The early Triassic rhynchosaur Mesosuchus browni and the interrelationships of basal archosauromorph reptiles

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Phil. Trans. R. Soc. Lond. B 1998 **353**, 501-541
doi: 10.1098/rstb.1998.0225

The Royal Society

The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles

David W. Dilkes[*]

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

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Restudy of the unique diapsid reptile *Mesosuchus browni* Watson, from the *Cynognathus* Assemblage Zone (late Early Triassic to early Middle Triassic) of the Burgersdorp Formation (Tarkastad Subgroup; Beaufort Group) of South Africa, confirms that it is the most plesiomorphic known member of the Rhynchosauria. A new phylogenetic analysis of basal taxa of Archosauromorpha indicates that Choristodera falls outside of the Sauria, Prolacertiformes is a paraphyletic taxon with *Prolacerta* sharing a more recent common ancestor with Archosauriformes than with any other clade, *Megalancosaurus* and *Drepanosaurus* are sister taxa in the clade Drepanosauridae within Archosauromorpha, and are the sister group to the clade Tanystropheidae composed of *Tanystropheus*, *Macrocnemus*, and *Langobardisaurus*. Combination of the phylogenetic relationships of basal archosauromorphs and their known stratigraphic ranges reveals significant gaps in the fossil records of Late Permian and Triassic diapsids. Extensions of the temporal ranges of several lineages of diapsids into the Late Permian suggests that more groups of terrestrial reptiles survived the end-Permian mass extinction than thought previously.

Keywords: fossil; phylogeny; reptile; South Africa; diapsid; Gondwana

1. INTRODUCTION

In 1911, D. M. S. Watson had the opportunity to examine a block of sandstone with the intermingled partial skeletons of several small reptiles in the private collection of Mr Alfred Brown. This block had been found in the *Cynognathus* Assemblage Zone near the town of Aliwal North in the Cape Province (now Eastern Cape Province) of South Africa (figure 1). Watson considered the skeletons to belong to a single new species that he named *Mesosuchus browni* in a preliminary note (Watson 1912*a*). However, it was

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[*] Address for correspondence: Department of Zoology, Erindale College, The University of Toronto, 3359 Mississauga Road, Mississauga, Ontario, Canada L5L 1C6 (`ddilkes@credit.erin.utoronto.ca`).

Phil. Trans. R. Soc. Lond. B (1998) **353**, 501–541
Received 24 October 1996 *Accepted* 10 March 1997

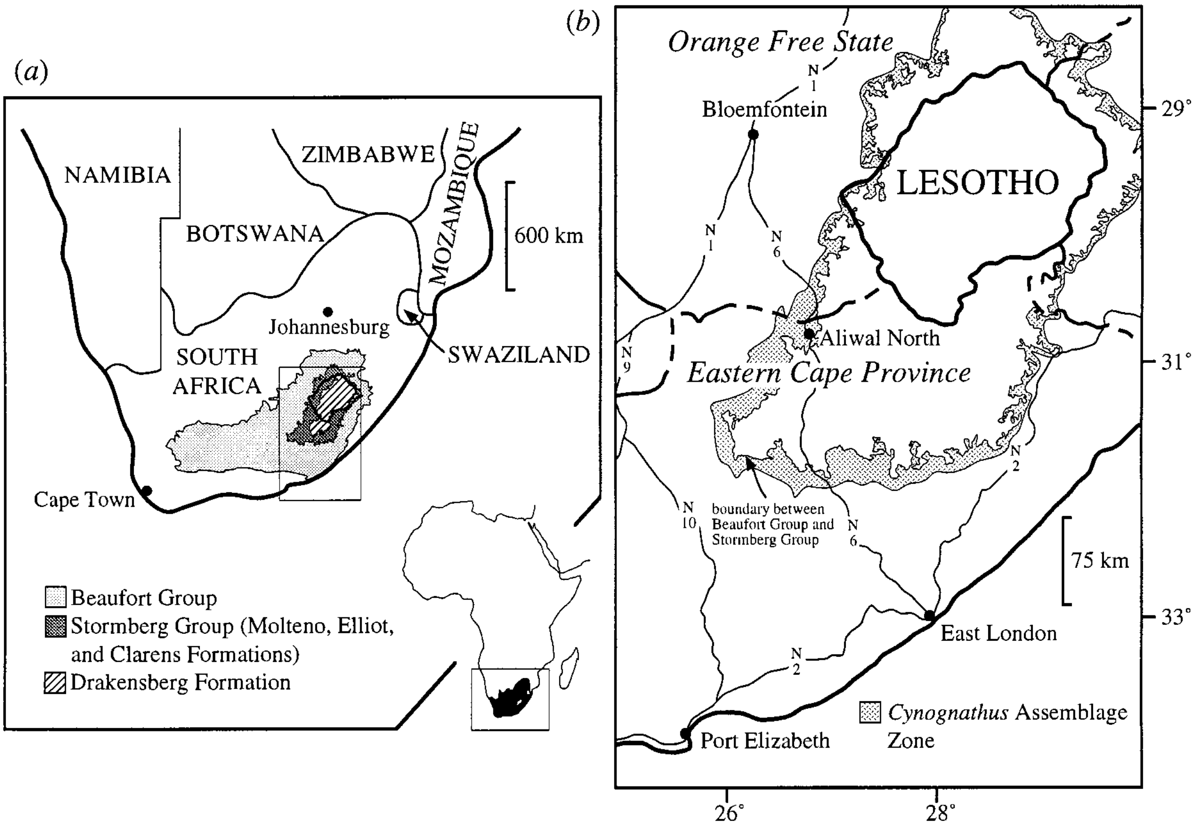

Figure 1. Maps of southern Africa. (*a*) Extent of the Beaufort and Stormberg Groups (Late Permian to Early Jurassic) and the Drakensberg mountains in South Africa; (*b*) enlarged map of Lesotho and regions of the Orange Free and Eastern Cape provinces. Exposures of *Cynognathus* Assemblage Zone derived from Kitching (1995).

apparent immediately to Robert Broom that the skeletons were actually of two distinct, though related, species (Broom 1913*a*). Broom designated an articulated skeleton with a single external naris and a pair of supposed acrodont premaxillary teeth as the type of *Mesosuchus*, and the remainder of the specimens were assigned to a new genus and species *Euparkeria capensis*. Watson's confusion is understandable given that the specimens he examined consisted only of an incomplete skull and articulated postcranium, numerous isolated cranial elements lacking from the single skull, and various parts of the axial and appendicular skeletons that could not be compared readily with the single, imperfect skeleton.

As the etymology of the name suggests, Watson (1912*a*) believed that *Mesosuchus* was an ancestral crocodile with close affinities to other presumed primitive crocodilians such as *Proterosuchus*, *Erythrosuchus* and *Ornithosuchus*. However, it is clear that the data for this opinion were derived from the skeletons of *Euparkeria*, in particular the slender lower jaw with thecodont implantation, the crocodilian-like ilium, and the construction of the tarsus and pes. Broom (1913*a*) recognized the great resemblance of *Mesosuchus* to the diaptosaurian (basal diapsid) reptile *Howesia* also from the *Cynognathus* Assemblage Zone near Aliwal North (Broom 1906). He concurred with Watson on the close relationship between *Ornithosuchus* and *Euparkeria*. In the same year, Broom (1913*b*) gave a more detailed description of both *Euparkeria* and *Mesosuchus*, reaffirming the affinities between *Euparkeria* and pseudosuchians, and between *Mesosuchus* and other rhynchocephalians such as *Howesia*, *Rhynchosaurus* and *Hyperodapedon*.

In 1921, the fossil collection of Mr Alfred Brown was purchased by the South African Museum, and a second specimen of *Mesosuchus* was discovered after further preparation of the blocks of sandstone from the type locality of *Mesosuchus* and *Euparkeria*. This new specimen provided additional information on the forelimb, pelvis and tarsus, but regrettably could not improve on knowledge of the skull because only an incomplete maxilla was found (Haughton 1921). Continued collecting from the type locality in 1924 by Mr A. W. Higgins uncovered two more specimens. One consists of a nearly complete skull in articulation with the cranial half of the skeleton (Haughton 1924) and the second specimen is an articulated vertebral column with most of the dorsals, both sacrals and a significant number of caudal vertebrae, a partial forelimb and both hindlimbs. The exquisitely preserved skull of the first specimen was considered by Broom (1925*a*, p. 6) to be 'one of the finest ever discovered in the history of palaeontology', and is the primary source for virtually all published data on the skull of *Mesosuchus*. The only published data on the second specimen are illustrations of the pedes (Carroll 1976).

Published data on the anatomy of *Mesosuchus* are limited. Information on the cranium and postcranium are found only in the early papers of Broom (1913*b*) and Haughton (1921, 1924). Broom's (1925*a*) restoration of the skull of *Mesosuchus* based upon SAM 6536 has been repeated, with little modification, in several subsequent publications (e.g. Romer 1956; Kuhn 1969; Carroll 1988). Malan (1963) discussed the unique dentition of *Mesosuchus*, and Carroll (1976) provided more detailed illustrations of the tarsus and pes than given in Haughton (1921) and compared them with those of *Noteosuchus*, *Howesia* and *Proterosuchus*. The skeleton of the endemic rhynchosaurian reptile *Mesosuchus browni* from the Early Triassic of South Africa is redescribed here, and a new phylogeny of Rhynchosauria and basal taxa of Archosauromorpha is presented.

2. SYSTEMATIC PALAEONTOLOGY

(a) ***Reptilia Laurent, 1768***
Diapsida Osborn, 1903
Archosauromorpha Huene, 1946
Rhynchosauria Osborn, 1903

Revised diagnosis. Archosauromorph diapsids characterized by a down-turned (beak-shaped) premaxilla, contact between the premaxilla and prefrontal, a median external naris, pitted depressions on the frontals and postfrontals, multiple rows of teeth on the maxilla, more than two rows of teeth on the dentary, flat jaw occlusion, very tall caudal neural spines with their height greater than three times their craniocaudal width, and a ratio of the lengths of the first and fourth metatarsals between 0.3 and 0.4.

(i) Mesosuchus *Watson, 1912*a

Type species. *Mesosuchus browni* Watson, 1912*a*.

Diagnosis. Same as for the only known species.

Mesosuchus browni *Watson, 1912*a

Diagnosis. Small rhynchosaurian diapsid characterized by the following autapomorphies: multiple rows of maxillary and dentary teeth with each row consisting of only a very small number of teeth, two premaxillary teeth that are approximately twice the size of the maxillary teeth, maxillary teeth inset medially and project below the internal naris, occlusion between vomerine teeth and dentary teeth, saddle-shaped vomers that overhang dorsally the premaxillary symphysis, length of axis neural spine greater than length of axis centrum, craniocaudally narrow neural spine of third cervical, prominent midventral groove on first two caudal centra.

Holotype. SAM 5882 is a partial rostrum, palate, braincase, lower jaws, sections of articulated presacral vertebral column, nine articulated caudal vertebrae, portions of scapula and pelvic girdle, and partial forelimb and hindlimbs.

Hypodigm. SAM 6046 is an incomplete right maxilla, an articulated series of the last ten presacrals, both sacrals, and first six caudals, partial forelimbs, left and right pelvic girdles, right hindlimb, elements of left tarsus. SAM 6536 is a virtually complete skull with lower jaws, articulated cervical vertebrae and ribs, dorsal vertebrae and ribs, complete left scapulocoracoid and partial right scapula, interclavicle, clavicles, distal end of left humerus, gastralia. SAM 7416 is an articulated vertebral column composed of the last dozen presacrals, both sacrals and at least the first 15 caudal vertebrae, fragments of right forelimb, pelvic girdle, complete right femur, right crus and partial left crus, and right and left tarsi and pedes.

Locality. As all definite specimens of *Mesosuchus* are from the same locality that yielded *Euparkeria*, any data on the exact location of the quarry for *Euparkeria* is relevant for *Mesosuchus*. After an attempt to relocate the collecting area for *Euparkeria*, Ewer (1965) concluded that all specimens had come from a single, now exhausted, site along a road between Aliwal North and Lady Grey. Although others have also investigated exposures of the *Cynognathus* Assemblage Zone around Aliwal North and claims of knowledge of the true location of the site have been made, the site remains unknown (B. S. Rubidge, personal communication).

Horizon. Middle zone of *Cynognathus* Assemblage Zone (Hancox *et al.* 1995) correlating with the upper two-thirds of the Burgersdorp Formation (Tarkastad Subgroup; Beaufort Group) according to Keyser & Smith (1979). The *Cynognathus* Assemblage Zone is the uppermost biozone of the Beaufort Group. Exposures are found along the border between the Beaufort Group and Stormberg Group. The age of the middle zone is uncertain as the *Cynognathus* Assemblage Zone appears to straddle the boundary between the Early (Scythian) and Middle (Anisian) Triassic. The traditionally accepted age for the entire *Cynognathus* Assemblage Zone is Scythian (e.g. Romer 1966), but recent field work has demonstrated the existence of at least three distinct faunal subdivisions (Hancox *et al.* 1995). Although the faunal elements of the middle zone of the *Cynognathus* Assemblage Zone are similar to certain European sequences (Ochev & Shishkin 1989), correlations between these sequences and the German Triassic sequence are tenuous because few taxa are shared.

3. DESCRIPTION

(a) ***Skull***

(i) *General features of skull*

Mesosuchus has a broadly triangular skull with a wide temporal region that tapers sharply along the orbits, expands abruptly at the prefrontals, then tapers to the blunt rostrum (figure 2). A large, median external naris located at the front of the rostrum faces dorsally and cranially. Orbits face laterally and slightly cranially. *Mesosuchus* can be distinguished from all other rhynchosaurs, with the possible exception of *Howesia* (Dilkes 1995), by the presence of a beak-like rostrum that is formed primarily by huge premaxillary teeth rather than by tapering, edentulous premaxillae. When the distortion of the quadrates is corrected, the craniomandibular joint is located farther caudally than shown by Broom (1925*a*). The lower temporal bar is incomplete.

The palate has a pronounced, sagittally elongated vault in ventral aspect that is formed primarily by the vomers. Towards the tip of the rostrum, the vomers contact the premaxillae at a level coincident with the maxillary tooth margin, but curve strongly dorsally towards the palatines, thus placing the choanae significantly above the tooth margin. In addition, the vomerine and palatine borders of the choana are recessed dorsally to withdraw further the choana from the oral cavity.

None of the lower jaws is complete, but in combination allow a reasonably complete composite (figure 3). An enlarged, upturned retroarticular process dominates the profile of the lower jaw and extends quite far behind the occiput (figure 4). There is no lateral mandibular fenestra, contrary to Broom (1913*a*,*b*).

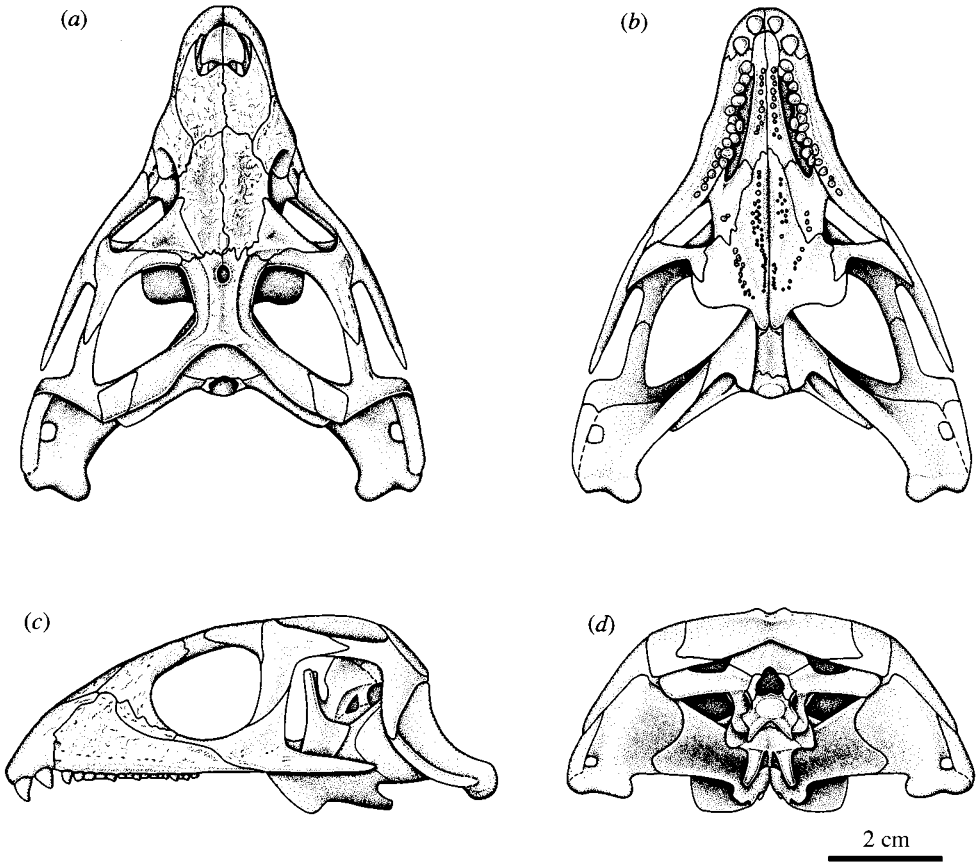

Figure 2. *Mesosuchus browni*. Reconstruction of skull in (*a*) dorsal; (*b*) ventral; (*c*) left lateral; and (*d*) occipital views.

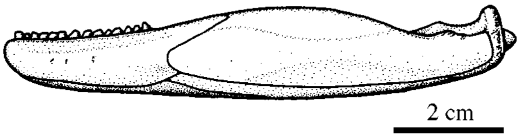

Figure 3. *Mesosuchus browni*. Reconstruction of lower jaw in left lateral view.

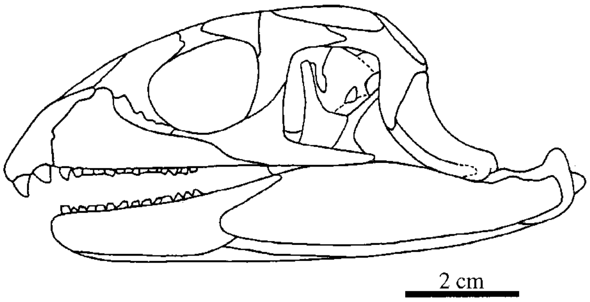

Figure 4. *Mesosuchus browni*. Reconstruction of skull and lower jaw in left lateral view.

Sculpturing of varying degrees of rugosity is present on most of the dermal skull bones with the exception of the squamosals and supratemporals (figures 5 and 6). It consists of an apparently random pattern of shallow to moderately deep, irregularly shaped pits. Sculpturing is extensive on the nasals and frontals, but is reduced in number and depth on the premaxillae, maxillae, prefrontals, jugals and postorbitals. Interspersed on the elevated areas about the pits are small, occasionally knob-like protuberances that are prominent on the nasals and frontals. No sculpturing is present on the lower jaw.

(ii) *Dermal bones of skull*

Each premaxilla is composed of a robust, median symphysis and a tapering extension (posterodorsal process) that contacts the prefrontal, a feature recognized as a synapomorphy of Rhynchosauria (Dilkes 1995). Haughton (1924) noted in his description of SAM 6536 that the premaxilla approached closely, but did not consider there to be any contact with the prefrontal. Judging by his illustrations, it would seem that only the right side of SAM 6536 was prepared, and as this side is damaged slightly by crushing to create an apparent separation of the premaxilla and prefrontal, his conclusion is reasonable. On the other hand, Broom (1925*a*) showed a substantial contact between the premaxilla and prefrontal in his reconstruction, but gave no comment. Contact between the premaxilla and prefrontal is shown clearly on the left side of SAM 6536 (figure 5*a*,*c*). The suture between the premaxilla and maxilla is complex with two large foramina present. A distinct notch in the maxilla contributes most of the border of a dorsal fenestra (figures 5*c*,*d*, 6*c*,*d*, and 7*a*,*b*) and appears to be the cranialmost of a series of maxillary foramina that extend across the lateral face of the maxilla and probably conveyed cutaneous

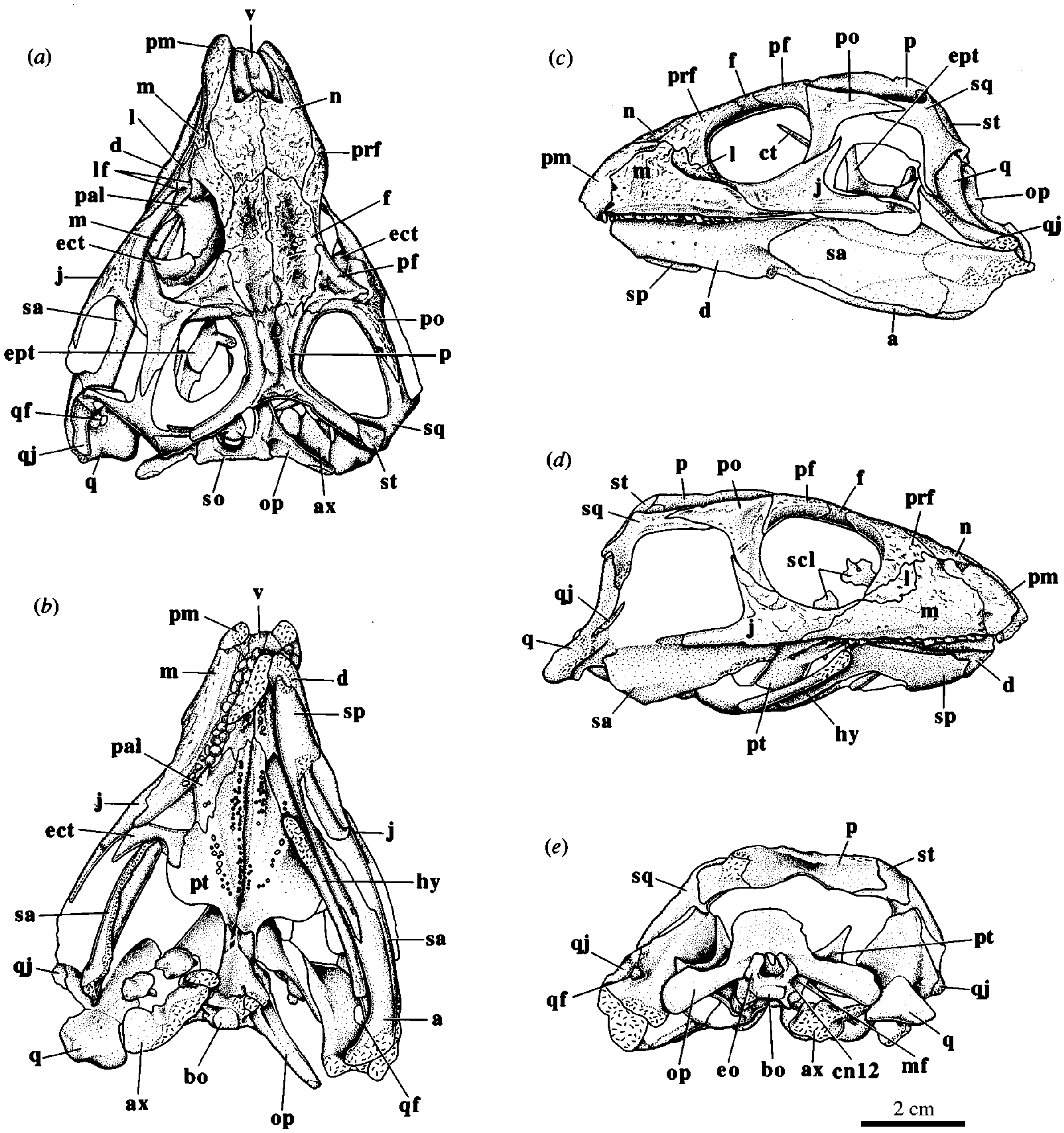

Figure 5. *Mesosuchus browni*. SAM 6536. Skull and partial lower jaws in (*a*) dorsal; (*b*) ventral; (*c*) right lateral; (*d*) left lateral; and (*e*) occipital views. For a list of abbreviations see Appendix 3(b).

blood vessels and nerves. The maxilla overlaps the premaxilla above and below this notch. A ventral foramen is immediately above the tooth-bearing margin, but is separated from the margin by a process of the maxilla that fits into a slot on the premaxilla.

Maxillary teeth are inset with a distinct lateral space between the teeth and the vertical face of the maxilla (figures 5*b*–*d*, 6*b*–*d* and 7*a*). The dorsal edge is constricted by the posterodorsal process of the premaxilla and elongate lacrimal. A large internal flange of the maxilla is visible within the median external naris that extends cranially along the medial side of the premaxilla virtually to the symphysis. In addition, this internal maxillary flange has a deep concavity for the dorsally expanded vomer.

The nasal forms most of the lateral and the entire caudal margins of the median external naris. Anteromedial projections of the nasals, although very short, are similar to those present in other diapsids where processes of the nasals and premaxillae form the medial strut between the paired external nares. A narrow internal flange of the nasal extends forward along the inner side of the premaxilla and the upper edge of the internal maxillary flange, but does not contact the vomer.

A lateral expansion of the prefrontal at the orbital margin divides it into distinct dorsal and lateral regions. An enlarged orbital process of the prefrontal contacts the palatine along the anteroventral border of the orbit.

