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Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*

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The osteology of an almost complete braincase of the rauisuchian archosaur *Batrachotomus kupferzellensis* Gower from the Middle Triassic of Germany is described. There is a possibly discrete epiotic ossification, the metotic fissure is undivided by bone (i.e. there is a metotic foramen), the medial wall of the otic capsule is mostly ossified, the cerebral branch of the internal carotid artery entered the lateral surface of the parabasisphenoid, the ventral ramus of the opisthotic is more prominent laterally than a strong subvertical ridge on the exoccipital and basioccipital that lies posterior to the external foramen for the hypoglossal nerve, and the perilymphatic foramen faces away from the otic capsule in a posterior direction. Braincase morphology in the rauisuchians *Saurosuchus galilei*, *Postosuchus kirkpatricki*, and *Tikisuchus romeri* is reviewed. A matrix of 27 braincase characters for 12 archosaurian taxa is analysed. The most parsimonious hypothesis is consistent with the currently orthodox view of archosaurian phylogeny, except in that aetosaurians are more closely related to crocodylomorphs than is any rauisuchian. This phylogeny is used in a brief interpretation of the evolution of derived braincase features present in extant crocodylians. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, 136, 49–76.

ADDITIONAL KEYWORDS: – Crurotarsi – Crocodylia – morphology – phylogeny – character evolution.

INTRODUCTION

Birds and crocodylians are the only extant members of the large diapsid clade Archosauria, a group that also includes dinosaurs, pterosaurs and many less familiar fossil groups of the Mesozoic. The origin of birds and their morphology has received much recent interest (e.g. see detailed reviews by Witmer (1991) and Padian & Chiappe (1998)) but the ancestry of crocodylian morphology has been relatively neglected in comparison. It is currently recognized that extant crocodylians are members of a clade, Crocodyliformes, that along with the Mesozoic Sphenosuchia comprise the clade Crocodylomorpha. The immediate relationships of Crocodylomorpha to other major clades of Mesozoic suchians such as Aetosauria, Ornithosuchia, and Rauisuchia (if this is indeed a clade – see Discussion in Gower, 2000) remain rather less resolved (Gower & Wilkinson, 1996).

Extant birds and crocodylians are clearly very different in gross form, but they share a number of derived similarities of the neurocranium, particularly of the otic region (e.g. Walker, 1972, 1985, 1990), a substantial proportion of which appear to have evolved independently in the two groups (Gower & Weber, 1998). Exactly where, when, and in what sequence the derived features of bird and crocodylian braincases were acquired requires a more detailed knowledge of archosaurian phylogeny, and also of braincase morphology in fossil taxa. Braincase osteology of non-crocodylomorph suchians is particularly poorly known. Detailed descriptions and/or figures are only available for a very few parasuchians (phytosaur; e.g. Camp, 1930, 1942; Chatterjee, 1978), rauisuchians (Chatterjee, 1985; Alcober, 2000), and aetosaurians (Case, 1922; Walker, 1961, 1985; Parrish, 1994; Gower & Walker, 2002), and no ornithosuchians.

The aim of this paper is to provide a detailed description of a well preserved braincase of the rauisuchian archosaur *Batrachotomus kupferzellensis* Gower. The

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osteology of rauisuchians is poorly known and their relationships remain unclear and controversial (Gower, 2000). In addition to providing data on the early evolution of the suchian braincase, this description also aims to improve our knowledge of the osteology of rauisuchians and to increase the data available for future phylogenetic analyses of Archosauria.

TERMINOLOGY AND ABBREVIATIONS

Braincase structure terminology follows Gower & Weber (1998). Archosauria is used in its traditional sense (e.g. Juul, 1994; Benton, 1999), with archosaurs in the sense of Gauthier (1986) referred to as crown-group archosaurs. The crown group has recently been named Avesuchia by Benton (1999). Systematic confusion means that Rauisuchia is also used here in its traditional sense (Gower, 2000), even though genera and species usually referred to this taxon might not constitute a monophylum.

Institutional abbreviations used are: BMNH, The Natural History Museum, London; ISI, Indian Statistical Institute, Calcutta; SMNS, Staatliches Museum für Naturkunde, Stuttgart; TTUP, Texas Tech University Palaeontology Collection, Lubbock; UCMP, University of California Museum of Palaeontology, Berkeley; UMMP, University of Michigan Museum of Palaeontology, Ann Arbor.

Abbreviations used in more than one figure are as follows: aar – anterior ampullary recess (external and anterior vertical semicircular canals open into this concavity), aur – auricular recess, bk – break in specimen, bo – basioccipital, bolr – lateral ridge on basioccipital, bor – basioccipital recess, bpt – basipterygoid process, bptf – basipterygoid facet, bs – parabasisphenoid, btbo – basal tuber of basioccipital, btbs – basal tuber of parabasisphenoid, cc – osseus common crus, cp – cultriform process of parabasisphenoid, cpr – crista prootica, dhv – position of opening for dorsal head vein plus associated sinus, dv – dorsal part of vestibule, eo – exoccipital, eolr – lateral ridge on exoccipital, eop – exoccipital pillar, eov – possible route of external occipital vein, ep – epiotic, fo – fenestra ovalis, g.pVII – groove probably for palatine ramus of facial nerve + palatine artery, l. – left, mcv – path of middle cerebral vein, mf – metotic foramen, np – notochordal pit, ob – otic bulla (ossified medial wall of vestibule of otic capsule), oc – occipital condyle, op – opisthotic, par – posterior ampullary recess (external and posterior vertical semicircular canals also open into this concavity), pp – paroccipital process, ppt – ridge possibly for attachment of protractor pterygoidei, pr – prootic, r. – right, s.ls – surface for articulation with laterosphenoid, so – supraoccipital, ug – unossified gap, V – position of foramen for trigeminal nerve, VII – position of passage of facial nerve, vrop –

ventral ramus of the opisthotic. In all figures, diagonal shading denotes a fracture surface, cross-shading denotes areas of matrix or artificial material.

MATERIAL AND METHODS

The braincase of *Batrachotomus kupferzellensis* described here is housed at the Staatliches Museum für Naturkunde, Stuttgart and catalogued as part of specimen SMNS 80260. The braincase is also known in SMNS 80261, but this is a heavily crushed, and much less informative example. *B. kupferzellensis* derives from Middle Triassic (Lettenkeuper, Anisian) deposits in Baden-Württemberg, southern Germany. For an overview of the known material and a description of the cranial osteology of this taxon see Gower (1999) and references therein.

The material was prepared mechanically, mostly soon after it was excavated in 1977. At this time, the two main pieces (dorsal and ventral) of the braincase of SMNS 80260 were bonded together artificially. These were separated in 1996 and a small amount of remaining matrix was removed using a blunt needle.

During the course of this study, comparisons were made with both original material of extant and fossil diapsids and with the literature. Chief sources of data are given in parentheses for the following taxa: *Sphenodon* (Gower & Weber, 1998; Säve-Söderbergh, 1947); other extant non-archosaurian diapsids (Säve-Söderbergh, 1947; Oelrich, 1956; pers. obs.); *Euparkeria capensis* (Evans, 1986; Welman, 1995; Gower & Weber, 1998); proterosuchids and erythrosuchids (Gower & Sennikov, 1996a,b; Gower, 1997; pers. obs.); phytosaurs (Camp, 1930, 1942; Chatterjee, 1978; pers. obs. of BMNH, ISI, and TTUP material); aetosaurians (Case, 1922; Walker, 1961, 1985; Parrish, 1994; Gower & Walker, 2002); *Postosuchus kirpatricki* (Chatterjee, 1985; Parrish, 1993; pers. obs. of TTUP material); *Saurosuchus galilei* (Alcober, 2000); sphenosuchian crocodylomorphs (Walker, 1990; Wu & Chatterjee, 1993); crocodyliform crocodylomorphs (Iordansky, 1973; Walker, 1990; pers. obs. of dried skulls in BMNH); birds (Walker, 1972, 1985, 1990; pers. obs. of dried skulls of a limited range of taxa).

DESCRIPTION OF SMNS 80260

The organization of this description approximately follows that given for the braincase of *Sphenosuchus acutus* by Walker (1990: 31–49). Firstly, the external surfaces including the inner ear are described, followed by the internal surface of the endocranial cavity. A horizontal fracture passes clean through the braincase of SMNS 80260 at a level just above the floor of the endocranial cavity. The braincase of this specimen is therefore currently in two pieces, termed here the ‘dorsal’ and ‘ventral’ pieces.

The braincase of SMNS 80260 is partly crushed but most of the three-dimensional details are preserved intact, if occasionally a little distorted. The left side of the braincase has been pushed in toward the midline more than the right, so that the specimen is now slightly asymmetrical. Additional preservational distortion means that the dorsal and ventral pieces of the specimen do not fit together precisely along the break through the right exoccipital pillar. The parabasisphenoid has been squashed so that its lower part, including the basipterygoid processes, has been pushed back almost to the level of the basal tubera of the element. The surface of the bone is generally well preserved apart from the numerous shear-cracks that run through the specimen in association with the distortion undergone during preservation. The hind part of the braincase of SMNS 80260 is largely complete except for some loss of bone from some of the edges bordering the main horizontal fracture through the specimen. Anteriorly, however, neither the cultriform process of the parabasisphenoid nor the laterosphenoids are preserved.

EXTERNAL SURFACE

Basioccipital

The basioccipital forms almost all of the hemispherical occipital condyle, upon which a shallow notochordal pit is visible (Fig. 1). There is no great development of

a condylar stalk, in that the base of the condyle lies only a short distance behind the posterior face of the basal tubera and the rest of the main body of the basioccipital (Figs 2, 3). The basal tubera of the basioccipital are a pair of ventrally projecting, bilobed structures separated by a median cleft. The more medial of each pair of lobes is larger and projects further ventrally. It also bears a ridge on its posterior surface that runs along the longitudinal axis of the lobe. Medially, between these larger lobes, the posteroventral edge of the basioccipital carries a small crescentic 'basioccipital recess', close to the suture between this element and the parabasisphenoid.

The smaller lobe of each basal tuber contacts the ventral ramus of the opisthotic as well as the basal tuber of the parabasisphenoid, and its lateral edge forms a subvertical ridge that is confluent with a lateral crista on the exoccipital (lateral exoccipital ridge; see below). A cleft marks the division between the larger and smaller tuberal lobe of each side of the basioccipital. Along with the basal tuber of the parabasisphenoid, this cleft forms the entrance to a gap that passes up between these elements (and perhaps the ventral surface of the ventral ramus of the opisthotic) an unknown distance towards the floor of the endocranial cavity. The inner surface of this channel is not covered with a layer of firmly ossified bone. Similar openings and channels in other diapsids have been termed 'pseudolagenar recess' in basal archosaurs (Gower & Sennikov, 1996a,b, 1997) and 'unossi-

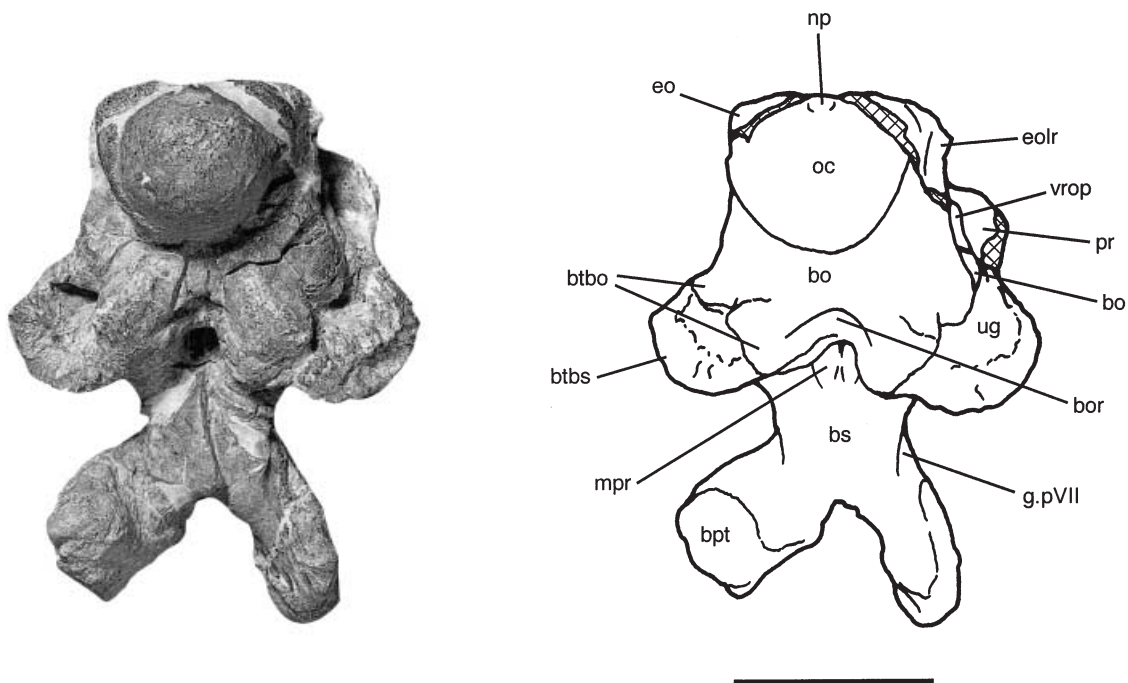


Figure 1. *Batrachotomus kupferzellensis* Gower. Ventral part of braincase of SMNS 80260 in posterior view. Scale bar = 30 mm mpr = median pharyngeal recess.

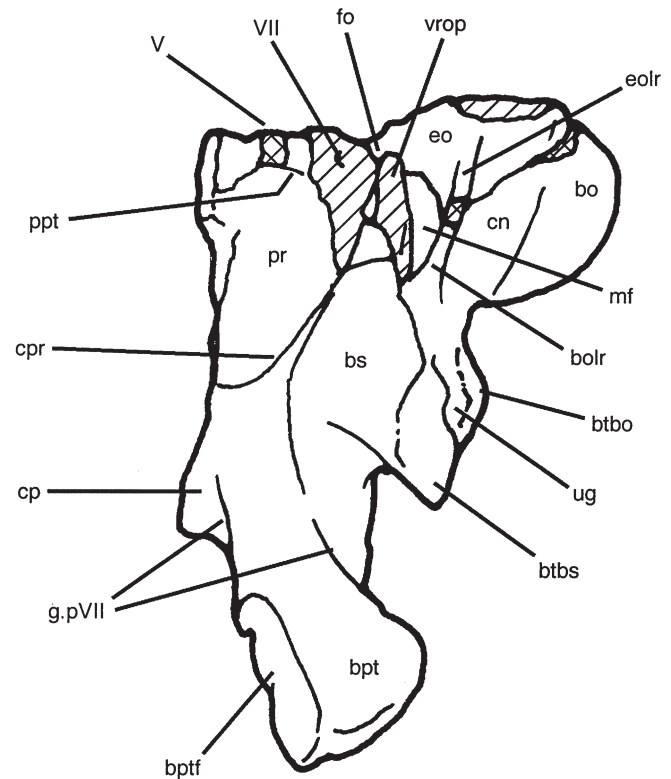


Figure 2. *Batrachotomus kupferzellensis* Gower. Ventral part of braincase of SMNS 80260 in left lateral view. See Figure 3 for scale. cn = condylar neck/stalk.

fied gap' in a wider range of diapsids (Gower & Weber, 1998). It is unclear whether this channel in SMNS 80260 extends anteriorly between elements far enough to enter the ventral end of the lagenar/cochlear recess. The anterior surface of the smaller lobe of each basal tuber of the basioccipital forms part of a large concavity that lies at the ventral end of the metotic foramen. At least part of this area probably housed the perilymphatic duct.

