur with Walker's diagnosis that all these ilia show a characteristic subvertical buttress, and similar architecture, and may be grouped within the Poposauridae. These specimens are briefly discussed below.

(i) *Stubensandstein ilium*. (Figure 26*a*, *b*.) Von Meyer (1861, plate 4, figs. 1 and 2) discussed a supposed parasuchid ilium from the Stubensandstein (Norian) of Germany. The ilium is very similar to that of the intermediate-sized *Postosuchus* (figure 24).

(ii) *Arizonasaurus*. (Figure 26*c*–*e*.) Welles (1947) reported a new pseudosuchian, *Arizonasaurus*, from the early Middle Triassic Moenkopi Formation of Arizona on the basis of fragmentary material. The left maxilla shows interdental plates, subnarial and antorbital openings. Unfortunately most of the alveoli are empty. However, several isolated teeth figured by him, are pointed, recurved and serrated, and may belong to the same genus. The ilium shows the subvertical buttress and long posterior process as in a poposaurid. Another juvenile specimen of ilium, tentatively referred to by Welles as *Anisodontosaurus*, is so similar to *Arizonasaurus* that there is no doubt as to their generic identity. Welles erected *Anisodontosaurus* as Reptilia incertae sedis because of its peculiar dental structure. The mandible contains peg-like blunt teeth, and the implantation is 'ankylothecodont' as in rhynchosaurs (Chatterjee 1974). It is clear that *Anisodontosaurus* is not a thecodontian, and the referred ilium belongs to a juvenile individual of *Arizonasaurus*.

(iii) *Archosaur from the Bromsgrove Sandstone Formation, England*. (Figure 26*f*.) Riley & Stutchbury (1836) described and subsequently (1840) figured various dinosaur bones from the late Triassic 'Magnesian Conglomerate', near Bristol, England, as representing a new genus *Thecodontosaurus*, but they did not provide a specific name. Morris (1843) rectified this omission while cataloguing the British fossils, and erected the species *Thecodontosaurus antiquus*. The type species is now considered as a prosauropod in the family Anchisauridae (Galton 1976). Later von Huene (1908) referred several isolated bones from the 'Lower Keuper Sandstone', now called the Bromsgrove Sandstone Formation of the midlands of England, to *Thecodontosaurus antiquus*.

A. D. Walker (1969) pointed out that several of these postcranial elements from the Middle

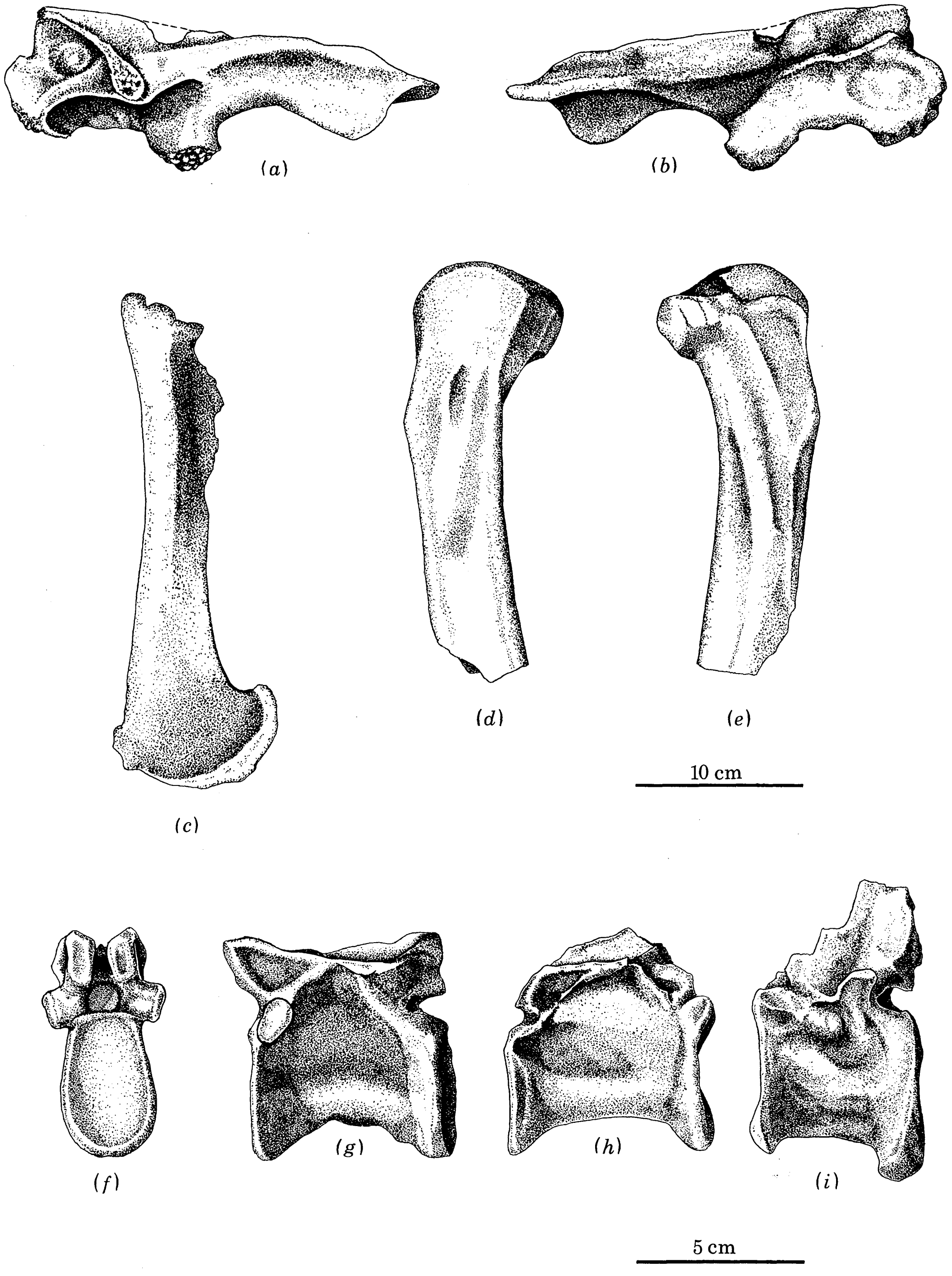

FIGURE 25. *Poposaurus gracilis* Mehl (1915). Holotype, specimen F.M.N.H. 357. (*a*) and (*b*) Left ilium, lateral and medial views; (*c*) conjoined pubes left lateral view, showing hook-like distal end; (*d*) and (*e*) posterior and anterior views of right femur (magn. ×0.25). (*f*) and (*g*) Anterior and lateral views of a dorsal vertebra; (*h*) lateral view of a dorsal vertebra; (*i*) lateral view of a caudal vertebra (magn. ×0.5).