The elongate, crescentic lacrimal overlaps the prefrontal and is itself overlapped by the maxilla. A pair of lacrimal foramina, one twice the size of the other, are situated on the orbital portion of the lacrimal and face inwards (figure 5*a*). Medial to these foramina the lacrimal contacts the lateral process of the palatine. There is also a broad

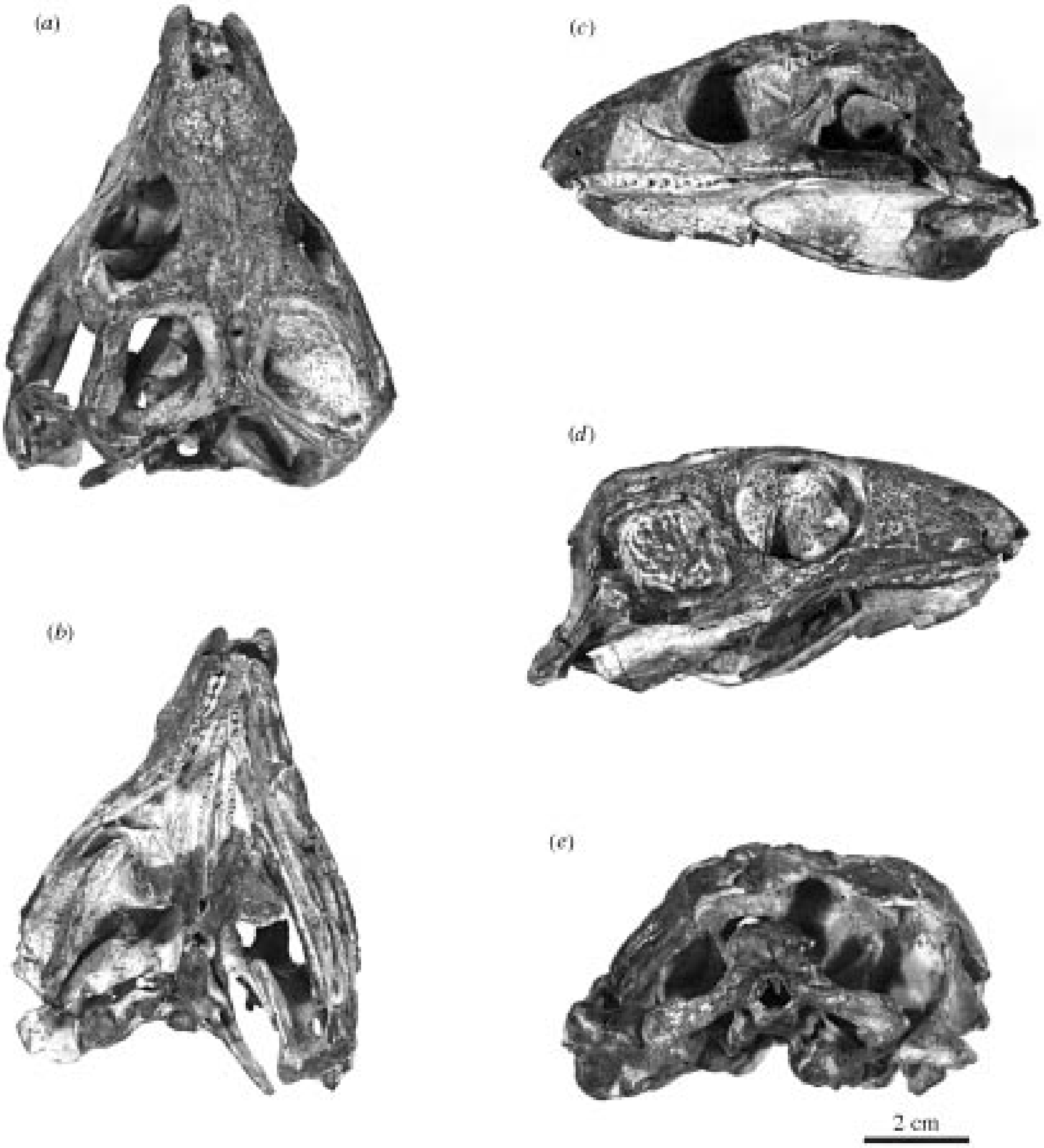

Figure 6. *Mesosuchus browni*. SAM 6536. Photographs of skull and partial lower jaws in (*a*) dorsal; (*b*) ventral; (*c*) right lateral; (*d*) left lateral; and (*e*) occipital views.

union between the lacrimal and jugal within the ventral orbital rim.

The dorsal depressions of the frontal of *Mesosuchus* are similar to those of *Howesia* (Dilkes 1995) and are found in other rhynchosaurs (Chatterjee 1974; Huene 1938). Contrary to Haughton (1924), the frontal does not enter the upper temporal fenestra.

The triradiate jugal has a posterior process that tapers to an apparently blunt point, as indicated by impressions in the matrix of SAM 6536 (represented by dashed lines in figure 5*c*,*d*), near the caudal edge of the lower temporal fenestra. Broom (1925*a*) claimed to see an articular facet on the right jugal for the quadratojugal, which constituted his primary morphological evidence for a complete lower temporal arch. However, the lateral surface of both jugals of SAM 6536 is smooth in the area of an expected facet. The posterior jugal process of *Howesia* is significantly shorter and terminates at the midpoint of the lower temporal fenestra (Dilkes 1995). Other rhynchosaurs have a complete lower temporal arch (Benton 1983; Huene 1938); however, it should be noted that although all species of *Rhynchosaurus* are restored with a jugal–quadratojugal contact (Benton 1990), none of the specimens has a complete jugal or quadratojugal. Hence, the morphology of the lower temporal arch is unknown currently for *Rhynchosaurus*.

The triangular postfrontal enters the upper temporal fenestra, but does not separate the postorbital and parietal. Most of the dorsal surface, medial to the thickened orbital rim, is occupied by a deep depression.

Three processes (anteroventral, posterodorsal and dorsomedial) of approximately equal length comprise the postorbital. The dorsomedial process forms a substantial portion of the smooth cranial rim of the upper temporal fenestra and contacts the parietal below the postfrontal. The anteroventral process reaches farther down the medial side of the jugal than suggested by its external exposure, but does not contact the ectopterygoid.

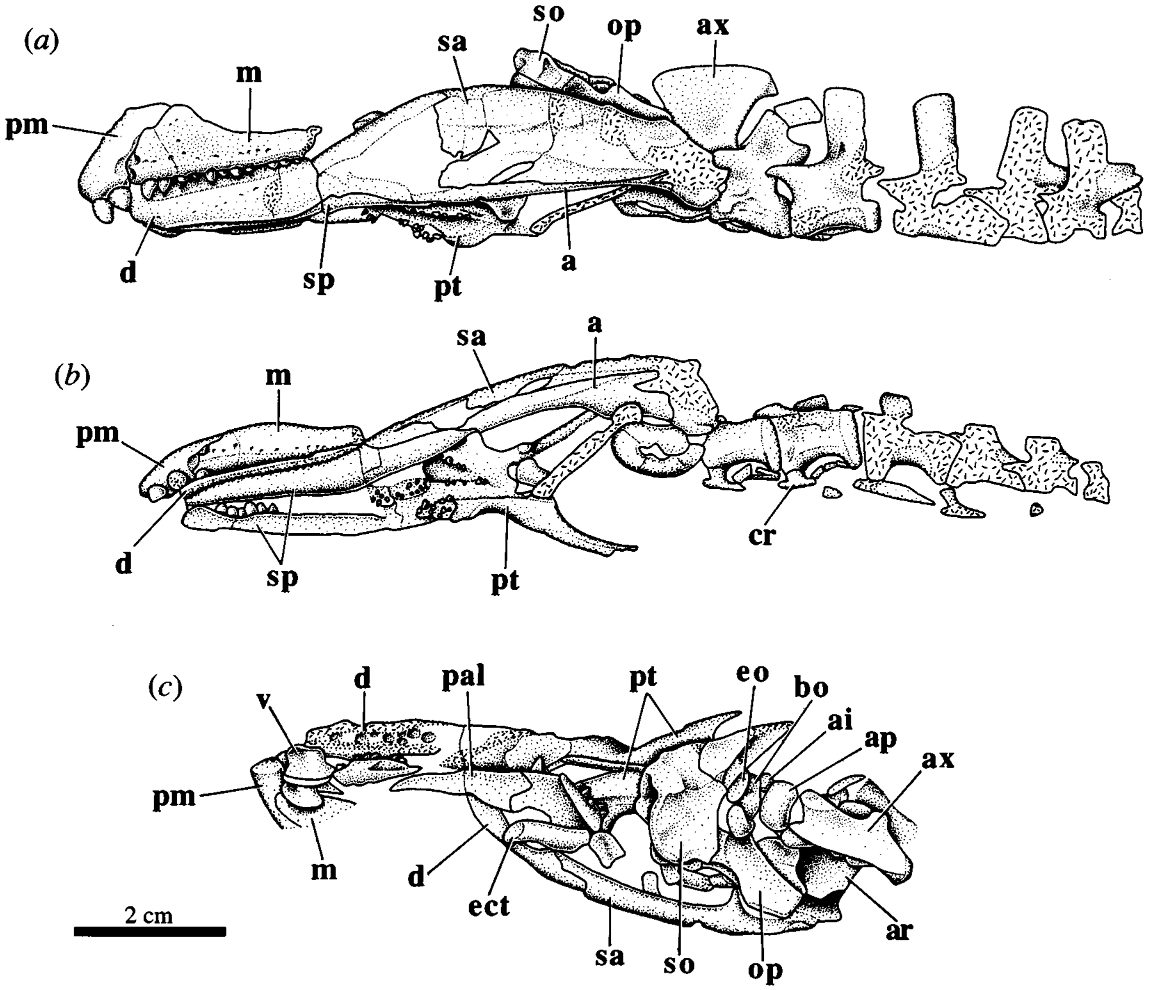

Figure 7. *Mesosuchus browni*. Holotype SAM 5882. Partial skull and jaws and cervical vertebrae in (*a*) left lateral; (*b*) ventral; and (*c*) dorsal views. For a list of abbreviations see Appendix 3(b).

Four distinct processes of the squamosal are present. An anterior process has a triangular groove for the postorbital and forms about two-thirds of the upper temporal arch. A ventral process extends to the ventral half of the lower temporal fenestra and resembles more closely that of *Proterosuchus* (J. Welman, personal communication) and *Prolacerta* (Gow 1975) than the abbreviated ventral process of *Howesia* (Dilkes 1995). A medial process has a broad articulation with the supratemporal and contacts the occipital wing of the parietal along the inner side of the temporal fenestra. A small, posteroventral process has a cup-shaped concavity for reception of the rounded dorsal head of the quadrate and is recessed medially for the paroccipital process of the opisthotic.

Both quadratojugals of SAM 6536 are incomplete, but the left is missing only the caudal portion next to the condyles of the quadrate. Each quadratojugal is a thin sheet of bone that lies dorsally against the cranial side of the squamosal and curves caudally onto the dorsolateral side of the quadrate to terminate just caudal to the quadrate condyles. Though fractured, the left quadratojugal has a smoothly finished surface in the area of the posterior process restored by Broom (1925*a*).

Mesosuchus has a Y-shaped skull table with the parietals fused medially in SAM 6536 with the exception of a short section caudal to the parapineal foramen. Each parietal of SAM 6536 has a tall, sculptured ridge along the medial border of the upper temporal fenestra. These parietal ridges approach medially just behind the parapineal foramen, but remain separated by a narrow, heavily sculptured gap. On the other hand, the parietals of one individual on an unnumbered block with three skeletons of *Euparkeria* and two skeletons of *Mesosuchus* currently on display at the South African Museum has completely fused parietals with a sharp, midline ridge. The ventrolateral flange of the parietal, presumably for attachment of adductor musculature, extends from its caudal contact with postorbital to its contact with the supratemporal and squamosal. The occipital wings of the parietals are tall, craniocaudal thin sheets that overlap the supratemporals occipitally.

The supratemporals of *Mesosuchus* (figures 5*e* and 6*e*) and *Howesia* (Dilkes 1995) occupy identical positions on the skulls and are extremely similar in shape. Each is a thin sheet sandwiched between the medial process of the squamosal cranially and the occipital wing of the parietal caudally.

Mesosuchus shares with *Howesia* (Dilkes 1995) and *Hyperodapedon gordoni* (Benton 1983) the presence of a sclerotic ring in the orbit (figures 5*d* and 6*d*).

(iii) *Dermal bones of palate*

The elongate vomers form most of the dorsally raised, medial border of the choanae. Cranial to the choana, each vomer is expanded dorsally along its contacts with the opposite vomer and the maxilla (figures 2*a*, 5*a*, 6*a* and 7*c*). The dorsal surface between these expanded contacts is convex in a craniocaudal direction. Unfortunately, little information on the dorsal side of the vomers in other basal archosauromorphs is available in the literature because it is covered usually by the nasals and premaxillae in those taxa with paired external nares. Separate vomers of *Prolacerta* (BP/1/2675) and *Euparkeria* (Gow 1970) lack the dorsal expansions present on the vomers of *Mesosuchus*. The derived rhynchosaur *Hyperodapedon* (Chatterjee 1974) has the dorsally expanded lateral contact between the vomer and maxilla. The vomer of *Howesia* is unknown (Dilkes 1995). A single row of irregularly placed vomerine teeth on a ridge increase in size cranially until the first two in the row are the same size as those at the front of the dentary.

In addition to its lengthy, slightly interdigitated suture with the pterygoid, the palatine has, in ventral aspect, contacts with the vomer cranially and medially and the maxilla laterally to form the caudal margin of the choana. The dorsal deflection of the choanal margin along the vomer is continued by the palatine and there is a prominent triangular groove at the caudal corner of the choana. Dorsally, the lateral process of the palatine extends above its contact with the maxilla to reach both the lacrimal and prefrontal (figure 5*a*). Palatine and ectopterygoid are separated ventrally along the medial rim of the suborbital fenestra (figure 5*b*), but are in contact dorsally (figure 5*a*). There are only a few, scattered teeth on the palatine.

The arch-shaped ectopterygoid spans the distance between the transverse flange of the pterygoid and the jugal to separate the suborbital fenestra and adductor chamber (figures 5*b* and 6*b*). The suture between the ectopterygoid and pterygoid is complex and consists, in ventral aspect, of the pterygoid overlapping the ectopterygoid at the suborbital fenestra followed by a reversal along the ventrolateral flange with the ectopterygoid overlapping the pterygoid. An identical sutural pattern is present in *Howesia* (Dilkes 1995), *Proterosuchus* (J. Welman, personal communication), *Euparkeria* (J. Welman, personal communication), and probably *Prolacerta* (D. W. Dilkes, personal examination of BP/1/2675). Camp (1945*a*) illustrated an ectopterygoid in an excellent specimen of *Prolacerta* that appears to conform to that of *Mesosuchus*.

A short dorsal flange extends along the length of the medial edge of each pterygoid. Although these dorsal flanges might have reinforced the midline suture of the pterygoids, two areas of partial separation are present (figures 5*b* and 6*b*). There is a small, oval gap immediately cranial to the basipterygoid articulation and a longer, slit-like separation that extends nearly to the vomers. The transverse flange is a simple posteroventrally directed region of the pterygoid and lacks any thickening along its caudal or lateral edges. The basipterygoid processes fit into deep dorsomedial recesses at the junction between the transverse flange and the quadrate ramus. The rim around each basicranial facet is incomplete dorsally where the epipterygoid is seated. Small flanges from the pterygoid cover the entire ventral side of the basicranial processes. The quadrate ramus is developed into two planes: one is an essential vertical, dorsoventrally tall sheet that is overlapped laterally for a significant distance by the quadrate and the other curves ventromedially over much of the ventral side of the parasphenoid and has a rectangular process that reaches caudally to the level of the occipital condyle (figures 2*b* and 5*b*). Three distinct fields of denticles are present on the pterygoid. One consists of numerous denticles of quite variable size on a raised ridge that extends anterolaterally across the pterygoid to the palatine. A second field is a single row of medially inclined teeth along the midline suture of the pterygoids just cranial to the basipterygoid processes. The third is a cranial continuation of the second field, but consists of a wider field on a raised ridge which narrows cranially to a single row of denticles. Virtually identical patterns of denticles are present in *Prolacerta* (D. W. Dilkes, personal observation of BP/1/2675), *Proterosuchus* (J. Welman, personal communication), and *Macrocnemus* (Peyer 1937).

(iv) *Quadrate and epipterygoid*

The quadrate is deeply concave caudally and has large lateral and medial large rami (figures 2, 5 and 6). The smaller lateral ramus has a complex, sinuous joint with the quadratojugal. This ramus is overlapped dorsally by the ventral process of the squamosal. The inner, pterygoid ramus extends nearly to the epipterygoid along the lateral side of the pterygoid. Dorsally, the quadrate has a rounded head that fits into the cavity on the posteroventral process of the squamosal. Composed of two, strongly convex facets of unequal size, the axis of the quadrate condyle meets the midline of the skull at an angle of 80°. A large quadrate foramen is situated next to the quadratojugal.

The quadrate of *Mesosuchus* shares the greatest number of similarities with the quadrates of *Howesia* (Dilkes 1995), *Prolacerta* (D. W. Dilkes, personal observation), *Proterosuchus* (Cruickshank 1972), *Macrocnemus* (Peyer 1937; Kuhn-Schnyder 1962) and *Euparkeria* (Ewer 1965). As restored conventionally (Carroll 1975*a*; Gow 1975), the quadrate of *Prolacerta* is given a vertical orientation and only a slight concavity. However, the quadrates of BP/1/2675 and BP/1/471 (not illustrated in Gow (1975) have much deeper concavities, and the correct orientation of the quadrate is shown clearly by BP/1/471 where the craniomandibular joint is caudal to the occipital condyle.

The epipterygoid of SAM 6536 (figures 5*a,c*) has an expanded base that rests along the dorsolateral surface of the quadrate ramus of the pterygoid and an incomplete dorsal process that reaches at least to the height of the anterior inferior process of the prootic (figure 2*c*). A ridge on the medial side of the dorsal process extends ventrally to a prominent buttress-like projection above a deep, oval depression that appears to be continuous with the larger basicranial facet on the pterygoid and evidently received a portion of the basipterygoid process. A virtually identical epipterygoid is present in *Prolacerta* (Gow 1975), including the medial ridge on the dorsal process (D. W. Dilkes, personal observation of BP/1/2675). The epipterygoids of *Proterosuchus* (J. Welman, personal communication) and *Euparkeria* are indistinguishable from those of *Mesosuchus* and *Prolacerta*.

(v) *Endocranium*

The exoccipitals of the holotype (SAM 5882) are preserved as separate elements, but could be exposed only

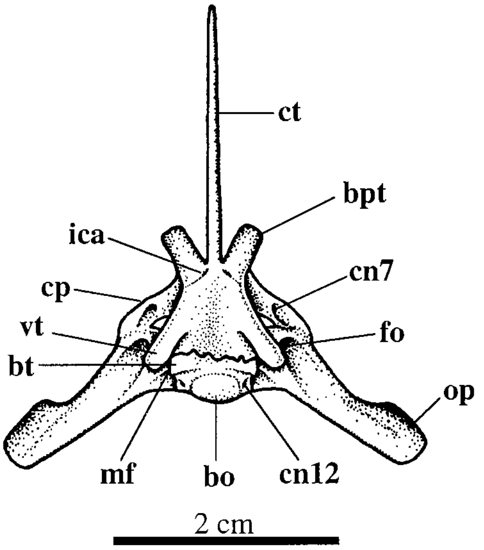

Figure 8. *Mesosuchus browni*. Reconstruction of braincase in ventral view. For a list of abbreviations see Appendix 3(b).

in dorsal aspect because the cervicals are in articulation with the basioccipital (figure 7*c*). The atlas–axis complex of SAM 6536 is separated from the occipital condyle, and the exoccipitals are distinct from the supraoccipital and opisthotic, but are fused ventrally to the basioccipital. Each exoccipital has a constricted base with a pair of foramina in a deep fossa probably for the exit of the hypoglossal nerve. This nerve apparently entered the exoccipital through two widely spaced internal foramina. Raised facets for the proatlas are present on the expanded, dorsal portion. Cranially, the exoccipital borders the metotic foramen through which probably passed the glossopharyngeal, vagus and accessory nerves.

The elongate, oval occipital condyle of the basioccipital faces posteroventrally. Between the occipital condyle and parasphenoid, the convex ventral surface is drawn ventrolaterally into a pair of basal tubera. Dorsal to these tubera there is a large process for contact with the ventral ramus of the opisthotic. It is unknown if the basioccipital contributes to the metotic foramen because it is fused indistinguishably to the exoccipitals.

The parasphenoid and basisphenoid are fused indistinguishably in *Mesosuchus* and will be described as a unit. The posterolateral corners of the triangular parasphenoidal plate are drawn downwards beyond the highly interdigitated basioccipital–parasphenoid suture into cristae ventrolaterales (figure 8). A foramen that probably conveyed the internal carotid lies posteromedial to the basipterygoid process at the cranial end of the vidian canal whose floor is continuous with the sharp lateral edge of the parasphenoid. The vidian canal probably carried the palatine branch of the internal carotid artery and the palatine (vidian) branch of the facial nerve. As there is only a single pair of dorsal foramina at the base of the cultriform process, it is likely that, in contrast to that of lizards (Oelrich 1956), only a cerebral branch of the internal carotid entered the foramina in the vidian canal and exited at the base of the cultriform process. The palatine branch of the internal carotid may have joined with the palatine nerve to continue forward along the ventral side of the basipterygoid process.

A tall transverse dorsum sella separates a cranial chamber from a larger caudal chamber, which contained the hindbrain and midbrain. The cultriform process extends along the dorsal edge of the medial expansion of the pterygoids until the midpoint of the orbit. It has a V-shaped cross-section with a shallow dorsal trough restricted to the base of the process. Width of the cultriform process is uniform throughout its length as in *Howesia* (Dilkes 1995), but in contrast to the tapering cultriform process of *Prolacerta* (Evans 1986). The cranial face of the dorsum sella is bisected by a ridge that, as in *Prolacerta*, apparently separated two concavities for the retractor bulbi and bulbaris muscles. There are no foramina for the abducens nerves in the dorsum sella. The most likely course for these nerves was along the dorsal rim of the dorsum sella.

The paroccipital process of the opisthotic is directed caudolaterally from its constricted basal contact with the exoccipital and supraoccipital. A ventral excavation of the paroccipital process reaches from the fenestra ovalis across at least half of the length of the process. Distally, the paroccipital process thins to a blade, which contacts the supratemporal and the posteroventral process of the squamosal. There is no contact with the quadrate. Below the base of the paroccipital process, a ventral ramus of the opisthotic forms the cranial border of the metotic foramen and the caudal border of the fenestra ovalis. The distal end of the ventral ramus is enlarged into a curved foot that has a broad contact with a similarly shaped process on the basioccipital above the basal tubera. There is an additional contact between the ventral ramus and the cristae ventrolaterales of the fused parasphenoid and basisphenoid. An expanded ventral ramus of the opisthotic was noted previously in *Mesosuchus* (Evans 1986, fig. 8), but the illustration of SAM 6536 in that paper does not show the rounded configuration of the ventral ramus because the left parasphenoid, opisthotic and basioccipital are damaged (figure 5*b*).

The prootic forms most of the lateral wall of the otic capsule. It joins the supraoccipital dorsally and the opisthotic caudally above the fenestra ovalis. Ventrally, its contact with the fused parasphenoid and basisphenoid is interrupted by a large, triangular gap, as in *Prolacerta* (Evans 1986). The crista prootica is a prominent ridge on the lateral face of the prootic that extends cranially from the upper rim of the fenestra ovalis to the front of the triangular gap (figure 8). Beneath the crista prootica, the prootic is recessed medially and probably received the internal jugular vein as in extant iguanid lizards (Oelrich 1956). A foramen that is probably for the facial nerve is present on the dorsomedial face of the crista prootica above the triangular gap (figure 8). *Prolacerta* also has a foramen for the facial nerve in a similar location (Gow 1975; D. W. Dilkes, personal observation), contrary to its reported absence by Evans (1986), as does *Euparkeria* (Welman 1995). *Hyperodapedon huxleyi* has a foramen for the facial nerve at the cranial end of the shortened crista prootica (Chatterjee 1974).

Immediately above the cranial terminus of the crista prootica, the anterior process of the prootic extends dorsally for at least half of the height of the prootic. The anterior process of *Mesosuchus* is more slender than that of *Prolacerta* (Evans 1986) and lacks the curvature of the latter genus. Between the anterior process and main body of the prootic is the deep trigeminal incisure for the passage of the trigeminal nerve. *Euparkeria* has a considerably wider trigeminal incisure and anterior process (Welman 1995). Middle and Late Triassic rhynchosaurs have shorter anterior processes and shallower trigeminal incisures (Benton 1983, 1990). As in *Prolacerta* (Evans 1986), the convex antero-dorsal margin of the prootic of *Mesosuchus* is rounded from the dorsal contact with the opisthotic to the bottom of the trigeminal incisure and probably indicates the location of the anterior semicircular canal. A large, dorsally convex and ventrally concave shelf projects medially from the internal surface of the prootic, cranial to the fenestra ovalis (not visible in figure 5*a*, which shows only a portion of the interior of the braincase). Below this shelf is a large cavity that probably held the vestibule of the inner ear.

The flat, rectangular supraoccipital of *Mesosuchus* with its low, median dorsal ridge (figures 5*e*, 6*e* and 7*c*) is extremely similar to that of *Howesia* (Dilkes 1995) and other basal archosauromorphs such as *Prolacerta* (Evans 1986; Gow 1975), *Proterosuchus* (Cruickshank 1972), *Euparkeria* (Ewer 1965), and *Tanystropheus* (Wild 1973). The dorsal margin of the supraoccipital of *Mesosuchus* is joined extensively along the occipital margin of the fused parietals by a straight central section and a pair of flanking sections directed posterolaterally at an angle similar to that of the occipital wings of the parietals. In sharp contrast, Middle and Late Triassic rhynchosaurs have a strongly arched supraoccipital with a reduced dorsal contact with the parietals (Benton 1983, 1990). In *Hyperodapedon*, this contact is located far cranial to the occipital margin of the parietals (Benton 1983).

A laterosphenoid is absent in *Mesosuchus*. Watson (1912*a*) described a laterosphenoid under the term epipterygoid with a deep notch for the optic nerve on the holotype, an observation that he maintained 45 years later (Watson 1957). Given the fragmented nature of the holotype and partial preparation of most of the bones cranial to the braincase, it is likely that he mistook some portion of the palate, perhaps the combination of the ectopterygoid and pterygoid (figure 7*c*), for a laterosphenoid.

(vi) *Lower jaw*

At least six elements are present in the lower jaw of *Mesosuchus*: dentary, splenial, surangular, angular, prearticular and articular. A coronoid is probably present, but judging by the articulation between dentary and surangular in the holotype (figure 7*a*), it is displaced ventrally from the dorsal edge of the lower jaw (figure 3).