Exoccipital

No sutural demarcation between exoccipital and opisthotic is detectable in SMNS 80260. Each element is described separately here with the assumption that, as in other diapsids (where known), the exoccipital is largely restricted to the pillar positioned between the foramen magnum and the metotic fissure/foramen. The ventral parts of the exoccipitals are in contact for most of their length so that the basioccipital is largely excluded from the ventral border of the foramen magnum. The preservational fracture that runs approximately horizontally through the braincase of SMNS

80260 passes through the bases of the exoccipital pillars, and in doing so it reveals the path of a single channel on each side for the hypoglossal nerve (Fig. 4). This channel runs in a slightly anterior as well as lateral direction, in passing from the endocranial cavity to the external surface of the braincase.

The lateral surface of the exoccipital is dominated by a conspicuous subvertical crista that forms the posterior margin of the metotic foramen (Figs 1–3). The crest ('lateral exoccipital ridge') extends further vertically than the rest of the exoccipital and contacts and continues onto the basal tuber of the basioccipital. The crest effectively divides the lateral surface of the exoccipital into two concave surfaces – anterolaterally and posterolaterally. The external hypoglossal foramen lies on the anterolaterally directed surface, close to the metotic foramen. This superficially resembles the condition in the early suchians *S. acutus* (Walker, 1990), *Dibothrosuchus elaphros* (Wu & Chatterjee, 1993), and *Stagonolepis robertsoni* (Walker, 1985), except that in these taxa the external foramina for the hypoglossal nerve lie posterior to the crest while in *B. kupferzellensis* the opposite is true.

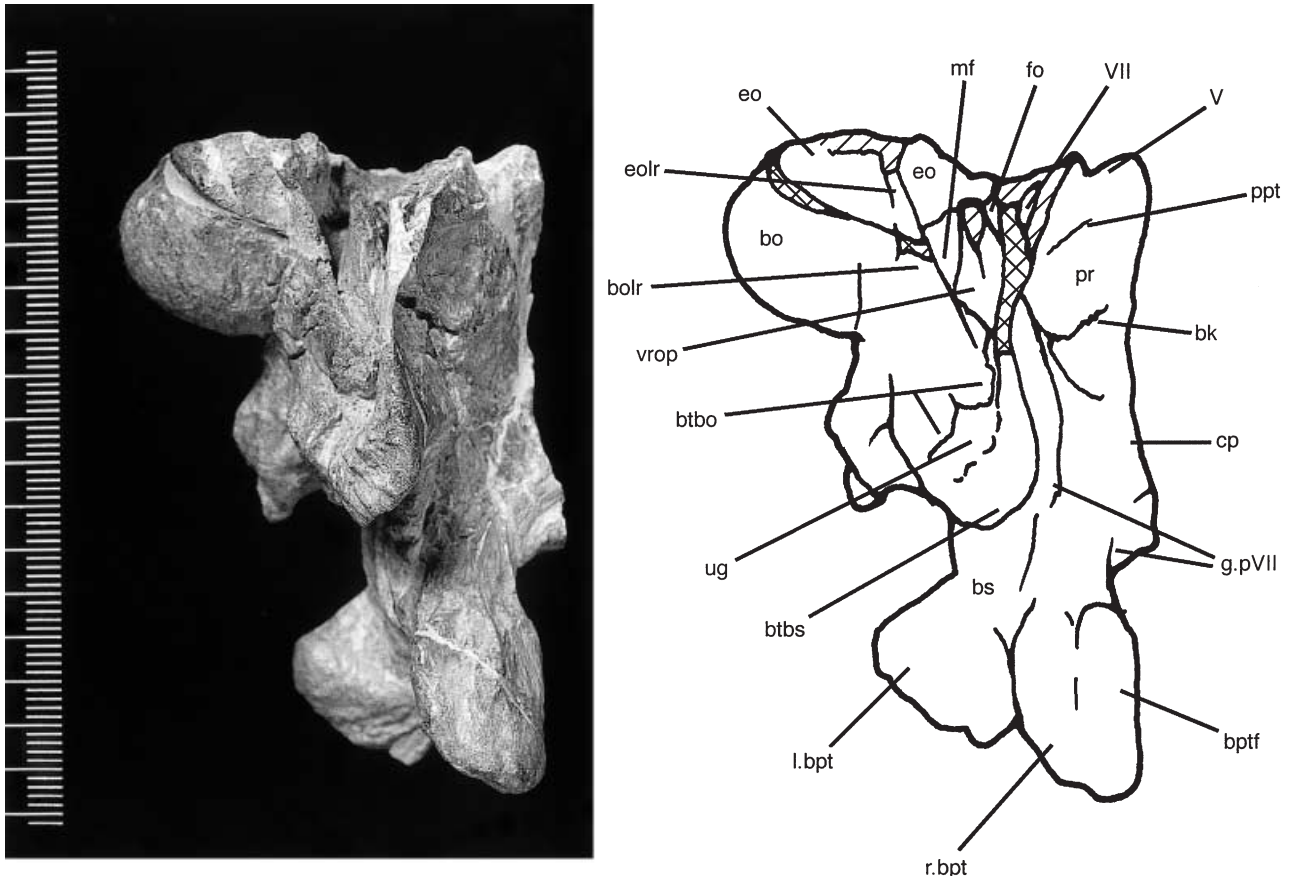


Figure 3. *Batrachotomus kupferzellensis* Gower. Ventral part of braincase of SMNS 80260 in right posterolateral view. Scale bar in mm.

The metotic fissure of SMNS 80260 shows no sign of having been subdivided by bone, and the entire posterior margin of the resulting metotic foramen is formed by the anterolateral face of the exoccipital pillar.

Supraoccipital

The supraoccipital of SMNS 80260 is complete. It is an approximately triangular element in posterodorsal view, being much wider than long (Fig. 5). Posteriorly, it forms the dorsal border of the foramen magnum. The dorsal surface of the element bears a midline dorsal ridge and a pair of anterolateral depressed facets for articulation with the ventromedial surface of the parietals. The lateral surfaces of these facets are irregular. Behind the facets for the parietal, the supraoccipital extends a lateral process over the proximodorsal edge of each of the proximal ends of the paroccipital processes of the opisthotics. The supraoccipital is also exposed on the anterior, unfinished surface of the braincase of SMNS 80260 (Fig. 6), and it might have made brief contact with the laterosphenoids.

Epiotic

The epiotic has only a very small exposure on the external surface of the braincase. It forms a thin, irregular strip between the lateral surface of the supraoccipital and prootics, immediately adjacent to the facet on the former element that articulates with the parietal. Indeed, it seems probable that the epiotic also contacted the parietal at this point, but the suture with the supraoccipital is difficult to trace, and it may be that these two elements are partially fused. The anterior view of the braincase of SMNS 80260 (Fig. 6) indicates that the epiotic also articulated with the laterosphenoids.

Opisthotic

The paroccipital processes of SMNS 80260 are largely formed by the opisthotic. They are relatively short and have strongly expanded, flattened distal ends. The posterior surface of each paroccipital process bears a low subhorizontal ridge near its dorsal edge, extending laterally away from the suture with the supraoccipital. When the parietal is articulated with the

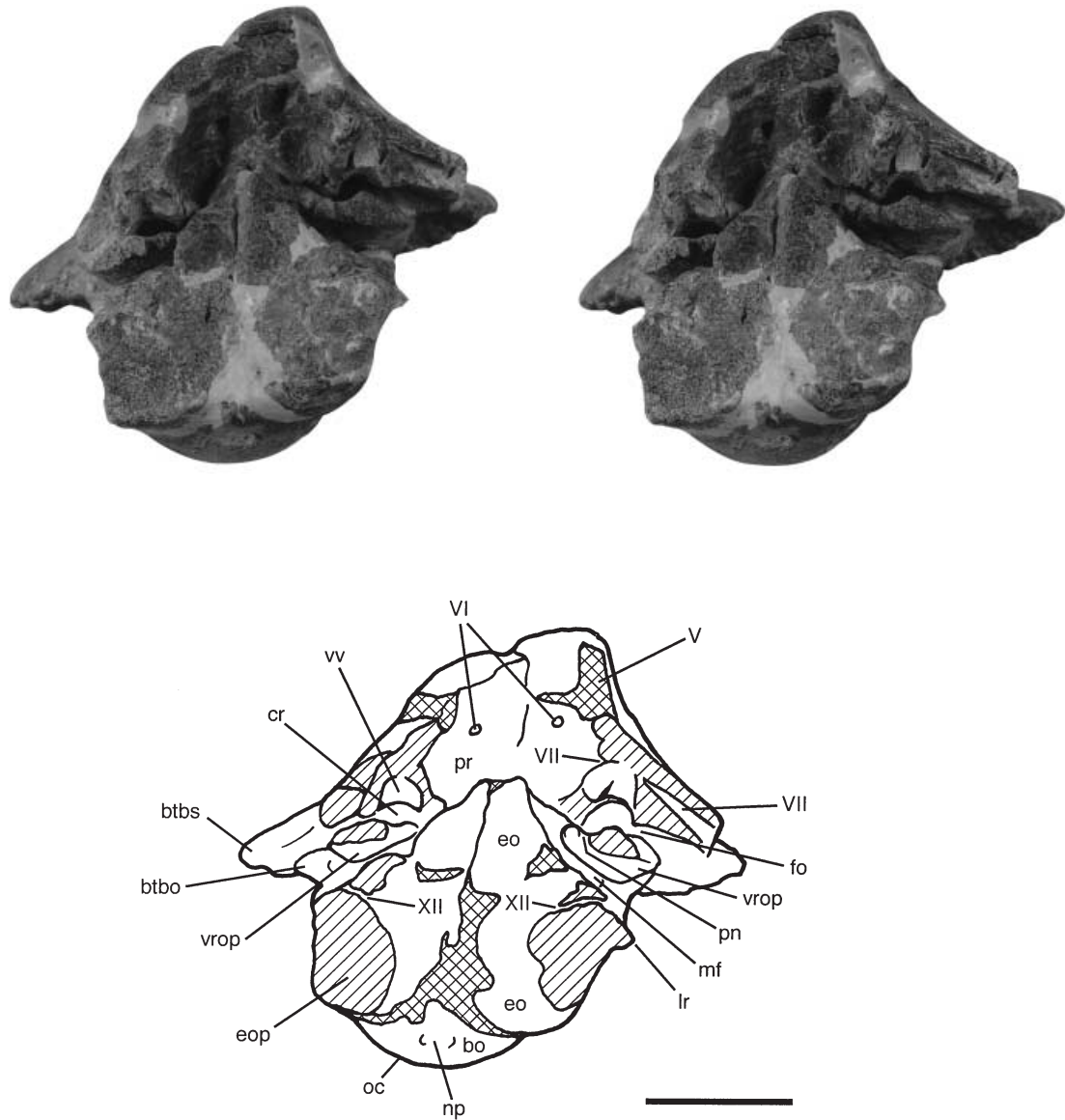


Figure 4. *Batrachotomus kupferzellensis* Gower. Stereopair photographs and diagram of ventral part of braincase of SMNS 80260 in dorsal view i.e. normal to fracture surface between ventral and dorsal pieces. Anterior is to the top of the figure. Scale bar = 15 mm cr = cochlear/lagenar recess; lr = lateral ridge; pn = notch in break through ventral ramus of the opisthotic for passage of perilymphatic duct; VI = foramen for abducens nerve; vv = ventral part of vestibule; XII = foramen for hypoglossal nerve.

braincase, the post-temporal fenestra is a narrow slit between the ventral surface of the parietal, the lateral tip of the supraoccipital and the dorsal edge of the paroccipital process of the opisthotic immediately above the subhorizontal ridge. Anteriorly (Fig. 6), one can envisage the post-temporal fenestra communicating with an anteromedially extending groove that lies along the supraoccipital-opisthotic suture. At its medial extent, at the junction of supraoccipital, opisthotic, prootic, and perhaps epiotic, there is a deep

subtriangular pit. This is seen on the left of SMNS 80260, but is obscured by crushing on the right side. The groove and pit are here interpreted as the possible route of the external occipital vein.

The anterior surfaces of the paroccipital processes of the opisthotics bear subvertical, narrow oval depressions just lateral to midway along their lengths (Fig. 6). A small amount of surface bone seems to have been stripped off at least the depression on the left side of SMNS 80260. It is unclear if these features are

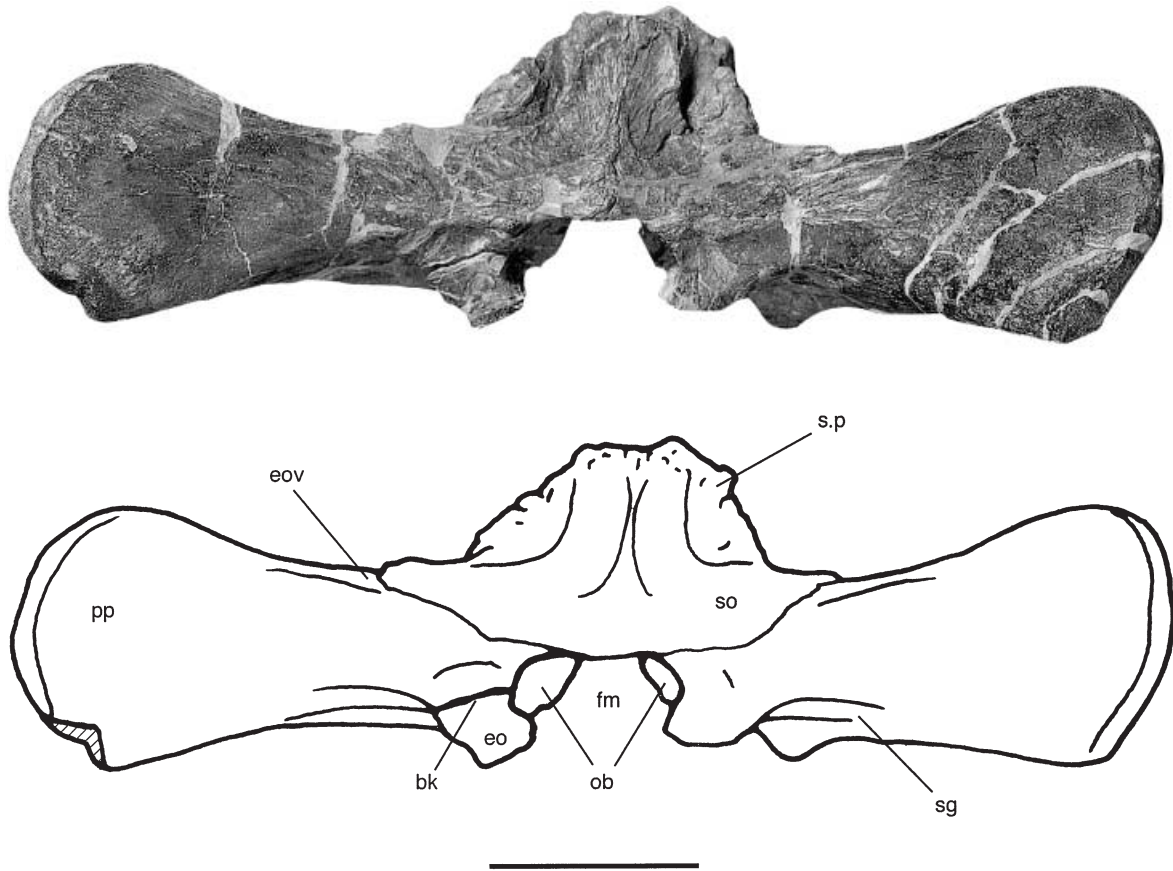


Figure 5. *Batrachotomus kupferzellensis* Gower. Dorsal part of braincase of SMNS 80260 in posterior view. Scale bar = 30 mm fm = foramen magnum; sg = stapedial groove; s.p = surface for articulation with parietal.

natural or if they have been developed or exaggerated during preservation. They perhaps represent a contact zone between the paroccipital process and the posterior surface of the central ridge of the dorsal end of the quadrate. The anterior surface of the paroccipital process lateral to this feature exhibits subhorizontal striae, most strongly developed towards the lower edge.