Triassic Bromsgrove Sandstone Formation, near Warwick and Bromsgrove, England, usually referred to *Thecodontosaurus*, are closely related to *Poposaurus*. The material includes articulated sacral vertebrae (Huxley, T. H., 1870, plate III, figs 9 and 10), an ilium (Owen 1842, plate 45, figs 16 and 17), and an ischium (von Huene 1908, fig. 228). The ilium has a short anterior but long posterior process, with partly open acetabulum, and a subvertical buttress above it. It looks like a primitive version of the Stubensandstein ilium and strongly suggests poposaurid affinity.

(iv) *Pelvis from the Dockum Group, Texas.* (Figure 26*g–i*.) Case (1922, 1943) described several curious pelves from the Dockum Group as parasuchid. Colbert (1961) and A. D. Walker (1969) rightly pointed out that they are not parasuchid, but show strong affiliation with the poposaurid type. One pelvis (Case 1943) is identical with that of *Postosuchus*, where the pubis has a pronounced hook.

The status of Triassic carnosaurs

Another group of reptiles, so called Triassic carnosaurs, need to be seriously considered in connection with the affinity of *Postosuchus*. Triassic carnosaurs have been a poorly known and confusing group. Various tooth-bearing elements from the Upper Triassic which indicated a large, upland, carnivorous habit (contrasting with long-jawed parasuchids of aquatic habits), were referred to carnosaurs (von Huene 1932). However the association of cranial and postcranial material of Triassic carnosaurs is highly disputed. Romer (1956) considered that there were two families within the Triassic carnosaurs: Palaeosauridae and Teratosauridae. A. D. Walker (1964) and Charig *et al.* (1965), on the other hand, considered these two groups as prosauropods.

A. D. Walker (1964) reviewed the systematics of the various Triassic carnosaurs in detail, and concluded that *Ornithosuchus*, *Sinosaurus* (only the type maxilla), and *Teratosaurus* (only the type maxilla) were the only known Triassic carnosaurs. He pointed out that, since in no case, in material referred to *Sinosaurus* and *Teratosaurus*, was there a direct proven association between skull and postcranial material, the latter may be prosauropodous in nature. He placed these three genera in the family Ornithosuchidae which is a senior synonym of Teratosauridae. I will discuss these three genera in detail to estimate their relationships with *Postosuchus*.

The anatomy of *Ornithosuchus* from the Lossiemouth Sandstone Formation of Scotland is now well known from Walker's account (1964). The skull of *Ornithosuchus* shows various carnosaurian traits, as does *Postosuchus*. Its acetabulum shows incipient fenestration. However Bonaparte (1971) demonstrated that *Ornithosuchus* was not a carnosaur, but rather an advanced theocodontian, similar to *Riojasuchus* of Argentina. His conclusion is based on the tarsal structure of *Riojasuchus*, in which the astragalus has a socket for receiving the peg of the calcaneum, the opposite condition to that in 'crocodile-normal' joint. Chatterjee (1982) termed this ankle joint 'crocodile-reverse' which is characteristic of the Suborder Ornithosuchia, of the Order Thecodontia.

Unfortunately the ankle joint of *Teratosaurus* and *Sinosaurus* is unknown, and their allocation to a proper group seems difficult. Von Meyer (1861) erected the monotypic species *Teratosaurus suevicus* from the Stubensandstein of Germany on the basis of a right maxilla (figure 27*b*). It exhibits blade-like and serrated teeth, 13 alveoli, interdental plates, 1 subnarial and 1 antorbital fenestrae. It is very difficult to differentiate between Carnosauria and Rauisuchia on the basis of the maxilla only. However, in the carnosaurs, there are two antorbital fenestrae located entirely within the maxilla, whereas in Rauisuchia there is one. In *Teratosaurus*, the anterior