The dorsal margin of the dentary is slightly concave along the dentigerous region. Dentary teeth are inset and present above the symphysis at the tip of the lower jaw. Beneath the inset row of dentary teeth there are several small foramina. The lateral surface of the dentary is convex, particularly cranial to the surangular, where there is a low ridge with a shallowly concave ventral margin. The symphysis is small and formed only by the dentary. Unlike Middle and Late Triassic rhynchosaurs, the dentary of *Mesosuchus* does not have diverging edentulous processes that project in front of the symphysis.

Most of the medial side of the dentary is covered by the splenial (figure 5*d*). Splenial and angular meet laterally along a lengthy suture that extends to the middle of the lower jaw, whereupon it turns abruptly dorsally on the medial side and the splenial overlaps the angular. No meckelian foramina are visible, but only a small part of the medial suture between the splenial and angular can be seen and the entire suture between the splenial and prearticular is unknown.

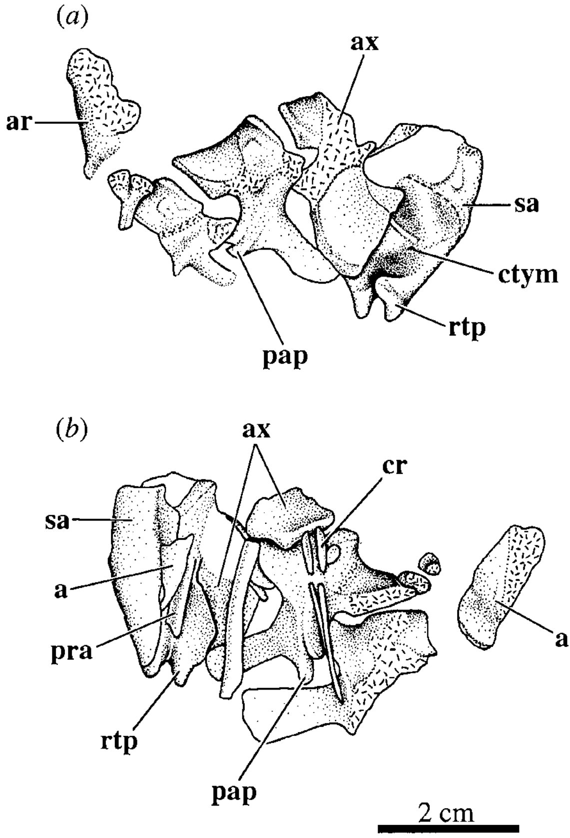

Figure 9. *Mesosuchus browni*. SAM 6536. (*a*) and (*b*) articular region, atlas, axis and third cervical vertebra. For a list of abbreviations see Appendix 3(b).

The angular has a long lateral exposure along the ventral margin of the lower jaw from the splenial to the articular (figures 5*b* and 9). Only a small section of the medial side of the angular is visible.

A pair of low ridges are present on the surangulars of SAM 5882 and 6536. Earlier reports (Broom 1913*a*,*b*) of a lateral mandibular fenestra on the lower jaw of *Mesosuchus* are incorrect, and an illustration of this fenestra on the holotype (Broom 1913*b*) may correspond vaguely with a poorly defined region of missing bone (figure 7*a*). There is a considerably smaller, oval gap in the surangular on the holotype lower jaw, but the broken edges of this gap show that it is merely the product of damage. Dorsally, the suture between the surangular and articular can be traced from the lateral side of the jaw only to the glenoid in SAM 6536. Presumably the surangular forms some portion of the lateral side of the glenoid as suggested by a median process of the surangular next to the left paroccipital process on the holotype (figure 7*c*) that forms the caudal rim of the adductor fossa.

Only a small section of the prearticular is preserved along the ventromedial surface of the right lower jaw of SAM 6536 (figure 9*b*). It appears to have been overlapped by the angular and in turn overlapped the articular. A groove

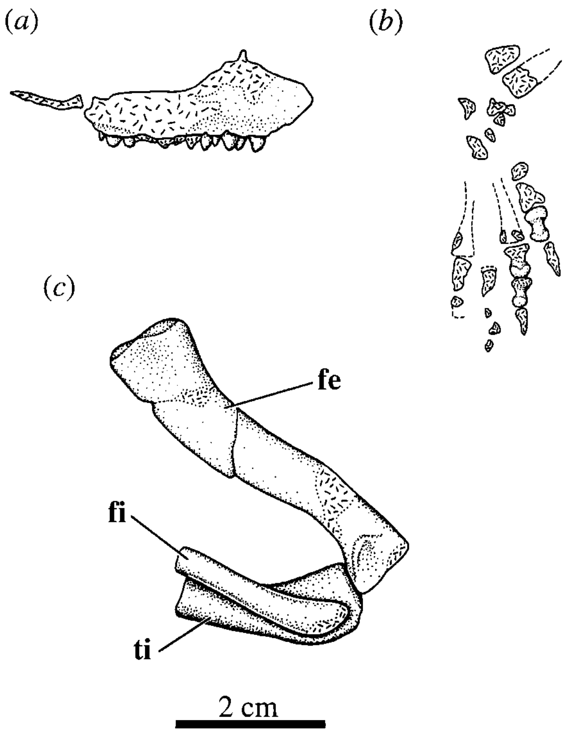

Figure 10. *Mesosuchus browni*. SAM 6046. (*a*) partial right maxilla; (*b*) partial manus; (*c*) partial right hindlimb. For a list of abbreviations see Appendix 3(b).

along the ventral surface of the retroarticular process continues onto the prearticular, but not on to the angular.

The articular forms the medial and probably most of the lateral portions of the glenoid and has a large, intricately constructed retroarticular process (figure 9). Immediately behind the glenoid fossa is a small foramen leading cranially into the body of the articular and presumably received the cordi tympani division of the hyomandibular ramus of the facial nerve as in lizards (Oelrich 1956). Caudal to this foramen the dorsal surface of the retroarticular process is concave. The caudal tip of the retroarticular process is divided by a deep cleft into lateral and medial projections. A groove extends ventrally from this notch along the articular onto the prearticular as described above. The medial projection reaches caudal to the lateral projection. It is oval in cross-section due to a slight lateromedial compression. The lateral projection is continuous ventrally with the remainder of the articular and extends dorsally above the level of the glenoid fossa. This dorsal extension ends in a blunt tip that is inflected over the cleft. A rugose finish covers the dorsolateral and dorsal surfaces of the lateral projection.

(vii) *Dentition*

All descriptions of the marginal teeth of *Mesosuchus* have stated that they are ankylosed to the jaws (Broom 1913*a*,*b*; Haughton 1921, 1924; Malan 1963; Watson 1912*a*). However, careful preparation of the maxillary dentition of SAM 5882, 6046 and 6536 has revealed a clear line of separation between the tooth and surrounding bone, thus indicating that the teeth are implanted in the jaws. Broken sections through the last maxillary tooth of SAM 5882 and damage to the caudal maxillary teeth of SAM 6046 show deep implantation, but it is uncertain if the mode of attachment should be described as thecodont. Two large premaxillary teeth overhang the front of the lower jaw in the type (figure 7*a*,*b*); SAM 6536 has only a splinter of the second premaxillary tooth (figures 5*b*,*c* and 6*b*,*c*). Each premaxillary tooth has a broad base and tapers only slightly for approximately three-quarters of its length, and then tapers more abruptly and is recurved. A circular cross-section is maintained throughout the teeth. The majority of the maxillary teeth are worn heavily to short, blunt pegs (figures 5, 6 and 7). However, the first two maxillary teeth of the holotype (figure 7*a*) and several teeth of SAM 6046 (figure 10*a*) are complete and conical.

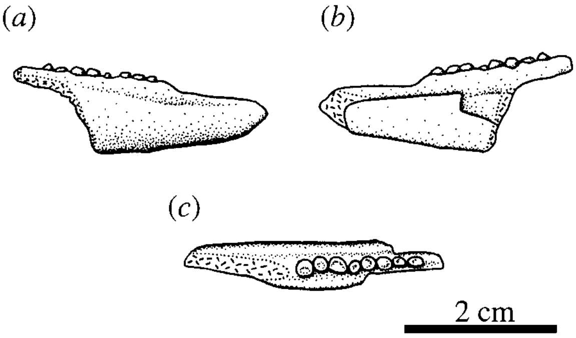

Figure 11. *Mesosuchus browni*. SAM 6536. Symphyseal region of right lower jaw in (*a*) lateral; (*b*) medial; (*c*) dorsal views.

Malan (1963) observed for the first time an intriguing zig-zag arrangement of the maxillary and dentary teeth of *Mesosuchus*. Her discussion and illustration (Malan 1963, fig. 8) of the maxillary teeth of SAM 6536 suggest that a pronounced zig-zag arrangement is true for virtually the entire row of teeth, when in actuality it is correct only for the middle section where the medial expansion of the maxilla is widest. The first and last four teeth are aligned in a row that is parallel to the maxilla. Teeth of the dentary have a simpler arrangement with only a slight zig-zag (figure 11).

Malan proposed two possible interpretations for this zig-zag arrangement. It could be the result of the superposition of alternating waves of tooth replacement that affect odd-numbered or even-numbered teeth on a slightly zig-zag arrangement of teeth. Alternatively, each tooth germ could have produced a pair of teeth with the older, labial tooth retained. In effect, rows of multiple teeth with only two teeth in each row.

The latter explanation seems to accord far better with the available evidence. The multiple-tooth rowed Early Permian *Captorhinus aguti* does exhibit in some instances a zig-zag pattern of teeth. In some individuals a section of multiple tooth rows has two or at most three teeth in each Zahnreihe (Bolt & DeMar 1975, fig. 7D). A zig-zag pattern is produced among these very short Zahnreihen that is extremely similar to the pattern observed in *Mesosuchus*.

Rhynchosaurs with clearly evident multiple rows of teeth had a mode of tooth replacement similar to that described for *Captorhinus* (Benton 1984). Teeth of these reptiles are arranged in Zahnreihen that are parallel to the jaw margin or extend between the posterolingual and anterolabial edges. New teeth are added posterolingually to several Zahnreihen simultaneously and are carried forward by posterolingual growth of the jaw element. Furthermore, the occlusal surface of the maxilla and

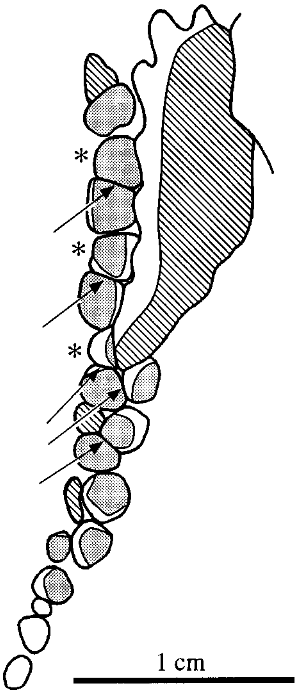

Figure 12. *Mesosuchus browni*. SAM 6536. Line drawing of exposed teeth of right maxilla in occlusal view. Surfaces of damaged bone and teeth are represented by cross hatching. Worn surfaces of teeth are shown by stippling. Arrows point to erosional surfaces between neighbouring Zahnreihen and asterisks indicate steps in alignment of Zahnreihen.

dentary is convex, and continuous lingual growth relocates teeth from the lingual side into occlusion and later into a more labial orientation. Resorption of bone cranially and labially prevents the older teeth from moving onto the labial surface. Consistent patterns of erosion between teeth of different ages can be used to identify Zahnreihen in *Captorhinus* (Bolt & DeMar 1975; Ricqlès & Bolt 1983) and rhynchosaurs (Benton 1984). According to the model of jaw growth and addition of teeth in *Captorhinus*, the oldest tooth is at the cranial end of each Zahnreihe, and older Zahnreihen in a region of multiple tooth rows are located labially. Teeth within a Zahnreihe are often eroded on their medial side by adjacent teeth in the younger, lingual Zahnreihe and occasionally on their caudal side by the next caudal tooth in that row. In addition, the cranial (i.e. labial) teeth of Zahnreihen are separated by steps in *Captorhinus* where the tooth of medially adjacent Zahnreihe is located lingually to the oldest tooth of the next older Zahnreihe.

Although only a right maxilla and partial right dentary of *Mesosuchus* are exposed occlusally, some of these erosional features and steps between Zahnreihen can be observed and support the hypothesis that *Mesosuchus* has multiple rows of teeth on at least the maxilla. Although the bases of the dentary teeth of SAM 6536 are close, the teeth are spaced far apart with little evidence of erosional contact (figure 11). Five sites of lingual erosion are visible in the zig-zag region of the maxilla (figure 12), which is consistent with the idea of these teeth belonging to different Zahnreihen. Erosion was the result of the addition of teeth to the younger, lingual Zahnreihe. Three instances of steps between adjacent Zahnreihen are present and contribute to the appearance of a zig-zag arrangement.

(b) *Postcranial skeleton*

(i) *Vertebrae*

No specimen of *Mesosuchus* has a complete, articulated vertebral column, but it is possible to estimate that there are a minimum of seven and probably eight cervical vertebrae based on SAM 5882 and 6536. Assuming a total of 25 presacral vertebrae as appears to be common for related taxa such as *Prolacerta* (Gow 1975), *Rhynchosaurus* (Benton 1990), *Hyperodapedon* (Benton 1983; Chatterjee 1974), and *Proterosuchus* (Cruickshank 1972), *Mesosuchus* has 17 dorsal vertebrae. Broom (1913*b*) estimated 26 presacral vertebrae for *Mesosuchus* based on the type specimen SAM 5882. There is no complete series of caudal vertebrae in any specimen of *Mesosuchus*, hence the true length of the tail is unknown. Similarly, the correct length of the tail is unknown for all other basal archosauromorphs. Those with an appreciable portion of the tail preserved, such as *Macrocnemus* (Peyer 1937), *Trilophosaurus* (Gregory 1945), and *Tanystropheus* (Wild 1973), suggest a long tail with a probable minimum of 40 vertebrae as is also true for the basal diapsids such as *Petrolacosaurus* (Reisz 1981).

There are no preserved proatlases. A small atlas intercentrum is present on the holotype wedged between the atlas centrum and basioccipital (figure 7*c*). Its size is smaller than expected given the robustness of this bone in *Hyperodapedon* (Benton 1983) and *Prolacerta* (Gow 1975), but it is possible that the remainder of the atlas intercentrum is hidden underneath the basioccipital and atlas pleurocentrum. The atlas pleurocentrum (centrum) is a considerably larger ovoid with a convex cranial side and a concave caudal side (figure 7*c*). A pair of loosely associated bones near the axis of SAM 6536 (figure 5*b*) are probably the atlas neural arches. Each has a roughly square outline with a notch on one side that presumably demarcates the dorsal arm that articulates with the prezygapophysis of the axis from the ventral arm that contacts the atlas pleurocentrum.

An axis intercentrum cannot be identified with certainty although a crushed, oblong bone next to the cranial edge of the axis centrum of SAM 6536 could be this element (figure 5*b*). Haughton (1924) identified this bone as the odontoid (axis intercentrum). The large neural spine of the axis has a restricted base and expands dorsally to attain a height greater than that of the remaining cervical neural arches. The dorsal edge of the neural spine is thin for much of its length, but greatly expanded at the caudal corner, possibly for attachment of *M. spinalis capitus*. The ventral edge of the axis centrum has a sharp ventral keel as in *Prolacerta* (BP/1/2675) and *Howesia* (Dilkes 1995). Only a small diapophysis is visible on the right side of the centrum of the holotype.

The third cervical vertebrae of the holotype and SAM 6536 are distinctly different from the other presacral vertebrae (figures 7*a* and 9). Each has a neural spine that is craniocaudally narrower than any of the succeeding vertebrae, a difference particularly pronounced in SAM 6536 (figure 9). In addition, the third cervical vertebra of each specimen possesses unique features not reported in any other basal archosauromorph. The third cervical vertebra of SAM 6536 has a large process above each postzygapophysis that does not articulate with any portion of the fourth cervical vertebra. In contrast, the type specimen has a narrow ridge along the cranial edge of the neural spine that terminates as a small process above the prezygapophysis (figure 7*a*). As neither of these processes in SAM 6536 and the holotype appear to articulate with any portion of the neighbouring vertebrae, their significance is uncertain. There is only a very small transverse process situated low on the centrum and near the cranial rim. Ventrally, the centrum has a pinched, but rounded margin, contrary to Haughton (1924).

The remaining cervical vertebrae have tall and craniocaudally narrow neural spines and robust zygapophyses (figure 7*a*). Transverse process appear to be in a similar position to that of the third cervical vertebra. Centra lack ventral keels.

The dorsal vertebrae may be distinguished from the cervicals by their shorter and craniocaudally broader neural spines with blunt tops and prominent transverse process situated on the pedicel of the neural arch below the prezygapophysis (figure 13). Although damaged, the neural spines of the last pair of dorsals are narrower craniocaudally than the other dorsals and resemble the neural spines of the sacrals. A shallow pocket is present on the neural arches above the transverse processes of the middle and caudal dorsals of SAM 6046. *Howesia* has deeper pockets on the neural arches of the last several dorsals (Dilkes 1995). Articular facets for the tuberculum and capitulum are confluent on all exposed transverse processes; those of the cranialmost three or four dorsals are not visible. Transverse processes of the dorsal vertebrae at the cranial end of the series are large, projecting laterally for a distance equal to half the length of the centrum. Those dorsal vertebrae in the middle and caudal regions are significantly shorter. All dorsal centra have a gently rounded ventral margin, are amphicoelous and non-notochordal. There is only a minor amount of bevelling for the intercentra.

Mesosuchus has two sacral vertebrae that are easily recognizable by their massive ribs (figures 13 and 14). A slight ridge on each sacral vertebrae of SAM 6046 may mark the boundary between the significantly enlarged transverse process and fused sacral rib (figure 13*a*). The shallow depressions on the neural arches of the dorsals are also present on the sacrals. The centra of the sacrals have similar dimensions to that of the dorsals and lack significant bevelling for intercentra. A shallow mid-ventral groove is present on the second sacral of SAM 7416 (figure 14), but apparently not the first sacral, which is exposed only on SAM 6046 (figure 13*c*).

Neural spines of the caudal vertebrae are very tall and craniocaudally narrower than the sacrals with a height to width ratio of at least 3 : 1 (figures 13 and 14). This ratio is maintained for a minimum of the first 11 vertebrae. Comparison of the proximal caudals of SAM 6046 and those more distal of SAM 7416 suggest a slight increase in height. *Rhynchosaurus* (Benton 1990) has caudal neural spines with a similar height to width ratio, but unlike *Mesosuchus* there is a more dramatic increase in the height of the spines from the first to sixth, with a maintenance of the same height for a further several vertebrae, and then a decrease to a small projection by about the twentieth vertebra. An additional difference between the caudal neural spines of *Mesosuchus* and *Rhynchosaurus* is found in the first three caudals, which are inclined caudally to a slight degree in *Mesosuchus*, but are vertical in *Rhynchosaurus*. Caudal neural spines with a similar ratio are also present in *Howesia* (Dilkes 1995); however, *Howesia* can be distinguished by its autapomorphic pronounced caudal inclination of the neural spines for at least the first dozen vertebrae.

Width of the caudal neural arch is considerably smaller than that of the dorsals and sacrals. This transition in width is achieved in the first caudal (figure 13*a*). The elongate lateral projections of the caudals are considered to be entirely transverse processes rather than fused ribs and processes because no line of fusion is visible unlike that between the sacral ribs and vertebrae. The transverse process of the first caudal projects laterally and somewhat caudally, and ends bluntly. Its length is greater than that of the centrum. Large transverse processes with little or no caudal orientation are present on at least the subsequent five caudals of SAM 7416 (figure 14). Those of the next seven caudals are broken, and the last two that are exposed have much shorter transverse processes with lengths less than that of their centra. Only a modest decrease in lengths of caudal centra relative to the sacrals is discernible across the first 14 caudals. The mid-ventral groove on the centrum of the second sacral is also present on the first two caudals (figures 13*c* and 14). These grooves are absent on the caudals of *Howesia* (Dilkes 1995) and *Prolacerta* (BP/1/2676).

The haemal arch has an expanded base with a large circular opening for the caudal artery and vein. Distal to this foramen, the thin haemal spine projects ventrolaterally and has an expanded distal tip similar to the haemal spines of *Howesia* (Dilkes 1995) and *Prolacerta* (BP/1/2676).

Intercentra are absent from the cervical vertebrae of *Mesosuchus*, but retained in the dorsal vertebrae (figures 13*c* and 14) as is also true for *Howesia* (Dilkes 1995), *Prolacerta* (BP\1\2676), and *Trilophosaurus* (Gregory 1945). Sizes of the intercentra vary considerably between SAM 6536 and 7416, which are individuals of comparable size. The transition from intercentra to haemal arch occurs between the second and fourth caudal vertebrae (figure 14).

(ii) *Ribs*

Ribs are present in *Mesosuchus* throughout the presacral series, with the probable exception of the atlas. None of the cervical ribs are complete, but it is clear that they are virtually identical to those of prolacertiformes and *Trilophosaurus* (Gregory 1945). Each is holocephalous and attached to the cranial–ventral corner of the centrum. A prominent anterior accessory process is found on the proximal head (figure 7*b*). The shaft is extremely narrow and at a right angle to the proximal head. With the probable exception of the last one or two cervical ribs, all lie approximately parallel to the vertebrae. Total length of the shaft was at least equal to the lengths of two centra (figure 9*b*), although it is possible that the lengths of the cervical ribs varied as in *Macrocnemus* (Rieppel 1989). All dorsal ribs have long and gently curved shafts with oval cross-sectional outlines. There is some distal flattening of the shaft.

Proximal dorsal ribs have a small separation between the tubercular and capitular heads, but all others are holo-

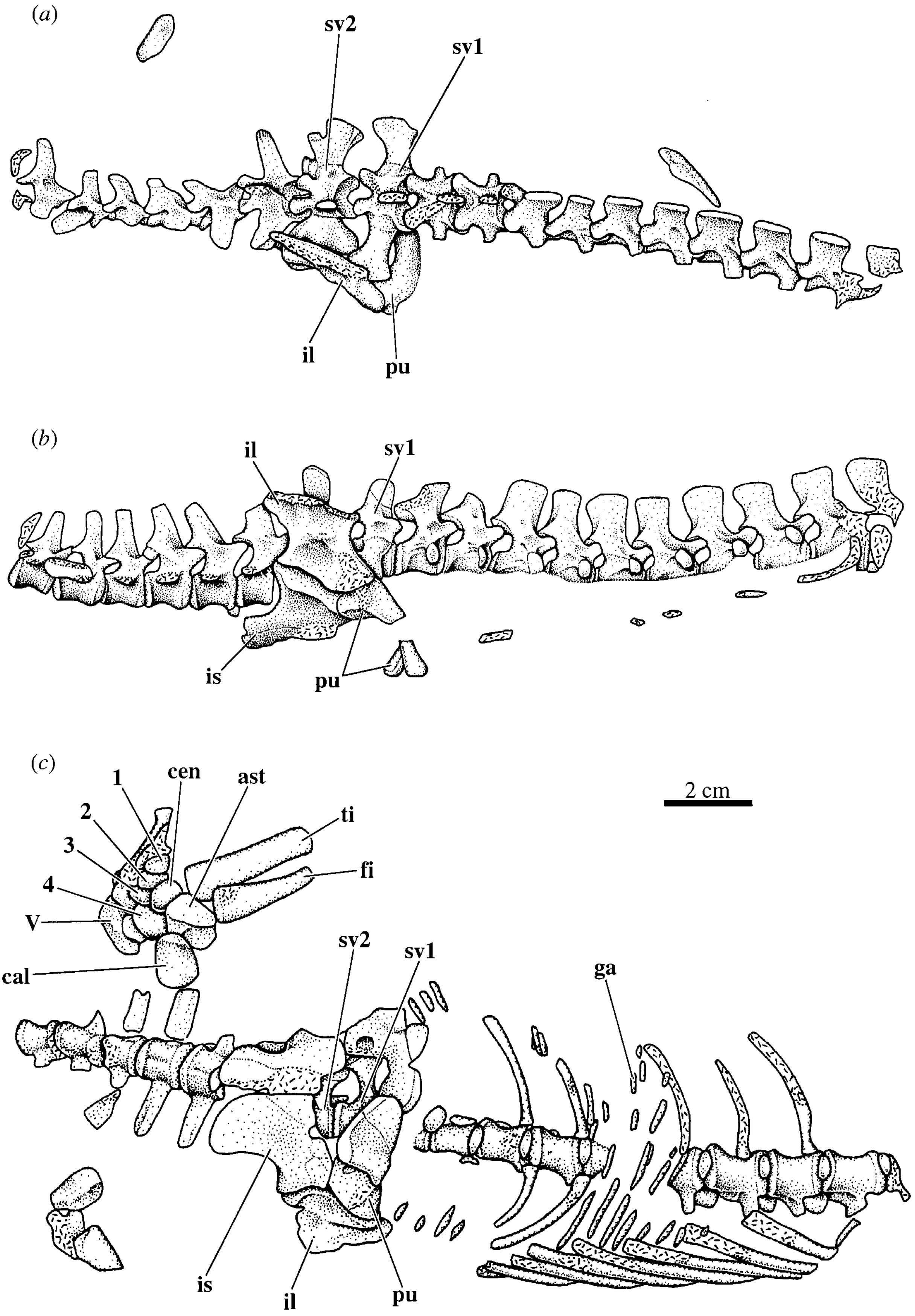

Figure 13. *Mesosuchus browni*. SAM 6046. Articulated series of dorsal, sacral and caudal vertebrae, pelvis and partial right hindlimb in (*a*) dorsal; (*b*) right lateral; and (*c*) ventral views. For a list of abbreviations see Appendix 3(b).