The posterior surface of the narrow ventral edge of the paroccipital process harbours the stapedial groove and, at its proximal end, the openings of the metotic foramen and fenestra ovalis. The ventral ramus of the opisthotic, separating the fenestra ovalis from the metotic foramen, is well defined in SMNS 80260. It can be seen externally in posterior (Fig. 1) and lateral (Figs 2, 3) views, although this is not as prominent as in some non-crown-group archosauromorphs (e.g. Evans, 1986; Gower & Sennikov, 1996a, 1997; Gower, 1997; Gower & Weber, 1998). The distal end of this ramus is moderately expanded and the suture it shares with the basioccipital is oblique, with the lateral side of the ventral ramus of the opisthotic extending further ventrally than the medial side.

Inner ear

The bony structure of the inner ear, the ossified part of the otic capsule, consists essentially of two partially differentiated cavities, the vestibule and the cochlear recess. The braincase of SMNS 80260 is slightly damaged on both sides just lateral to the cochlear recesses, but it seems fairly certain that the lateral surface of the braincase did not bear any clear indication of the position or orientation of the cochlear recess in the form of a 'cochlear prominence', such as is present in crocodylomorphs (e.g. Walker, 1990). Instead, the upper part of the recess is clearly positioned medial to a substantial, undifferentiated lateral part of the prootic that ends at the crista prootica, and, at the lower end, the parabasisphenoid also contributes to masking its location in external view.

The recess itself is much deeper, more tubular, and more clearly defined than that documented for non-crown-group archosaurs (Walker, 1990; Gower & Sennikov, 1996a; Gower, 1997; Gower & Weber, 1998). It is subcircular in cross-section (Fig. 4) and descends approximately 11 mm vertically below the vestibule. Preparation or exposure of the ventral end is perhaps

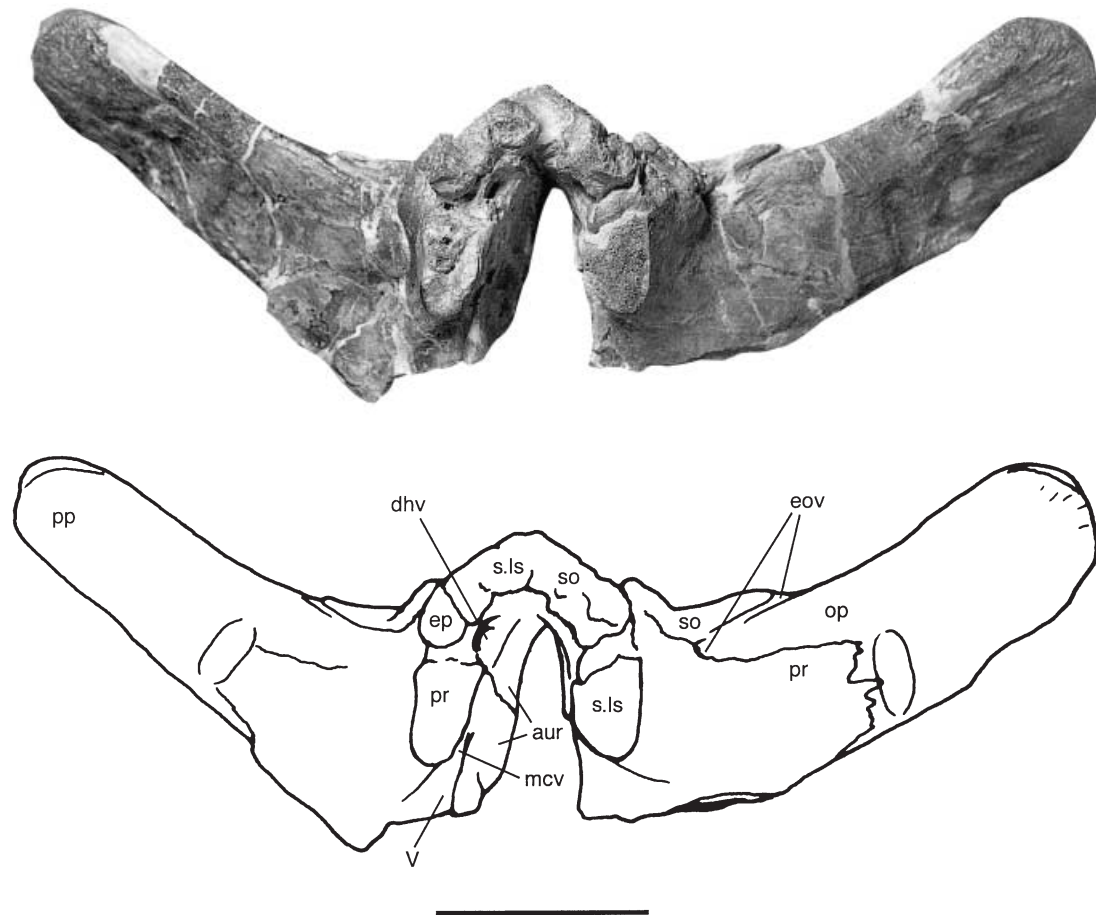


Figure 6. *Batrachotomus kupferzellensis* Gower. Dorsal part of braincase of SMNS 80260 in anterior view. Scale bar = 30 mm.

not complete, but there is nothing to suggest that it did not remain fairly straight for the whole of its length. In SMNS 80260, the dorsal end of the subcircular cross section of the recess is divided into approximately two halves – the curved anterior margin is formed largely by the prootic, and the less strongly curved posterior margin is formed by the anterior surface of the ventral ramus of the opisthotic beneath the position of the perilymphatic foramen. There are also clear indications, at the ventral end of the recess, that contributions are made by the parabasisphenoid, anterolaterally, and by the basioccipital, posterolaterally. The parabasisphenoid contribution occurs as a result of the dorsal wing of the element passing between the distal end of the ventral ramus of the opisthotic and the crista prootica, while the basioccipital contribution is associated with the oblique suture this element forms with the ventral ramus of the opisthotic. Despite this, the full extent of these contributions is not yet clear. There is no indication of whether the floor of the lagenar/cochlear recess is com-

pletely ossified or whether it is confluent with the unossified gap lying between the basioccipital, basioccipital, and parabasisphenoid. Such a continuous unossified channel is present in *Sphenodon* (Gower & Weber, 1998) and the erythrosuchid *Garjainia prima* (= *Vjushkovia triplicostata*; see Gower & Sennikov, 2000) and was termed the ‘pseudolagenar recess’ by Gower & Sennikov (1996a,b) because the potentially cochlear end was not well defined and should probably not therefore be interpreted as decisively indicating the presence of an elongated cochlea.

In SMNS 80260, the recess appears to maintain approximately the same cross-section for all of its length. While the exact length of the lagena/cochlea is difficult to estimate, the elongate and well defined, tubular nature of the recess is interpreted as indicating that a more elongated, cochlear-like organ had developed, in comparison to the sac-like and relatively short lagena of extant lepidosauromorphs (e.g. Oelrich, 1956) and presumably non-crown-group archosaurs (e.g. Gower & Sennikov, 1996a; Gower,

1997; Gower & Weber, 1998) and perhaps even phytosaurs (Case, 1928; Camp, 1930; Walker, 1990).

The dorsal limit of the cochlear recess is marked by a transversely concave surface on the posterolateral edge of the prootic. At this dorsal limit, the recess joins the anterior part of the lower end of the vestibule. The boundary between these cochlear (or lagenar) and vestibular parts of the otic capsule is clearly indicated by a low ridge, but it is not demarcated by the presence of a definite crest of bone (Fig. 4). In this manner, *B. kupferzellensis* resembles non-crown-group archosaurs and contrasts with, for example, extant lizards (e.g. Oelrich, 1956), the extinct crocodylomorph *S. acutus* (Walker, 1990), and extant birds and crocodylians (A.D. Walker, pers. comm.; pers. obs.). Hasse, 1873 termed the dividing crest in crocodylians the crista vestibuli, and Oelrich (1956) termed the similar structure in *Ctenosaura pectinata* the lagenar crest. Another difference between this region in *B. kupferzellensis* and extant crocodylians, is that in the former the lagenar/cochlear recess extends essentially ventrally from the bottom of the vestibule, while in the latter the recess is geniculate and lies ventrolateral to the vestibule.

Except for a small part of the anteroventral corner of its floor, the vestibule is preserved in the dorsal piece of SMNS 80260 (Fig. 7). Here it is essentially a subspherical, three-cornered chamber, with the surfaces linking these corners being decidedly convex. The corners are situated in approximately anterior, posterior and dorsal positions, and each one is marked by concavities that presumably harbour fossae and foramina that indicate the position of ampullae and the path of the semicircular canals. On the basis of comparisons with extant and extinct diapsids, where the underlying pattern is very conservative (pers. obs.), interpreting the relationship between these vestibular features and the soft tissues that they relate to is relatively simple. The dorsalmost corner lies within the epiotic and it probably houses what was the ventral opening of the sinus superior utriculi, i.e. it holds the osseous crus communis. The anteroventral corner lies in the prootic and it contains a large concavity that holds the anterior opening of the external semicircular canal and the ventral opening of the anterior vertical semicircular canal (both visible on both sides), as well as a space that would have been occupied by the anterior ampulla. The posteroventral fossa is formed by opisthotic, and it is interpreted as probably housing the ventral opening of the posterior vertical semicircular canal and the posterior opening of the external semicircular canal, as well as a recess for the posterior ampulla.

Allowing for a little loss of bone during preservation and preparation, the medial wall of the vestibule can be considered to be very nearly completely ossified by

the epiotic, prootic, and opisthotic, with these elements meeting at a Y-shaped suture (Figs 7, 8). This level of ossification resembles the condition in many crown-group archosaurs and squamates, and contrasts with non-crown-group archosauromorphs and *Sphenodon* in which this medial wall is ossified to a much lesser degree (Gower & Weber, 1998).

As a result of the horizontal break running through the braincase of SMNS 80260, it is difficult to interpret the detailed form of the ventral ramus of the opisthotic with great confidence. However, the break has revealed a notch in the broken dorsal surface of each ramus on the ventral piece of the braincase (Fig. 4). This lies just medial to the mid point of the width of each ramus and is interpreted as the ventral border of the perilymphatic foramen. This notch passes back through the opisthotic in a posterior or perhaps slightly posteromedial direction. On both sides, it is not entirely clear whether the piece of the ramus medial to the notch is finished or broken – and thus whether the bony part of the opisthotic loop was complete (with a loop closure suture; Walker, 1990) or incomplete and perhaps finished with cartilage in life (as in *Sphenodon*). There is a suggestion, particularly on the right side, that the subhorizontal surface of the ventral ramus medial to the notch was finished, indicating that a loop closure suture was probably not present, but confirmation of this interpretation will probably require better preserved material. What is clear, is that the perilymphatic notch/loop is in a more medial position than the expanded and more laterally deflected perilymphatic foramen of aetosaurians (Walker, 1985, 1990; Gower & Walker, 2002) and crocodylomorphs (Walker, 1990). The perilymphatic foramen in *B. kupferzellensis* is also smaller relative to the size of the ventral ramus of the opisthotic than in aetosaurians and crocodylomorphs.

Prootic

The prootic forms much of the lateral wall of the endocranium. The anterior margin of the element is broadly notched by its contribution to the border of the trigeminal foramen. The lateral fossa surrounding this foramen is bordered dorsally and ventrally by a pair of subhorizontal ridges that mark a transition to much thicker areas of bone. The more ventral of these ridges has been recorded also in noncrown-group archosauromorphs where it has been interpreted as the site of origin of the protractor pterygoidei (e.g. Gow, 1975; Benton, 1983; Gower & Sennikov, 1996a). A small cleft harboured by the overhang of the ridge dorsal to the trigeminal foramen, seen most clearly on the right side of SMNS 80260 (Figs 6, 8), partly subdivides the trigeminal foramen. Based on its spatial relation to features on the internal surface of the