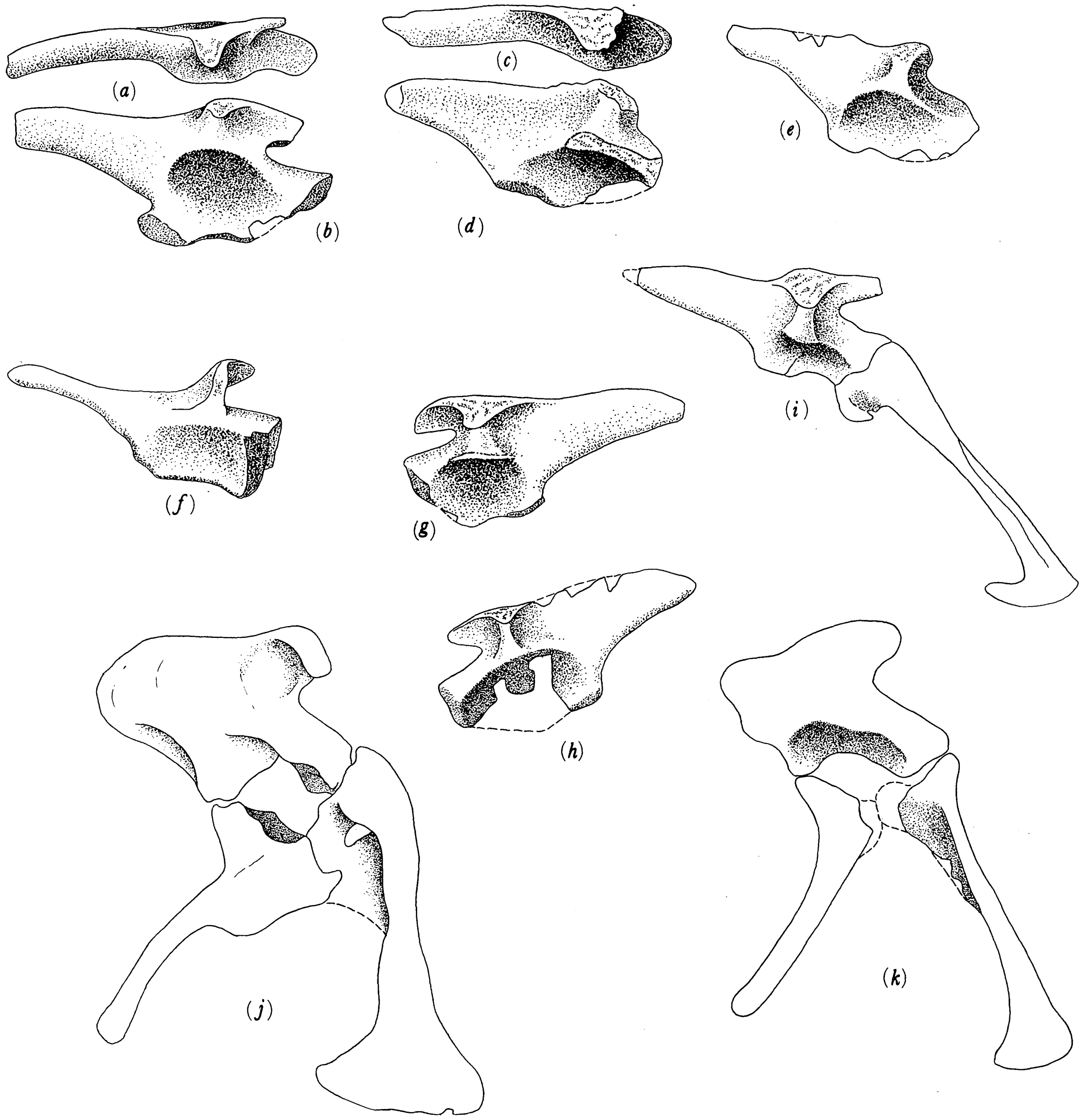

FIGURE 26. Pelvic girdles of poposaurid and Triassic saurischians. (*a*) and (*b*) Dorsal and lateral views of a right ilium from the Stubensandstein of Germany; the specimen may belong to *Teratosaurus* (after Meyer 1861); (*c*) and (*d*) dorsal and lateral views of right ilium of *Arizonasaurus* from the Middle Triassic Holbrook Member of Arizona (after Welles 1947); (*e*) lateral view of the right ilium of *Arizonasaurus*, originally referred to *Anisodontosaurus* by Welles (1947) from the Holbrook Member of Arizona; (*f*) left ilium in lateral view, referred here as Warwick poposaur; from the Middle Triassic Bromsgrove Sandstone of England (after Owen 1842); (*g*) lateral view of a left ilium referred herein as *Postosuchus*, from the Triassic Dockum Group of Texas (after Case 1922); (*h*) left ilium in lateral view, referred herein as *Postosuchus*, from the Triassic Dockum Group of Texas (after Case 1922); (*i*) lateral view of right ilium and pubis, from the Triassic Dockum Group of Texas, referred herein as *Postosuchus* (after Case 1943); (*j*) lateral view of right pelvis of *Herrerasaurus* from the early Upper Triassic Ischigualasto Formation of Argentina (after Reig 1963); (*k*) lateral view of right pelvis of *Staurikosaurus* from the early Upper Triassic Santa Maria Formation of Brazil (after Colbert 1970).

antorbital fenestra is absent as in Rauisuchia. In fact the size and proportion of the maxilla, and the number of teeth correspond very well with that of *Postosuchus* (figure 27*c*). In rauisuchids, the maxillary dental count is lower than 13. Welles (1947) suggested that the maxilla of *Teratosaurus* may actually belong with the Stubensandstein ilium of von Meyer (1861), discussed earlier. If this association could be substantiated, the poposaurid affinity of *Teratosaurus* would be strengthened.

Young (1948) described *Sinosaurus triassicus* from the Upper Red Bed of Lufeng, China on the basis of a left maxilla, jaw fragments and isolated teeth. The maxilla (figure 27*a*) shows large serrated teeth, interdental plates, and traces of subnarial and antorbital fenestrae. Unfortunately the maxilla is incomplete and the total dental count is unknown. However, there is one antorbital fenestra present in the maxilla, as is seen in Rauisuchia. Young concluded that *Sinosaurus* and *Teratosaurus* are extremely similar. If this is true *Sinosaurus* seems to be a potential rauisuchian, but its allocation into the proper family is not possible at this stage owing to a lack of associated postcranial material. All the Triassic carnosaurs (*sensu* A. D. Walker 1964), *Ornithosuchus*, *Teratosaurus*, and *Sinosaurus* which were approaching the theropod level of organization, appear to be advanced thecodontians. True carnosaurs were probably evolved in post-Triassic time.

Herrerasaurus and Staurikosaurus

See figure 26*j*, *k*. Mention should be made at this point of two contemporaneous carnivorous saurischians, namely *Herrerasaurus* and *Staurikosaurus*, as they exhibit a footed pubis like *Postosuchus*. *Herrerasaurus* is known from the Ischigualasto Formation of Argentina (Reig 1963), and *Staurikosaurus* from the Santa Maria Formation of Brazil (Colbert 1970). Except for the footed pubis, both the genera are well advanced over *Postosuchus*, and show various dinosaurian hallmarks in the pelvis (highly perforated acetabulum) and hind-limb (femur with well-developed fourth trochanter and mesotarsal ankle joint). Currently their taxonomy is obscure. Galton (1977) referred these two genera to Saurischia *incertae sedis*. It appears that an expanded pubic foot has evolved independently on several occasions among archosaurs, as first pointed out by A. D. Walker (1969), in poposaurids, *Herrerasaurus*, and *Staurikosaurus* during the Triassic, and in several theropods and in *Archaeopteryx* during Jurassic and Cretaceous times.

(*c*) *Outline of classification*

From the preceding discussion it will be apparent that the rauisuchians were the dominant terrestrial carnivores during the Middle and Upper Triassic, both in Laurasia and Gondwana. *Postosuchus* is considered here to be an advanced rauisuchian and grouped with *Poposaurus*, *Teratosaurus*, *Arizonasaurus* and the Warwick archosaur in the Family Poposauridae Nopsca, 1928 (which has a priority over Teratosauridae von Huene (1932). The Poposauridae is regarded as the sister group of the Rauisuchidae within the Infraorder Rauisuchia (Chatterjee 1982). The inferred phylogenetic relations of poposaurids may be represented in figure 28.

A revised classification of Rauisuchia is appended listing only the type species and geological horizons (data on Rauisuchidae mainly after Krebs (1976)).

Order Thecodontia Owen, 1859
  Suborder Pseudosuchia Zittel 1887–1890.
    Infraorder Rauisuchia von Huene, 1942 (for diagnosis see §11).
      Family Rauisuchidae von Huene, 1942.