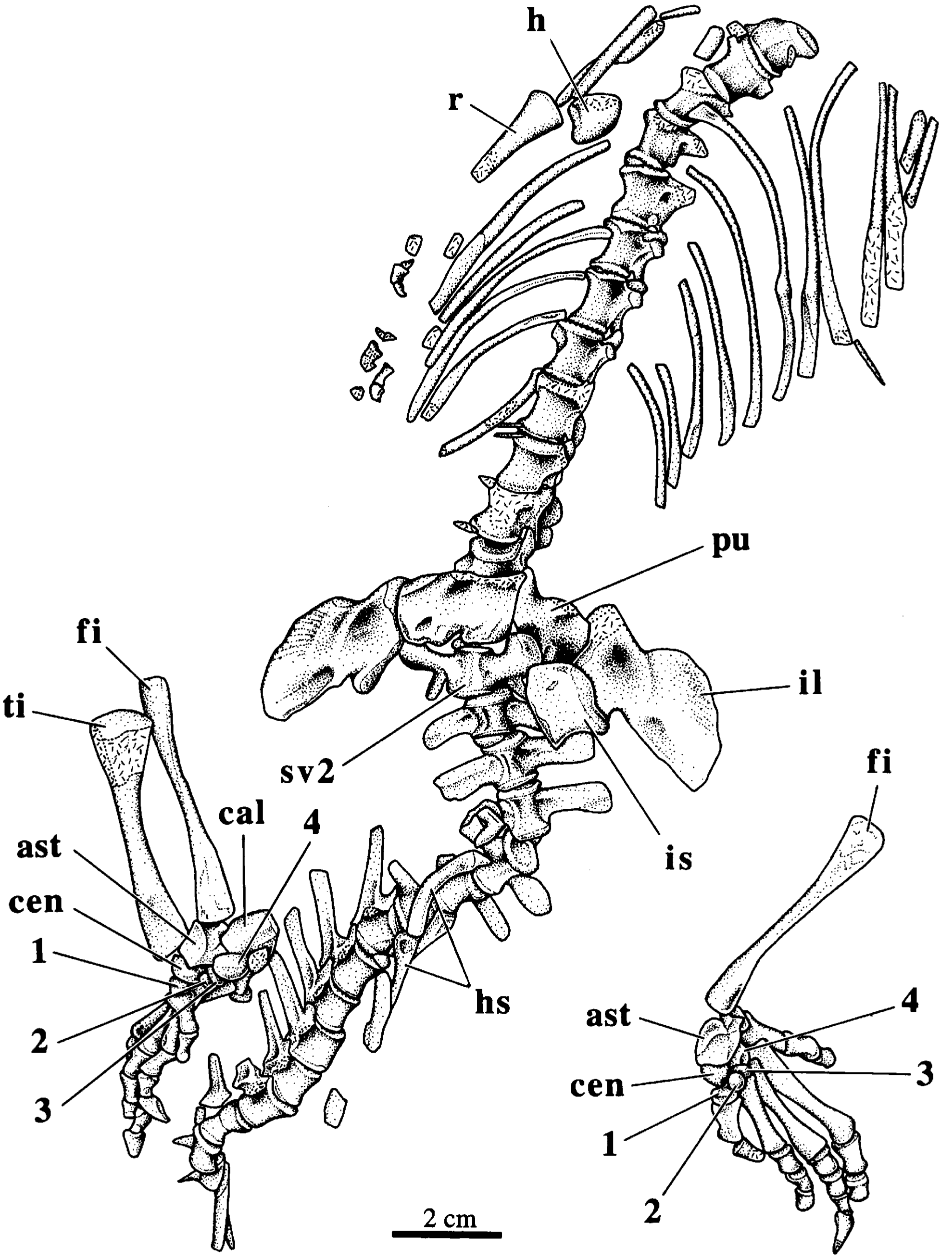

Figure 14. *Mesosuchus browni*. SAM 7416. Partial postcranial skeleton in ventral view. For a list of abbreviations see Appendix 3(b).

cephalous. The sacral ribs of *Mesosuchus* are virtually identical to those of *Howesia* (Dilkes 1995) and *Prolacerta* (Gow 1975) and extremely similar to those of *Macrocnemus* (Rieppel 1989). From their greatly enlarged bases, each sacral rib expands to a massive buttress against the inner side of the ilium. The first sacral rib has an oval distal expansion that overlaps the anterolateral corner of the second sacral rib as in *Macrocnemus*. The second sacral rib of *Mesosuchus* is bifurcated. A large process with a flat, truncated end projects posterolaterally from the base of the sacral rib (figures 13*a* and 14). A bifurcated second sacral rib has been reported in *Howesia* (Dilkes 1995), *Prolacerta* (Gow 1975), *Macrocnemus* (Rieppel 1989) and *Langobardisaurus* (Renesto 1994*a*), and is present in many extant lizards (Hoffstetter & Gasc 1969). This bifurcation in *Mesosuchus*, *Howesia*, *Prolacerta* and *Euparkeria* consists of a blade-like posterolateral projection with a flat, truncated end that does not contact the ilium, whereas the same projection in *Macrocnemus* and *Langobardisaurus* has a bluntly pointed terminus. *Protorosaurus* does not have a bifurcate second sacral rib (Meyer 1856, plates VI and IX). In addition, and contrary to published reports, a bifurcate second sacral rib is also present in *Euparkeria* and *Proterosuchus*. In her description of the sacral vertebrae of *Euparkeria*, Ewer (1965) stated only that the second sacral rib was expanded distally. However, after examination of SAM 6049, upon which her description was based, it is clear that the space between the expanded articular portion of the rib and the posterior process is filled with matrix of identical colour to that of the fossilized bone. Other clearly bifurcated second sacral ribs are present in SAM 7696 and 7710. The trifurcation of the second sacral rib of *Proterosuchus* reported by Cruickshank (1972) is apparently the result of his misinterpretation of a long, matrix-filled dorsal depression as evidence of an additional anterior process. Examination of QR 1484 showed only a single, broad articular surface for the ilium and a large posterior process.

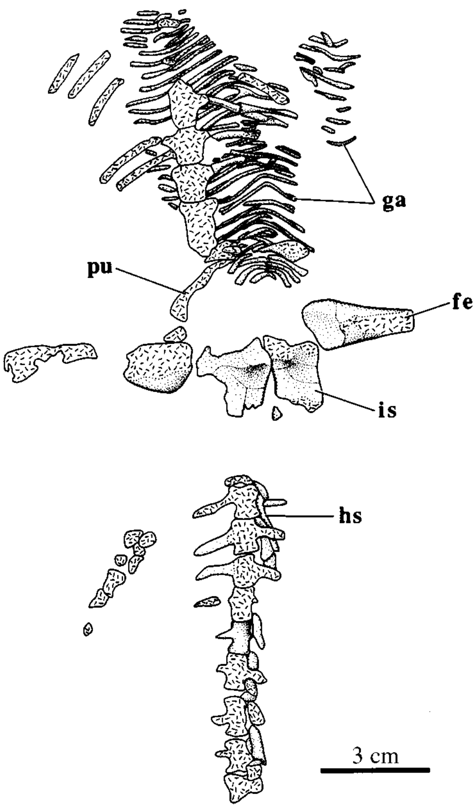

Figure 15. *Mesosuchus browni*. Holotype SAM 5882. Partial postcranial skeleton in dorsal view. For a list of abbreviations see Appendix 3(b).

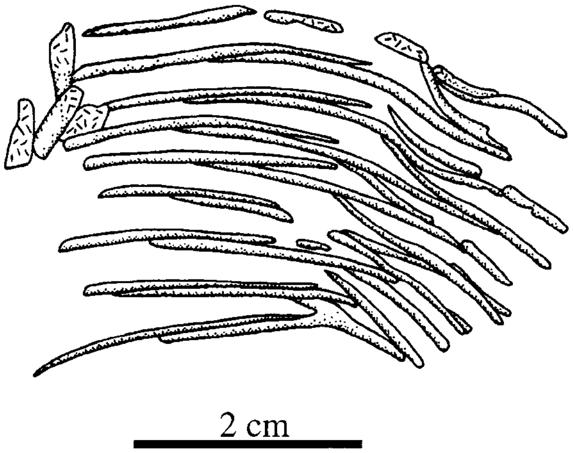

Figure 16. *Mesosuchus browni*. SAM 6536. Gastralia.

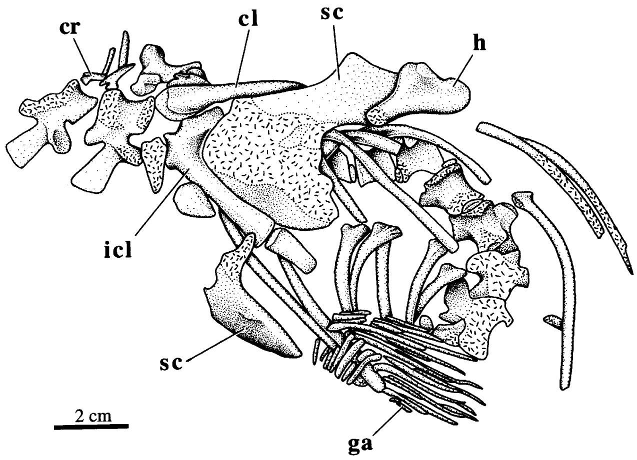

Figure 17. *Mesosuchus browni*. SAM 6536. Partial pectoral girdle, cervical and dorsal vertebrae, and gastralia. For a list of abbreviations see Appendix 3(b).

(iii) *Gastralia*

Gastralia are incomplete in all specimens, but appear to cover virtually the entire ventral thoracic and abdominal regions. The largest set of preserved gastralia suggests that at least 30 were present originally. Most gastralia are thin, elongate rods that taper at each end, with the exception of the last four rows, which are shorter and wider (figures 15–17), as is also true for *Howesia* (Dilkes 1995). All gastralia have a cranial curvature with the degree of curvature varying from a V-shape to a broader U-shape. Each repeated section of gastralia of *Mesosuchus* consists of a central element, overlapped along its cranial side by a straight or slightly curved lateral element that is itself overlapped laterally by a third element. Occasionally, the central element will have an anterolateral projection on its cranial side.

Gastralia are present in the majority of known basal archosauromorphs; however, there is considerable variability rendering comparisons difficult. *Mesosuchus* shares the presence of a gastralium composed of a single, median element overlapped cranially by lateral elements with *Champsosaurus* (Erickson 1985), *Hyperodapedon* (in spite of the apparent division of some medial elements) and *Rhynchosaurus*. *Champsosaurus* differs from rhynchosaurs in that its medial element is bent caudally rather than cranially. Other archosauromorphs have apparently unique constructions of gastralia. A gastralium of *Euparkeria* (Ewer 1965) has two cranially bent medial elements, some of which have an anterior process very similar to that on some medial elements of *Mesosuchus*. On the other hand, *Proterosuchus* (Cruickshank 1972; D. W. Dilkes, personal examination of QR 1484) appears to lack medial gastrial elements and often there is only a pair of very long lateral elements that overlap along the midline. Yet a further variation is present in *Tanystropheus* (Wild 1973) where two medial elements dovetail along the midline and are overlapped distally by long lateral elements.

(iv) *Pectoral girdle*

Morphology of the scapulocoracoid of *Mesosuchus* (figure 17) is extremely similar to that of *Prolacerta* (Gow 1975) in both its overall configuration and the fusion of the scapula and coracoid, but stands in sharp contrast to the pectoral girdles of Middle and Late Triassic rhynchosaurs. In these rhynchosaurs, the scapula and coracoid are unfused and the scapula has an essentially vertical orientation, with the probable exception of *Stenaulorhynchus* (Huene 1938). *Proterosuchus* has a pectoral girdle with a similar construction to *Mesosuchus*, but the scapula and coracoid are separate (Cruickshank 1972). The tall, narrow scapula of *Euparkeria* (Ewer 1965) resembles that of *Rhynchosaurus* and *Hyperodapedon* (Benton 1983, 1990). A pronounced acromion for the clavicle is present on the cranial border of the scapula of *Mesosuchus*. Immediately above the acromion, the scapula is constricted and then expands dorsally. The dorsal edge appears to be unfinished suggestive of a cartilaginous suprascapula. Little information can be

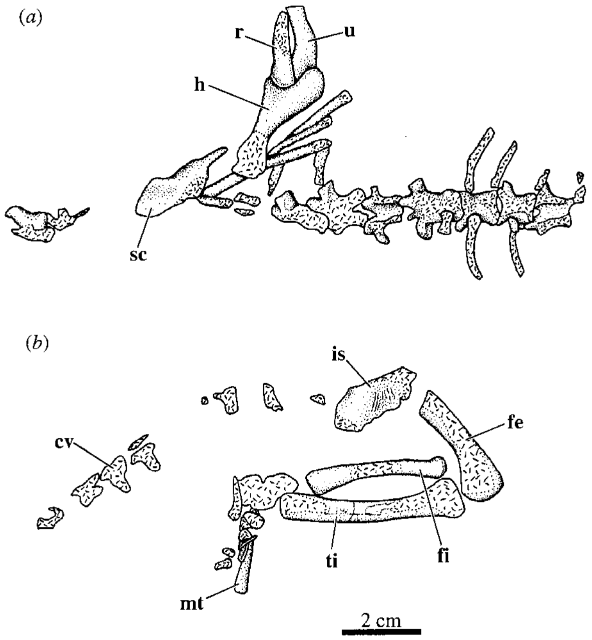

Figure 18. *Mesosuchus browni*. Holotype SAM 5882. (*a*) Partial left forelimb; (*b*) partial left hindlimb. For a list of abbreviations see Appendix 3(b).

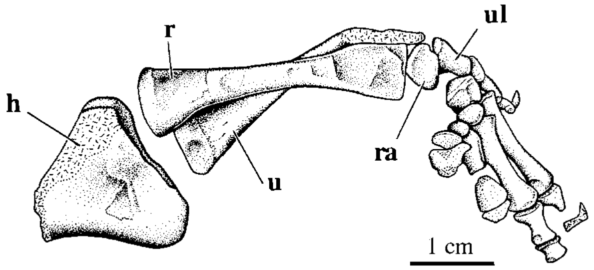

Figure 19. *Mesosuchus browni*. SAM 6046. Partial left forelimb. For a list of abbreviations see Appendix 3(b).

obtained on the glenoid other than it shares a similar 'screw-shape' and primarily lateral orientation with the glenoids of *Prolacerta* and *Proterosuchus*, unlike the 'screw-shaped', but caudally open glenoids of other rhynchosaurs and *Euparkeria*. There is no evidence of a foramen in the single known coracoid of *Mesosuchus*.

The T-shaped interclavicle has a long caudal stem with a modest expansion (figure 17). It appears to end abruptly, but a small apparently additional ossification immediately behind the interclavicle of SAM 6536 is probably its continuation, because this ossification tapers to a blunt point just caudal to the rear margin of the coracoid in common with other amniotes. The ventral surface of the caudal stem is convex. The crossbar is curved dorsally along the cranial edge of the coracoid and overlaps the clavicles. A deep notch is present on the crossbar between the clavicular facets. A similar notch is also present on the interclavicles of *Prolacerta* (Gow 1975), *Proterosuchus* (contrary to Cruickshank (1972) and D. W. Dilkes, personal observation of QR 1484 and GHG 363), and *Macrocnemus* (Rieppel 1989).

The clavicle has a modestly expanded ventral portion that is overlain by the interclavicle and tapers gradually dorsally (figure 17). It appears to have reached dorsally to the upper edge of the scapula.

(v) *Forelimb*

Only the distal end of the humerus is preserved (figures 17–19). Ectepicondylar and entepicondylar foramina are absent, and there is no supinator crest. The capitellum is a hemispherical, slightly convex facet that is offset from the ventral surface. The trochlear notch is distinct.

The radius and ulna have slightly compressed shafts and greatly expanded and flattened proximal and distal ends (figures 18 and 19). An olecranon process is not present on the ulna.

Most of the manus can be reconstructed from the incomplete forelimbs of SAM 6046 (figures 10*b* and 19). Six carpals are preserved in the carpus of the left forelimb of SAM 6046 (figure 19). Three of the carpals are considerably larger than the others. One has a square outline with rounded corners and a shallow, lateral notch and is associated with the radius. A second is near the ulna, but is more elongate and lacks a notch. These carpals are probably the radiale and ulnare, respectively, although it is also possible that the carpal identified as a radiale is the intermedium and the radiale is absent. Four distal carpals are present and articulate with metacarpals one to four. The first three distal carpals are ovoid in shape and the fourth is significantly larger and has a slight dorsal ridge. Only the expanded proximal end of the first metacarpal is present. Measurements of the metacarpals of SAM 6046 given by Haughton (1921) are correct with the exception of metacarpal one which, as stated above, is incomplete. The phalangeal counts for the digits are uncertain.

(vi) *Pelvic girdle*

The ilium of *Mesosuchus* (figures 13 and 14) is virtually identical in both shape and size to the ilia of *Howesia* (Dilkes 1995), *Noteosuchus* (Carroll 1976) and *Prolacerta* (Gow 1975) (figure 20). All have a broad anterior projection, a larger posterior projection and a slightly convex dorsal margin. A series of vertical striations covers the cranial two-thirds of the lateral surface of the iliac blade above the dorsal rim of the acetabulum of *Mesosuchus*. There is an elongate, shallow depression caudal to this striated region.

The pubis has an expanded, dorsoventrally convex cranial surface that extends posteromedially from the prominent processes lateralis to the midline suture with the opposite pubis (figure 13). Caudal to the pubic symphysis, the pubis is concave. Immediately cranial to the transverse suture between the pubis and ischium is a large, oval obturator foramen. A portion of the pubic boundary of a diamond-shaped median gap between the pubes and ischia, also present in other rhynchosaurs (Benton 1983, 1990; Dilkes 1995), is preserved on the left pubis of SAM 6046.

Beneath its robust contribution to the acetabulum, the ischium is flat and uniformly thick. The lateral margin is deeply concave, far more so than in *Rhynchosaurus* (Benton 1990) or *Hyperodapedon* (Benton 1983), but identical to that of *Howesia* (Dilkes 1995) and *Noteosuchus* (Carroll 1976). *Stenaulorhynchus* (Huene 1938) shares a deep lateral concavity of the ischium with Early Triassic rhynchosaurs. Caudally, the ischium is elongated with an extensive ischiadic symphysis.

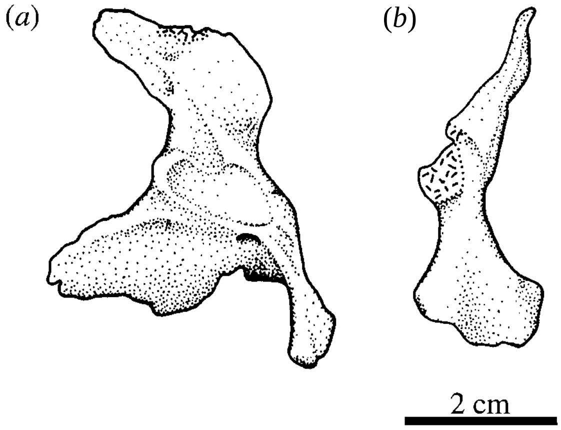

Figure 20. *Prolacerta broomi*. BP/1/2676. Right pelvis in (*a*) lateral; and (*b*) cranial views.

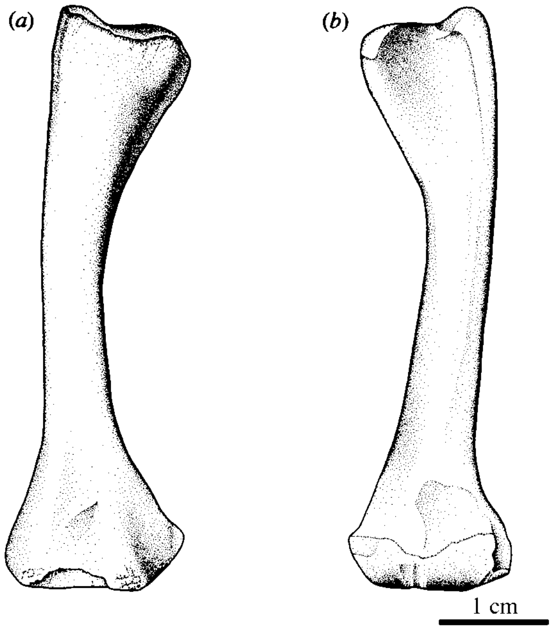

Figure 21. *Mesosuchus browni*. SAM 7416. Right femur in (*a*) dorsal; and (*b*) ventral views.

(vii) *Hindlimb*

The femur has a relatively flat, proximal articular surface that continues for a short distance onto the ventral side of the internal trochanter (figure 21). The shaft has a sigmoidal curvature (figures 10*c* and 21). Distal condyles are equal in size, and their continuous articular surfaces are restricted to the ventral side. A low, straight ridge on the ventral side extends from the caudal margin of the intertrochanteric fossa to just above the shallow popliteal fossa. As noted in previous descriptions of South African rhynchosaurs (Carroll 1976; Dilkes 1995), the femora of *Mesosuchus*, *Howesia* and *Noteosuchus* are virtually identical. Though incomplete in all described specimens, the femur of *Rhynchosaurus* appears to resemble very closely the femora of the South African rhynchosaurs (Benton 1990). *Stenaulorhynchus* and *Scaphonyx* retain the sigmoidal curvature of the femoral shaft, but the articular ends are more expanded and the shaft appears shorter (Huene 1938, 1942). *Hyperodapedon* has a robust femur with a virtually straight shaft (Benton 1983). The femora of *Euparkeria* (Ewer 1965; D. W. Dilkes, personal examination of SAM 6047), *Prolacerta* (Gow 1975) and *Trilophosaurus* (Gregory 1945) are strikingly similar to the femora of the South African rhynchosaurs, although much longer relative to the tibia in the latter two taxa. In contrast, *Proterosuchus* has a more robust femur with a straight shaft (Cruickshank 1972).

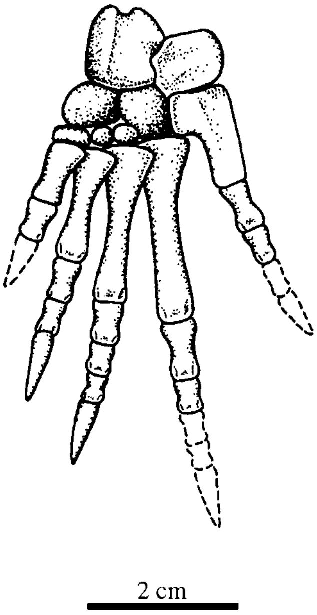

Figure 22. *Mesosuchus browni*. Reconstruction of left pes in dorsal view.

The length of the tibia of SAM 7416 is 83% that of the femoral length, similar to the value of 90% reported for *Noteosuchus* (Carroll 1976). Available femora of *Howesia* are incomplete, and it can only be stated that the femur and tibia did not differ greatly in length (Dilkes 1995). The descriptions of the tibiae of *Noteosuchus* (Carroll 1976) and *Howesia* (Dilkes 1995) fit the tibia of *Mesosuchus* with no modification. The fibula of *Mesosuchus* is identical to those of the other Early Triassic rhynchosaurs.

The confusion generated by Haughton's (1921) illustration of the tarsus of *Mesosuchus* for discussions of tarsal evolution (e.g. Hughes 1968) was cleared by Carroll (1976) who showed that *Mesosuchus*, *Howesia* and *Noteosuchus* share virtually identical tarsal elements. The sole remaining discrepancy between the tarsus of *Howesia* and *Mesosuchus*, specifically the apparent alignment of the centrale, astragalus and calcaneum into a single row (Carroll 1976), which is a feature present in all later rhynchosaurs, was resolved by Dilkes (1995). Thus, in terms of both the morphology of the individual elements and their positions within the tarsus, no significant differences exist between the tarsi of Early Triassic rhynchosaurs.

Proximally, the astragalus has a quadrangular, laterally facing articular facet for the fibula. The ventral margin of the fibular facet is indented slightly for the reception of the dorsal edge of the calcaneum (figure 22). Below the fibular facet, there is a small constriction followed by a great expansion to form the body of the astragalus, thus giving the element an L-shape noted in numerous other early

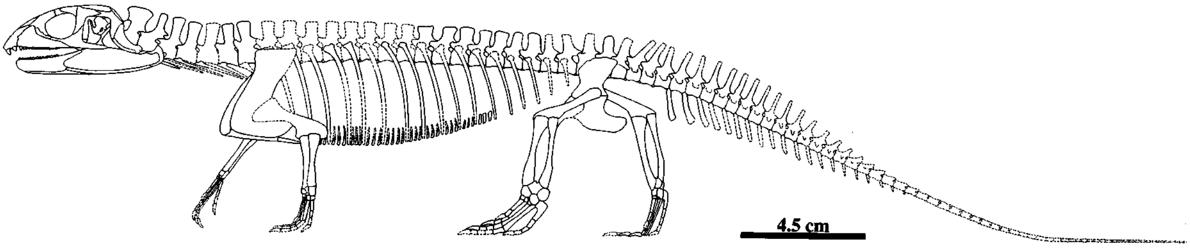

Figure 23. *Mesosuchus browni*. Reconstruction of skeleton in left lateral view.

amniotes. The lateral side of this constriction forms part of the perforating foramen between the astragalus and calcaneum. A region of finished bone separates the fibular facet from the considerably larger, convex, medial facet for the tibia. Distally, the astragalus presents a highly convex, continuous articular surface for the centrale, fourth distal tarsal and calcaneum. Most of the articular surfaces for the tibia, centrale, fourth distal tarsal and calcaneum are present on the dorsal side of the astragalus.

The calcaneum is a large, flat, rectangular element. Only a slight notch marks the contribution of the calcaneum to the perforating foramen. Proximal to this notch, a small projection fits into the ventral indentation of the fibular facet on the astragalus noted above. Distal to the notch, a second small projection forms a corner between the notch and the recessed face for the calcaneal facet of the astragalus. The articular surface for the fourth distal tarsal is continuous with astragalar facet, but is convex rather than recessed. A prominent ridge on the dorsal side extends from the distal portion of the astragalar–calcaneal joint to the tip of the lateral tuber.

Lying distal to the astragalus and calcaneum is the enlarged centrale. It is smoothly rounded and ovoid in shape with a slightly flattened proximal side for the astragalus and a rounded distal side that contacts the first, second and third distal tarsals. Four distal tarsals are present in the tarsus of *Mesosuchus*. Unlike the others, the first distal tarsal is disk-like in shape with flat proximal and distal surfaces for the astragalus and first metatarsal, respectively. Second and third distal tarsals vary in shape from small spheres to ovoids and are either comparable in size to the first distal tarsal (figure 14) or slightly larger (figure 13). The fourth distal tarsal is the largest of the series. It tends to be ovoid in shape with only poorly defined articular regions for the astragalus, calcaneum, fourth distal tarsal and fifth metatarsal.