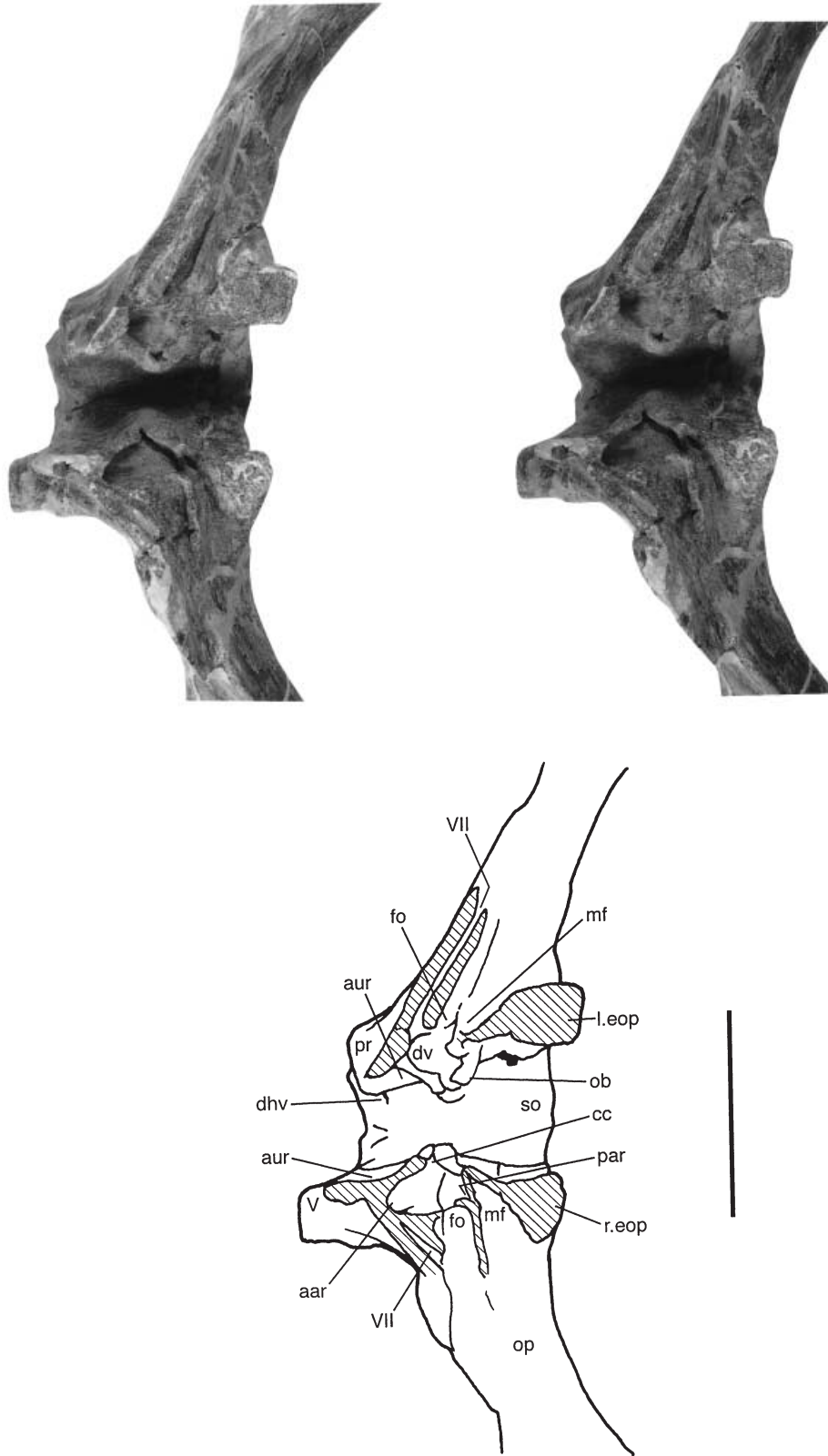


Figure 7. *Batrachotomus kupferzellensis* Gower. Stereopair photographs and diagram of dorsal part of braincase of SMNS 80260 in ventral view i.e. normal to fracture surface between ventral and dorsal pieces. Anterior is to the left of the figure. Scale bar = 30 mm.

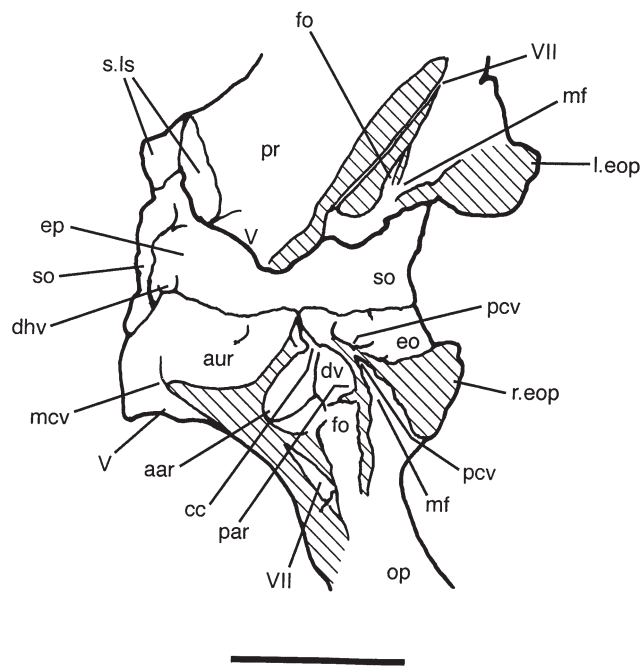
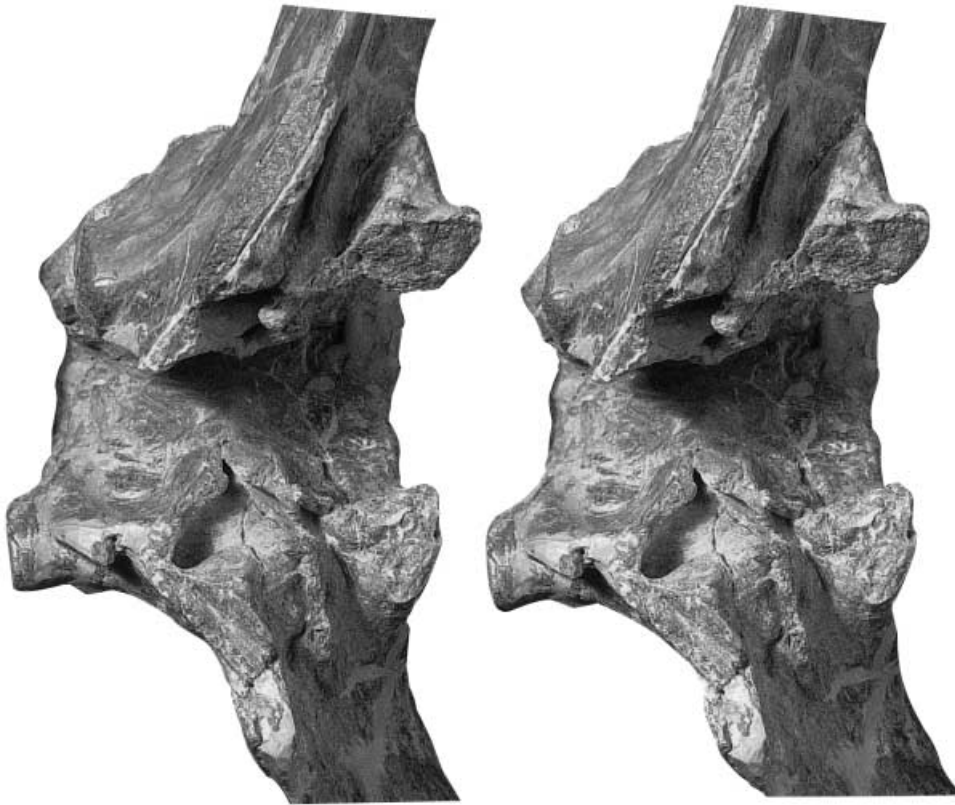


Figure 8. *Batrachotomus kupferzellensis* Gower. Stereopair photographs and diagram of dorsal part of braincase of SMNS 80260 in left ventrolateral view. Anterior is to the left of the figure. pcv = probable path of posterior cerebral/cephalic vein (this is associated with a depression for a sinus on the wall of the endocranial cavity). The diagram is of a slightly more lateral view than the stereo pair photographs, such that the latter show part of the interior of the left vestibule. Scale bar = 20 mm.

endocranium (see below) and comparisons with living taxa (e.g. crocodylians, pers. obs.; *Ctenosaura pectinata*, Oelrich, 1956), the more dorsal and slightly posterior part can be interpreted as marking the passage of the middle cerebral vein, and the lower and slightly more anterior part as for the trigeminal nerve.

Posteriorly, the prootic extends back over the proximalateral surface of the paroccipital process as a thin sheet. Dorsal to the trigeminal foramen, the prootic contacts the epiotic and supraoccipital along an irregular suture in a region that articulates with ventromedial 'sockets' on the parietals (Gower, 1999).

The crista prootica has been partly destroyed by the horizontal fracture through the specimen. Ventrally, it seems to have been barely raised above the surrounding lateral braincase surface but this might at least partly be the result of compression during preservation. Its anteroventral overlapping (laterally) of the parabasisphenoid can be clearly detected (Figs 2, 3). The position of the foramen of the facial nerve can be located on the right side of the ventral part of SMNS 80260 (Fig. 4), behind the crista prootica at a point level with the posterior end of the horizontal lateral ridge below the trigeminal foramen. A small pit within the broken lateral surface of the prootic probably marks its position on the left side of the ventral part of the specimen (Fig. 2). Grooves along the ventral fracture surface on the dorsal part of SMNS 80260 indicate the passage of the facial nerve parallel to the ventral edge of the paroccipital process (Figs 7, 8). There is no intrinsic evidence that there was more than a single, combined opening for the hyomandibular and palatine and branches of the facial nerve, but the horizontal fracture through the specimen and loss of some bone at this point makes this a detail that ideally would be checked against better preserved material.

Behind the path of the bony channel for the facial nerve, and beneath the floor of the fenestra ovalis, the posteromedial part of the prootic forms the cochlear recess with the ventral ramus of the opisthotic, as described above (see inner ear).

Anteriorly, the thickened part of the prootic beneath the trigeminal foramen meets its antimere along the midline and forms the roof to the hypophyseal fossa. This part of the prootic is not upturned (see character 4 of Gower & Sennikov, 1996a) and the external abducens foramen, while not visible, probably lies on the underside of a horizontal surface because it can not be located on the better preserved anterior surface of the prootic (that additionally probably articulated with the laterosphenoid). Whether the external foramen lies wholly within prootic (or partly in parabasisphenoid) is also unknown because of fractures in SMNS 80260 that pass from the dorsal end of the hypophyseal fossa back through the ventral ends of the prootics.

Parabasisphenoid

The parabasisphenoid of *B. kupperzellensis* is distinctly verticalized, although this has clearly been exaggerated by preservational distortion in SMNS 80260, in which the basiptyergoid processes lie almost directly below the basal tubera. In posterior view (Fig. 1), the basal tubera resemble a pair of roughly finished scoops – the upper concave surfaces of which contribute to the unossified gaps between this element and the basioccipital (basal tubera) and opisthotics (ventral rami). The dorsolateral edge of each basal tuber of the parabasisphenoid is sandwiched between the anteroventral surface of the ventral ramus of the opisthotic and the posteromedial surface of the prootic. It thus forms at least a small part of the floor of the fenestra ovalis, and probably the distal end of the cochlear recess.

Posteromedially, between the basal tubera and just below its suture with the basioccipital, the parabasisphenoid holds a deep depression of small diameter (Fig. 1). This is generally rounded, but there is a small indication both dorsally and ventrally that its floor becomes partially subdivided by low midline ridges. This apparently blind pit is interpreted as the median pharyngeal recess (Witmer, 1997). Similar depressions in other suchians have often been termed the median eustachian foramen, following the nomenclature frequently employed for crocodyliforms, where the apparently equivalent depression (which may be at least partly within basioccipital) is not blind, but instead communicates with the true (lateral) eustachian tubes. The basioccipital recess is partially subdivided but blind in the crocodylomorph *Sphenosuchus acutus* (Walker, 1990). Wu & Chatterjee (1993) reported that the subdivided basioccipital recess in the crocodylomorph *Dibothrosuchus elaphros* communicates with the eustachian tubes, but it is unclear whether this is an inference based on the condition in crocodyliforms or if this was actually observed in the slightly crushed material they studied. The equivalent concavity in at least some aetosaurians is a large, deep, hemispherical to conical, closed depression that occupies much of the area between the closely spaced basal tubera and basiptyergoid processes (e.g. Case, 1922; Parrish, 1994).

In posterior view (Fig. 1), the parabasisphenoid is strongly waisted below the basal tubera and above the basiptyergoid processes. The latter processes are approximately the same size as the basal tubera, and thus do not resemble the relatively much larger comparative structures in crocodylians and the sphenosuchian crocodylomorphs *S. acutus* (Walker, 1990) and *D. elaphros* (Wu & Chatterjee, 1993). There is no indication of any foramina for the entrance of the cerebral branches of the internal carotid arteries on the posterior surface of the parabasisphenoid, such as is seen in non-crown-group archosaurs and archosauromorphs

(e.g. Benton, 1983; Evans, 1986; Gower & Sennikov, 1996a; Gower & Weber, 1998). Instead, the foramen for this blood vessel is interpreted as lying on the lateral surface of the parabasisphenoid, in a groove that arcs from behind the posterior edge of the crista prootica on to the posterodorsal edge of the basiptyergoid process, on the lower edge of the broad notch that separates the basal tuber of the parabasisphenoid from the basiptyergoid process. The groove passes ventromedially around the base of the basiptyergoid process before extending anterodorsally along the lateral surface of the base of the cultriform process of the parabasisphenoid. There are no foramina along that part of the groove that passes around the basiptyergoid process.

Based on comparisons with *Sphenodon* (Säve-Söderbergh, 1947; pers. obs.) and reconstructions of soft tissues proposed for a range of fossil archosaurs (e.g. Walker, 1961, 1990; Gower & Sennikov, 1996a, 1997; Gower, 1997; Gower & Weber, 1998), this groove and the probable position of an entrance foramen allow a reconstruction of the paths of the internal carotid artery and palatine branch of the facial nerve. The palatine branch of the facial nerve is interpreted as being transmitted to the base of the cultriform process of the parabasisphenoid outside of bone. Thus there were no bony Vidian canals in *B. kupferzellensis*. The palatine artery would have probably branched from the cerebral branch of the internal carotid near the point that the latter vessel entered the braincase. The palatine artery would have passed to the base of the cultriform process in an open (not enclosed in bone) channel in association with the palatine branch of the facial nerve.

The basiptyergoid process bears a well defined facet for articulation with the pterygoid. This facet comprises an oval region on the ventrolateral surface of the process that wraps around the ventral edge and onto a small area of the posterior end of the ventromedial surface of the process. The articulation with the pterygoid was evidently non sutural. The cultriform process is incomplete except for its tall, laterally compressed base that bears a dorsal gutter forming the floor of the hypophyseal fossa (Fig. 9). Here, the ventral end of the hypophyseal fossa bears a deep, incompletely prepared pit that probably houses the foramina for the entrance of the cerebral branches of the internal carotid arteries into the fossa. The vast majority of the hypophyseal fossa is formed by the parabasisphenoid as it passes up between the ventrolateral wings of the paired prootics. There is no evidence that the parabasisphenoid would have contacted the laterosphenoid in the region preformed by the pila antotica.

Laterosphenoid

The laterosphenoid is not preserved in SMNS 80260, but there is good evidence of its existence. This element seems to be ossified in all archosaurs and an area for its articulation with the ventral surface of the frontal of SMNS 52790 and SMNS 80260 can clearly be detected. The long and narrow form of this area on the frontal has been interpreted (Gower, 1999: 19) as an indication that the laterosphenoid of *B. kupferzellensis* is relatively long and slender in comparison with other known suchian archosaurs.