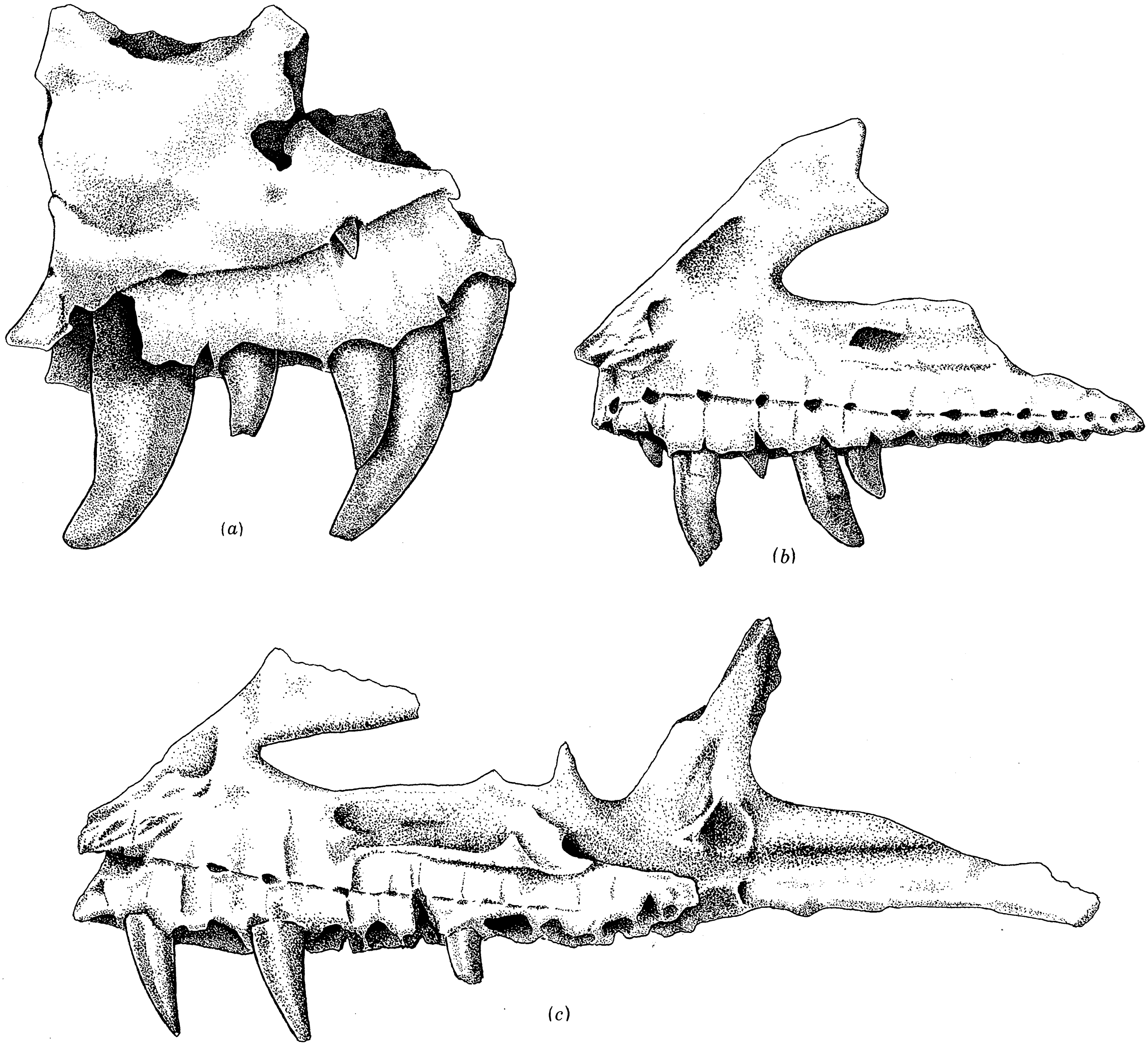

FIGURE 27. (*a*) Medial view of left maxilla of *Sinosaurus* (after Young 1948); (*b*) medial view of right maxilla of *Teratosaurus* (after Meyer 1861); (*c*) medial view of right maxilla of *Postosuchus*. Note, *Teratosaurus* and *Postosuchus* are very similar which suggest close relationships.

Quadrupedal, maxillary teeth less than 12, cervicals short, ilium horizontal in advanced genera, subvertical buttress above acetabulum absent; acetabulum closed, pubis rod-like.

Genus: *Rauisuchus* von Huene, 1942
Type species: *Rauisuchus tiradentes* von Huene, 1942
Santa Maria Formation, Brazil; middle or early late Triassic.
Genus: *Prestosuchus* von Huene, 1942
Type species: *Prestosuchus chiniquensis* von Huene, 1942

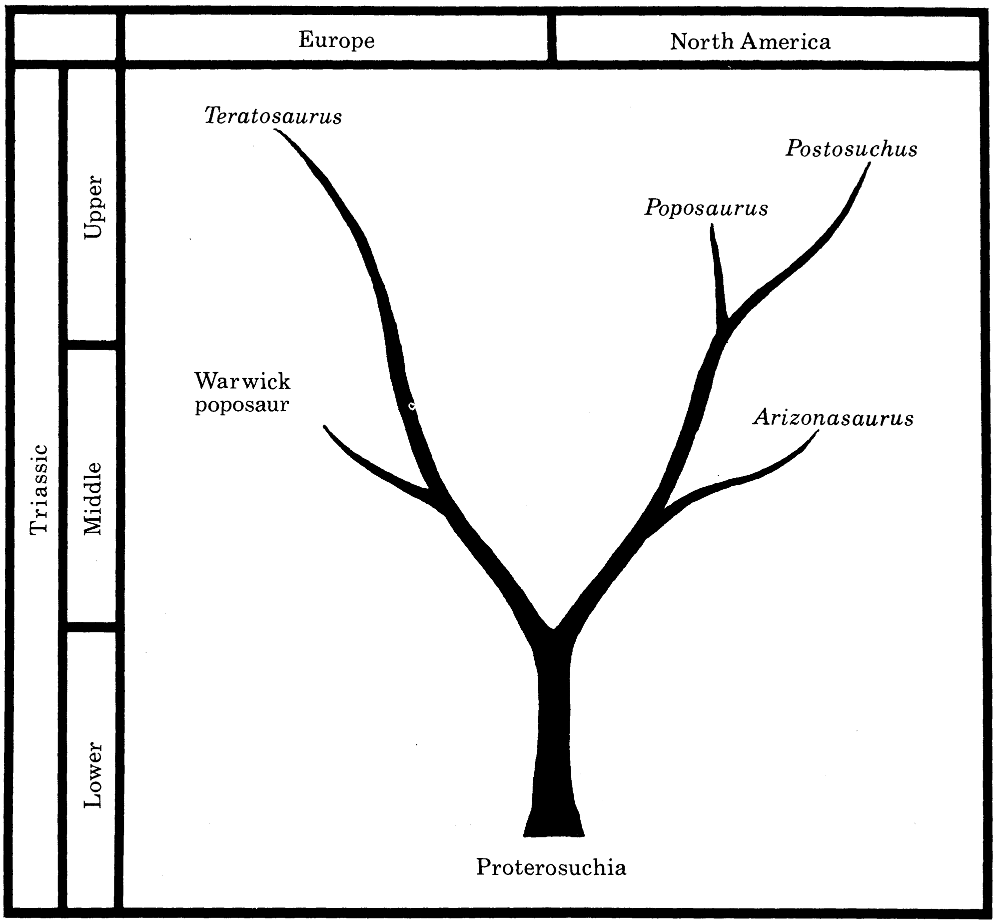

FIGURE 28. Suggested phylogeny of the different genera of *Poposauridae*.