Metatarsals one to four increase sequentially in length. Each has expanded proximal and distal ends that are set at an angle, so the proximal ends overlap and the distal ends lie in the plane of the pes. The fifth metatarsal has a large, medially directed head that contacts primarily the fourth distal tarsal, but also the calcaneum. A distinct neck separates the head with its expanded articular end from the shaft. Only pedal digits two and three are complete with phalangeal formulae of three and four, respectively. A single phalanx is preserved on digit one of both pedes and two are visible on digits four and five of the left pes. The probable phalangeal counts of digits one, four and five are two, five and four, respectively, based on other archosauromorphs with similar pedal morphologies such as *Noteosuchus* (Carroll 1976), *Trilophosaurus* (Gregory 1945) and *Macrocnemus* (Rieppel 1989). The unguals are long and recurved.

(c) *Reconstruction*

A composite reconstruction of the skeleton of *Mesosuchus* is given in figure 23. The neck is short relative to the length of the dorsal vertebrae, with the apparent length reduced further by the enlarged retroarticular process of the mandible. Although proportions are derived from different individuals, the hindlimb is clearly longer than the forelimb. The ratio of the lengths of the tibia of SAM 7416 and the radius of SAM 6046 is 1.45. The difference is greater for the manus and pes where the ratio between the lengths of the fourth metatarsal of SAM 7416 and the fourth metacarpal of SAM 6046 is 1.80. The elongated neural spines of the first dozen caudal vertebrae and the large haemal spines give the tail a pronounced dorsoventral expansion.

4. PHYLOGENETIC RELATIONSHIPS

(a) *Taxonomic history of rhynchosaurs*

Soon after the first description of a rhynchosaur (Owen 1842), comparisons were made between rhynchosaurs and the extant sphenodontid *Sphenodon*. Owen (1845, 1859) argued that *Rhynchosaurus* was related to the South African synapsid *Dicynodon*, and suggested that the edentulous tusk-like bones of *Rhynchosaurus* were analogous to the premaxillae and represented both the termination of a forward progression of the tusks seen in species of *Dicynodon* and an extreme version of the toothed beak of *Sphenodon* (referred to by Owen as *Rhynchocephalus*). Soon after the publication of an important monograph on the anatomy of *Sphenodon* (Günther 1867), Huxley (1869, 1887) noted further similarities between *Sphenodon* and the second recorded rhynchosaur *Hyperodapedon*. According to his observations of *Hyperodapedon*, both shared beak-like rostrums in which the premaxillae formed either the entire beak (*Hyperodapedon* and its close relative *Rhynchosaurus*), or the base of the beak (*Sphenodon*) and upper dentition on fused maxillae and palatines separated by a groove into which a single row of dentary teeth inserted. He proposed (1887) the group Sphenodontina, which was composed of Rhynchosauridae (*Rhynchosaurus* and *Hyperodapedon*) and Sphenodontidae (*Sphenodon* and relatives). Others (e.g. Woodward 1898; Zittel 1893) followed Huxley's argument and placed rhynchosaurs close to *Sphenodon*.

A more detailed description of *Hyperodapedon* (Burckhardt 1900), revealed that the characters listed by Huxley as evidence of affinities of rhynchosaurs with *Sphenodon* were incorrect. Burckhardt considered the premaxillary beak to be in no way comparable to the toothed premaxillae of *Sphenodon*, and interpreted the upper dentition as entirely palatal. Instead of the close affiliation supported by Huxley, Burckhardt argued that rhynchosaurs were a separate lineage of rhynchocephalians, as the group was defined by Boulenger (1891) to include a restricted group of true rhynchocephalians consisting of *Sphenodon* and its immediate allies and a second group Proterosauria [sic].

In his landmark paper on reptilian classification, Osborn (1903) concurred with Burckhardt that there was no evidence of a special relationship between rhynchosaurs and *Sphenodon*. The new order Rhynchosauria was proposed as one of several equivalent orders of reptiles in a new superorder Diaptosauria. Osborn's only attempt at a phylogenetic consideration of rhynchosaurs was to suggest tentatively a link with the parareptile *Procolophon*.

The discoveries of *Howesia* and *Mesosuchus* failed initially to resolve the phylogenetic position of rhynchosaurs, because although similarities between these taxa and rhynchosaurs were noted, *Howesia* and *Mesosuchus* were nonetheless interpreted as part of the basal radiation of diaptosaurians. As a consequence, proposals for relationship were vague and classifications quite divergent. The great resemblance between the enlarged dental area of *Howesia* with its numerous teeth and the tooth plates of *Hyperodapedon* and *Rhynchosaurus* impressed Broom (1906), and he concluded that *Howesia* was a primitive gnathodont, his term for Rhynchosauria. Furthermore, he considered gnathodonts to be more closely related to phytosaurs, which unlike Osborn (1903), he included in Diaptosauria. At the same time though he attached evolutionary significance to the similar tarsi of *Howesia* and *Sphenodon* despite the more distant relationship of rhynchocephalians according to his scheme. In his study of *Mesosuchus* and *Euparkeria* (Broom 1913*b*), he discussed *Mesosuchus* separately from the gnathodonts and implied a possible connection with the pseudosuchian thecodonts such as *Euparkeria*, but chose to not advance any new classificatory scheme until knowledge was gained of the probable Permian ancestral diapsids.

Youngina capensis (Broom 1914, 1922) from the *Dicynodon* Assemblage Zone of South Africa furnished an almost ideal ancestral type for diapsids, and had special relevance to the problem of the origin of lizards and the identity of the bones of the temporal region. A new thecodontian suborder Eosuchia was created for *Youngina* and it came to dominate evolutionary thinking among palaeontologists for the next several decades as the central evolutionary stock for many or all other diapsids. Two classifications of reptiles appeared soon after the discovery of *Youngina*, and represented the first attempts to modify the influential work of Osborn (1903) in the light of the new knowledge of early diapsids. Watson (1917) followed Broom and recognized *Youngina* as a basal thecodont in a family Eosuchidae to which he added *Eosuchus colletti* (Watson 1912*b*). A new primitive, probably thecodontian, family Howesiidae was erected for *Howesia*, and questionably to also include *Mesosuchus* and *Proterosuchus*. Watson's uncertainty as to where to place *Mesosuchus* and *Proterosuchus* could be attributed to the fact that the single character (presence of multiple rows of teeth) given as diagnostic for Howesiidae was known only for *Howesia*. Watson's classification retained elements of Osborn's, specifically the presence of the orders Rhynchocephalia, Proganosauria and Protorosauria, but he followed the idea of a closer affinity between *Sphenodon* and rhynchosaurs as expressed in earlier classifications (e.g. Boulenger 1891) and placed rhynchosaurs (*Rhynchosaurus*, *Hyperodapedon*, *Stenometopon* and ?*Palacrodon*) outside thecodonts as a family in the order Rhynchocephalia. Independently to Watson, Williston (1917) published a new classification of Reptilia where he recognized the three major subclasses of Anapsida, Synapsida and Diapsida, and included a new subclass Parapsida for those groups with only an upper temporal opening (Ichthyosauria, Proganosauria, Protorosauria and Squamata). Rhynchosaurs were retained as a basal branch of the diaptosaurian diapsids close to the origin of rhynchocephalians. Later, Williston (1925) revised his classification of reptiles and reintroduced rhynchosaurs to Rhynchocephalia.

The discovery of additional specimens of *Mesosuchus*, in particular the highly informative skull of SAM 6536, seemed to only emphasize the uniqueness of *Howesia* and *Mesosuchus*. On examining SAM 6536, Haughton (1924) noted similarities with numerous other early diapsids, but could not detect convincing evidence for membership in a specific group. Instead, he suggested that a new suborder of diaptosaurian reptiles Mesosuchidia be established for *Mesosuchus* and perhaps *Howesia*. Although Mesosuchidia is now a largely forgotten taxonomic rank, as it appeared in only a few subsequent classifications and without a diagnosis (e.g. Benton 1983, 1985), *Howesia* and *Mesosuchus* were considered to be unique rhynchocephalians, and attempts were made to convey their relationships with other rhynchosaurs. For example, Nopsca (1928) retained Watson's (1917) family Howesiidae, but moved *Proterosuchus* to the thecodonts and added *Noteosuchus*, *Askeptosaurus* (regarded currently as a thalattosaur) and *Polysphenodon* (regarded currently as a sphenodontid) to the howesiids. *Mesosuchus* was placed with other rhynchosaurs in the family Rhynchosauridae to indicate its closer affinities, but as a separate subfamily. Similarly, Huene (1956) separated *Mesosuchus* from other rhynchosaurs at the rank of subfamily, but included *Howesia* with the Middle and Late Triassic rhynchosaurs. Chatterjee (1969, 1974, 1980) classified *Howesia* and *Mesosuchus* with other rhynchosaurs in Rhynchosauria. In the first two of his papers on rhynchosaurs, he erected three grades of evolution that he equated with subfamilies. The third paper in 1980 was modified to suggest a dichotomy in the lineage of rhynchosaurs in the Middle Triassic. All three phylogenies included *Howesia* and *Mesosuchus* as the most primitive grade.

A. S. Romer had perhaps the most profound influence upon the classification of Reptilia through a series of editions of vertebrate palaeontology textbooks (Romer 1933, 1945, 1966), his revision of Williston's textbook of reptilian osteology (Romer 1956), and papers (Romer 1967, 1971). His argument that diapsids did not share a common ancestor, but are divided properly into two major divisions, Archosauria and Lepidosauria, became the widely accepted viewpoint (e.g. Camp 1945*b*; Kuhn 1966, 1969). One consequence of his subdivision of Diapsida was the inclusion of Rhynchocephalia (along with the rhynchosaurs) in Lepidosauria rather than with archosaurs (Watson 1917; Nopsca 1928) or as part of a basal radiation of diapsids distinct from squamates (Osborn 1903; Williston 1917, 1925).

The orthodox classification of rhynchosaurs with rhynchocephalians was questioned by several authors (e.g. Hughes 1968; Carroll 1976; Brinkman 1981). Recent phylogenetic studies (Benton 1985; Chatterjee 1986; Evans 1988; Laurin 1991) reaffirmed the existence of two major branches of diapsid phylogeny, Lepidosauromorpha and Archosauromorpha, and transferred Rhynchosauria from lepidosaurs to the archosauromorphs to join the prolacertiformes, *Trilophosaurus*, and basal archosauriforms such as *Euparkeria* and *Proterosuchus*. Although the importance of *Howesia* and *Mesosuchus* was emphasized in at least two major studies of diapsid evolution (Benton 1985; Evans 1988), their potential impact upon hypotheses of early archosauromorph phylogeny remained unaddressed largely because neither study demonstrated that the cladogram given was the most parsimonious, and only limited and often incorrect published data were available for the South African rhynchosaurs. A more rigorous study of Rhynchosauria (Benton 1990) presented the most parsimonious tree along with relevant statistics, but was limited to only the relationships among rhynchosaurs. A second cladistic analysis of Rhynchosauria incorporating new data on *Howesia* (Dilkes 1995) gave results very similar to those of Benton (1990). The phylogenetic study of Archosauromorpha given in this paper is the first to incorporate data on the basal rhynchosaurs *Howesia* and *Mesosuchus*, the basal South African archosauromorphs *Euparkeria*, *Proterosuchus* and *Prolacerta*, and the neodiapsid *Youngina*, based on personal observation of all specimens housed in South African institutions.

(b) *Materials and methods*

Six genera of rhynchosaurs are included in the phylogenetic analysis: *Hyperodapedon* (Benton 1983; Chatterjee 1974), *Scaphonyx* (Benton 1983; Huene 1942; Sill 1970), *Rhynchosaurus* (Benton 1990), *Stenaulorhynchus* (Benton 1983; Huene 1938), *Howesia* (Dilkes 1995) and *Mesosuchus*. The Indian rhynchosaur *Paradapedon* is synonymous with *Hyperodapedon* (Benton 1983). Several other genera of rhynchosaurs have been erected, but on small portions of the skeleton, principally the tooth-bearing bones. These additional genera are: *Mesodapedon* and *Supradapedon* (Chatterjee 1980), *Acrodenta* (Dutuit 1976), *Isalorhynchus* (Buffetaut 1983) and *Otischalkeria* (Hunt & Lucas 1991). An additional, unnamed rhynchosaur is known from Nova Scotia, Canada (Baird 1963), and may be *Scaphonyx* (Hunt & Lucas 1991). The problem of deciding whether certain taxa should be included in a phylogenetic analysis when most of their character states are unknown was addressed recently (Benton 1990; Wilkinson & Benton 1995). The six additional rhynchosaurs listed above were excluded by Benton (1990) because less than two-thirds of the character states could be determined. Using the method of safe taxonomic reduction, which identifies clearly those taxa that do not alter a basic tree structure, Wilkinson & Benton (1995) were able to exclude the same set of taxa.

Exclusion of taxa by the search for actual or potential redundancy of combinations of character states assumes that each taxon is valid. Unless there is an unequivocal autapomorphy present, large amounts of missing data are often a clue that one is dealing with either a part of an established taxon or merely an unidentifiable fragment. Most and perhaps all of the taxa excluded by Wilkinson & Benton (1995) appear to be invalid taxa or at best questionable. The holotype of *Mesodapedon* from the Middle Triassic of India is a partial left dentary. Two maxillae were designated as referred specimens (Chatterjee 1980). The dentary has two fields of teeth that enter into the maxillary grooves, as in *Stenaulorhynchus* (Benton 1984). Two maxillary grooves are present. The longer, medial groove extends the length of the maxilla and the shorter, lateral groove is restricted to the caudal half, again as in *Stenaulorhynchus*. All other diagnostic features are also true for *Stenaulorhynchus*, and it is likely that the Indian material belongs to this genus. *Supradapedon* from the Late Triassic of East Africa was described originally as *Scaphonyx stockleyi* (Boonstra 1953) and consists of a single left maxillary tooth plate. It agrees very well with the maxillary plates of *Scaphonyx* and *Hyperodapedon* and probably belongs to one of these taxa (Benton 1983; Raath *et al.* 1992; D. W. Dilkes, personal examination). Illustrations of the three tooth-bearing bones of *Acrodenta* (Dutuit 1976) are strongly suggestive of a captorhinid (J.-M. Dutuit, personal communication, cited in Hunt & Lucas (1991)). *Acrodenta* has been shown to be a captorhinid with unique acrodont dentition (Jalil & Dutuit 1996). *Isalorhynchus* from the Ladinian (Middle Triassic) of Madagascar is probably from a juvenile because there is little significant wear on the teeth (Buffetaut 1983). There is a single groove on the maxilla, two rows of teeth medial to the groove and a single row lateral to the groove. These features are consistent with a juvenile of *Rhynchosaurus*. However, a juvenile *Rhynchosaurus* has lingual maxillary teeth, which are clearly absent on *Isalorhynchus*. Proper taxonomic assessment of *Isalorhynchus* should await the collection of mature individuals. The 'Texas rhynchosaur' of Benton (1990) and Wilkinson & Benton (1995) has been described (Hunt & Lucas 1991) as a new genus and species *Otischalkia elderae*. Diagnostic features include a humerus with a proximal expansion that is as wide as the proximal end, which differs from the humeri of *Hyperodapedon gordoni* and *Stenaulorhynchus* where the proximal expansion is wider; a smaller deltopectoral crest than in *Stenaulorhynchus*; and the presence of a hooked supinator process (known only in *Stenaulorhynchus*). The proportions of the humerus of *Otischalkia* are different from those of *Hyperodapedon gordoni*, but are very similar to those of the Indian species of *Hyperodapedon*, *H. huxleyi* (Chatterjee 1974) including the size of the deltopectoral crest. One other distinction between the humeri of *Otischalkia* and *Stenaulorhynchus* is the larger size of the capitellum relative to the trochlea. However, the proportions of the capitellum and trochlea of *Otischalkia* resemble those of both species of *Hyperodapedon* (Chatterjee 1974; Benton 1983). A hooked supinator process, which is shown in the illustration of the holotype, but is absent in the photographs of the holotype and referred humerus, may be a valid diagnostic feature. An unassociated femur assigned to *Otischalkia* lacks any diagnostic features of rhynchosaurs and so must be considered with scepticism. Thus, with the possible exception of *Otischalkia*, none of the above discussed taxa have any clear autapomorphies or a combination of derived characters that would distinguish them from other rhynchosaurs.

No formal synonymies will be declared because I have not examined personally the specimens. All of these taxa will be excluded from the phylogenetic analysis owing to this uncertainty.

In addition to the rhynchosaurs *Hyperodapedon*, *Scaphonyx*, *Rhynchosaurus*, *Stenaulorhynchus*, *Mesosuchus* and *Howesia*, the following taxa were included in the phylogenetic analysis: *Petrolacosaurus*, *Youngina*, *Gephyrosaurus*, Squamata, *Prolacerta*, *Macrocnemus*, *Tanystropheus*, *Protorosaurus*, *Megalancosaurus*, *Langobardisaurus*, *Drepanosaurus*, *Trilophosaurus*, *Proterosuchus*, *Euparkeria*, *Champsosaurus*, *Cteniogenys* and *Lazarussuchus*. These taxa were coded for 144 characters. Many characters were taken from data matrices and character lists in the literature (Benton 1985, 1990; Evans 1986, 1988; Laurin 1991; Dilkes 1995) with and without modification, but a significant number are new and include information from the South African diapsids that was heretofore unknown or misinterpreted. A recently described new prolacertiform diapsid *Langobardisaurus* (Renesto 1994*a*) and new data on the highly derived diapsids *Megalancosaurus* (Renesto 1994*b*) and *Drepanosaurus* (Renesto 1994*c*) from the Late Triassic of northern Italy were included. The resultant data matrix of dimensions 23 × 144 was analysed on a Macintosh LC 630 with the branch-and-bound algorithm of PAUP 3.1.1 to derive the most parsimonious trees. Characters with multiple states for a taxon were interpreted as polymorphism. All characters were run with equal weight. Optimization of characters was performed by delayed transformation (DELTRAN).

Multistate characters are becoming increasingly the norm in morphologically based phylogenies, particularly when one is attempting to delineate character states for morphometric and meristic variables. Although the topic of continuing discussion (e.g. Hauser & Presch 1991; Hauser 1992; Lipscomb 1992; Wilkinson 1992; Slowinski 1993), there is little current consensus on the question of whether or not multistate characters should be ordered. Investigation of the possible effect of ordering character states upon the resolution (i.e. number of polytomies) of cladograms has produced either no clear and uniform effect (Hauser & Presch 1991) or an increase in resolution (Slowinski 1993) depending on whether one orders all multistate characters in a data matrix or only a subset of these characters. Evidently, any increase in resolution is dependent largely on the subjective choice of which multistate characters are to be ordered and how the connections between ordered states are expressed (i.e. linear or branching if there are four or more character states). Transformation series analysis (Mickevich 1982) has been offered as a more objective means of ordering states whereby the initial hypotheses of order and transformations of characters indicated on the cladogram are compared and new cladograms generated with the character transformations from the previous cladogram. This iterative procedure continues until no new cladograms are produced. Transformation series analysis has been criticized on the grounds that it may reject a hypothesis of order in which the most similar states are adjacent for another hypothesis that maximizes overall congruence between hypotheses of order and resolution of a cladogram (Lipscomb 1992). An alternative approach that stresses both similarity and congruence (Lipscomb 1992) has also been criticized (Barriel & Tassy 1993).

I will adopt a pragmatic approach and perform one analysis with all multistate characters unordered and a second analysis with a selection of multistate characters ordered. Those characters selected to be ordered exhibited a clear morphocline of character states or meristic change. Character 15 may be ordered linearly according to the amount of reduction of the lacrimal. From the plesiomorphic state of a lacrimal that reaches the external naris, the reduction of the lacrimal can lead first to its exclusion from the external naris by the contact between the maxilla and nasal, and then with further reduction to its separation from the nasal by the contact between the maxilla and prefrontal. Character 64 can be ordered linearly by the increase in number of tooth rows. The remaining characters selected for ordering (81, 88, 123, 124) attempt to express morphometric differences and can be ordered linearly according to either an increase or decrease in physical dimensions.

Strength of the phylogenetic signal in the data matrix is measured by the g_1 test for skewness (Hillis & Huelsenbeck 1992) based on a subsample of 100 000 random trees selected by PAUP. Stability of clades on the most parsimonious cladogram(s) is assessed by two means: bootstrap (Felsenstein 1985) and branch support (Bremer 1994). Bootstrapping is by far the most widely used procedure to quantify support for clades due largely to its availability through PAUP and apparent ease of interpretation of the results. It is a resampling technique in which the ideal, but rarely attainable, procedure of repeated sampling from a population is replaced by repeated sampling with replacement from the original sample. The error generated through bootstrap resampling is a representation of the error associated with resampling from the population. A number of criticisms, summarized recently by Sanderson (1995), have been advanced against statistical approaches to phylogenetic reconstruction in general and the bootstrap in particular, of which perhaps the most important is that it may not be valid to assign confidence limits to a cladogram. Alternatively, one can view the bootstrap as a means of gaining some insight into the relative support for clades for the more practical purpose of determining the stability of phylogenetic taxonomies. Given the controversial nature of randomization in phylogenetics, bootstrap values will be interpreted as relative indicators of clade stability in this paper. The second index of clade stability, branch support, is simply the number of extra steps required to collapse a clade on the strict consensus tree of less than parsimonious trees (Bremer 1994). Most values of branch support were determined by saving those trees found during a heuristic search that were up to ten steps longer than the most parsimonious tree. Memory limitations of the computer restricted this approach to only ten extra steps. For those few clades with stronger support, branch support values were calculated by the converse constraints option of PAUP.

(c) *Results*

Virtually identical trees were produced whether one treats all multistate characters as unordered or if those few multistate characters identified above are ordered (figure 24). A strong phylogenetic signal is present in the data matrix ($g_1 = -0.785$, $p \ll 0.01$). Two most parsimonious trees are the result when all multistate characters are unordered (figure 24*a*). Each tree has a length of 365

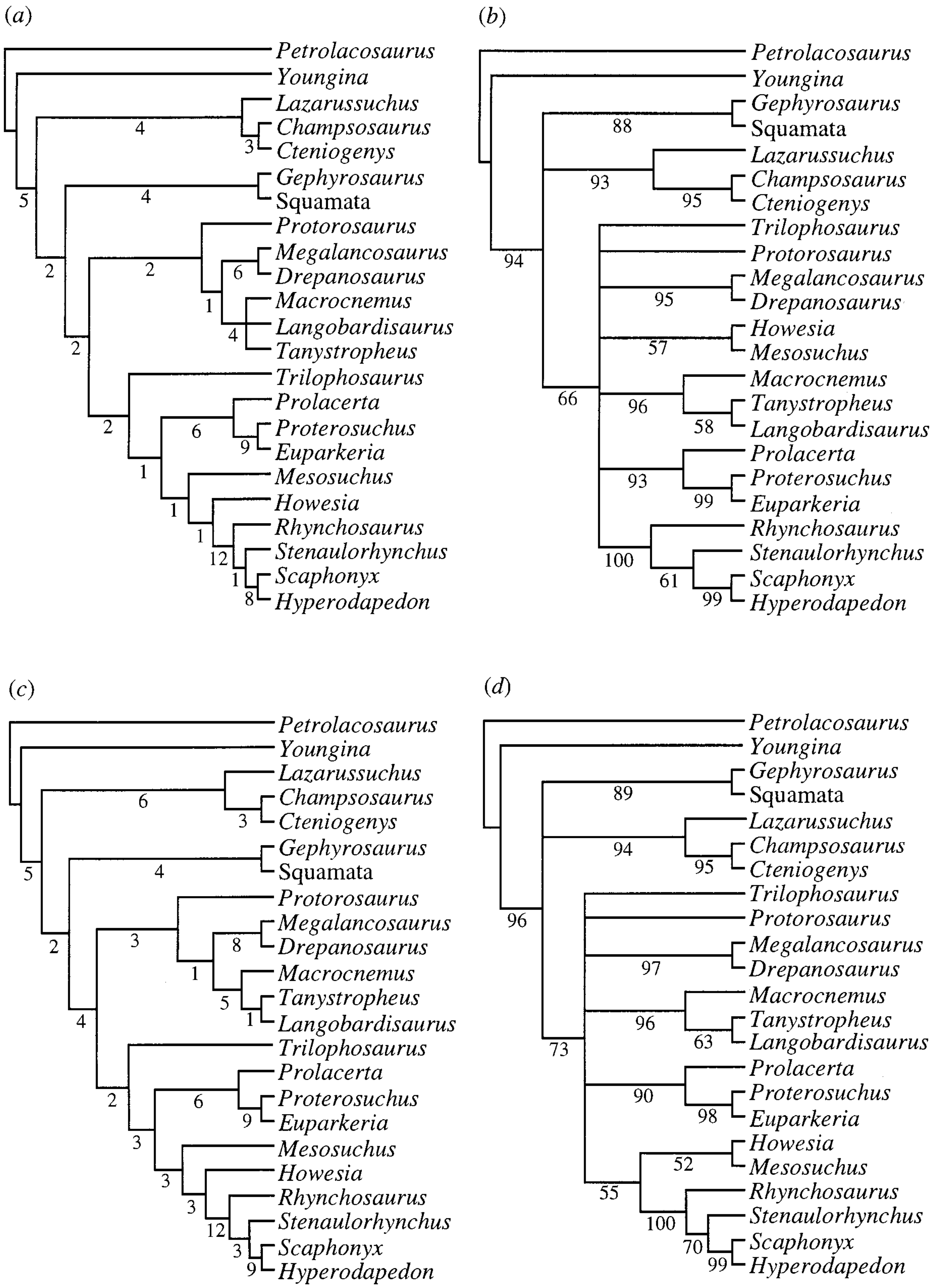

Figure 24. Most parsimonious trees with bootstrap proportions and branch support values. (*a*) and (*b*) All multistate characters run unordered. (*a*) Majority-rule consensus tree of most parsimonious trees with branch support values for each node; (*b*) majority-rule consensus tree with bootstrap proportions; (*c*) and (*d*) multistate characters 15, 64, 81, 88, 123, and 124 run ordered. (*c*) Most parsimonious tree with branch support values for each node; (*d*) majority-rule consensus tree with bootstrap proportions.