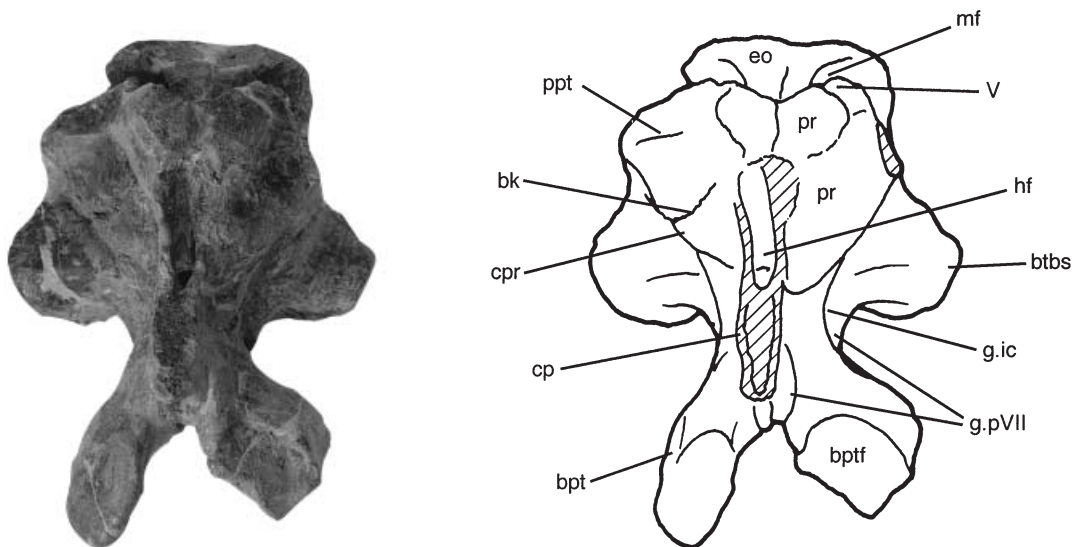


Figure 9. *Batrachotomus kupferzellensis* Gower. Ventral part of braincase of SMNS 80260 in anterior view. See Figure 1 for scale. g. ic = groove for cerebral branch of internal carotid artery; hf = hypophyseal fossa.

INTERNAL SURFACE
(FIGS 4, 7, 8)*Basioccipital*

The basioccipital is not exposed at the posterior part of the floor of the endocranial cavity because of midline contact between the exoccipitals. It does appear to be exposed further anterolaterally, between the anterolateral margin of each exoccipital and the lateral surface of the base of the ventral ramus of the opisthotic. Thus the basioccipital contributes to the floor of the metotic foramen. Although the basioccipital is exposed here, at the lateral edge of the endocranial cavity, exposure along the midline is prevented by contact between the posterior end of the prootics, and between the prootics and exoccipitals.

Exoccipital

The exoccipitals make midline contact on the posterior part of the floor of the endocranial cavity. Here the floor is flat to slightly concave transversely. The anterior end of the exoccipitals are tapered. Their anterior margins mark the point of an abrupt drop of approximately 5 mm down onto the middle part of the floor of the endocranial cavity and, laterally, a greater drop down onto the floor of the metotic foramen. The internal foramen for the hypoglossal nerve lies slightly posterior to the external foramen, so that the nerve passed through the exoccipital pillar in a slightly posteromedially anterolaterally aligned channel.

The metotic foramen is a tall, narrow, subvertical slit (Figs 2, 3). Above its dorsal end, the internal aspect of the exoccipital exhibits a very distinctive feature, most clearly seen on the right side (Fig. 8). A small foramen passes through the braincase immediately above the dorsal end of the metotic foramen. This passes downwards and slightly backwards out through the braincase wall, originating within a well marked depression on the inner wall of the endocranial cavity on the concave posterodorsal surface of the otic bulla. This depression has a gently tapering anterodorsal end and an incised, semicircular posteroventral margin that is formed by a narrow splint of bone that forms the ventral border to the foramen by bridging across the dorsal end of the metotic foramen. The depression is interpreted as part of a vascular sinus, and the foramen as possibly transmitting the posterior cerebral/cephalic vein or an equivalent vessel.

The route of the posterior cerebral/cephalic vein in diapsids is somewhat confused in the literature. However, Dendy (1909: 413) reported that in *Sphenodon* the posterior cephalic vein passes “outwards, downwards, and backwards, above and behind the *ductus endolymphaticus*, to the jugular foramen, through which it leaves the cranial cavity just behind the audi-

tory capsule, in company with the ninth, tenth, and eleventh cranial nerves”. Dendy also reports that this vessel adheres close to the inner surface of the cranial wall and that its position is easily recognized after removal of the brain. The same vein has been reported as leaving the braincase via the foramen magnum in, for example, lizards (e.g. Dendy, 1909) and crocodylians (e.g. Grosser & Brezina, 1895; Bruner, 1907), and even as shifting from the metotic fissure to the foramen magnum in later ontogenetic stages of crocodylians (Hochstetter, 1906; van Gelderen, 1924–25). Thus the reality, consistency, and significance of this possible difference does not appear to be emphatic from a brief investigation of the literature. Walker (1990: 48, 89, fig. 30) described a ‘reniform cavity’ in *S. acutus*, positioned above the internal dorsal end of the metotic foramen. This holds several small foramina, and a gutter passes from its lower end in to the dorsal end of the metotic foramen. Walker (1990: 89) found only slight indications of the presence of the depression in skulls of extant crocodylians. I can confirm this, and report that in at least some specimens, one of the several foramina in this region is larger than the others and forms a decidedly ventrally and laterally directed passage that bears at least a superficial resemblance to the lower end of the depression and the foramen described in *B. kupferzellensis*. A hair passed through this foramen in dried skulls of crocodylians emerges into the middle ear cavity below and behind the perilymphatic foramen. The wall of the endocranial cavity above and behind the otic bulla of extant crocodylians is associated with several venous sinuses, and thus it is possible that the foramina observed in crocodylian skulls, in *S. acutus* (including the gutter), and in SMNS 80260 were associated with venous drainage, although this clearly represents an area for further investigation. Whatever its soft-tissue associations, the presence of a small foramen here in *B. kupferzellensis* is perhaps a derived state among archosaurs. A similar feature can also be detected in *Postosuchus kirkpatricki* (see below).

No suture can be detected between the exoccipital and opisthotic on the internal surface of the braincase of *B. kupferzellensis*. The only slight indication of a possible suture lies on the right side of SMNS 80260, where the anterior end of the splint of bone that forms the ventral margin of the venous sinus (described above) meets the posterior wall of the otic bulla. However, this might instead be a suture within a compound opisthotic + exoccipital as it encloses the passage of the vein. A suture exists within the compound opisthotic + exoccipital here in at least some extant crocodylians (pers. obs. of *Crocodylus* spp.), between the posterior surface of the otic bulla and the anterodorsal end of the ‘exoccipital pillar’, enclosing the larger foramen that occurs in this region.

Supraoccipital

The demarcation of supraoccipital from epiotic is not very clear on the internal surface of the braincase. The supraoccipital certainly forms the ceiling to the posteriormost part of the endocranial cavity because it contributes to the dorsal border of the foramen. It probably also forms the ceiling to the anteriormost part of the endocranial cavity that is preserved in SMNS 80260 (Figs 6, 8). The supraoccipital may even form the whole of the midline of the ceiling, but this is not entirely clear. The epiotic certainly forms the majority of the upper part of the walls of the posterior part of the endocranial cavity. Anterior to the supraoccipital, the parietals probably formed the endocranial ceiling.

Epiotic

The epiotic forms a considerable portion of the dorso-lateral walls of the interior surface of the endocranial cavity. It forms a little more than the upper third of the ossified medial wall of the otic bulla, that is visible through the foramen magnum (Fig. 5). This medial wall is better preserved on the right, where the confluence of the epiotic, opisthotic, and prootic probably marked the location of the endolymphatic foramen. The basis for this suggestion is largely that an alternative position for this foramen cannot be detected, as well as comparison with sphenosuchian and crocodyli-form crocodylomorphs (Walker, 1990; pers. obs.). Anterior to the vestibule, the medial surface of the epiotic bears the dorsal limit of the shallow auricular (floccular) recess as it extends up from the prootic.

Each of the dorsolateral corners of this portion of the endocranium of SMNS 80260 holds a deep subtriangular pit within a fossa. On the right side, this appears to lie within the anterodorsal corner of the epiotic (Fig. 8), but on the left it is possible that the supraoccipital forms its anterodorsal edge. Similar pits are seen in a wide range of extant and extinct diapsids, and in *B. kupferzellensis* this probably represents the passage of the dorsal head vein, with the fossa surrounding the pit probably indicating the position of a venous sinus.

Opisthotic

The opisthotic forms the posteroventral part of the otic bulla. The ventral ramus of the opisthotic forms the perilymphatic foramen, which is described above (inner ear section). The medial edge of the ventral ramus is thinner than the lateral edge. The suture between the ventral ramus and the basioccipital is oblique, such that below the position of the perilymphatic foramen, the ventral ramus becomes less and less medially extensive.

Prootic

The prootic forms part of the floor and lateral walls of the mid part of the endocranial cavity, and contributes to the anteroventral portion of the otic bulla. It also holds a little more than half of the auricular recess. Both the left and right recesses of SMNS 80260 hold a single well marked, presumably vascular foramen that enters the bone in a posteroventral direction. A groove passes around the anterior edge of the auricular recess and down to the trigeminal foramen. This is interpreted as indicating the passage of the middle cerebral vein. There was probably communication between the upper part of this groove and the presumably sinus-holding fossa that surrounds the foramen for the dorsal head vein on the anterodorsal part of the epiotic. Indication of this venous connection is weak in SMNS 80260, but it might have partly been preserved on the posterior edge of the medial surface of the (missing) laterosphenoid.

The ventral part of SMNS 80260 shows the opposite prootics meeting along the midline on the floor of the endocranial cavity (Fig. 4). Here the floor is concave transversely, more so than the posterior part of the cavity where the floor is formed by the exoccipitals. The prootics extend back to meet the anterior end of the exoccipitals along the midline. Immediately lateral to this and medial to the cochlear/lagenar recess, the posterior edge of the prootic contacts the anterior end of the basioccipital. This is visible on the right side of SMNS 80260, but obscured by crushing on the left of the specimen. The part of the floor formed by the prootics is marked by a pair of foramina for the abducens nerves, which seem to lie entirely within these elements. Posterolateral to the abducens foramen, the prootic forms an overhang in the ventrolateral edge of the endocranial cavity. The posterior part of this overhang is formed by the anteroventral limit of the otic bulla, and it harbours the internal foramen for the passage of the facial nerve through the braincase wall. There are no clear indications of foramina that might have transmitted branches of the acoustic nerve, probably as a result of loss of detail along the fracture surface between the dorsal and ventral pieces of SMNS 80260.

Parabasisphenoid

The parabasisphenoid does not seem to be exposed in the walls or floor of the endocranial cavity of SMNS 80260.

BRAINCASE STRUCTURE IN OTHER RAUISUCHIANS

Rauisuchian osteology in general is poorly known (Gower, 2000), and braincase structure has been fig-

ured and/or described for only a handful of taxa. Braincase structure is here reviewed for those rauisuchians in which it is best known.

SAUROSUCHUS GALILEI

Saurosuchus galilei Reig is known from the Upper Triassic Ischigualasto Formation of Argentina. Braincase elements were not among the original material described by Reig (1959) or in two subsequent descriptive accounts (Reig, 1961; Sill, 1974), but a good and largely complete braincase was preserved in the specimen figured and described in detail by Alcober (2000). In overall form, the braincase of *S. galilei* resembles that of *B. kupferzellensis* rather more than that of the rauisuchians *Postosuchus kirkpatricki* and *Tikisuchus romeri*, in that the parabasisphenoid is fairly short from its dorsal to ventral edges (plesiomorphic condition). *S. galilei* braincase characters that are plesiomorphic for crown-group archosaurs include the absence of a semilunar depression and parabasisphenoid intertuberal plate, a lateral position on the parabasisphenoid for the entrance of the cerebral branch of the internal carotid artery, and a metotic foramen (i.e. an undivided metotic fissure). The lateral edge of the exoccipital bears a subvertical ridge, but this is not as prominent as in *B. kupferzellensis*. This ridge lies posterior to the single external foramen for the hypoglossal nerve, and there is some indication (left side of Alcober's fig. 7A) that it extends down onto the dorsal part of the basioccipital. The posterior surface of the braincase shows a large unossified gap between the basal tuber of the basioccipital, ventral ridge of the opisthotic, and parabasisphenoid. The opposite exoccipitals and prootics meet along the midline. The pila antotica was ossified by prootic and parabasisphenoid, so that there is no contact between laterosphenoid and parabasisphenoid. Alcober's fig. 8 shows that the base of the cultriform process of the parabasisphenoid bears a groove on its lateral surface, in an equivalent position to that described for *B. kupferzellensis* and interpreted as indicating the route of the palatine branch of the facial nerve and perhaps the palatine artery.

Alcober identified the presence of a 'presphenoid' in *S. galilei*, articulating with the laterosphenoid and prootic anterior to the single undivided opening for the middle cerebral vein and trigeminal nerve. Indeed, the limits of this element were identified as including a border to the trigeminal opening. Examination of Alcober's figures shows the 'presphenoid' to be in a position occupied by the anteroventral portion of the laterosphenoid in a wide range of other Triassic archosaurs. Thus the suture between laterosphenoid and 'presphenoid' might alternatively represent a break in the (incomplete) posterior portion of laterosphenoid,

extending from a potential zone of weakness at the trigeminal foramen. Fractures in this position have been observed in some Triassic archosaurs, but the pattern described by Alcober is consistent on both sides of the specimen, and I have not examined the material first hand.

POSTOSUCHUS KIRKPATRICKI

Postosuchus kirkpatricki Chatterjee is known from the Upper Triassic of the south-western United States of America (Chatterjee, 1985; Long & Murry, 1995). It has a confused taxonomic history (Long & Murry, 1995; Gower, 2000), but it seems that the documented braincase material from the type locality can be relatively confidently associated with the species name *P. kirkpatricki*. Chatterjee (1985: fig. 7) figured three views of a composite restoration of the braincase of *P. kirkpatricki* and described and interpreted aspects of the osteology. The braincase of the holotype (TTUP 9000) is currently largely obscured by paint and plaster applied during the restoration of the skull. My observations of this specimen were aided by access to photographs (provided by S. Chatterjee) taken of the specimen prior to restoration. I also examined the other TTUP *P. kirkpatricki* braincase, no. 9002.

My observations agreed with the view presented by Chatterjee (1985) in terms of the general proportions and in many of the sutural relations and detailed features. I concur that there is a single opening for cranial nerves IX–XI (metotic foramen), a laterally positioned entrance of the cerebral branch of the internal carotid artery, and an unossified gap between the basal tubera of the basioccipital and parabasisphenoid that was probably filled with cartilage in life. Some other details merit further discussion.