Santa Maria Formation, Brazil; middle or early late Triassic.
Genus: *Procerosuchus* von Huene, 1942
Type species: *Procerosuchus celer* von Huene, 1942
Santa Maria Formation, Brazil; middle or early late Triassic.
Genus: *Mandasuchus* Charig, in von Huene, 1956 (nomen nudum)
Type species: *Mandasuchus tanyauchen* Charig, 1967 (nomen nudum)
Manda Formation, East Africa; middle Triassic
Genus: *Stagonosuchus* von Huene, 1938
Type species: *Stagonosuchus nyassicus* von Huene, 1938 (= *S. major* (Haughton, 1932))
Manda Formation, East Africa; middle Triassic.
Genus: *Luperosuchus* Romer, 1971
Type species: *Luperosuchus fractus* Romer, 1971
Chañares Formation, Argentina; middle Triassic.
Genus: *Saurosuchus* Reig, 1959
Type species: *Saurosuchus galilei* Reig, 1959
Ischigualasto Formation, Argentina; late Triassic
Genus: *Fasolasuchus* Bonaparte, 1981

Type species: *Fasolasuchus tenax* Bonaparte, 1981
Los Colorados Formation, Argentina; late Triassic.
Genus: *Heptasuchus* Dawley, Zawiskie and Cosgriff, 1979
Type species: *Heptasuchus clarki* Dawley, Zawiskie and Cosgriff, 1979
Chugwater Formation, Wyoming; late Triassic.
Genus: *Ticinosuchus* Krebs, 1965
Type species: *Ticinosuchus ferox* Krebs, 1965
Grenzbitumenzone, Monte San Giorgio, Switzerland; middle Triassic.

Family Poposauridae Nopsca, 1928.

Facultatively bipedal, gracile, maxillary teeth 13; cervicals elongate; ilium vertical with subvertical buttress above acetabulum; acetabulum partly open; pubis with prominent hook at the distal end.

Genus: *Poposaurus* Mehl, 1915
Type species: *Poposaurus gracilis* Mehl, 1915
Chugwater Formation, Wyoming; late Triassic.
Genus: *Postosuchus* n.gen.
Type species: *Postosuchus kirkpatricki* n.sp.
Dockum Group, Texas; late Triassic.
Genus: *Teratosaurus* von Meyer, 1861
Type species: *Teratosaurus suevicus* von Meyer, 1861
Stubensandstein, Germany; late Triassic.
Genus: *Arizonasaurus* Welles, 1947
Type species: *Arizonasaurus babbitti* Welles, 1947
Moenkopi Formation, Arizona; middle Triassic
Genus: Warwick poposaur, unnamed
Type species: Warwick poposaur, unnamed
Bromsgrove Sandstone Formation, England; middle Triassic
Genus: *Sinosaurus* Young, 1948, Rauisuchia *incertae sedis*
Type species: *Sinosaurus triassicus* Young, 1948
Upper Red Beds, Lufeng, China; late Triassic–early Jurassic

12. The evolution of tyrannosaurs

Carnosaurs were highly successful predators during the Jurassic and Cretaceous periods. The Infraorder Carnosauria (*sensu* Charig 1973) includes four families: Allosauridae, Tyrannosauridae, Deinocheiridae, and Spinosauridae. The Family Deinocheiridae was erected on a single incomplete specimen of *Deinocheirus* from the Upper Cretaceous of Mongolia, and is currently considered as a giant ornithomimid (Galton 1982) and is therefore not a carnosaur. The Family Spinosauridae contains highly specialized theropods showing extremely elongated neural spines, up to 1.5 m long, and is of doubtful position among carnosaurs (Romer 1956). Its allocation must be deferred until better material is available.

Tyrannosaurs resemble larger versions of allosaurs, but major differences have led many palaeontologists to believe that they cannot be direct descendants (Osborn 1912). A. D. Walker (1964) suggested that allosaurids and tyrannosaurids represent separate phyletic lines that diverged in late Triassic time. Although allosaurids and tyrannosaurids share many common characters such as bipedal gait, highly carnivorous habit, loose mandibular symphysis with intramandibular kinesis, flexible palate, and similar postcranial features, they may be distinguished by a suite of contrasting characters summarized in table 10.

Table 10. Contrasts between Allosauridae and Tyrannosauridae

	Allosaurus-like forms	*Tyrannosaurus*-like forms
general		
(1)	size: 10 m long, estimated live mass 2300 kg	size: 15 m long, estimated live mass 7500 kg
(2)	skull, slender, moderately high, mesokinetic, quadrate streptostylic	skull robust, very high, akinetic, quadrate immovable
(3)	fronto-parietal crest wide	fronto-parietal crest narrow
(4)	postorbital-jugal bar behind orbit nearly vertical; postorbital loosely articulated	ventral process of the postorbital has a forward projection in the orbit; postorbital strongly articulated
(5)	squamosal–quadratojugal border behind lower temporal opening nearly vertical	squamosal–quadratojugal bar has a forward projection
(6)	skull fenestrae large, bony bars between them slender	skull fenestrae small, bony bars expanded
(7)	dental formula: 5+17/15	dental formula: 4+12/14
(8)	premaxillary teeth non-incisiform	premaxillary teeth incisiform
(9)	deep cavity between basioccipital and basisphenoid	no such cavity in this region
(10)	surangular foramen small	surangular foramen large
(11)	retroarticular process weak	retroarticular process strong
postcranial		
(12)	front limb 42% of hind	front limb 26% of hind
(13)	manus 70% of pes; three functional digits in manus	manus 28% of pes; two functional digits in manus
(14)	ilium with short anterior process	ilium with long anterior process
(15)	ischium long and expanded distally	ischium short with tapering distal end
(16)	ankle joint: advanced mesotarsal-reverse (AM-R) type	ankle joint: advanced mesotarsal-normal (AM-N) type

Significance of the ankle structure

In recent years, it has been recognized that a number of structurally distinct kinds of ankle joints are present in archosaurs, which may provide a useful clue to the phylogeny and classification of these groups. Bonaparte (1971) pointed out two distinct types of astragalo-calcanear joints among archosaurs on the basis of the relative positions of the peg and socket. One is like that of extant crocodilians in which the astragalus has a peg that fits into a socket of the calcaneum. The tarsus of *Postosuchus* is a good example of this pattern. The second category is seen in advanced ornithosuchids in which the peg is on the calcaneum and the socket on the astragalus. Chatterjee (1978*a*) termed these two types of ankle joint crocodile-normal (CN) and crocodile-reverse (CR) respectively. From a functional point of view, the astragalus forms part of the crus, the calcaneum part of the pes. The peg and socket joint between the astragalus and the calcaneum allows a rotational movement between them.