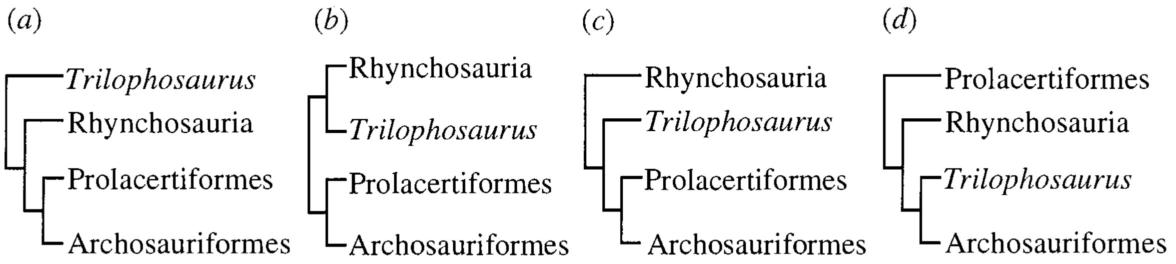

Figure 25. Hypotheses of interrelationships of basal archosauromorphs according to (*a*) Benton (1985); (*b*) Chatterjee (1986); (*c*) Evans (1988) and Gauthier *et al*. (1988); and (*d*) Gauthier (1994).

steps, a consistency index of 0.464 excluding uninformative characters (rescaled consistency index (CI) = 0.308), and a retention index (RI) of 0.646. The strict consensus tree has a polytomy of *Macrocnemus*, *Langobardisaurus* and *Tanystropheus*. A single most parsimonious tree is produced with ordered multistate characters (figure 24*c*). This tree requires 369 steps, has a CI of 0.459 excluding uninformative characters (rescaled CI = 0.307), and an RI of 0.651.

There are several notable features of the cladograms. The clade Rhynchosauria is present with the arrangement of taxa proposed by Dilkes (1995). Choristoderes form a clade as expected, but are not included in Archosauromorpha in contrast to the conclusions of most recent, cladistically based studies (Gauthier *et al.* 1988*a*; Evans 1990; Rieppel 1993). Evans & Hecht (1993) argued tentatively that choristoderes are not archosauromorphs, but their results cannot be reproduced because a data matrix was not provided. Support for a placement of Choristodera outside of Sauria is rather weak with branch support values of only 2 and bootstrap values of less than 50%. Perhaps the least expected result was the demonstration that Prolacertiformes is paraphyletic. *Prolacerta* shares a more recent common ancestry with Archosauriformes than with any taxon designated customarily as a prolacertiform. The remaining prolacertiforms form a clade that branches off at the base of Archosauromorpha. A close similarity between *Prolacerta* and *Proterosuchus* had been noted by Benton (1985); however, he also considered inclusion of *Proterosuchus* in Archosauria (equivalent to Archosauriformes in this paper) rather than Prolacertiformes to be supported equally by his data. The shared presence of a downturned premaxilla and distally expanded haemal spines supported a sister group relationship between *Prolacerta* and *Proterosuchus* according to Benton (1985). Both characters were included in this study, but failed to support the node of *Prolacerta* and Archosauriformes because *Prolacerta* does not have a downturned premaxilla and a distally expanded haemal spine is an ambiguous character state with a wider distribution. *Protorosaurus* is the basal member of a reduced prolacertiform clade, with the highly autapomorphic Late Triassic diapsids *Megalancosaurus* (Renesto 1994*b*) and *Drepanosaurus* (Renesto 1994*c*) from northern Italy forming a well-supported clade as shown by the high branch support and bootstrap values. Contrary to Berman & Reisz (1992), the clade Drepanosauridae (herein considered to include *Megalancosaurus*, *Drepanosaurus* and probably *Dolabrosaurus*) is an archosauromorph taxon rather than a member of the lepidosauromorphs.

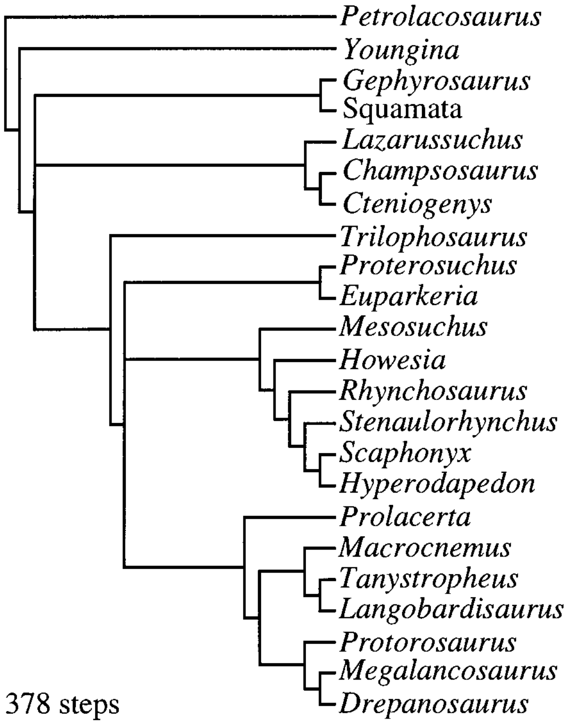

Figure 26. Strict consensus tree of most parsimonious trees based upon data matrix in this paper and consistent with monophyly of Prolacertiformes.

Macrocnemus, *Tanystropheus* and *Langobardisaurus* also form a robust clade, but there is little support for any hypothesis of their interrelationships.

The branch support and bootstrap values are in general agreement for the relative stability of the clades for the analyses of unordered and ordered multistate characters. Ordering of multistate characters increases support for several clades according to the branch support values, in particular the support for Rhynchosauria and the sister group relationship between rhynchosaurs, *Prolacerta* and Archosauriformes, but an increase in bootstrap values occurs for only a few clades. The primary difference between the majority-rule consensus trees of bootstrap results for unordered and ordered multistate characters is the retention of Rhynchosauria only when the selected multistate characters are ordered. However, the support for Rhynchosauria remains weak at just slightly above 50%. Both sets of bootstrap results show a sister group relationship between *Mesosuchus* and *Howesia* in contrast to the relationship depicted in the most parsimonious trees.

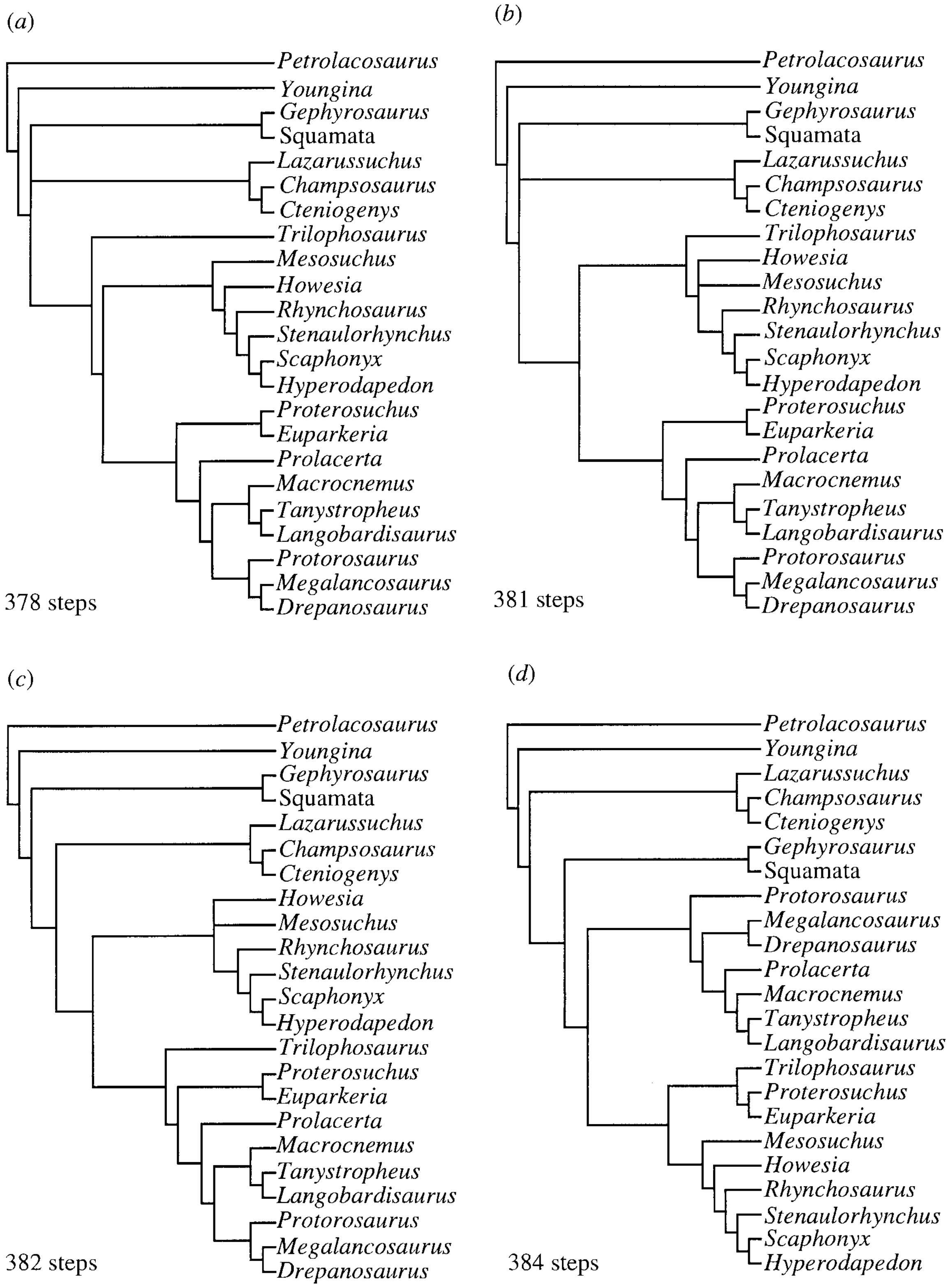

Figure 27. Strict consensus trees of most parsimonious trees based upon data matrix in this paper and consistent with hypotheses of (*a*) Benton (1985); (*b*) Chatterjee (1986); (*c*) Evans (1988) and Gauthier *et al*. (1988); and (*d*) Gauthier (1994).

5. DISCUSSION

(a) *Topological constraints*

A series of topological constraints analyses were performed to investigate: (i) the effect of forcing monophyly of Prolacertiformes upon the structure of the most parsimonious tree(s); and (ii) alternative arrangements of Rhynchosauria, *Trilophosaurus*, a monophyletic Prolacertiformes and Archosauriformes as hypothesized by Benton (1985), Chatterjee (1986), Evans (1988) and Gauthier (1994) (figure 25). The interrelationships of basal archosauromorphs were analysed also in two recent phylogenetic studies on sauropterygian reptiles (Rieppel 1993, 1994). The results of these studies will not be considered in this paper

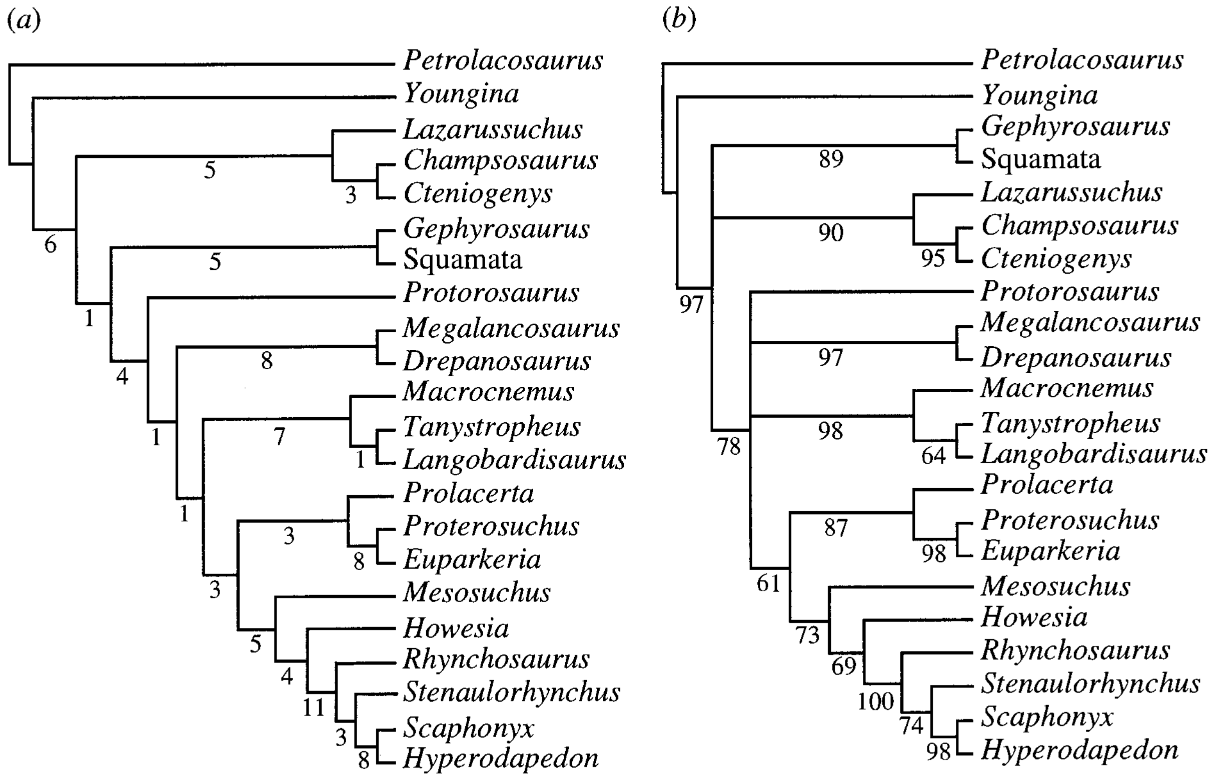

Figure 28. Deletion of *Trilophosaurus* from data matrix. (*a*) Most parsimonious tree with branch support values; (*b*) majority-rule consensus tree with bootstrap proportions.

because in the first study the largely redundant taxa of Protorosauria (derived from the data matrix of Gauthier *et al.* (1988*a*)) and Prolacertiformes were included, and in the second study an unresolved polytomy was present among most archosauromorphs. In each topological constraints analysis, relationships within each taxon and between the remaining taxa were not specified *a priori* to allow the maximum flexibility in obtaining the shortest tree. All trees were found through heuristic searches with a random addition sequence using ten replicates and the tree-bisection–reconnection branch-swapping option selected. Character states were optimized using DELTRAN. Given the nearly identical results regardless of whether or not some multistate characters were ordered, all topological constraints analyses were performed with the same set of ordered multistate characters.

The results of the search for the shortest tree with a monophyletic Prolacertiformes are three trees of length 378 steps (figure 26), nine steps longer than the single most parsimonious tree with no constraints. A polytomy is present between Archosauriformes, Rhynchosauria and Prolacertiformes. Interestingly, with the forced inclusion of *Prolacerta* it comes to occupy the most basal position within Prolacertiformes, and *Protorosaurus* is shifted higher up the hierarchy to become the sister taxon to the clade of *Megalancosaurus* and *Drepanosaurus*. This pattern of relationships within an enforced monophyletic Prolacertiformes is maintained throughout the resultant trees from the other topological constraints analyses.

Two most parsimonious trees, each with a length of 378 steps, are also obtained when the analysis is constrained to give the hypothesized relationships of Rhynchosauria, *Trilophosaurus*, Prolacertiformes and Archosauriformes according to Benton (1985) (figure 27*a*). The hypothesis of Chatterjee (1986) is found in four shortest trees of 381 steps (figure 27*b*), the two shortest trees with the hypothesis of Evans (1988), which differ from that of Benton (1985) only in the reversal of the positions of Rhynchosauria and *Trilophosaurus*, are slightly longer at 382 steps (figure 27*c*), and the more recent hypothesis of Gauthier (1994) is the longest at 384 steps (figure 27*d*). If the shortest tree is the preferred one because it conveys best the information in the data matrix, then all hypotheses that entail a monophyletic Prolacertiformes must be rejected in favour of the hypothesis that *Prolacerta* is the sister taxon of Archosauriformes.

Prolacertiforms are characterized by all authors who accept their monophyly as an early lineage of archosauromorphs that branched off at least in the Late Permian, and are distinguished most readily by elongated necks. In the earliest member *Protorosaurus* from the Late Permian of Germany and Britain, this elongation is moderate with cervical vertebrae about twice the length of a dorsal vertebra. However, later prolacertiforms have greatly elongated cervical vertebrae with the most extreme condition seen in *Tanystropheus* from the Middle and Late Triassic of Europe in which a cervical vertebra is three to four times the length of a dorsal vertebra, and the neck is lengthened further by an increase in the number of cervicals. In addition to the elongation of the centra, the neural spines of the cervicals are reduced in height. However, elongated cervicals (character 81, state 2) with reduced neural spines (character 82) are forced to evolve independently in the most parsimonious tree obtained in this study because *Trilophosaurus*, which has the plesiomorphic characters of short cervicals with tall

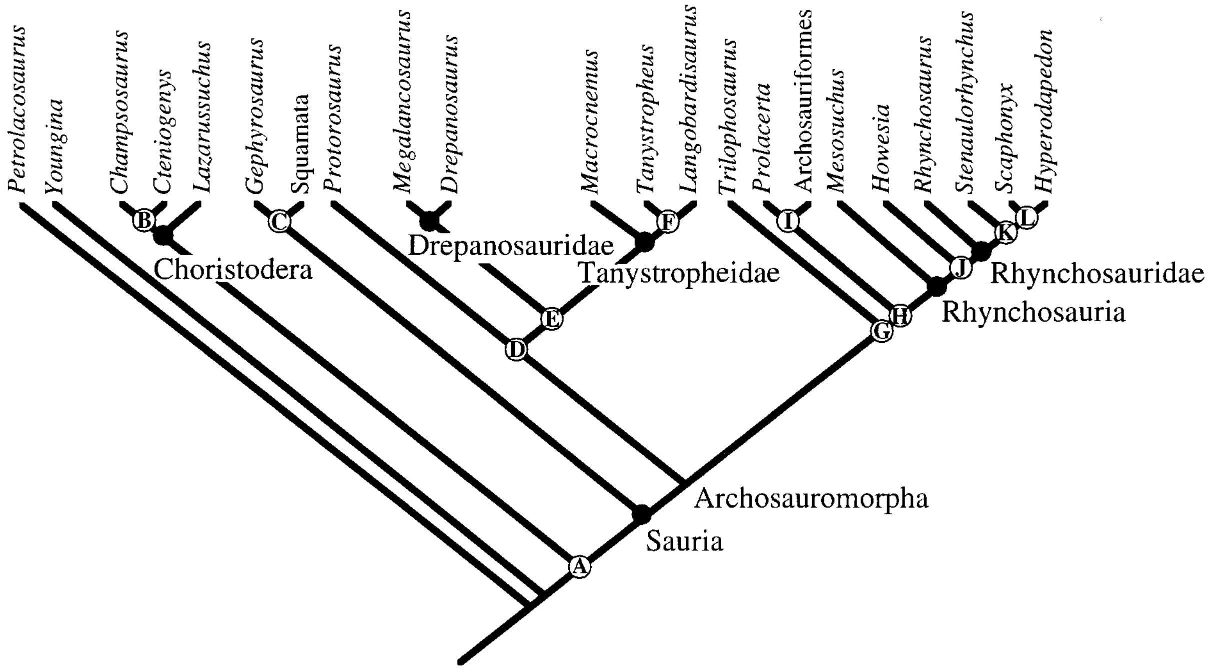

Figure 29. Phylogenetic tree of basal archosauromorphs. Diagnoses for each node designated by a capital letter are given in appendix 2.

neural spines, is placed between *Prolacerta* and the remaining prolacertiforms. Other characters forced to evolve independently by the inclusion of *Trilophosaurus* are the contact between the centrale and the tibia, a ratio of the lengths of digits 3 and 4 of between 0.8 and 0.9, a ratio of the lengths of nasal and frontal of >1.0, and a snout that is $\geqslant 50\%$ of the total skull length.

(b) *Deletion of* Trilophosaurus

To investigate further the effect of including in a phylogenetic analysis a highly derived member of a lineage for which no basal taxa are known presently, *Trilophosaurus* was excluded and the data matrix rerun as above with the same multistate characters ordered. A single most parsimonious tree was found (figure 28*a*). It has a length of 354 steps, a CI excluding uninformative characters of 0.479 (rescaled CI = 0.326), and an RI of 0.662. There is overall good agreement between the branch support (figure 28*a*) and bootstrap values (figure 28*b*). Those nodes with a very low branch support tend to collapse on the bootstrap majority-rule consensus tree. A large increase in support for Rhynchosauria occurred as shown by the change in branch support from 3 to 5 and bootstrap proportions from 55 to 73. The majority of relationships found in the most parsimonious tree are retained with the notable exception of the clade of prolacertiforms that excludes *Prolacerta*. This clade collapses and forms a series of branches at the base of Archosauromorpha. The well-supported smaller clades of *Megalancosaurus* and *Drepanosaurus*, and *Macrocnemus*, *Tanystropheus* and *Langobardisaurus* remain intact. With the exclusion of *Trilophosaurus*, elongated cervical vertebrae (>1.5 times the length of a dorsal vertebra), reduced cervical neural spines, contact between the tibia and centrale, and ratio of 0.8–0.9 between digits 3 and 4 of the pes now diagnose unambiguously only single nodes. In addition, the lengths of the snout relative to the skull and the nasal relative to the frontal reverse to the plesiomorphic character state in rhynchosaurs.

(c) *Definitions and diagnoses*

A phylogenetic tree derived from the cladogram with ordered multistate characters is given in figure 29. Major nodes with significant support as shown by branch support and bootstrap values are labelled. The node Rhynchosauria is also labelled even though its support is less than expected, particularly when all multistate characters are run unordered. Despite the relative weakness of this node, rhynchosaurs remain easily diagnosable by a number of unambiguous characters, some of which are unique to the clade. Furthermore, as demonstrated above, one factor in the relative instability of the clade Rhynchosauria is the presence of *Trilophosaurus* in the data matrix. Removal of this single taxon produced a strong increase in support for Rhynchosauria. Although the clade of all prolacertiforms minus *Prolacerta* is seemingly as stable as Rhynchosauria, the collapse of this clade following simply the exclusion of *Trilophosaurus* demonstrates a weakness not revealed by either branch support or the bootstrap. It is not named for this reason. Only node-based and stem-based definitions of clades are used according to the principles of phylogenetic taxonomy (de Queiroz & Gauthier 1990, 1992, 1994). The form of the definitions follows that prescribed by de Queiroz & Gauthier (1990) and Bryant (1996). Apomorphy-based definitions are avoided because the assumption of homology of the apomorphy may be invalid within a different phylogenetic hypothesis or character optimization, and the form of the apomorphy is dependent on how one delineates the character for analysis (Bryant 1994; Schander & Thollesson 1995). For each named clade on the phylogenetic tree, a definition and diagnosis are given. The number for each character in a diagnosis matches that in the list of characters in Appendix 1. A full list of apomorphies for each node is in Appendix 2.

(i) *Sauria*

Definition

The most recent common ancestor of Lepidosauria and Archosauria and all of its descendants. This definition is identical to that given by Gauthier *et al.* (1988*a*).

Diagnosis

4. An incomplete lower temporal arch.
34. Absence of the anteroventral process of the squamosal.
35. Absence of a anterior process of the quadratojugal.
42. Craniocaudally elongate ectopterygoid that does not reach caudal edge of transverse flange of pterygoid.
47. Presence of the crista prootica.

Comments on diagnosis

Ever since the first attempt to divide reptiles according to the nature of their temporal fenestration (Woodward 1898), the lack of a lower temporal bar in squamates has been considered by all workers with few exceptions (e.g. Williston 1917) to be an evolutionary loss of a temporal bar that is present in early diapsids. The discoveries of *Youngina* (Broom 1914, 1922, 1925*a*), and in particular *Prolacerta* (Camp 1945*a*,*b*), which supposedly shared homologous features with both *Youngina* and squamates removed any lingering doubts as to the diapsid status of squamates. *Sphenodon* with its complete lower temporal arch and fixed quadrate has long been assumed to be a primitive reptile or more colourfully as a 'living fossil'. Its close relationship to squamates suggested that the loss of the lower temporal arch was diagnostic of squamates. However, several Late Triassic and Early Jurassic sphenodontians have a gap between the jugal and quadrate, and demonstrate that a complete lower temporal arch is a secondary development within sphenodontians (Whiteside 1986; Wu 1994). Recent phylogenetic studies of Sauropterygia (Rieppel 1993, 1994) have provided evidence that these Mesozoic marine reptiles are specialized lepidosauromorphs that have lost the lower temporal arch. An incomplete lower temporal arch was diagnostic of Lepidosauromorpha, although this result was found only when turtles were included and ACCTRAN optimization chosen (Rieppel 1994). In the present study, an incomplete lower temporal arch is diagnostic of Sauria, which necessitates the secondary development of a complete lower temporal arch in two lineages: *Rhynchosauria* and Archosauriformes.

(ii) *Choristodera*

Definition

The most recent common ancestor of *Lazarussuchus*, *Cteniogenys* and *Champsosaurus* and all of its descendants. Lists of synapomorphies have been given in several recent studies to support hypotheses of interrelationships of choristoderes and the relationships of the clade with other diapsids (Evans 1988, 1990; Evans & Hecht 1993), but a phylogenetic definition of the clade is lacking in all of these papers.

Diagnosis

2. Elongation of snout to greater than 50% of the total length of the skull.
38. Contact present between vomer and maxilla.
116. Lateral tuber of calcaneum present.
125. Contact between the prefrontals along the midline.
127. Mandibular symphysis is extended caudally.
128. Incorporation of first caudal vertebra into sacrum.
129. Nearly or fully vertical caudal zygapophyses.

Comments on diagnosis

Contact between the vomer and maxilla has occurred independently several times in basal archosauromorphs. Choristoderes have a vomer–maxilla contact perhaps as a consequence of the caudal shift of the internal nares. The vomer and maxilla contact in *Euparkeria* and *Proterosuchus* although in the former it is due primarily to a medial process of the maxilla (Gow 1970), and in the latter the palatal shelf of the premaxilla is enlarged and the vomer and maxilla connect only along the cranial rim of the internal naris (J. Welman, personal communication).

