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New data on the braincase of the aetosaurian archosaur (Reptilia: Diapsida) *Stagonolepis robertsoni* Agassiz

DAVID J. GOWER and ALICK D. WALKER

Department of Zoology, The Natural History Museum, London SW7 5BD, UK

New data on the braincase of the aetosaurian archosaur *Stagonolepis robertsoni* Agassiz are presented, based on new preparation, synthetic casting, and interpretation of fossil material from the Triassic Elgin Sandstones, Scotland. The metotic fissure is not divided by bone. The perilymphatic foramen is completely bound by bone, and faces away from the otic capsule in a posterolateral direction. A prominent subvertical ridge on the anterolateral edge of the exoccipital and upper part of the basioccipital cannot be directly associated with the subcapsular process of the chondrocranium of extant crocodilians. This ridge projects laterally beyond the ventral ramus of the opisthotic, and lies anterior to the external foramina for the hypoglossal nerve. The overall structure of the braincases (especially the otic region) of *S. robertsoni* and other aetosaurians, where known, is more similar (in terms of derived archosaurian characters) to those of crocodylomorphs than are the braincases of other major suchian groups. This provides evidence for the currently unorthodox hypothesis that, among major suchian clades, Aetosauria and Crocodylomorpha are each others' closest relatives. Support for this hypothesis is found in features of the palatine and prefrontal that have not been considered in recent studies of suchian phylogeny. This alternative phylogenetic hypothesis demands further investigation but, combined with the new morphological data that it explains, it provides a framework for the understanding of the evolution of the derived and distinctive braincase structure of extant crocodilians. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society,* 2002, **136**, 7–23.

ADDITIONAL KEYWORDS: – Suchia – Crocodylomorpha – morphology – phylogeny – character evolution.

INTRODUCTION

Aetosaurians are a highly distinctive clade of Middle and Upper Triassic suchian archosaurs (e.g. Walker, 1961; Parrish, 1994; Heckert & Lucas, 2000). Their relationships to other major suchian groups, including crocodylomorphs, rauisuchians and ornithosuchians is currently unclear (Gower & Wilkinson, 1996). Phylogenetic relationships within Aetosauria are also mostly unclear, but there is currently consensus that *Aetosaurus* is the earliest branching genus to have been considered, and that *Stagonolepis* is one of the earliest branching genera among the non-*Aetosaurus* aetosaurians. Walker's (1961) monograph on *Stagonolepis robertsoni* made this one of the best known aetosaurian taxa, along with *Longosuchus meadei* (= *Typothorax meadei*) and *Desmatosuchus haplocerus*

(= *D. spurensis*). Since Walker's monograph, there have been few detailed studies of the (especially cranial) anatomy of other aetosaurians (but see study of *L. meadei* by Parrish, 1994). Further work on aetosaurian anatomy should improve estimates of aetosaurian in-group relationships and the phylogenetic position of the clade within Archosauria, thus paving the way for improved understanding of the group's evolution.

Braincase structure is relatively well known in some sphenosuchian and crocodyliform crocodylomorphs (e.g. Walker, 1990), but details are less clear for other groups of suchians, including aetosaurians. Greater knowledge of aetosaurian braincase structure will assist understanding of the evolution of suchian braincases – particularly the origin of the highly distinctive crocodilian pattern. Walker (1961) presented braincase data for *S. robertsoni*, but further preparatory, comparative, and interpretative work has since

Correspondence. David J. Gower. E-mail: D.Gower@nhm.ac.uk

been conducted. Brief comments regarding some of this new work were published (Walker, 1972, 1985, 1990) or privately distributed (by A.D.W.) as reprint annotations and summary correction sheets, but many details have never been formally or informally reported or their implications discussed. The aim of this communication is to present new information on the braincase of *S. robertsoni*, to comment on previous interpretations where relevant, and to place the new data in a broader context by assessing the implications they have for suchian phylogeny and braincase evolution.

TERMINOLOGY AND ABBREVIATIONS

Morphological terminology follows Gower & Weber (1998). Institutional abbreviations used are: BMNH, The Natural History Museum, London; ISI, Indian Statistical Institute, Calcutta; MCZD, University of Aberdeen Zoology Department; TMM, Texas Memorial Museum, Austin; TTUP, Texas Tech University Palaeontology Collection, Lubbock; UCMP, Museum of Palaeontology, University of California; ZMUC, Zoological Museum, University of Copenhagen.