Two other types of ankle joints are known among archosaurs. In the dinosaurian ankle, the joint is mesotarsal, where the hinge movement occurs between the proximal and distal rows of tarsals. However, the astragalus has an ascending process for locking the tibia, and the calcaneum is reduced and lacks the 'heel'. A primitive version of the mesotarsal joint is seen in proterosuchians, where the astragalus and calcaneum articulate with each other by means of double convexo-concave complementary joints, with a perforating foramen between them. The calcaneum has a laterally extending tuber. To differentiate between these two types of mesotarsal joints, Chatterjee coined the terms advanced-mesotarsal (AM) for the dinosaurian ankle joint, and primitive-mesotarsal (PM) for the primitive thecodontian ankle joint.

The origin of dinosaurs from different thecodontian lineages is not clear at this moment. Bonaparte (1969), Krebs (1963), and Welles & Long (1974) argued that the AM joint cannot be derived from CN or CR joint. On the other hand, Charig (1972), A. D. Walker (1977), Cruickshank (1979), and Chatterjee (1982) maintained that such derivation did occur. The ankle of *Postosuchus*, being a transitional between CN and AM joint, supports this contention.

Some of the modifications of the ankle joint of *Postosuchus* toward the AM joint is as follows:

(i) rotation of the distal end of the tibia with the development of a postero-lateral notch to obtain efficient union with the astragalus;

(ii) initial development of the ascending process of the astragalus.

The calcaneum of *Postosuchus*, however, is still in the thecodontian grade with the retention of the posterior tuber on which some of the ankle flexors were inserted. With the development of fully improved dinosaur-like posture, the massive calcaneal tuber would be unnecessary, and the ankle flexors could be attached directly on the metatarsus. In the crocodile the heel ossifies from a separate centre (Walker, A. D., 1972). During the evolution of the dinosaurian tarsus, vertical compression, due to large body mass, seems to have caused the calcaneal heel to lose ossification. Freed from its connection with the heel, the calcaneum became small, firmly fixed with the astragalus, and perfected the mesotarsal joint. A reduced or vestigial calcaneal heel has been reported in the prosauropod *Riojasaurus* (Bonaparte 1971), the thecodontian *Lagosuchus* (Bonaparte 1975) and the coelurosaur *Saltopus* (Walker 1970). This implies that the AM joint could have evolved from a crocodiloid joint. The calcaneum of *Postosuchus* without tuber is not far from that of a theropod. Many theropods retain the vestiges of peg and socket joint, either in CN or CR fashion, thus indicating a close structural affinity (Chatterjee 1982). It is possible to recognize strict homologies between the ankle of *Postosuchus* and counterparts in the Triassic and later dinosaurs (figure 29).

Although both allosaurs and tyrannosaurs show mesotarsal ankle joints, the nature of the articulation between astragalus and calcaneum is quite different in each family. In *Allosaurus*, there is an incipient socket in the astragalus which receives a peg-like process of the calcaneum. In *Tyrannosaurus*, the reverse is the case where the incipient peg of the astragalus fits into a socket of the calcaneum. Chatterjee (1982) accordingly, named the former type as 'advanced mesotarsal-reverse' (AM-R), and the latter as 'advanced mesotarsal-normal' (AM-N) type. I believe that tyrannosaurs could be evolved from a *Postosuchus*-like animal, as indicated by the correlation between the ankle structure and other anatomical details. The reasons for this hypothesis will be discussed below.

The origin of tyrannosaurs

The family Tyrannosauridae represents the culmination of carnosaur evolution. It possibly made its first appearance at the top of the early Cretaceous of Mongolia; its main occurrence, however, is in the late Cretaceous of North America, East Asia, India, Argentina and Africa. Except for the North American and Mongolian forms, the rest of the material is based on incomplete material, and thus comparison of *Postosuchus* will be restricted to *Tyrannosaurus*. The