Presence of lateral tuber of the calcaneum is cited customarily as a synapomorphy of Archosauromorpha (Benton 1985; Evans 1988), but according to the phylogeny presented in this paper it appeared independently in choristoderes, drepanosaurids, and the common ancestor of *Trilophosaurus*, *Prolacerta*, archosauriforms and rhynchosaurs.

(iii) *Archosauromorpha*

Definition

Protorosaurus and all other saurians that are related more closely to *Protorosaurus* than to Lepidosauria. This stem-based definition should replace the node-based definition of Laurin (1991) because, as stated in that paper and according to the phylogenetic relationships advanced herein, it would exclude *Protorosaurus*, Drepanosauridae and Tanystropheidae. Furthermore, a stem-based definition of Archosauromorpha would be consistent with the stem-based definition of Lepidosauromorpha (Gauthier *et al.* 1988*b*).

Diagnosis

8. Presence of a posterodorsal process of the premaxilla.
26. Presence of a sagittal crest.
77. Presence of slender and tapering cervical ribs that lie at low angle to vertebrae.
97. Presence of a notch on the cranial margin of the interclavicle.
102. Dorsal margin of ilium composed of a small anterior process and a larger posterior process.
109. Absence of medial centrale of carpus.

Comments on diagnosis

The presence of slender and tapering cervical ribs that lie at a low angle to the vertebrae has been used previously to diagnose Prolacertiformes (Carroll & Currie 1991; Evans 1988) or as a synapomorphy of Prolacertiformes and Archosauriformes (Benton 1985). However, its presence in *Trilophosaurus* (Gregory 1945) and the paraphyly of the prolacertiforms shifts the character to the base of Archosauromorpha.

A notch on the cranial margin of the interclavicle was known previously only for *Macrocnemus* (Peyer 1937; Rieppel 1989) and *Prolacerta* (Gow 1975). In combination with the paraphyly of prolacertiforms, this character is also shifted to the base of Archosauromorpha.

(iv) *Drepanosauridae*

Definition

The most recent common ancestor of *Megalancosaurus*, *Drepanosaurus* and *Dolabrosaurus* (Berman & Reisz 1992) and all of its descendants. Although *Dolabrosaurus* was not included in the data matrix, it shares numerous diagnostic vertebral characters, particularly of the caudal region, with this pair of taxa that support a closer relationship with them than with any other group of archosauromorphs.

Diagnosis

88. Proximal caudal vertebrae with neural spines that are greater than 3.0 times the craniocaudal length of the neural spines.
92. Loss of gastralia.
102. Presence of a large anterior projection on the ilium.
116. Presence of a lateral tuber on the calcaneum.
124. Ratio of the lengths of digits 3 and 4 $\geqslant 0.9$.
129. Nearly or fully vertical caudal zygapophyses.
139. Expanded distal ends of caudal neural spines.
140. Expanded distal ends of first 5–6 dorsal vertebrae.
141. Cranial curvature of haemal spines.

Comments on diagnosis

Presence of only an anterior projection on the ilium, expansion of the distal ends of the caudal neural spines, expansion of the distal ends of the first five to six dorsal vertebrae and cranial curvature of the haemal spines are autapomorphic characters of drepanosaurids. Very tall caudal neural spines (height > 3.0 times their craniocaudal length) evolved independently in drepanosaurids and rhynchosaurs.

(v) *Tanystropheidae*

Definition

The most recent common ancestor of *Macrocnemus*, *Tanystropheus* and *Langobardisaurus* and all of its descendants.

Diagnosis

73. Profile of dentary–coronoid–surangular is concave caudal to coronoid.
85. Height of dorsal neural spines is less than their length.
88. Height of proximal caudal neural spines is less than their length.
117. Contact between tibia and centrale.
120. Absence of second distal tarsal.

(vi) *Rhynchosauria*

Definition

The most recent common ancestor of *Mesosuchus* and *Howesia* and all of its descendants.

Diagnosis

6. A premaxilla that is down-turned relative to the maxilla.
7. Contact between premaxilla and prefrontal.
10. A single, median external naris.
20. Pitted depression on the dorsal surface of the frontal.
21. Pitted depression on the dorsal surface of the postfrontal.
61. Multiple rows of teeth on the maxilla.
64. More than two rows of teeth on the dentary.
65. Flat jaw occlusion.
88. Height of proximal caudal neural spines is greater than 3.0 times their length.
123. Ratio of metatarsals I and IV between 0.3 and 0.4.

Comments on diagnosis

At least two unique characters, the pitted depression on the dorsal surface of the frontal and multiple rows of maxillary teeth are present in rhynchosaurs. With the possible exception of *Howesia*, all rhynchosaurs have a premaxilla that is down-turned relative to the maxilla. A down-turned premaxilla has evolved independently in *Proterosuchus*. In the most often cited source on *Prolacerta* (Gow 1975), a slight ventral deflection is restored for the premaxilla and has been interpreted as possibly homologous to the down-turned premaxilla of *Proterosuchus* (Benton 1985). However, in another restoration (Carroll 1975*a*), the premaxilla has a horizontal ventral margin. Only a single known specimen of *Prolacerta* (BP/1/471) has the premaxillae in articulation and can be examined from all perspectives. The right premaxilla of this specimen is displaced ventrally, but the left retains its proper relationship with the maxilla and shows no significant ventral orientation.

(vii) *Rhynchosauridae*

Definition

The most recent common ancestor of *Rhynchosaurus*, *Stenaulorhynchus*, *Scaphonyx* and *Hyperodapedon* and all of its descendants.

Diagnosis

19. Ratio of lengths of frontals and parietals is $\leqslant 1.0$.
23. Ratio of the lengths of the anteroventral and posterodorsal processes of postorbital is < 1.0.
39. Contact between ectopterygoid and jugal is less than or equal to area of contact between ectopterygoid and pterygoid.
41. Contact between ectopterygoid and palatine along lateral margin of suborbital fenestra excluding maxilla.
42. Ectopterygoid has an extensive ventral contact with pterygoid that is posteroventrally elongate and reaches the lateral corner of the transverse flange.
54. A pillar-like supraoccipital.
62. Two grooves on occlusal surface of maxilla.
65. Blade and groove occlusion.
67. Absence of teeth on the palatine.
73. Profile of dentary–coronoid–surangular is concave caudal to coronoid.
87. Second sacral rib is not bifurcate.
91. Distal width of haemal spine is equivalent to the proximal width.
104. Absence of an anterior apron of the pubis.
112. A transverse row of three proximal tarsals consisting of the astragalus, calcaneum and centrale.
115. Perforating foramen between distal ends of tibia and fibula.
118. Absence of contact between the centrale and distal tarsal four.
129. Nearly or fully inclined caudal zygapophyses.
142. A simple overlap between ectopterygoid and pterygoid.

Comments on diagnosis

Rhynchosauridae is the most strongly supported clade in the phylogeny. Four characters are autapomorphic: contact between the ectopterygoid and palatine along lateral margin of suborbital fenestra to exclude maxilla, a blade and groove pattern of occlusion, astragalus, calcaneum and centrale in a transverse row, and the absence of contact between the centrale and distal tarsal four. Numerous other characters are related to the profound change in the shape of the skulls of rhynchosaurids in comparison with other basal archosauromorphs. Their shorter and broader skulls are shown by a ratio of frontals and parietals that is $\leqslant 1.0$ and the change in the proportions of the postorbital. The reorganization of the palate is shown, in addition to the autapomorphic contact between the palatine and ectopterygoid, by the reduced contact between the ectopterygoid and jugal, an extensive overlap between the ectopterygoid and pterygoid, and absence of teeth on the palatine. Reversals are frequent. The reduction of the contact between the ectopterygoid and jugal, non-bifurcate second sacral rib, haemal spines with equal proximal and distal widths, absence of an anterior apron on the pubis, and a simple overlap between the ectopterygoid and pterygoid are all reversals.

(d) *Taxonomic status of* Noteosuchus colletti

Described originally as *Eosuchus colletti* (Watson 1912*b*), this small diapsid from the *Lystrosaurus* Assemblage Zone (Early Triassic) near Grass Ridge, Cradock District, Eastern Cape Province, is based on a single articulated skeleton lacking a skull. The skeleton is preserved in a heavily worn nodule that was split open into three blocks. Watson was convinced that *Eosuchus* was a thecodont and subsequently linked it with *Youngina* in a family of primitive thecodonts (Watson 1917). Broom (1925*b*) noted that the generic name was preoccupied and suggested the replacement name of *Noteosuchus*. He pointed out that most of the evidence put forth by Watson to support his hypothesis that *Noteosuchus* was a thecodont was derived from comparisons with a confusion of material that belonged to both *Mesosuchus* and *Euparkeria*. Instead of affinities with thecodonts, Broom argued that *Noteosuchus* was close to the common ancestor of gnathodonts, rhynchocephalians, pelycosimians (based on *Erythrosuchus*) and phytosaurs. Although at least one early paper (Nopsca 1928) recognized that *Noteosuchus* is a rhynchosaur, with the promotion of Eosuchia as a primitive grade of diapsids that lived in the Late Permian and Early Triassic, *Noteosuchus* was listed in most subsequent papers (e.g. Huene 1939; Romer 1956; Kuhn 1969) as an eosuchian.

A far more detailed study by Carroll (1976) furnished clear evidence that *Noteosuchus* is a rhynchosaur, which is supported in this study by the presence of very tall caudal neural spines and a ratio of lengths of metatarsals I and IV between 0.3 and 0.4. Although Carroll observed correctly that the postcranial skeletons of *Noteosuchus*, *Howesia* and *Mesosuchus* are extremely similar, several features of *Howesia* and *Mesosuchus* were unrecognized, and additional comparisons among these taxa are warranted.

Noteosuchus lacks the deep pockets on the neural arches of the dorsals and sacrals and the caudal inclination of the proximal caudal neural spines that are found in *Howesia* (Dilkes 1995). On the other hand, *Noteosuchus* shares with *Mesosuchus* the diagnostic character of the presence of a distinct midventral groove on the centra of the first pair of caudal vertebrae. In addition, *Noteosuchus* and *Mesosuchus* share a flattened first distal tarsal. The absence of diagnostic features of *Howesia* and the presence of one diagnostic feature of *Mesosuchus* suggests that *Noteosuchus* and *Mesosuchus* are synonymous. Unfortunately, the majority of diagnostic characters for *Mesosuchus* are found in the skull. Without information on the skull of *Noteosuchus*, it would be premature to declare a formal synonymy of these taxa. If correct, then *Mesosuchus* would be the senior synonym because Watson (1912*a*) erected *Mesosuchus* two pages earlier than *Noteosuchus*.

(e) *Stratigraphic calibration of phylogeny*

Combination of the hypothesized phylogenetic relationships of basal archosauromorphs and their known stratigraphic ranges indicates significant gaps within the fossil record of Late Permian and Early Triassic diapsid reptiles (figure 30). Although few Late Permian diapsids are known, their presence at various branch points throughout the phylogeny serves to pull down into the Late Permian lineages that do not appear in the fossil record until the Triassic. The oldest known saurians are from the Late Permian and consist of the archosauriform *Archosaurus* from Zone IV of the Vladimir region in Russia, *Protorosaurus* from the Kupferschiefer of Germany (Seeley 1888) and the equivalent Marl Slate of Britain (Evans 1993), which are late Tatarian in age (Sues & Munk 1996), and the South African lepidosauromorphs *Saurosternon* and possibly *Palaeagama* (Carroll 1975*b*) from the Karoo. Extensions to the Late Permian are indicated for the lineages with *Prolacerta*, *Trilophosaurus*, rhynchosaurs, and the lineage leading to the common ancestor of drepanosaurids and tanystropheids. The missing portion of the lineage with *Trilophosaurus* is particularly large at about 30 million years, and emphasizes the highly autapomorphic nature of this taxon and the difficulty of establishing its phylogenetic relationships without basal taxa of the lineage. There are also significant temporal range extensions within clades of basal archosauromorphs. *Langobardisaurus* from the middle Norian is the sister taxon of *Tanystropheus* which appears first in the Middle Triassic and establishes a minimal time of divergence of these taxa at the Anisian–Ladinian boundary. The Middle Triassic is also the minimal time of divergence of the drepanosaurids and tanystropheids. Rhynchosaurs are represented by selective taxa from the Early, Middle and Late Triassic. Large gaps in their record exist between the Middle and Late Triassic species whereas those of the Early and Middle Triassic are separated by a slightly smaller gap. Minimal time of divergence of the choristoderes is the Late Permian as indicated by other studies (Storrs & Gower 1993). This gap in the fossil record of choristoderans extends for approximately 40 million years from the Rhaetian to Tatarian. Thus, it is clear that the fossil record of diapsid reptiles in the Late Permian is a woefully inadequate representation of their actual diversity. The incompleteness of the terrestrial record during the Late Permian and Early Triassic is well known and clearly a factor in the low diversity of Late Permian diapsids. Various explanations have been offered to account for the dramatically different faunas of the Late

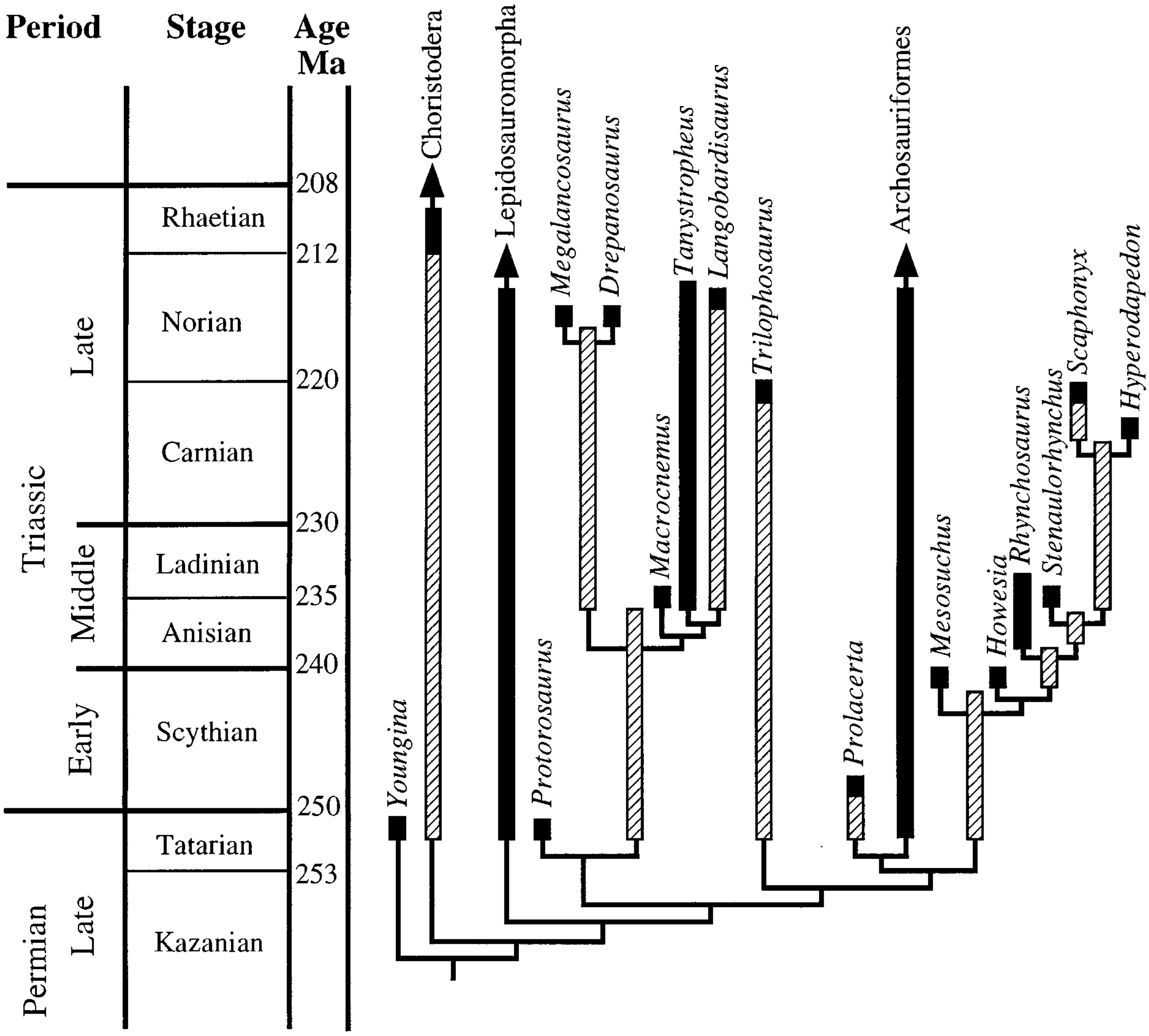

Figure 30. Most parsimonious tree with stratigraphic ranges of Permian and Triassic diapsids included in this study. Black bars represent known temporal ranges and bars with cross hatching are missing portions of lineages derived from minimum time of divergence of clades.

Permian and Early Triassic, but have concentrated on the absence (real or an artefact of fossil record) of Late Permian taxa in the Early Triassic (Maxwell 1992). The large missing segments demonstrated for lineages of early archosauromorphs in the Triassic indicate that, at least for diapsids, one must also consider the problem of the absence of basal members in the Late Permian. Calibration of a phylogeny by stratigraphic ranges of fossil taxa will lead to predictions of downward range extensions. When these range extensions cross the boundary of a mass extinction such as the end-Permian event, the patterns of diversity may change dramatically with inevitable consequences for proposed explanations of the extinction event.

6. CONCLUSIONS

New data on *Mesosuchus*, as well as corrections to published data on the other South African basal archosauromorphs *Prolacerta*, *Euparkeria* and *Proterosuchus*, has had a profound impact on the hypothesized early phylogeny of Archosauromorpha. In particular, *Mesosuchus* is a key taxon because it possesses several derived characters that link it strongly with rhynchosaurs, but also numerous plesiomorphic characters that indicate a close relationship with *Prolacerta* and archosauriforms. Early members of a lineage can possess a unique combination of plesiomorphic and derived characters, and when incorporated into a phylogenetic analysis can generate fewer most parsimonious trees, more stable trees (as measured by different indices such as the bootstrap and branch support), and a better fit between the fossil record and tree.

Not surprisingly, the nodes with the strongest support are those consisting of highly derived taxa. Thus, rhynchosaurids, archosauriforms, tanystropheids, drepanosaurids and choristoderes have large branch support and bootstrap values. Many of these clades also have long segments missing from their fossil record. A more extreme case is found in derived taxa that are isolated in the fossil record. One example is *Trilophosaurus*, which has a highly autapomorphic skull that is also poorly known due to the difficulty of identifying sutures. The absence of basal members is at the root of their morphological distinctiveness, and, at the same time, responsible for the recognition of only a few synapomorphies between members of each lineage. The weakness of those nodes linking highly derived lineages is shown by lower branch support and bootstrap values.

The new phylogeny of basal archosauromorphs is more parsimonious than any proposed previously. Despite its greater robustness in several areas, support for relationships between several groups is weak due to the lack of early members in most lineages in the Late Permian and Early Triassic. Without knowledge of the basal members of these lineages, it is impossible to determine whether any of the characters shared among the derived taxa are homologous. Thus, discovery of these basal taxa will ultimately prove to be instrumental in generating more reliable phylogenetic hypotheses of Archosauromorpha.

I thank Dr Bruce Rubidge of the Bernard Price Institute for Palaeontological Research in Johannesburg, South Africa, for his enthusiastic support, Dr Gillian King (formerly of the South African Museum) for arranging the loans of the specimens of *Mesosuchus*, Dr Chris Gow (BPI for Palaeontological Research) for discussions of the anatomy of *Prolacerta*, Johann Welman (National Museum, Bloemfontein) for allowing me to examine *Euparkeria* and *Proterosuchus*, John Merck Jr (University of Texas at Austin) for providing new data on the skull of *Trilophosaurus*, Dr Silvio Renesto (Università degli Studi di Milano, Italy) for providing photographs of *Langobardisaurus*, Gary Kruger (BPI for Palaeontological Research) for assistance with photography and Richard Lewis (Principal Technician of the BPI for Palaeontological Research) for keeping the vibrotool operating while I prepared the specimens. I also thank Dr Robert Carroll for allowing me to use his copy of PAUP. Comments and suggestions by Dr David Norman and an anonymous reviewer are appreciated and improved the manuscript significantly.

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APPENDIX 1.

Description of characters used in the cladograms. The number in parentheses (0, 1, 2, or 3) refers to the character state listed for the character.

1. Dimensions of skull. Midline length greater than maximum width (0) or midline length less than maximum width (1).
2. Relative length of snout. $<50\%$ of total skull length (0), or $\geqslant 50\%$ of total skull length (1).
3. Upper temporal fenestra. Oval in outline and not elongated caudally (0) or elongated caudally with inner surface of parietal and squamosal facing dorsally (1).
4. Lower temporal fenestra. Present and closed ventrally (0), present and open ventrally (1) or absent (2).
5. Antorbital fenestra. Absent (0) or present (1).
6. Shape of premaxilla. Horizontal ventral margin (0) or down-turned ventral margin (1).
7. Premaxilla and prefrontal. No contact (0) or contact present (1).
8. Shape of maxillary ramus of premaxilla. Contributes only to ventral border of external naris (0) or extends as a posterodorsal process to form caudal border of external naris (1).
9. Premaxilla and cranial part of dentary. Teeth present (0) or edentulous (1).
10. External nares. Separate (0) or single, medial naris (1).
11. External nares location. Marginal (0) or close to midline (1).
12. External nares shape. Rounded (0) or elongate (1).
13. Shape of cranial margin of nasal at midline. Strongly convex with anterior process (0) or transverse with little convexity (1).
14. Septomaxilla. Present (0) or absent (1).
15. Lacrimal. Contacts nasal and reaches external naris (0), contacts nasal but does not reach naris (1) or does not contact nasal or reach naris (2).
16. Maxilla. Horizontal ventral margin (0) or convex ventral margin (1).
17. Form of suture between premaxilla and maxilla above dentigerous margin. Simple vertical or diagonal contact (0) or notch present in maxilla (1).

18. Ratio of lengths of nasal and frontal. $\leqslant 1.0$ (0) or >1.0 (1).
19. Ratio of lengths of frontals and parietals. >1.0 (0) or $\leqslant 1.0$ (1).
20. Shape of dorsal surface of frontal next to sutures with postfrontal and parietal. Flat to slightly concave (0) or longitudinal depression with deep pits is present (1).
21. Shape of dorsal surface of postfrontal. Flat or slightly concave towards raised orbital rim (0) or depression present with deep pits (1).
22. Postorbital and parietal contact. Present (0) or absent (1).
23. Ratio of lengths of anteroventral and posterodorsal processes of postorbital. >1.0 (0) or <1.0 (1).
24. Postfrontal. Excluded from upper temporal fenestra (0) or entering upper temporal fenestra (1).
25. Median contact of parietals. Suture present (0) or parietals fused with loss of suture (1).
26. Parietal table. Broad (0), constricted without sagittal crest (1) or sagittal crest present (2).
27. Parapineal foramen. Present (0) or absent (1).
28. Shape of median border of parietal. Level with skull table (0) or drawn downwards to form ventrolateral flange (1).
29. Postparietal. Present (0) or absent (1).
30. Tabular. Present (0) or absent (1).
31. Supratemporal. Present (0) or absent (1).
32. Subtemporal process of jugal. Robust with height $>50\%$ of length (0) or slender with height $<50\%$ of length (1).
33. Lateral surface of jugal above maxilla. Continuous (0) or lateral shelf present (1).
34. Anteroventral process of squamosal. Broad ventrally with distal width that is approximately equal to dorsoventral height (0), narrow ventrally with distal width less than dorsoventral height (1) or absent (2).
35. Quadratojugal. Present with anterior process (0), present without anterior process (1) or absent (2).
36. Quadrate. Covered laterally (0) or exposed laterally (1).
37. Quadrate emargination. Absent (0), present without conch (1) or present with conch (2).
38. Contact between vomer and maxilla. Absent (0) or present (1).
39. Contact between ectopterygoid and jugal. Restricted with area of contact approximately equal to or less than contact between ectopterygoid and pterygoid (0) or ectopterygoid expanded caudally (1).
40. Contact between ectopterygoid and maxilla. Absent (0) or present (1).
41. Elements contributing to lateral border of suborbital fenestra. Ectopterygoid, palatine and maxilla (0) or ectopterygoid and palatine contact to exclude maxilla (1).
42. Shape of ectopterygoid along suture with pterygoid. Transversely broad (0), posteroventrally elongate and does not reach lateral corner of transverse flange (1) or posteroventrally elongate and reaches corner of transverse flange (2).
43. Orientation of basipterygoid processes. Anterolateral (0) or lateral (1).
44. Parasphenoid teeth. Present (0) or absent (1).
45. Foramen for entrance of internal carotid arteries. Lateral wall of braincase (0) or ventral surface of parasphenoid (1).
46. Club-shaped ventral ramus of opisthotic. Absent (0) or present (1).
47. Lateral surface of prootic. Continuous and slightly convex (0) or crista prootica present (1).
48. Anterior inferior process of prootic. Absent (0) or present (1).
49. Abducens foramina. In dorsum sella (0) or between prootic and dorsum sella (1).
50. Laterosphenoid. Absent (0) or present (1).
51. Position of occipital condyle. Even with craniomandibular joint (0), cranial to craniomandibular joint (1) or caudal to craniomandibular joint (2).
52. Paroccipital process. Ends freely (0) or reaches suspensorium (1).
53. Post-temporal fenestra. Large (0) or small (1).
54. Supraoccipital. Plate-like (0) or pillar-like (1).
55. Tooth implantation. Subthecodont (0), ankylothecodont (1) or pleurodont (2).
56. Caniniform teeth. Present (0) or absent (1).
57. Serrated teeth. Absent (0) or present (1).
58. Curvature of teeth. Absent (0) or present (1).
59. Cross-sectional shape of teeth. Oval (0) or laterally compressed (1).
60. Maxillary tooth plate. Absent (0) or present (1).
61. Number of tooth rows on maxilla. Single row (0) or multiple rows (1).
62. Number of grooves on maxilla. None (0), one (1) or two (2).
63. Location of maxillary teeth. Only on occlusal surface (0) or on occlusal and lingual surfaces (1).
64. Number of tooth rows on dentary. One (0), two (1) or more than two (2).
65. Jaw occlusion. Single-sided overlap (0), flat occlusion (1) or blade and groove (2).
66. Vomerine teeth. Present (0) or absent (1).
67. Palatine teeth. Present (0) or absent (1).
68. Teeth on palatine ramus of pterygoid. Present in two fields (0), present in one field (1), present in three fields (2) or absent (3).
69. Teeth on transverse flange of pterygoid. Single row (0), multiple rows (1) or absent (2).
70. Depth of lower jaw measured at maximum height of adductor fossa relative to length of jaw from tip to articular. $<25\%$ (0) or $>25\%$ (1).
71. Jaw symphysis. Formed largely or wholly by dentary (0) or formed only by splenial (1).
72. Divergence of dentaries cranial to symphysis. Absent (0) or present (1).
73. Dentary–coronoid–surangular profile. Horizontal to convex (0) or concave caudal to coronoid (1).
74. Retroarticular process. Absent (0), present and small and formed by articular (1), present and large and formed by articular (2) or present and formed by fused articular and prearticular (3).
75. Upturned retroarticular process. Absent (0) or present (1).
76. Lateral mandibular fenestra. Absent (0) or present (1).
77. Slender and tapering cervical ribs at low angle to vertebrae. Absent (0) or present (1).
78. Cervical rib accessory process. Absent (0) or present (1).
79. Postaxial cervical intercentra. Present (0) or absent (1).
80. Dorsal vertebrae intercentra. Present (0) or absent (1).
81. Ratio of lengths of centra of mid-cervical and mid-dorsal vertebrae. $\leqslant 1.0$ (0), >1.0 and <1.5 (1) or >1.5 (2).