Abbreviations used in more than one figure are as follows: bf – unidentified bone fragment, bo – basioccipital, bs – parabasisphenoid, eo – exoccipital, f – frontal, fo – fenestra ovalis, h – hole (artefactual) in specimen, lr – lateral ridge of exoccipital/basioccipital, ls – laterosphenoid, mf – metotic foramen, p – parietal, pf – perilymphatic foramen, pp – paroccipital process, pt – pterygoid, q – quadrate, sq – squamosal, vrop – ventral ramus of opisthotic, XII – foramen for hypoglossal nerve.

MATERIAL AND METHODS

Stagonolepis robertsoni is known from the Triassic Elgin Sandstones of Scotland (see Walker, 1961). The material under consideration here is the University of Aberdeen Zoology Museum specimen MCZD 2, collected in 1935 by George Thompson from the West Quarry, Lossiemouth. The MCZD prefix indicates that it was formerly in the collection of Marischal College, Aberdeen, Zoology Department (Walker, 1961). MCZD 2 is currently in various separate, articulating blocks of matrix numbered MCZD 2-1 to 2-7. Part 2-1 comprises postcranial material, while the skull is represented in parts 2-2 to 2-7. The skull (approximate length 19 cm, Walker, 1961: 111) has been somewhat dorsoventrally compressed during preservation. Preservation is unusual and variable. In parts, the bone surface is well preserved, allowing observation of some fine details. In other areas, the preserved bone has eroded away leaving faithful natural moulds in the hard, iron-rich sandstone. In some cases bone frag-

ments have been manually removed in order to fully prepare these natural moulds for the making of artificial casts. Preservation as bone and natural moulds occurs sometimes together in close proximity on the same block of matrix. Block 2-2 has two main surfaces; one shows, in bone, the anterior of the palate and upper jaws in ventral view (Walker, 1961: fig. 31), and the other is the underside of the anterior part of the skull roof, mostly preserved as a natural mould but with bone around the upper margin of the antorbital fenestra. An artificial cast of this surface is shown in Walker's (1961) fig. 30. Block 2-3 is the counterpart to the upper surface of 2-2, and shows a natural mould of the upper surface of the anterior of the skull roof. Walker (1961: fig. 27) showed an artificial cast of this. Block 2-4 is the bone of the left side of the posterior part of the skull, and this is the piece mostly under consideration here. Block 2-5 is currently in four separate, articulating blocks. It preserves, in a mixture of bone and natural moulds, the right side of the condylar and otic parts of the braincase, fragments of the anterior presacral vertebrae and dorsal osteoderms, and the right side of the posterior and middle parts of the skull. Block 2-6 is a natural mould of the anterior tips of the premaxillae, and block 2-7 is a natural mould of part of the ascending process of the right maxilla.

The main block of MCZD 2 that provides the basis for the new data presented here is MCZD 2-4 (Fig. 1; photographs presented by Walker, 1961: figs 26, 28, 29). Mechanical preparation of this block with a hand-held needle was undertaken in several phases by A.D.W. after 1961, right up to the middle of 1999. Additionally, a PVC cast (made by A.D.W. in 1979) was taken of the natural mould of the right otic region of MCZD 2-5, once all remnants of bone were removed. This is stored among the MCZD 2 material. Information gleaned from MCZD 2 was used in Walker's (1961: 123–127; figs 4, 5) description and composite reconstructions of the braincase of *S. robertsoni*. Apart from his 1961 paper, comments and/or figures on the braincase of this taxon were presented by Walker in subsequent papers in 1972, 1985 and 1990.

DESCRIPTIVE ACCOUNT

MCZD 2-4, LEFT SIDE OF BRAINCASE WITH BONE PRESERVED

Lateral aspect
Figure 2 shows the external surface of the left otic region in ventral view. The fenestra ovalis and metotic foramen lie within a 'stapedial groove' that broadens medially. This groove is bordered anteriorly by a strong crista prootica, and posteriorly by a subvertical lateral ridge on that part of the exoccipital that forms