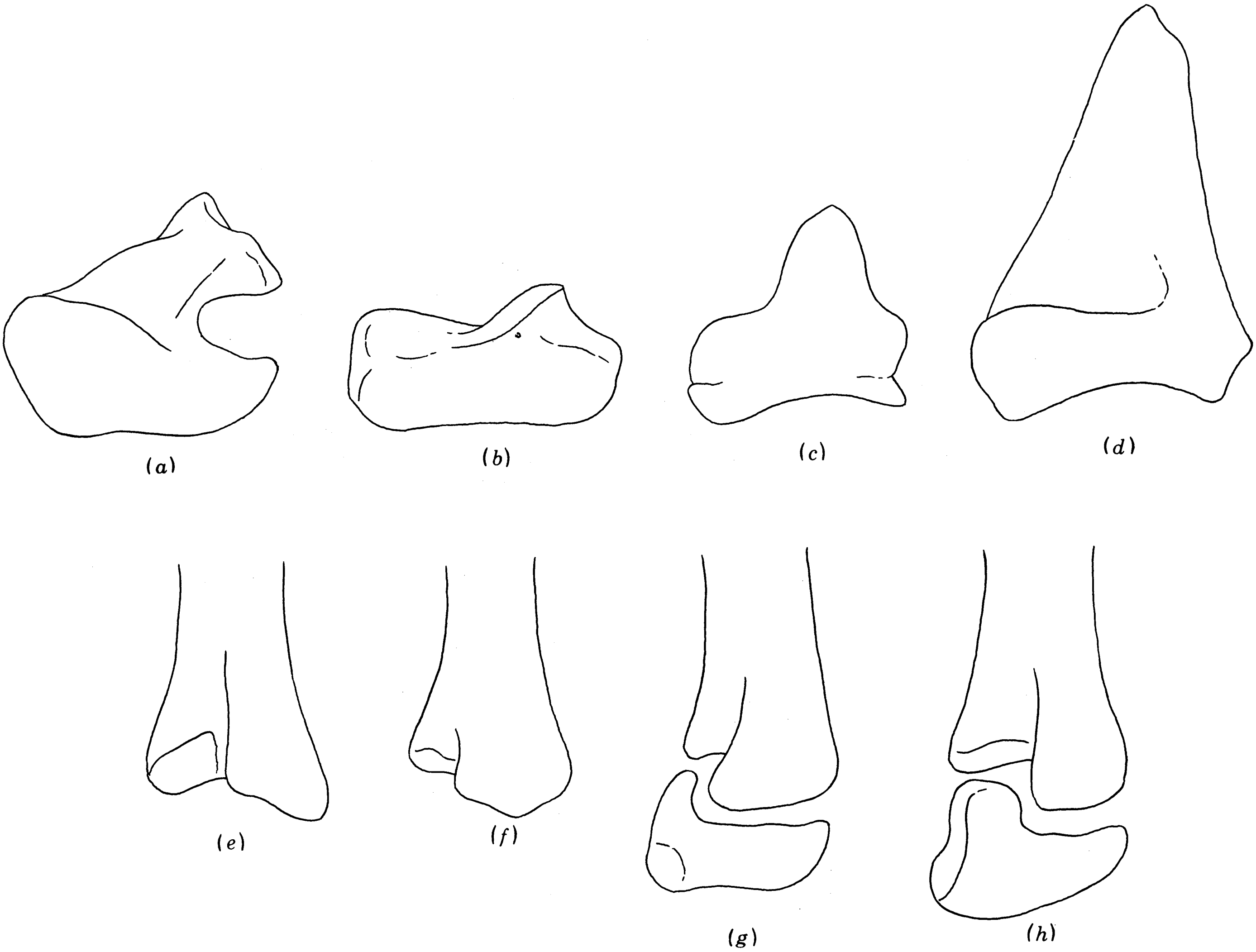

FIGURE 29. Comparisons of tibia-astragalar connection. (*a*)–(*d*) Anterior views of the left astragalus showing the development of the ascending process. (*a*) *Postosuchus*; (*b*) a new podokesaur from the Triassic of India; (*c*) *Allosaurus* (after Madsen 1976); (*d*) *Albertosaurus* (after Lambe 1917). (*e*)–(*h*) Posterior views of the left tibia showing the notch for the ascending process of the astragalus. (*e*) *Postosuchus*; (*f*) *Barapasaurus* (after Jain *et al.* 1975); (*g*) *Massospondylus* (after Charig *et al.* 1965); (*h*) *Diplodocus* (after Charig *et al.* 1965).

family contains seven genera: *Tyrannosaurus*, *Tarbosaurus*, *Albertosaurus*, *Daspletosaurus*, *Indosuchus*, *Alioramus*, and *Prodeinodon* (Olshevsky 1978). A comparison of *Postosuchus* with *Tyrannosaurus* offers more positive evidence of probable phyletic relationships (table 11).

It thus appears from this table that a suite of tyrannosaurian traits were already developed in *Postosuchus*, and thus supports the contention that this reptile may be close to the ancestry of tyrannosaurs. So far no definite tyrannosaurs are known from Jurassic sediments. This implies a long hiatus of the fossil record between *Postosuchus*- and *Tyrannosaurus*-bearing horizons, and future discovery may fill this important gap. Probably allosaurs took the role of large terrestrial predators during Jurassic time, as did *Postosuchus* during the late Triassic. From the primitive *Postosuchus*-like stock, the progressive morphological changes leading to *Tyrannosaurus* could be traced by the following evolutionary development (figure 30).

TABLE 11. COMPARISON OF DIAGNOSTIC CHARACTERS BETWEEN *POSTOSUCHUS* AND *TYRANNOSAURUS*

	Postosuchus-like animal		*Tyrannosaurus*-like animal
skull			
(1)	skull length 55 cm, slightly longer than femur (50 cm)	(1)	skull length 1.4 m, slightly longer than femur (1 m)
(2)	skull kinesis: dorsal roof akinetic, palate flexible, quadrate fixed, loose symphysis, intramandibular kinesis present	(2)	skull kinesis: dorsal roof akinetic, palate flexible, quadrate fixed, loose symphysis, intramandibular kinesis present
(3)	nares terminal large; nasal long	(3)	nares terminal large; nasal long
(4)	premaxillae and nasals narrow, and beak-like	(4)	premaxillae and nasals narrow, and beak-like
(5)	two antorbital fenestrae, strong shelf over posterior one; accessory foramina in jugal and lacrimal absent	(5)	three antorbital fenestrae, no shelf over posterior one; accessory foramina in jugal and lacrimal present
(6)	orbit deep with forward projection of postorbital	(6)	orbit deep with forward projection of postorbital
(7)	lower temporal opening divided by a forward projection of squamosal-quadratojugal	(7)	lower temporal opening partially divided by a forward projection of squamosal-quadratojugal
(8)	teeth highly serrate recurved with large canine teeth	(8)	teeth highly serrate, recurved with large canine teeth
(9)	dental formula: 4+13/15, interdental plates present	(9)	dental formula: 4+12/14, interdental plates present
(10)	prominent dorso-lateral ridge over the orbit formed by lacrimal, prefrontal, postorbital and squamosal	(10)	dorso-lateral ridge formed only by postorbital
(11)	frontal slightly depressed along mid-line; skull table very wide across frontals	(11)	frontal highly depressed along mid-line; skull table very narrow across frontals
(12)	T-shaped parietals, lateral branch highly crested; frontals do not take part in supratemporal fenestrae	(12)	T-shaped parietals, lateral branch highly crested; frontals take part in supratemporal fenestrae
(13)	interpterygoid vacuity narrow, paired plate-like vomers	(13)	interpterygoid vacuity wide, single diamond-shaped vomer
(14)	braincase deep, highly projecting basipterygoid process	(14)	braincase deep, highly projecting basipterygoid process
(15)	surangular fenestra large	(15)	surangular fenestra large
(16)	retroarticular process prominent	(16)	retroarticular process prominent
postcranial			
(17)	posture: facultative bipedal	(17)	posture: obligatory bipedal
(18)	neck long, hyposphene-hypantrum in dorsals, sacrals co-ossified, 4	(18)	neck short, hyposphene-hypantrum in dorsals, sacrals co-ossified 5
(19)	limb disparity: fore-limb 64% of hind, manus 39% of pes, five functional digits in manus	(19)	limb disparity: fore-limb 26% of hind, manus 28% of pes, two functional digits in manus
(20)	ilium with short anterior and long posterior process	(20)	ilium with long anterior and posterior process
(21)	acetabulum slightly open, subvertical buttress above it	(21)	acetabulum fully open, subvertical buttress above it
(22)	ischium rod-like with slightly expanded distal end	(22)	ischium rod-like with tapering distal end
(23)	pubis with expanded foot	(23)	pubis with expanded foot
(24)	femur lacking lesser trochanter, weakly sigmoid and longer than tibia	(24)	femur with lesser trochanter, straight, and longer than tibia
(25)	tibia and fibula closely apposed; distally tibia has an antero-lateral notch for ascending process of astragalus	(25)	tibia and fibula closely apposed; distally tibia lacks notch, astragalus laps the distal end of tibia anteriorly
(26)	pes symmetrical, digitigrade, digit III longest and robust, I and V reduced	(26)	pes symmetrical, digitigrade, digit III longest but reduced proximally, I lost
(27)	ankle joint: crocodile-normal (CN) type, calcaneum large with a tuber, ascending process of astragalus small	(27)	ankle joint: advanced mesotarsal-normal (AM-N) type, calcaneum small, without tuber; ascending process of astragalus very large
(28)	scutes present	(28)	scutes absent