There is a strong subvertical ridge on the lateral surface of the exoccipital and upper part of the basioccipital, but this lies posterior, not anterior, to the single external foramen for the hypoglossal nerve (seen on the left side of TTUP 9002), so that this foramen is not (*contra* Chatterjee, 1985: fig. 7) visible in posterior view. This ridge runs down onto the dorsolateral edge of the basal tubera of the basioccipital. It is stronger than the corresponding ridge in *B. kupferzellensis* and, as in *Stagonolepis robertsoni* (Gower & Walker, 2002) and crocodylomorphs (Walker, 1990), it extends further laterally than the ventral ramus of the opisthotic. Unlike the situation in *B. kupferzellensis*, the basal tubera of the basioccipital are barely bilobed, and there is no clear recess on the posterior surface of the basioccipital between the tubera. The sutural relations between opisthotic and prootic on the paroccipital process are not clear. The foramina for the cerebral branches of the internal carotid arteries are within depressions that lie close to

the midline, where the parabasisphenoid is very narrow. Chatterjee identified a separate presphenoid ossification articulating with the laterosphenoid and parabasisphenoid. Chatterjee's (1985: fig. 7) reconstruction of this region presents a highly unusual arrangement for a Triassic archosaur. The known part of the laterosphenoid is shown as sandwiched between the prootic and the base of the cultriform process of the parabasisphenoid, and as forming the anteroventral half of the border to the trigeminal foramen and even part of the crista that overhangs that part of the parabasisphenoid pierced by the foramen for the cerebral branch of the internal carotid foramen. This region is incompletely preserved in TTUP 9002, and it does not provide support for this reconstruction. The surface of TTUP 9000 (photographs and direct observation) is poorly preserved and difficult to interpret. At least that part of the laterosphenoid-prootic suture depicted as lying immediately posteroventral to the trigeminal foramen might be instead interpreted as an artefactual crack. I suggest that determination of the exact pattern of elements here, including the possible presence of a presphenoid, requires additional material. There are several features for which it is not possible, in the known specimens, to ascertain the condition with any confidence including the presence/absence of a discrete epiotic, the exact path of the abducens and facial nerves through the braincase wall, and the entire shape of the cultriform process of the parabasisphenoid.

The endocranial cavity is exposed in TTUP 9002. The exoccipitals meet along the midline and, anteriorly, they appear to be separated here from the prootics by exposure of the parabasisphenoid and basioccipital. As in *B. kupferzellensis*, there is a abrupt drop in the level of the floor of the endocranial cavity from the hind part formed by the exoccipitals to the mid part in front of this. On each side, close to the lateral edge of the floor of the endocranial cavity, there are two clearly defined cup-like depressions. The more posterior of these (visible in Parrish, 1993: fig. 7A) lies just in front of the base of the exoccipital pillar and is here interpreted as the floor of the metotic foramen. The more anterior depression lies a short distance in front of this and is here interpreted as the lagenar/cochlear recess. This is not as deep as in crocodylomorphs, but it is better defined than in non-crown-group archosaurs and phytosaurs (Walker, 1990; Gower & Weber, 1998). Its upper, anterior limit is not marked by any sign of a crista demarcating the border between the lower end of the vestibule and the upper end of the lagenar recess. On the left side of TTUP 9002, the lagenar/cochlear recess lies along the basioccipital-parabasisphenoid suture. Anteriorly, in the same specimen, the opposite prootics seems to make midline contact. TTUP 9002 also presents evidence that

P. kirkpatricki closely resembled *B. kupferzellensis* in possessing a separate foramen possibly for the passage of the posterior cerebral/cephalic vein. Seen best on the left side, the wall of the endocranial cavity immediately above the metotic foramen bears a crescent-edged depression that is interpreted as the position of a venous sinus. A foramen within this depression passes through the thin anterior edge of the exoccipital pillar to emerge immediately above the external opening of the metotic foramen. This is also visible on the right side of TTUP 9002, but the medial surface is partly broken.

In addition to TTUP 9000 and TTUP 9002, Chatterjee (1985: 407) referred a third braincase to *P. kirkpatricki*, UMMP 7473. This had previously been figured by Case (1922: pl. 13), who referred this isolated braincase to the dinosaur *Coelophysis*. Chatterjee considered it to differ from the braincase of Known *Coelophysis* and instead found that UMMP 7473 "corresponds so well" with the TTUP braincases referred to *P. kirkpatricki* that he proposed that it represented the same taxon. I have examined UMMP 7473 and believe that Chatterjee's taxonomic identification is not correct. The specimen is incomplete (see figures in Case, 1922), consisting of the occipital condyle, the endocranial cavity, and the proximal parts of the parabasisphenoid and paroccipital processes. The region of the fenestra ovalis, ventral ramus of the opisthotic and perilymphatic foramen has been obliterated during preservation/preparation on both sides and is marked now by only a single large hollow. The suture between exoccipitals and the condylar portion of the basioccipital cannot be detected. The structures labelled 'bpt' by Case are not the basiptyergoid process as such, but rather the incomplete parts of the parabasisphenoid that would have supported these processes. The part of the parabasisphenoid that has been preserved does resemble that of *P. kirkpatricki* in that it consists of a pair of thin subvertical plates of bone that border a transversely narrow but deep median pharyngeal recess. Additionally, a small depression is positioned just above this recess and between the ventral edge of the basal tubera of the basioccipital, resembling a similar feature in TTUP 9000 and 9002. The endocranial cavity of UMMP 7473 is also exposed. Features observable here include well ossified otic bullae, well marked fossae indicating the position of venous sinuses and the passage of the dorsal head veins, shallow auricular fossae, and an abrupt step down on the floor of the endocranial cavity anterior to the front end of the exoccipitals. These features are consistent with this specimen being *P. kirkpatricki*, but they are also found in a wider range of Triassic archosaurs.

Foramina that are interpreted as being for the entrance of the cerebral branches of the internal

carotid arteries are positioned on the lateral surfaces of the parabasisphenoid – one of the few indications (Gower & Weber, 1998; Parrish, 1993) that the braincase of UMMP 7473 probably belongs to a crown-group archosaur. However, the one important difference between this specimen and the known braincases of *P. kirkpatricki* lies in the position of the external foramen for the hypoglossal nerve. This is posterior to a very strong subvertical ridge on the lateral surface of the exoccipital. Among crurotarsans, this arrangement is known to certainly occur only in aetosaurians and crocodylomorphs (see below; Gower & Walker, 2002). It is not possible for me to completely rule out that UMMP 7473 might be from an ornithomimid, but this may partly reflect my unfamiliarity with braincase osteology in taxa from that group.

Apart from Chatterjee's (1985) original figures of the braincase of *P. kirkpatricki*, two other interpretations have been published (Chatterjee, 1991: fig. 28b), Parrish, 1993: fig. 7). Chatterjee (1991: fig. 28b) presented a modified version of his previous (1985) reconstruction of the braincase of *P. kirkpatricki* in lateral view. Sutural relations remained largely the same (except for a smaller prootic contribution to the paroccipital process), but a few changes in detail were made. A small foramen was now indicated positioned above the metotic foramen, this was identified as the posterior tympanic recess (Chatterjee, 1991: 335, fig. 28b), a pneumatic diverticulum of the tympanic cavity. This is here interpreted as possibly representing the passage of the posterior cerebral/cephalic vein through the braincase (see above). In addition, two further possible pneumatic depressions were accentuated relative to the earlier reconstruction, posterodorsal (not visible in TTUP 9002, pers. obs.) to the trigeminal opening, and in the region of the foramen for the cerebral branch of the internal carotid artery.

Parrish (1993: 300) claimed that *P. kirkpatricki* possesses a 'wedgelike, dorsoventrally expanded parasphenoid rostrum' and that this is a derived feature shared with rauisuchian and crocodylomorph suchians including *Lotosaurus* and *Dibothrosuchus*. The exact meaning of 'wedgelike' in this context is unclear. This description has also been used to describe the condition seen in crocodylians where the rostrum does not taper proximally, but rather expands dorsoventrally before ending at an abrupt blunt edge. This contrasts with the condition in which the rostrum is longer than it is high and it tapers to a point proximally. This latter condition is probably plesiomorphic for suchians (and archosaurs as a whole) because it is present in erythrosuchids and proterosuchids (Gower & Sennikov, 1996a; Gower, 1997), *Euparkeria capensis* (Welman, 1995; Gower & Weber, 1998) and phytosaurs (Camp, 1930; Chatterjee, 1978; pers. obs.). The parabasisphenoid rostrum is incomplete in the known

specimens of *P. kirkpatricki* (including that figured by Parrish, 1993: fig. 7) as well as of *Dibothrosuchus elaphros* (Wu & Chatterjee, 1993: 68). The rostrum of the crocodylomorph *Sphenosuchus acutus* tapers anteriorly in lateral view and is not wedge-shaped (Walker, 1990).

Parrish (1993: 302) also identified a synapomorphy for his clade Paracrocodylomorpha (comprising Crocodylomorpha + Poposauridae, the latter represented by *P. kirkpatricki*): "Foramen at basioccipital/basisphenoid juncture junction... In crocodylomorphs and *Postosuchus*, this is the exit for the eustachian tubes". A similar opening/pit (present in many, even non-crown-group archosaurians) is more probably an unossified gap that was plugged with cartilage in life (see review by Gower & Weber, 1998).

Long & Murry (1995) proposed a revision of material referred to *P. kirkpatricki*. This included referral of additional braincase material to this species. However, these specimens (e.g. UCMP A269/27479; Long & Murry, 1995: fig. 125) are fragmentary and I suggest that their identification must remain in question for the time being.

TIKISUCHUS ROMERI

Tikisuchus romeri Chatterjee & Majumdar is a rauisuchian from the Upper Triassic Tiki Formation of India, known from a single incomplete specimen, ISI R 305. The osteology of this taxon has been described only briefly by Chatterjee & Majumdar (1987). These authors figured a restoration of the braincase in posterior view and presented the following description: 'braincase very deep with elongated and well pronounced basipterygoid processes; supraoccipital tapers dorsally and makes a movable contact with parietal' (Chatterjee & Majumdar, 1987: 788). Furthermore, they (p. 787) included 'ossified laterosphenoid' in a list of archosaurian features possessed by the specimen.

I have re-examined this material as part of this study. The surface preservation of ISI R 305 is very crumbly, and sutures and other details are hard to make out. In addition, several regions of the braincase are not preserved or could not be located at the time of this study. This makes it impossible to comment on the laterosphenoids (which could not be located), exoccipitals, metotic region, fenestra ovalis. The paroccipital processes are fairly short with strong distal expansions. The basioccipital bears dorsal facets that indicate that the ventral ends of the exoccipitals met along the midline to form the ventral border of the foramen magnum. The basal tubera of the basioccipital are barely bilobed. There is no sign that the entrance foramina for the cerebral branches of the internal carotid arteries were located on the posterior or pos-

teroverventral wall of the parabasisphenoid. The anterolateral surfaces of the same element are even less perfectly preserved, but I tentatively interpret that this is where the foramina for the cerebral branch of the internal carotid artery are positioned.

The braincase of *T. romeri* resembles that of *P. kirkpatricki*, particularly in the elongated region of the parabasisphenoid between the basiptyergoid processes and the basal tubera, and in the way this region harbours a dorsoventrally elongate median pharyngeal recess. This is a derived feature within Suchia, and it represents a potential synapomorphy shared by *P. kirkpatricki* and *T. romeri* to the exclusion of other known suchians, including *B. kupferzellensis* (although the braincase UMMP 7473 appears to possess a similar feature, see above). One clear difference between the parabasisphenoids of *P. kirkpatricki* and *T. romeri* lies in the presence of paired short hook-like (in the transverse plane) processes on the parabasisphenoid of the latter taxon. These are not apparent in Chatterjee & Majumdar's (1987) figure 2, but they can be clearly detected on the posterior surface of the element between the bases of the basiptyergoid processes.

In summary, rauisuchian braincases are slowly becoming better known. The braincases of *B. kupferzellensis*, *S. galilei*, *P. kirkpatricki* and *T. romeri* share many features. Most of these are apparently plesiomorphic for Archosauria (e.g. undivided metotic foramen, external foramina for hypoglossal nerve not posterior to subvertical ridge), some are probably derived for Archosauria (e.g. well ossified otic bullae, lateral foramen for the cerebral branch of the internal carotid artery), but few if any seem to be both derived for Suchia and restricted to rauisuchians. The elongate median pharyngeal recess of *P. kirkpatricki* and *T. romeri* is perhaps the only such character. *B. kupferzellensis* and *P. kirkpatricki* share a separate foramen possibly for the posterior cerebral/cephalic vein above the dorsal end of the metotic foramen, but a probable equivalent is also present in at least some crocodylians, and the condition in *S. galilei* and *T. romeri* is unknown.

CRUROTARSAN PHYLOGENY AND THE EVOLUTION OF SUCHIAN BRAINCASES

There are two intimately related issues here – whether the patchy current knowledge of crurotarsan braincase osteology provides any potentially useful evidence for resolving the phylogenetic interrelationships of Crurotarsi, and also how much we can learn about early suchian braincase evolution by optimizing character states on a framework phylogeny for crurotarsans. The approach taken to explore these issues is one of constructing and analysing a character-taxon

matrix for braincase characters among some non-crown-group archosaurs and some crurotarsans. In focusing on these taxa, an initial assumption has been made that the archosaur evolutionary tree consists of a crown group comprising a bird- and a crocodylian-lineage, plus a series of non-crown-group taxa (Gower & Wilkinson, 1996). It has also been accepted that certain higher taxa are members of the crocodylian rather than bird-lineage (i.e. they are crurotarsans rather than ornithodirans), for example, phytosaurs, rauisuchians, aetosaurians, and sphenosuchian crocodylomorphs. Among crurotarsan and noncrown-group higher taxa, Ornithosuchia and Proterochampsidae will not be considered any further here because satisfactory braincase specimens or published descriptions are currently unavailable to me. Similarly, some singleton taxa with poorly preserved and/or documented braincases have not examined for this study and are thus excluded from further consideration. These include *Gracilisuchus stipanicorum* and *Erpetosuchus granti*. Braincase evolution in early ornithodirans is beyond the scope of this study and will not be considered further here.

The approach adopted here means that braincase characters identified through this and previous studies are used both to construct a phylogenetic hypothesis, and to investigate crurotarsan braincase evolution by optimizing them on the very same phylogenetic hypothesis. Some workers might be concerned here with issues of circularity in argumentation, but I do not share these concerns in this instance because (1) the phylogenetic hypothesis derived from braincase data is broadly concordant with currently orthodox views of archosaur phylogeny (see below); (2) this study is intended to be an exploration of braincase data, rather than to be the final word on either archosaurian phylogeny or archosaurian braincase evolution; (3) rather than being viciously circular, future workers are free to start from an entirely new position and set of assumptions.

TAXA

The terminal taxa employed here are the proterosuchid *Proterosuchus fergusi*, the erythrosuchid *Garjainia prima*, the euparkeriid *Euparkeria capensis*, phytosaurs, the rauisuchians *B. kupferzellensis*, *S. galilei*, *P. kirkpatricki*, and *T. romeri*, aetosaurians, and sphenosuchian (*D. elaphos*; *S. acutus*) and crocodyliform (*Crocodylus* sp.) crocodylomorphs. Sources of data are largely as given in Material and Methods. Characters are scored for phytosaurs on the basis of information in Chatterjee (1978) and personal observations of BMNH R38037 and R42745 (both probably *Nicrosaurus meyeri*, A. Hungerbühler, pers. comm.). Ingroup variation among phytosaurs has not been

studied in detail. Similarly, the aetosaurian terminal taxon has been scored largely on the basis of data for *Stagonolepis robertsoni* (Walker, 1961, 1985; Gower & Walker, 2002), but also for *Desmatosuchus spurensis* (Case, 1922) and *Longosuchus meadei* (Parrish, 1994; Gower & Walker, 2002). As with the phytosaurs, it may be that some of the scorings here do not represent the only or even the plesiomorphic condition for the clade as a whole. The included erythrosuchid, *G. prima*, is the senior subjective synonym of *Vjushkovia triplicostata* (Gower & Sennikov, 2000). Data for this taxon were taken from Gower & Sennikov (1996a). Crocodyliformes and crocodylians are represented through personal observation of dried skulls of *Crocodylus* sp.