Figure 1. *Stagonolepis robertsoni* Agassiz. General views of left posterodorsal corner of skull and braincase of MCZD 2-4 in (from top to bottom) lateral, medial, ventral and dorsal views. o = orbit; pf = postfrontal; po = postorbital; prf = prefrontal; utf = upper temporal fenestra. Scale bar in mm.
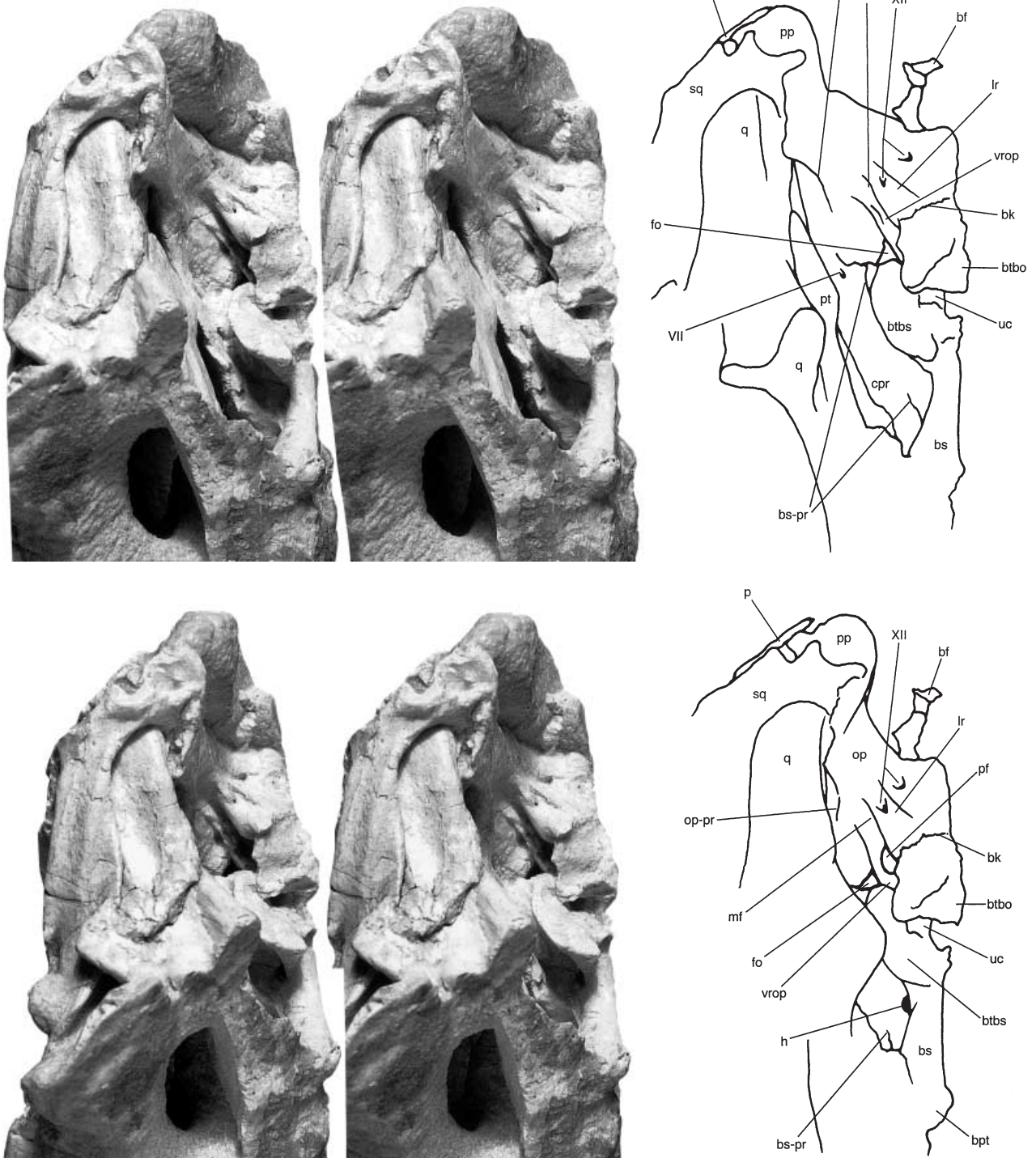
Figure 2. *Stagonolepis robertsoni* Agassiz. External view of left otic region of braincase of MCZD 2-4 in ventral (A) and posterolateroventral (B) views. Anterior is to the bottom of the figure. For scale see Fig. 1. bk = break in specimen; bpt = basipterygoid process; bs-pr = parabasisphenoid-prootic suture; btbo = basal tuber of basioccipital; btbs = basal tuber of parabasisphenoid; cpr = crista prootica; op = opisthotic; op-pr = opisthotic-prootic suture; uc = unossified channel/cleft; VII = foramen for facial nerve.

a pillar between the metotic foramen and foramen magnum. This ridge extends down onto the upper part of the basioccipital. The crista prootica harbours a posteriorly directed opening for the facial (VII) nerve. There is a small amount of local fracturing in this region and some small pits, but there only appears to be a single verifiable opening for the passage of this nerve. For example, a pit some 4 mm anteroventral to the undoubted facial foramen does not have any matrix in the bottom of it and cannot be verified as a second external foramen.