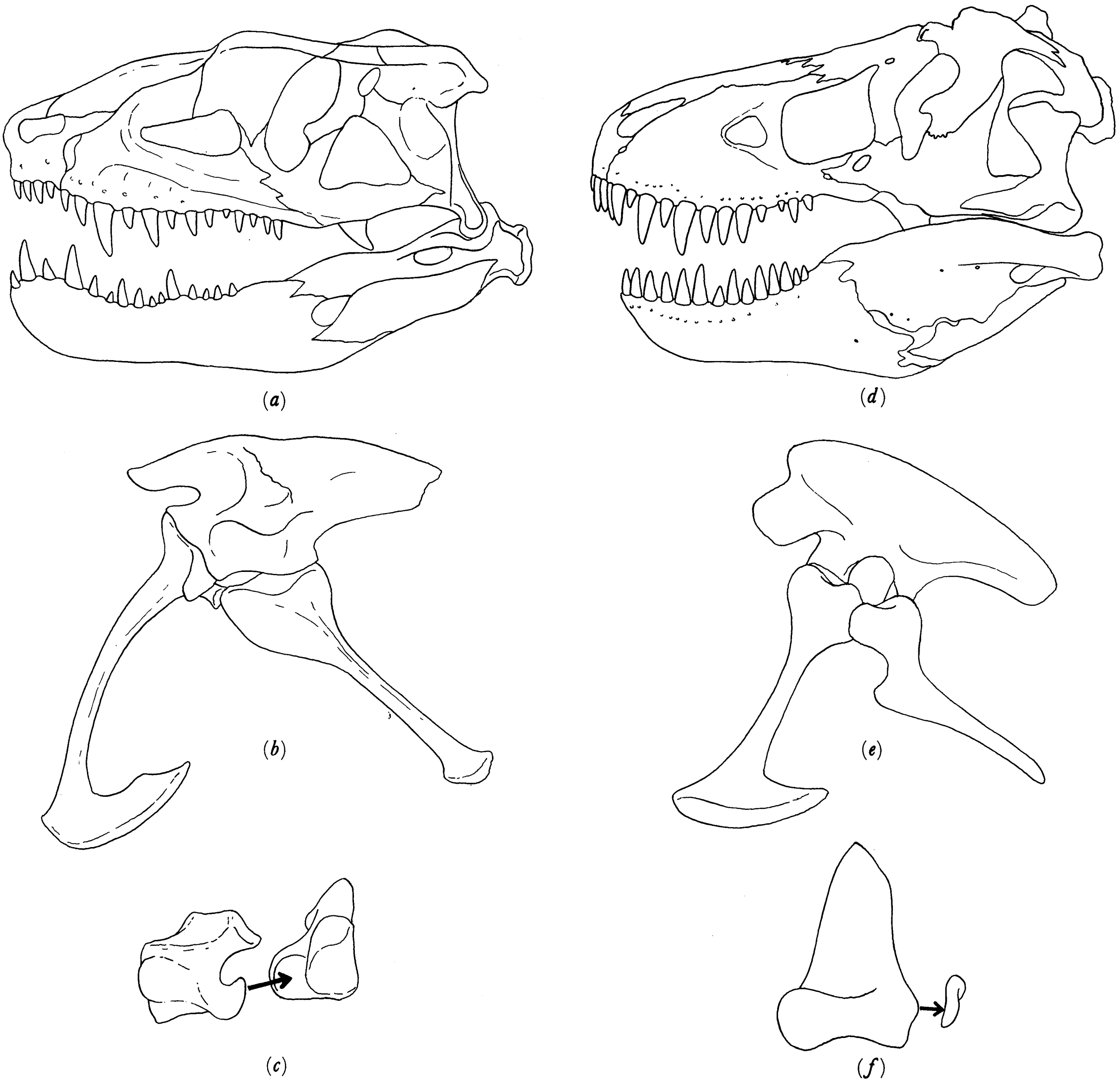

FIGURE 30. Comparisons between *Postosuchus* and *Tyrannosaurus*. (*a*), (*b*), (*c*) Skull, pelvis and ankle joint of *Postosuchus*; (*d*), (*e*), (*f*) skull, pelvis and ankle joint of *Tyrannosaurus* (after Osborn 1912, 1916; Lambe 1917). In the ankle joint, arrow indicates the position of socket opposite to the corresponding peg.

(i) Increase of over-all size from 4 m to 15 m in length.

(ii) Enlargement of skull. Additional fenestrations (such as in lacrimal, jugal, maxilla, surangular, ectopterygoid, and palatine) were developed probably to lighten the bones without loss of strength.

(iii) Loss of dorso-lateral crest over the orbit so the skull became more narrow and rounded allowing large stereoscopic vision.

(iv) Antero-posterior abbreviation of skull, reduction of marginal teeth.

(v) Change of posture from facultatively bipedal to obligatory bipedal; the front limb reduced to a grasping organ with two functional digits; pelvis and hind limb highly modified to support the body weight and to accommodate the powerful muscles. Some of the modifications in this region include the following:

(*a*) Acetabulum completely open, so that highly inturned head of femur could rotate freely in a vertical plane. Large iliac crest with strong anterior process, ischium became short and tapered distally, strong ilio-sacral joint with five sacrals.

(*b*) Femur robust, fairly straight with development of lesser trochanter.

(*c*) Metatarsals closely apposed, digit III narrow proximally, I lost: development of mesotarsal joint with strong ascending process of astragalus for locking tibia.

(*d*) Loss of dermal armour.

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