CHARACTERS

Some of the characters used here have been employed previously elsewhere, while others represent a first attempt to explore potential phylogenetic information represented by observed variation among taxa. The character-taxon matrix is shown in Table 1.

(1) Foramina for entrance of cerebral branches of internal carotid arteries into braincase positioned on the posterior (0), posterolateral (1), or anterolateral (2) surface of the parabasisphenoid.

In phytosaurs, the foramina are on the lateral surface of the parabasisphenoid, but only just anterior to the notches between the basal tubera and basipterygoid processes (Chatterjee, 1978; pers. obs.). This is morphologically intermediate between the condition in non-crown-group archosaurs (foramina on posterior surface, Parrish, 1993: character 7; Gower & Weber,

1998) and more derived suchians (foramina in a more anterodorsal position, on the lateral surface of the parabasisphenoid). The partially lateral position in phytosaurs is here assumed to be partly homologous with the more lateral position in those suchians more closely related to crocodylomorphs. This character is ordered 0-1-2, following the recommendation of Wilkinson (1995).

(2) Lateral surface of exoccipital without subvertical crest (0), with clear crest lying anterior to external foramina for hypoglossal nerve (1), or with clear crest present anterior to external foramina for hypoglossal nerve (2).

In the plesiomorphic archosaurian condition (e.g. Gower & Sennikov, 1996a), there is no lateral exoccipital crest or sharp ridge; the lateral surface is instead smoothly rounded. This condition appears to be retained in phytosaurs (although faint indications of a crest are perhaps sometimes present) and *S. galilei* (Alcober, 2000). A crest is present in some other rauisuchians, and perhaps in all aetosaurians and crocodylomorphs, with only the latter two taxa having external hypoglossal foramina positioned behind this ridge. This character is ordered 0-1-2 in this analysis, on the basis that the hypoglossal foramina lie on an anterolateral surface on the anterior of the exoccipital pillar in those taxa lacking a ridge.

(3) Ventral ramus of the opisthotic extends further laterally than lateralmost edge of exoccipital (0), or the converse arrangement (1).

Although the plesiomorphic condition of this character for archosauromorphs and archosaurians is clearly a laterally extensive ventral ramus of the opisthotic (Gower & Sennikov, 1996a), it seems likely that there

Table 1. Taxon-character matrix showing distribution of braincase character states among archosaurian taxa. See text for details of characters, taxa, and sources of data

	12345	1 67890	12345	2 67890	12345	67
<i>Proterosuchus fergusi</i>	00000	000??	00000	00000	?000?	00
<i>Garjainia prima</i>	00000	00000	00001	00000	?0000	00
<i>Euparkeria capensis</i>	00000	00000	00000	10010	00010	01
Phytosaurs	10000	00100	00000	10010	?0010	01
<i>Saurosuchus galilei</i>	21000	011??	0000?	10000	?001?	01
<i>Batrachotomus kupferzellensis</i>	21000	01110	0000?	00010	00101	11
<i>Tikisuchus romeri</i>	2??00	011??	0?00?	?10??	?????	?1
<i>Postosuchus kirkpatricki</i>	21100	01110	0000?	?101?	???1?	11
Aetosaurians	22111	011??	0000?	?00??	1111?	01
<i>Sphenosuchus acutus</i>	22111	11111	11112	10111	11111	01
<i>Dibothrosuchus elaphos</i>	22110	111??	11112	10111	11???	01
<i>Crocodylus</i> sp.	22111	11111	11112	10101	1111?	11

is some homoplasy in this character, at least within Archosauria. For example, within Erythrosuchidae *G. prima* (= *V. triplicostata*) possesses the plesiomorphic state, but *Erythrosuchus africanus* and *Shansisuchus shansisuchus* possess the derived state (Gower & Sennikov, 1996a: character 5; Gower, 1997). Within Crurotarsi, the derived state is found in crocodylomorphs and aetosaurians, but also marginally in *P. kirkpatricki* (pers. obs.).

(4) *Region of braincase between fenestra ovalis and posterior edge of occipital condyle relatively short along longitudinal axis (0), or elongated (1).*

There are clearly difficulties associated with delineating and recognizing 'short' from 'elongated', but this character is employed as an initial attempt to capture the observed variation. The derived state (1) is present in aetosaurians (e.g. Gower & Walker, 2002) and crocodylomorphs (e.g. Walker, 1990; pers. obs.), and thus covaries with the presence of exoccipital pillars in which the external hypoglossal foramina lie posterior to subvertical lateral ridges. The presence of the derived state does not covary with an elongated condylar stalk. In phytosaurs, for example, the stalk supporting the condyle is long but the actual exoccipital pillar and the region between the end of the condyle and the fenestra ovalis are not here considered to be elongated. A morphometric analysis has not been conducted, and future work might scrutinize this character in more detail.

(5) *Ventromedial surfaces of opposite exoccipitals do (0), or do not (1), meet along the midline on the floor of the endocranial cavity.*

Among the taxa considered here, the plesiomorphic state (0) covaries with the absence of a basioccipital contribution to the border of the foramen magnum (not always the case – see character 17 of Gower & Sennikov, 1996a), and midline contact between the opposite prootics. A single character is used here.

(6) *Pneumatization of bony elements of the middle ear cavity absent or restricted (0), or well developed (1).*

Well developed middle ear pneumaticity is here considered to be confined to sphenosuchian and crocodyli-form crocodylomorphs. Large median pharyngeal recesses (e.g. *P. kirkpatricki*, aetosaurians) and depressions on the lateral surfaces of the parabasisphenoid (e.g. *P. kirkpatricki*) are not considered to be unequivocal indications of extensive middle ear pneumatization, and are not here incorporated as part of the derived state (1) of this character. The sphenosuchian *S. acutus*, in contrast, is scored as derived because it has clear pneumatic sinuses that pass right through the parabasisphenoid and invade the basiptyergoid processes (Walker, 1990).

(7) *Medial wall of vestibule incompletely ossified (0) or almost completely ossified (1).*

As Gower & Weber (1998) point out, this character is problematic in terms of delineating clear character states because of largely unknown ontogenetic and individual variation in most taxa. However, while non-crown-group archosauromorphs have largely medially open vestibules (that were probably finished in unossified tissue), crocodylomorphs, aetosaurians, and rauisuchians have well ossified medial vestibule walls that form bony otic bullae. The situation in phytosaurs is not entirely clear, but individuals with an essentially completely ossified medial vestibule wall have not been observed or apparently reported, and so this taxon is scored as exhibiting the plesiomorphic state (0).

(8) *Semilunar depression on lateral surface of basal tuber of parabasisphenoid present (0), or absent (1).*

This structure is known only in non-crown-group archosauromorphs (see Gower & Sennikov (1996a: character 11), Gower, 1997, Gower & Weber, 1998).

(9) *Well defined recess for lagena/cochlea absent or short and strongly tapered (0), or present, and elongated and tubular (1).*

As discussed above, recognition of the derived state (1) is complicated by the probable continuation of the ventral end of the lagenar recess into the unossified gap between the ventral ramus of the opisthotic and the basal tubera of basioccipital and parabasisphenoid. Thus, while *G. prima* (= *V. triplicostata*) might be interpreted as having a potentially elongated lagenar recess, this is not a well defined structure that is clearly tubular in nature (Gower & Sennikov, 1996a) and this taxon is therefore scored here as possessing the plesiomorphic state.

(10) *Crista vestibuli absent (0), or present (1).*

The crista vestibuli is a term established by Hasse (1873: 721–722, pl. XXXIII, fig. 11) for the thin crest of bone that demarcates and partially separates the lagenar/cochlear portion of the ossified part of the otic capsule from the vestibular portion. Plesiomorphically in archosaurs (e.g. Walker, 1990; Gower & Weber, 1998), the lagenar region is at most only poorly differentiated. Even in crown-group archosaurs such as *B. kupferzellensis*, where the lagenar region is clearly observable (and a cochlea may even have been present), the demarcation between vestibule and lagenar/cochlear recess is nothing more than a change in angle of an essentially continuous surface. Crocodylians and the sphenosuchian *S. acutus* (the pronounced rim described by Walker (1990: 37, fig. 22)) share the derived presence of a crista vestibuli. The condition is

unknown in many fossil taxa, including aetosaurians. The derived condition is present also in at least extant birds (where it is variably developed; A. D. Walker, pers. comm.) and lizards (e.g. lagenar crest of Oelrich, 1956; inferior cisternal crest of Baird, 1970: 202). Currently orthodox views of amniote phylogeny suggest that these multiple occurrences (crocodilians, birds, lizards) are convergent, but this is worthy of further study.

(11) *Lagenar/cochlear prominence absent (0), or present (1).*

The cochlear prominence (Walker, 1990) is an external feature present on the prootic (and opisthotic) of extinct and extant crocodylomorphs (Walker, 1990; pers. obs.) whereby the lateral surface of the part of the braincase that forms the lateral wall of the lagenar/cochlear recess is locally thickened so as to mark externally the position of the recess. Walker (1990: 95) reports that it is also present in birds. No such feature is present in non-crown-group archosaurs or apparently in non-crocodylomorph crurotarsans (pers. obs.).

(12) *Distal end of the ventral ramus of the opisthotic does not, or barely, makes contact with prootic anteroventral to fenestra ovalis (0), or has extended contact with prootic (1).*

In the plesiomorphic condition (state 0; e.g. *G. prima* = *V. triplicostata*, Gower & Sennikov, 1996a; *Erythrosuchus africanus*, Gower, 1997; *Euparkeria capensis*, Welman, 1995), the ventral end of the fenestra ovalis is usually closed by brief (if any) opisthotic-prootic contact. This may be accompanied by much greater contact between opisthotic and parabasisphenoid. In the derived condition (state 1), there is much greater vertical contact between the prootic and the anterior surface of the distal end of the ventral ramus of the opisthotic immediately below the fenestra ovalis (e.g. *Sphenosuchus acutus*, Walker, 1990: fig. 28a).

(13) *Eustachian tubes not enclosed by bone (0), or partially or fully enclosed (1).*

In diapsids plesiomorphically, there is no indication in bony elements of the route taken by the eustachian tubes. This plesiomorphic condition is present in non-crown-group archosauromorphs and archosaurs (e.g. Gower & Weber, 1998) and is retained in many crurotarsan lineages. Within Suchia, only crocodylomorphs seem to show bony indications of the positions of the true eustachian tubes. In the sphenosuchian *Sphenosuchus acutus* there are open grooves (Walker, 1990), while the sphenosuchian *Dibothrosuchus elaphros* would appear to have at least partially enclosed lateral tubes (Wu & Chatterjee, 1993). The tubes are fully enclosed in bone in extant crocodilians.

(14) *Contact between quadrate and prootic absent (0), present (1).*

Prootic-quadrate contact is seen only in crocodylomorphs among non-crown-group archosaurs and crurotarsans. Sphenosuchians have nonsutural contact (e.g. Walker, 1990; Wu & Chatterjee, 1993), while a sutural articulation is present in extant crocodilians.

(15) *External foramen for abducens nerves between parabasisphenoid and prootic (0), within prootic only (1), within parabasisphenoid only (2).*

This character is unordered here because the relationship between the three states is unclear, at least within Archosauromorpha, where state 0 would seem to be the plesiomorphic condition (see also Gower & Sennikov, 1996a: character 3).

(16) *External foramina for passage of abducens nerves on underside of a horizontal surface (0), or on the anterior of a more vertical, upturned process (1).*

See character 4 of Gower & Sennikov (1996a).

(17) *Parabasisphenoid relatively short dorsoventrally (0), or substantially elongated in the region between the basal tubera and the basiptyergoid processes, such that the median pharyngeal recess is dorsoventrally extended and trough-like (1).*

Parrish (1993: 300) hypothesized that the derived state “posteroventrally open trough formed by elongated and conjoined basiptyergoid processes” is a synapomorphy of his *Rauisuchia* (= his *Rauisuchidae* + *Crocodylomorpha* + *Gracilisuchus stipanicorum*). Contrary to Parrish, this condition is not present in *B. kupferzellensis* (see above) or crocodylomorphs, and instead I consider it restricted to *P. kirkpatricki* and *T. romeri* among documented forms.

(18) *Basiptyergoid processes of moderate size (0), or markedly enlarged (1).*

In Archosauromorpha plesiomorphically, the basiptyergoid processes and basal tubera of the parabasisphenoid are of comparable size. The basiptyergoid processes of crocodylomorphs are much enlarged, to a point where they are clearly larger than the basal tubera of the parabasisphenoid.

(19) *Supraoccipital excluded from dorsal border of foramen magnum by dorsomedial midline contact between opposite exoccipitals (0), or supraoccipital contributes to border of foramen magnum (1).*

(20) *Pila antotica ossified mainly by prootic and laterosphenoid, such that laterosphenoid-basisphenoid contact is absent (0), or pila antotica ossified largely by laterosphenoid and basisphenoid, with contact occurring between these two elements anterior to the trigeminal foramen in the adult braincase (1).*

The derived state 1 is present in crocodylians, birds and lepidosaurs. A laterosphenoid ossification is absent in the latter group, but the basisphenoid contributes to the ossification of the pila antotica (e.g. Evans, 1986). This might be another multiple braincase convergence in these three extant groups (see brief discussion by Gower & Weber, 1998: 399).

(21) *Perilymphatic foramen with an incompletely ossified border (0), or border entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop (Walker, 1985), incorporating a loop closure suture (Walker, 1990: 37) with itself (1).*

State 0 is plesiomorphic for archosaurs based on the condition in, for example, *Sphenodon*, rhynchosaur (Benton, 1983; pers. obs.), *Prolacerta* (Evans, 1986) and non-crown-group archosaurs (e.g. Walker, 1990; Gower & Weber, 1998). Among crurotarsans, the derived state is present with certainty only in aetosaurians (Gower & Walker, 2002) and crocodylomorphs (Walker, 1990). A completely bony border to the perilymphatic foramen is also present (presumably convergently) in squamates and birds (Walker, 1990).

(22) *Perilymphatic foramen in a medial position and orientated so as to transmit the perilymphatic duct out of the otic capsule in a posteromedial or posterior direction (0), or foramen positioned more laterally so that duct is transmitted posterolaterally/laterally and the foramen is at least partly visible in lateral view (1).*

Walker (1985, 1990; see also Gower & Walker, 2002) recognized and highlighted this character. The plesiomorphic state (0) is present in *Sphenodon* among extant diapsids (pers. obs.) and in non-crown-group archosaurs (e.g. Gower & Weber, 1998; pers. obs.). It is also retained in several early crurotarsans including phytosaurs and rauisuchians. The presumably derived state is observed, among suchians, in aetosaurians (Gower & Walker, 2002) and crocodylomorphs (Walker, 1985, 1990). The condition in incompletely prepared or preserved fossil material can be determined from the orientation of the ventral ramus of the opisthotic.