82. Dimensions of cervical neural spine. Tall with height and width approximately equal (0) or long and low with height $<$ width (1).
83. Notochordal canal. Present in adult (0) or absent in adult (1).
84. Neural arches of mid-dorsals. Shallowly excavated (0) or deeply excavated (1).
85. Dorsal neural spine height. Tall (0) or low with height $<$ length (1).
86. Trunk ribs. Most dichocephalous (0) or most holocephalous (1).
87. Second sacral rib. Not bifurcate (0), bifurcate with caudal process pointed bluntly (1) or bifurcate with caudal process truncated sharply (2).
88. Proximal caudal neural spine height. Moderately tall with height/length >1.0 and <2.0 (0), low with height/length <1.0 (1), tall with height/length >2.0 and <3.0 (2) or very tall with height/length >3.0 (3).
89. Ratio of lengths of caudal transverse processes and centra. $\leqslant 1.0$ (0) or >1.0 (1).
90. Proximal caudal ribs. Recurved (0) or project laterally (1).
91. Distal width of haemal spine. Equivalent to proximal width (0), tapering (1) or wider than proximal width (2).
92. Gastralia. Absent (0) or present (1).
93. Cleithrum. Present (0) or absent (1).
94. Coracoid process. Small (0) or large (1).
95. Clavicular shape. Broad proximally (0) or narrow proximally (1).
96. Interclavicle proximal shape. Broad diamond (0) or gracile anchor (1).
97. Cranial margin of interclavicle. Smoothly convex (0) or notch present between clavicles (1).
98. Caudal stem of interclavicle. Little change in width along entire length (0) or expansion present (1).
99. Shape of scapular blade. Tall and rectangular (0), low with deep caudal concavity (1) or tall and very narrow (2).
100. Pelvic girdle. Unfenestrated (0) or thyroid fenestra present (1).
101. Acetabulum. Elongate (0) or circular (1).
102. Dorsal margin of ilium. Posterior process only (0), large posterior process and smaller anterior process (1), equally developed anterior and posterior processes (2) or large anterior projection (3).
103. Processus lateralis. Present (0) or absent (1).
104. Anterior apron of pubis. Absent (0) or present (1).
105. Relative contributions of pubic elements to acetabulum. Primarily the ilium (0) or approximately equal contributions from each element (1).
106. Femoral humeral ratio of lengths. 1 : 1 (0) or femur $>$ humerus (1).
107. Entepicondylar foramen. Present (0) or absent (1).
108. Ectepicondylar foramen. Absent (0) or present (1).
109. Medial centrale of carpus. Present (0) or absent (1).
110. Femoral distal surfaces. Unequal (0) or equal (1).
111. Relative proportions of femur. Distal width/total length $\leqslant 0.3$ (0) or distal width/total length >0.3 (1).
112. Number of proximal tarsals in a transverse row. Two consisting of astragalus and calcaneum (0) or three consisting of astragalus, calcaneum and centrale (1).
113. Astragalus–calcaneum articulation. Concave–convex absent (0) or concave–convex present (1).
114. Lepidosaurian ankle joint. Absent (0) or present (1).
115. Perforating foramen. Between astragalus and calcaneum (0) or between distal ends of tibia and fibula (1).
116. Lateral tuber of calcaneum. Absent (0) or present (1).
117. Centrale. Present and does not contact tibia (0) or present and contacts tibia (1).
118. Centrale. Present and contacts distal tarsal 4 (0) or present and does not contact distal tarsal 4 (1).
119. First distal tarsal. Present (0) or absent (1).
120. Second distal tarsal. Present (0) or absent (1).
121. Fifth distal tarsal. Present (0) or absent (1).
122. Fifth metatarsal. Straight (0), hooked without deflection (1) or hooked with deflection of proximal head (2).
123. Ratio of lengths of metatarsals I and IV. $\geqslant 0.4$ (0), <0.4 and $\geqslant 0.3$ (1) or <0.3 (2).
124. Ratio of lengths of digits 3 and 4. $\leqslant 0.8$ (0), >0.8 and <0.9 (1) or $\geqslant 0.9$ (2).
125. Prefrontals. Separate along midline (0) or meet along midline (1).
126. Pterygoids. Join cranially (0) or remain separate (1).
127. Symphysis. Small (0) or extended caudally (1).
128. First caudal. Separate from sacrum (0) or incorporated in to sacrum (1).
129. Caudal zygapophysis. Inclined (0) or nearly or fully vertical (1).
130. Basicranial joint. Metakinetic (0) or fused (1).
131. Neurocentral sutures. Closed in adult (0) or open in adult (1).
132. Sacral and caudal ribs. Fused to centra (0) or free (1).
133. Odontoid prominence on atlas pleurocentrum. Absent (0), or present (1).
134. Cranial margin of cervical neural arch. Straight (0) or notched to form overhang (1).
135. Shape of astragalus. L-shaped with broad base (0) or elongate (1).
136. Crown of marginal teeth. Single point (0) or tricuspid (1).
137. Lumbar region. Not differentiated (0), ribs of last few presacrals project laterally and are not expanded (1) or ribs of last few presacrals fused or lost, project laterally and are not expanded distally (2).
138. First phalanx of digit 5. Shorter than or equal to length of first metatarsal (0) or significantly longer than the first metatarsal (1).
139. Distal ends of caudal neural spines. Not expanded (0) or expanded (1).
140. Distal ends of first five to six dorsal neural spines. Not expanded (0) or expanded (1).
141. Curvature of haemal spines. No curvature (0) or cranial curvature present (1).
142. Suture between ectopterygoid and pterygoid. Simple overlap of ectopterygoid and pterygoid (0) or complex overlap between ectopterygoid and pterygoid (1).
143. Distal ends of cervical neural spines. No expansion (0) or expansion present in form of flat table (1).
144. Pubic apron on ilium. Absent (0) or present (1).

APPENDIX 2.

List of apomorphies of taxa and clades. As not all clades in the most parsimonious cladogram are named, I follow the distinction between a clade and a taxon (named clade) of de Queiroz & Gauthier (1994). Those clades without a name are designated by a capital letter that corresponds to those of figure 29. Characters 15, 64, 81, 88, 123 and 124 were ordered linearly. Data matrix was analysed with PAUP 3.1.1. DELTRAN character optimization was selected. Ambiguous character states are indicated by an asterisk and reversals are indicated by a negative sign. Derived states for multistate characters are surrounded by brackets.

Youngina: 22, 34(1), 36*, 37(1)*, 46, 49*, 74(1), −78, −88(0), −91(0), 102(1), 143.

Node A: 15(2), 29, 30, 40, 92, 93*, 103, 107, 121.

Choristodera: 2, 11*, 27*, 38, 79*, 80*, 96*, 116, 122*, 125, 127, 128, 129.

Node B: 3*, 10, 18*, 23*, 69(1)*, 83*, 130*, 131, 132, 133*.

Sauria: 4, 34(2), 35(1), 36*, 42(1), 47, 69(2)*.

Node C: 25*, 37(2)*, 55(2), 73, 74(3)*, −78(0), 96*, 100, 108, 114, 115, 122(2), 144.

Archosauromorpha: 8, 12*, 24*, 26(2), 27*, 37(1)*, 68(2)*, 74(2)*, 77, 79*, 83*, −91(0)*, 97, 102(1), 109.

Node D: 2, 18, 81(2), 82.

Node E: 11*, 80*, 100, 124(1), 134.

Drepanosauridae: 88(3), −92, 99(2)*, 102(3), 116, 124(2), 139, 140, 141.

Tanystropheidae: 43*, 73, 85, −88(0), 89*, 99(1)*, 105*, 117, 120, 122(1)*, 135*.

Node F: 119, 136, 137(2)*, 138.

Node G: 14*, 45, 48*, 51(1)*, 84*, 113, 116, 117, 122(1)*.

Node H: 11*, 39, 49*, 75, 87(2), 88(2)*, 89*, 91(2)*, −103, 104, 124(1), 142*.

Node I: 2, −15(1)*, 17*, 18, −24, −26(0), 46*, 53, 58, 59, 126, 143.

Archosauriformes: −4, 5, −29, −35(0), 38*, 43, 50, 57, 76, −79, 96.

Rhynchosauria: 6, 7, 10, 20, 21, 25*, 38*, 61, 64(2), 65(1), 88(3), 98*, 123(1).

Node J: 13, 16, 55, 60, 63.

Rhynchosauridae: 9*, 19, 23, 33, −35(0)*, −39(0), 41, 42(2), 54, 62(2), 65(2), 66*, 67, 68(3)*, 71*, 72*, 73, −87(0), −91(0), 96*, −97*, −104, 112, 115, 118, 129, −142.

Node K: −4*, −77*, −78*, −84*, −88(2), 102(2), 111, 124(2).

Node L: 1, 22, −32, 43, −51(0), −62(1), −63, −64(1), 70, −75, 80, −89*.

APPENDIX 3.

(a) *List of institutional abbreviations*

BP/1/	Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
GHG	Geological Survey, Pretoria, South Africa
QR	National Museum, Bloemfontein, South Africa
SAM	South African Museum, Cape Town, South Africa

(b) *List of anatomical abbreviations*

a	angular
ai	atlas intercentrum
ap	atlas pleurocentrum
ar	articular
ast	astragalus
ax	axis
bo	basioccipital
bpt	basipterygoid process
bt	basal tubera
cal	calcaneum
cen	centrale
cl	clavicle
cn	cranial nerve
cp	crista prootica
cr	cervical rib
ct	cultriform process
ctym	cordi tympani foramen
cv	caudal vertebra
d	dentary
ect	ectopterygoid
eo	exoccipital
ept	epipterygoid
f	frontal
fe	femur
fi	fibula
fo	fenestra ovalis
ga	gastralia
h	humerus
hs	haemal spine
hy	hyoid
ica	internal carotid foramen
icl	interclavicle
il	ilium
is	ischium
j	jugal
l	lacrimal
lf	lacrimal foramina
m	maxilla
mf	metotic foramen
mt	metatarsal
n	nasal
op	opisthotic
p	parietal
pal	palatine
pap	posterior accessory process
pf	postfrontal
pm	premaxilla
po	postorbital
pra	prearticular
prf	prefrontal
pt	pterygoid
pu	pubis
q	quadrate
qf	quadrate foramen
qj	quadratojugal
r	radius
ra	radiale
rtp	retroarticular process
sa	surangular
sc	scapula
scl	sclerotic ring
so	supraoccipital
sp	splenial
sq	squamosal
st	supratemporal
sv1	sacral vertebra 1
sv2	sacral vertebra 2
ti	tibia
u	ulna
ul	ulnare
v	vomer
vt	cristae ventrolaterales
1–4	distal tarsals 1–4

APPENDIX 4.

Data matrix used in this study. Headings are characters 1–44, see Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Petrolacosaurus (Pe)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Youngina (Y)	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1
Gephyrosaurus(G)	0	0	0	1	0	0	0	0	0	0	0	1	0	?	2
Squamata (Sq)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
Prolacerta (Pr)	0	1	0	1	0	0	0	1	0	0	1	1	0	?	1
Macrocnemus (Ma)	0	1	?	1	0	0	0	1	0	?	1	1	0	?	2
Tanystropheus (Ta)	0	1	0	1	0	0	0	1	0	0	1	1	0	?	2
Trilophosaurus (Tr)	0	0	1	?	0	0	0	1	1	0	0	1	0	1	1
Howesia (Ho)	?	?	0	1	0	?	1	?	?	1	1	1	1	?	2
Mesosuchus (Me)	0	0	0	1	0	1	1	1	0	1	1	1	0	1	2
Rhynchosaurus (R)	0	0	0	?	0	1	1	1	1	1	1	1	1	1	2
Scaphonyx (Sc)	1	0	0	0	0	1	1	1	1	1	1	1	1	1	2
Stenaulorhynchus (St)	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2
Hyperodapedon (Hy)	1	0	0	0	0	1	1	1	1	1	1	1	1	1	2
Proterosuchus (Ph)	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1
Euparkeria (E)	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Champsosaurus (Ch)	0	1	1	0	0	0	0	1	0	1	1	0	0	0	2
Cteniogenys (Ct)	0	1	1	0	0	0	0	0	0	1	1	0	?	?	2
Lazurussuchus (L)	0	1	?	?	0	0	0	0	0	0	1	1	0	?	2
Protorosaurus (Po)	0	1	0	1	0	0	?	1	0	0	?	?	?	?	2
Megalancosaurus (Mg)	0	1	?	?	?	0	?	1	0	0	1	1	?	?	?
Langobardisaurus (Ln)	?	?	0	?	?	0	?	?	0	?	?	?	?	?	?
Drepanosaurus (D)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Y	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0
G	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	2	1
Sq	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	?	0	2	2
Pr	0	1	1	0	0	0	0	0	0	0	0	0&1	1	1	1	0	1	0	2	1
Ma	0	0	1	0	0	0	0	0	1	0	1	1	1	?	?	?	1	0	2	1
Ta	0	0	1	0	0	0	2	0	1	1	2	0	1	1	1	0	1	0	2	2
Tr	0	0	0	0	0	0	0	?	1	0	2	1	1	1	1	?	1	0	?	?
Ho	1	?	0	0	1	1	0	0	1	1	2	1	1	1	1	0	1	0	2	?
Me	0	1	0	0	1	1	0	0	1	1	2	0	1	1	1	0	1	0	2	1
R	1	0	0	1	?	?	0	1	0	1	2	1	1	1	1	0	1	1	2	0
Sc	1	0	0	1	1	1	1	1	1	1	2	1	1	1	1	?	0	1	2	0
St	1	0	0	1	1	1	0	1	0	1	2	1	1	1	1	?	1	1	2	0
Hy	1	0	0	1	1	1	1	1	1	1	2	1	1	1	1	1	0	1	2	0
Ph	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	2	0
E	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	2	0
Ch	0	0	1	0	0	1	0	1	1	0	1	1	1	1	1	1	1	0	0	0
Ct	0	0	1	1	0	0	0	1	0	0	0	1	1	?	?	?	1	0	?	0
L	0	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?	?	?	?
Po	0	?	1	0	?	?	?	0	?	1	2	1	1	?	?	?	0	0	2	?
Mg	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ln	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
D	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Y	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0
G	1	2	0	0	1	0	1	0	1	1	?	?	?	?	?	1	?	?	?	2
Sq	1	2	1	0	1	0	1	1	1	0	0	1	1	0	0	2	1	0	1	2
Pr	1	1	0	?	1	0	1	0	1	1	1	1	1	1	0	1	1	1	0	0
Ma	1	1	?	?	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?	0
Ta	1	1	0	0	1	0	2	1	1	0	?	1	0	?	0	0	1	0	0	0
Tr	1	1	0	0	?	0	?	0	1	1	?	1	1	?	0	1	1	0	0	1
Ho	1	1	?	1	1	0	1	0	1	?	?	?	?	?	0	1	?	0	0	1
Me	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1	?	0	0	0
R	1	1	?	0	1	1	2	0	1	1	0	1	1	1	0	1	1	0	1	1
Sc	1	1	1	0	1	1	2	1	1	1	0	1	1	?	0	0	1	0	1	1
St	1	1	1	0	1	1	2	0	1	1	0	1	1	?	0	1	1	0	1	1
Hy	1	1	1	0	1	1	2	1	1	1	0	1	1	1	0	0	1	0	1	1
Ph	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0
E	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Ch	0	0	1	0	1	0	0	?	1	0	0	0	0	0	0	2	1	0	0	0
Ct	?	0	1	0	1	0	0	0	1	0	?	0	0	0	0	?	1	?	?	0
L	?	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Po	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0
Mg	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Ln	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
D	?	?	?	?	?	?	?	?	?	?	?	?	?	?		?	?	?	?	?

	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Y	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
G	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	3	0
Sq	1	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	1	3	0
Pr	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	1	2	1
Ma	1	0	1	0	0	0	0	0	0	0	0	0	2	2	0	0	0	1	2	0
Ta	1	0	0	0	0	0	0	0	0	0	0	1	3	2	0	0	0	1	2	0
Tr	1	0	0	0	0	0	0	0	0	0	1	1	3	2	0	0	0	1	2	0
Ho	1	0	0	0	1	1	0	1	2	1	?	0	?	2	?	?	?	0	2	1
Me	1	0	0	0	0	1	0	0	2	1	0	0	2	2	0	0	0	0	2	1
R	1	0	0	0	1	1	2	1	2	2	1	1	3	2	0	1	1	1	2	?
Sc	1	0	0	0	1	1	1	0	0	2	1	1	3	2	1	1	1	1	2	0
St	1	0	0	0	1	1	2	1	2	2	1	1	?	2	0	1	1	1	2	1
Hy	1	0	0	0	1	1	1	0	1	2	1	1	3	2	1	1	1	1	2	0
Ph	1	1	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	1
E	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1
Ch	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ct	1	0	0	0	0	0	0	0	0	0	?	0	1	1	0	0	0	?	?	?
L	1	0	0	0	0	0	0	0	?	0	?	0	?	?	?	?	?	?	?	?
Po	1	0	0	1	0	0	0	0	0	0	0	0	?	?	0	0	0	0	?	?
Mg	1	0	0	0	0	0	0	0	0	0	?	?	?	?	0	?	0	0	?	?
Ln	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0	?	?	?
D	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
Pe	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Y	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	?	0	1
G	0	0	0	0	0	0	?	0	0	1	1	0	1	0	1	2	1	1	0	1
Sq	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	1	1	1
Pr	0	1	1	1	0	2	1	1	1	0	1	2	2	1	1	2	1	1	0	1
Ma	0	1	1	1	1	2	1	1	?	1	1	1	0	1	1	1	1	1	0	1
Ta	0	1	1	1	1	2	1	1	0	1	1	0	0	1	1	0	1	1	0	0
Tr	0	1	1	1	0	0	0	1	1	0	1	0	1	?	1	0	1	1	0	1
Ho	0	?	?	1	0	?	0	1	?	0	?	2	3	1	1	2	1	?	?	?
Me	0	1	1	1	0	1	0	1	1	0	1	2	3	1	1	2	1	1	1	0
R	0	?	?	?	?	0	0	1	?	0	1	0	3	0	1	0	1	1	0	?
Sc	0	0	0	1	1	0	0	1	0	0	1	0	2	0	1	?	1	1	0	?
St	0	0	0	1	0	0	0	1	0	1	?	1	2	1	1	0	?	1	0	1
Hy	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	1	1	1	0	?
Ph	1	1	1	0	0	?	0	1	1	0	1	1	2	1	1	2	1	1	0	1
E	1	1	1	0	0	0	0	1	1	0	1	2	2	1	1	1	1	1	0	1
Ch	0	0	1	1	1	0	0	1	0	0	1	0	1	1	1	1	1	1	0	1
Ct	?	?	?	1	1	0	0	1	0	0	?	?	?	0	?	?	?	?	?	?
L	?	0	1	1	1	0	0	0	0	0	1	0	?	?	1	?	1	?	?	1
Po	0	1	1	1	?	2	1	?	?	0	1	0	2	?	?	2	1	?	?	?
Mg	0	?	?	1	1	2	1	1	1	0	1	0	3	?	?	2	0	1	0	?
Ln	?	1	1	1	1	2	1	1	?	1	?	1	0	1	1	?	1	1	0	1
D	?	?	?	?	?	?	?	1	?	0	1	0	3	0	1	0	0	1	?	?

	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
Pe	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Y	0	0	0	0	?	1	1	0	0	0	1	0	0	0	1	0	0	0	?	0
G	1	0	?	0	1	1	0	1	0	0	1	0	1	?	?	0	0	0	1	1
Sq	1	0	0	0	1	1	0	1	0	0	1	1	1	0	1	0	?	0	1	1
Pr	0	1	0	0	0	1	1	0	1	0	1	1	0	1	1	0	0	1	0	0
Ma	0	1	0	1	1	1	1	0	0	1	1	1	0	?	1	0	0	0	0	0
Ta	0	?	0	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	0	?
Tr	0	?	1	0	0	1	1	1	0	0	1	1	0	1	1	0	0	1	0	0
Ho	?	?	?	?	0	1	1	0	1	0	?	1	0	?	1	?	0	1	0	0
Me	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	0
R	1	0	1	0	0	1	1	0	0	0	1	1	0	?	?	0	1	1	0	1
Sc	1	?	1	0	0	1	2	0	0	0	1	1	0	?	1	1	1	1	0	1
St	1	0&1	1	0	0	1	2	0	0	0	1	1	0	?	1	1	1	1	0	1
Hy	1	0	0	0	0	1	2	0	0	0	0	1	0	1	1	1	1	?	0	1
Ph	1	1	0	0	0	1	1	0	0	0	1	1	0	?	1	0	0	1	0	0
E	1	?	0	0	0	1	1	1	1	0	1	1	0	?	1	0	0	1	0	1
Ch	1	0	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0
Ct	?	?	?	?	?	1	0	?	?	?	?	1	0	?	?	?	?	?	?	?
L	1	?	?	0	?	?	0	?	?	?	1	1	0	?	1	0	0	?	0	?
Po	?	?	?	0	0	1	?	?	?	0	1	1	0	?	1	0	0	?	0	0
Mg	?	?	?	2	?	1	3	1	0	?	1	1	0	?	1	0	0	0	0	0
Ln	?	?	?	2	1	1	?	1	0	?	1	1	0	?	1	0	0	1	0	0
D	?	?	?	2	1	1	3	1	0	?	1	1	0	?	1	0	0	?	1	0

	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Y	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	?	0	0
G	0	?	?	?	?	?	2	?	?	0	0	0	0	0	0	0	0	0	0	?
Sq	0	?	?	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0	0	?
Pr	1	1	0	0	0	?	1	0	1	0	1	0	0	0	0	0	0	0	1	0
Ma	0	1	0	0	1	1	1	0	1	0	?	0	0	0	0	0	0	?	1	1
Ta	0	?	?	1	1	1	1	0	2	0	0	0	0	0	0	0	0	?	1	1
Tr	1	1	0	0	0	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0
Ho	1	1	0	0	0	1	1	?	?	0	?	?	0	0	0	0	0	?	?	0
Me	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
R	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0
Sc	1	1	1	0	0	1	1	1	2	0	0	0	0	?	0	0	0	0	0	0
St	1	1	1	0	0	1	1	2	2	0	0	0	0	?	0	0	0	0	0	0
Hy	0	1	1	0	0	1	1	2	2	0	0	0	0	1	0	0	0	0	0	0
Ph	1	1	0	0	0	1	1	1	?	0	1	0	0	0	0	0	0	?	0	0
E	1	?	?	1	1	1	1	0	?	0	1	0	0	?	0	0	0	0	0	0
Ch	1	?	?	?	?	1	1	0	?	1	0	1	1	1	1	1	1	1	0	0
Ct	?	?	?	?	?	?	?	?	?	1	0	1	?	1	1	1	1	1	?	?
L	1	?	?	1	1	1	1	?	?	1	0	1	1	1	?	0	0	?	0	0
Po	0	0	0	0	0	1	0	0	0	?	?	0	0	0	?	0	0	?	0	1
Mg	1	0	0	0	0	1	0	0	2	?	?	0	?	1	?	0	0	?	1	0
Ln	0	1	0	1	1	1	1	0	1	?	?	0	0	?	?	0	0	?	1	1
D	1	0	0	0	0	0	0	0	2	?	?	?	0	1	?	0	?	?	?	?

	136	137	138	139	140	141	142	143	144
Pe	0	0	0	0	0	0	0	0	0
Y	0	0	0	0	0	0	0	1	0
G	0	0	?	0	0	0	0	0	1
Sq	0	0	0	0	0	0	0	0	1
Pr	0	0	0	0	0	0	1	1	0
Ma	0	1	0	0	0	0	?	1	0
Ta	1	2	1	0	0	0	0	0	0
Tr	0	1	0	0	0	0	?	0	0
Ho	0	?	0	0	?	0	1	0	0
Me	0	0	0	0	0	0	1	0	0
R	0	0	?	0	0	0	0	0	0
Sc	0	0	?	0	0	0	0	0	0
St	0	0	0	0	0	0	?	?	?
Hy	0	0	0	0	0	0	0	0	0
Ph	0	1	0	0	0	0	1	1	0
E	0	0	0	0	0	0	1	1	0
Ch	0	0	0	0	0	0	?	0	0
Ct	0	?	?	0	?	?	0	?	?
L	0	0	0	0	0	0	?	1	0
Po	0	?	0	0	0	0	?	0	0
Mg	0	0	0	1	1	1	?	0	?
Ln	1	2	1	0	0	0	?	1	?
D	?	0	0	1	1	1	?	?	0