(23) *Foramen for trigeminal nerve and middle cerebral vein combined and undivided (0), or at least partially subdivided by prootic (1).*

In Archosauria plesiomorphically (state 0), the prootic contribution to the trigeminal foramen is smooth and undifferentiated, even where the route of the middle cerebral vein can be detected on the inner wall of the prootic (e.g. *Erythrosuchus africanus*, Gower, 1997). In the aetosaurian *Stagonolepis robertsoni* (Walker, 1961, 1990), the anterior of the prootic has two embayments – for separate openings for the trigeminal nerve and middle cerebral vein. Crocodylomorphs (e.g. Walker,

1990; pers. obs. of dried crocodylian skulls) have a single foramen that shows some indication of at least a partial bony subdivision of the exits of the vein and nerve. A partial subdivision is also seen in *B. kupferzellensis*. The emphasis for this character is here placed on the prootic because the laterosphenoid is less well known in many fossils. Bony subdivision of nerve and vein represents some ossification within the region that lies between these structures. Future work might investigate how this varies (perhaps with ontogeny) within taxa.

(24) *Prominent subhorizontal ridge on lateral surface of prootic below trigeminal foramen present (0), or absent (1).*

This ridge has been interpreted as a possible site of origin for the m. protractor pterygoidei. It might be difficult to determine the state of this character in small or poorly preserved material (e.g. Gower & Weber, 1998: 377), but there is a clear difference between larger and well preserved material with, for example, *G. prima* possessing, and *S. acutus* lacking the ridge. The absence of the ridge (the derived state) might have different causes in different taxa. For example, both *Erythrosuchus africanus* (Gower, 1997) and *S. acutus* (Walker, 1990) lack the ridge, but in *S. acutus* this might be associated with the greatly reduced area between the trigeminal foramen and the crista prootica. This is another character that would benefit from further study, particularly drawing on information from extant taxa. This character was employed by Gower & Sennikov (1996a: character 6).

(25) *Auricular recess largely restricted to prootic (0), or extends onto internal surface of epiotic/supraoccipital (1).*

The plesiomorphic condition is clearly present in, for example, *E. africanus* (Gower, 1997), and less so in phytosaurs (pers. obs. of BMNH 38037) where the fossa seems to reach the supraoccipital, but without really extending onto it. In the derived condition (e.g. *B. kupferzellensis*, Fig. 8), the fossa extends a long way onto the epiotic/supraoccipital. In extant crocodylians, the auricular fossa is very shallow, if actually present, so that this taxon is scored as uncertain for this character.

(26) *Additional foramen passing above and into the dorsal end of the metotic foramen absent (0), or present (1).*

This foramen is interpreted as a possibly discrete passage for the posterior cerebral/cephalic vein (see above). It is present in at least *B. kupferzellensis*, *P. kirkpatricki*, and probably extant crocodylians (see above). This character is somewhat problematic on several levels. This area is often not well preserved,

prepared or clearly visible in fossil material. Additionally, its configuration in those taxa where it has been observed suggests that its presence might only be dependent on a small amount of additional ossification. For example, there seems to be an open groove here in *S. acutus* (Walker, 1990) and it is debatable how different this situation is to that in, for example, *B. kupferzellensis* other than slightly more ossification of the soft-tissue separating the vein from other structures passing through the metotic foramen, in the latter taxon. However, this feature seems clearly to be absent in, for example, *Sphenodon*, rhynchosaurs (e.g. Benton, 1983; pers. obs.), and non-crown-group archosaurs (e.g. Gower & Sennikov, 1996a; Gower & Weber, 1998), so that the derived condition, foramen present, might have evolved (perhaps more than once) only within Suchia.

(27) *Parabasisphenoid intertuberal plate present (0), absent (1).*

See character 2 of Gower & Sennikov (1996a).

Several characters that are not immediately pertinent to the scope of this study have not been included here. These are characters for which at least one of the states would be scored in only a single taxon included in this analysis and thus are parsimony uninformative. These include the large hemispherical median pharyngeal recess present in some aetosaurians (see Parrish, 1994: character 14; Gower & Walker, 2002); the median parabasisphenoid tubercle of *G. prima* (= *V. triplicostata*, see character 23 of Gower & Sennikov, 1996a); the small transverse hook-like processes on the posteromedial edge of the basiptyergoid processes of *T. romeri* (see above); the subdivided metotic fissure of crocodylians (see Gower & Weber, 1998), and many other characters present only in crocodylians among those taxa considered here.

Some other potentially informative characters are excluded here because of difficulties in formulating and/or recognizing states, particularly in small samples of imperfectly preserved fossils. These include the number of external foramina for the hypoglossal nerves, the presence of a discrete epiotic ossification, and the presence of a 'presphenoid' ossification.

ANALYSIS

These 27 characters were scored for 12 taxa and analysed using parsimony as implemented in PAUP* Version 4.0b6 (Swofford, 1998). Trees were rooted with *Proterosuchus*. A parsimony matrix randomization permutation tail probability test (Faith & Cranston, 1991) on 100 permutations of the complete data set resulted in a minimum possible score of 0.01. This allows rejection of the null hypothesis that the data are no more hierarchically structured than are com-

parable but random, phylogenetically uninformative data – a recommended minimum requirement of any matrix to be used for phylogenetic inference (Faith & Cranston, 1991). A Branch and Bound (BB) search recovered five most parsimonious trees (MPTs) of 37 steps in length. The strict consensus of these MPTs is shown in Figure 10. Support for each node on the strict consensus was measured using the decay index (Bremer, 1988; Donoghue *et al.*, 1992) and bootstrap proportions (Felsenstein, 1985), the latter based on 1000 BB replicates and a maximum of 100 trees held for each iteration. Significance of length differences between optimal and suboptimal hypotheses was tested for in PAUP using Templeton tests (Templeton, 1983).

PHYLOGENY

The phylogeny (Fig. 10) recovered from analysis of the braincase data presented in Table 1 is largely consistent with the currently orthodox view of archosaur phylogeny (Gower & Wilkinson, 1996; see also subsequent analysis by Benton, 1999). Thus, crocodylians and sphenosuchians comprise a crocodylomorph clade; raiisuchians, aetosaurians and crocodylomorphs form a clade to the exclusion of phytosaurs and noncrown-group archosaurs; *Euparkeria* is more closely related to the included crown-group taxa than is the representative erythrosuchid (*G. prima*). The outstanding area of disagreement between the present analysis and the current orthodoxy lies in the relative position of raiisuchians, aetosaurians, and crocodylomorphs. There is currently consensus (Gower & Wilkinson, 1996; Benton, 1999) that crocodylomorphs are more closely related to at least some raiisuchians (at least *Postosuchus*) than to aetosaurians. Braincase data analysed here instead support a sister-group relationship between aetosaurians (*Stagonolepis*) and crocodylomorphs, among the taxa included in this study. The most parsimonious interpretation of the braincase data analysed here does not support raiisuchian monophyly. However, this is the weakest part of the tree and some character incongruence, combined with missing data especially for *P. kirkpatricki* and *T. romeri*, mean that alternative arrangements of the raiisuchians can be enforced with small additions to tree length.

Bootstrap proportions and decay indices are good to reasonable (considering the size of the data set) for all nodes except those immediately adjacent to the raiisuchians *B. kupferzellensis*, *P. kirkpatricki*, and *T. romeri*. The most robust groupings in the unconstrained MPTs (those with a decay index $> + 2$) are a significantly ($P \leq 0.1$) better fit to the data than are at least some of the shortest trees not including these groupings (see Fig. 10).

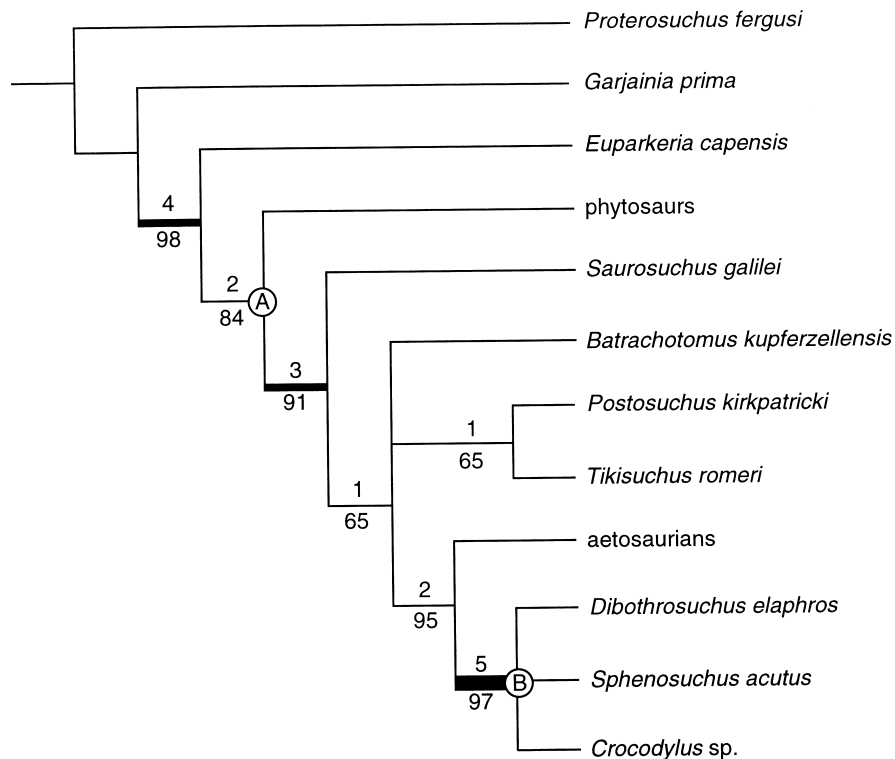


Figure 10. Strict consensus tree of five most parsimonious trees (MPTs) retrieved by parsimony analysis of data in Table 1. These MPTs have a length of 37 steps, a consistency index of 0.811, and a retention index of 0.889. Numbers above and below nodes represent decay indices and bootstrap proportions, respectively. Node A represents Crurotarsi (and all crown-group archosaurs here, in the absence of any ornithodiran taxa), node B represents Crocodylomorpha. The two nodes marked with medium thickness internal branches indicate that some (but not all) of the shortest trees not including those nodes are a significantly worse fit to the data than are the unconstrained MPTs (as measured by the Templeton test; $P \leq 0.1$). The single node (B) marked with the thickest internal branch indicates that all of the shortest trees not including that node are a significantly worse fit to the data than are the unconstrained MPTs. Constrained shortest trees lacking other nodes (thin internal branches) are not a significantly worse fit to the data.

BRAINCASE EVOLUTION

Although not all parts of the phylogenetic hypothesis recovered here (Fig. 10) are as robust as would be wished, this tree is used as the framework for a preliminary interpretation of crurotarsan, and especially suchian, braincase evolution. Missing data allows several alternative equally parsimonious optimizations for some of the characters on this tree. Focus here is on the acquisition of those characters that are derived for extant crocodylians but that are absent in non-crown-group archosaurs and in phytosaurs (the first branch off the crurotarsan lineage among those taxa considered here). Assuming that the currently orthodox view of the content of Crurotarsi and Ornithodira is correct, this therefore covers derived braincase characters that evolved after the divergence of the crocodylian- and bird-lineages from their last common ancestor. The conclusions presented here partly echo some

themes presented by Walker (1985, 1990; see also Gower & Walker, 2002).

Some derived crocodylian braincase features apparently absent in the last common ancestor of birds and crocodylians (see Gower & Weber, 1998) were probably acquired by the ancestral suchian, after the phytosaurs branched off the crocodylian lineage. These include a fully lateral position on the parabasisphenoid for the entrance of the cerebral branches of the internal carotid foramina, and a more completely ossified medial wall of the vestibular part of the otic capsule. A second suite of characters were acquired at some unknown point between the origin of the branch leading to phytosaurs and the origin of the last common ancestor of crocodylomorphs and aetosaurians. These are a well-defined and elongated lagenar/cochlear recess, a partial bony subdivision of the foramen for the passage of the trigeminal nerve and the middle cerebral vein through the braincase wall, and a

subvertical crest or ridge on the lateral surface of the exoccipital (and basioccipital). Some important derived features of the crocodylian otic region were acquired after the origin of rauisuchian lineages and before the origin of the last common ancestor of aetosaurians and crocodylomorphs. These include a complete perilymphatic loop, a posterolaterally directed perilymphatic foramen, greater prominence of the exoccipital lateral ridge (also acquired, perhaps independently, in *P. kirkpatricki*), passage of the hypoglossal nerve posterior to this exoccipital ridge, and an elongated region between the fenestra ovalis and the occipital condyle. Several derived crocodylian braincase features were acquired after the origin of the aetosaurian lineage but before the origin of the last common ancestor of crocodylomorphs, including a cochlear prominence, quadrate-prootic articulation, enlarged basiptyergoid processes, extensive tympanic pneumaticity, and at least partial bony enclosure of the eustachian tubes. Subsequent to the origin of sphenosuchian crocodylomorphs, ancestors to crocodylians evolved a subdivided metotic fissure (and associated discrete secondary tympanic window), a sutural articulation between the prootic and quadrate and the pterygoid and basiptyergoid process, and many other features (e.g. geniculate cochlear recess and others; see Walker, 1990).

DISCUSSION

There are several caveats associated with the findings of the current study. Firstly, the phylogeny of Mesozoic archosaurs is clearly still in need of further attention. Most of the characters analysed here not been used in previous studies of basal archosaur phylogeny and, while the phylogenetic hypothesis presented in Figure 10 might not be correct, these braincase data are certainly worthy of further investigation. For now, it might be noted that the unorthodox proposal that aetosaurians are more closely related to crocodylomorphs than are any rauisuchians also receives support from at least two detailed characters of the skull, namely the form of the palatine and the presence of a ventromedial process of the prefrontal (see Gower & Walker, 2002). Other caveats are that the promising phylogenetic signal in these braincase data has yet to be subjected to a wider range of archosaurian taxa. The phylogeny derived from braincase data might also be perturbed by the addition of other braincase characters. A further caveat is the preliminary nature of this study because braincase morphology is still not well understood in basal archosaurs. Good braincase specimens have not been found, prepared or described for many taxa and understanding of individual and ontogenetic variation is extremely poor even

in most of those taxa where good specimens have been documented.

These caveats aside, the main findings of the current study are that braincase morphology represents a relatively untapped resource of phylogenetic data. It suggests that aetosaurians are closer relatives of crocodylomorphs than any well known rauisuchian. Mapping braincase character states onto this phylogenetic framework suggests that some of the many derived features of the braincase of crocodylians were acquired successively in the evolution of the ancestors of crocodylians and successively larger clades including them and sphenosuchians, aetosaurians, rauisuchians, and phytosaurs, and that these evolutionary changes can be detected in the fossil record. Additional work is required to further flesh out and/or test this interpretation, and to extend the study to basal ornithomirans.

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