The fenstra ovalis is bound by the prootic, opisthotic, and parabasisphenoid. Fractures and associated telescoping of adjacent areas, as well as the position of the upper ends of the basal tubera of the basioccipital and parabasisphenoid, indicate that some preservational distortion has undoubtedly occurred in this region of the specimen. Thus it is not possible to accurately determine the original size and shape of the fenestra ovalis. The fenestra is separated from the metotic foramen by a slender, laminar ventral ramus of the opisthotic that is set back within the stapedial groove. The posterolateral edge of the ventral ramus of the opisthotic bears a shallow depression that is perhaps the result of preservational distortion. Towards its ventral end, the opisthotic ramus holds a large and rounded foramen that is interpreted as transmitting the perilymphatic duct. The ventral ramus is orientated such that its lateral edge lies further anterior than its medial edge. Thus, the perilymphatic foramen provides a posterolateral exit for the perilymphatic duct out of the otic capsule, and is partly visible in lateral view. The medial edge of the ventral ramus of the opisthotic is not complete, so that this left side of MCZD 2-4 does not provide decisive information on whether that part of the perilymphatic foramen enclosed in bone was open or closed medially (but see description below of synthetic cast of the right otic region of MCZD 2-5).

The metotic foramen reveals no indication of the embryonic metotic fissure having been subdivided by any bony structure. Thus, the glossopharyngeal, vagal, and accessory (IX, X, XI) nerves probably would have left a single bone-bordered opening. This means that there is no decisive indication that a secondary tympanic window or membrane was present, and thus there is no fossilized structure that can be termed fenestra rotunda/pseudorotunda. The metotic foramen is a dorsoventrally elongated slit, and its posterior border is formed by the subvertical ridge on the lateral surface of the exoccipital/basioccipital. As in crocodylomorphs (e.g. *Sphenosuchus acutus*, Walker, 1990; *Crocodylus* sp., pers. obs.), this ridge is situated at the anterior edge of the exoccipital pillar and lies in front of the external foramina for the hypoglossal nerve. In other suchian archosaurs (e.g. *Saurosuchus galilei*,

Alcober, 2000; *Batrachotomus kupferzellensis*, Gower, 2002b; *Parasuchus hislopi*, pers. obs. of ISI R44; other phytosaurs, pers. obs. of BMNH 38037; 42745 and TTUP 9230) an exoccipital ridge is absent, or more rounded and less pronounced. In these other taxa, the ridge (or lateralmost point of the exoccipital pillar) also lies relatively further back along the exoccipital and behind the external foramen/foramina for the passage of the hypoglossal nerve, which is generally close to the metotic foramen, on an anterolaterally rather than posterolaterally orientated surface. There are two foramina for the hypoglossal nerve on the left side of MCZD 2. The more posterior of these is larger and, despite some crushing here, it clearly lies a little above the level of the smaller, anterior opening, which is positioned on the posterolateral edge of the exoccipital ridge. The anteriormost foramen is considered to be too small to be likely to represent a distinct opening for the vagus nerve (X). The anterolateral position of the subvertical exoccipital ridge presents a posterolateral concavity on the outer surface of the exoccipital pillar.

Below the otic region, the preserved portions of the parabasisphenoid and basioccipital are partly crushed. Features distinguishable here include the flared parabasisphenoid tuber, the unossified cleft between this and the basioccipital tuber (a perhaps largely closed equivalent of the unossified gap in some earlier archosauromorphs and *Sphenodon*, see Gower & Sennikov, 1996, 1997; Gower & Weber, 1998), and the arched and concave ventral surface of the parabasisphenoid. A depression flanked by the ventral end of the crista prootica and the flared basal tuber of the parabasisphenoid represents the probable position of the entrance of the cerebral branch of the internal carotid artery into the braincase. There is a hole here that breaks through to the medial aspect of MCZD 2-4 that probably does not represent the actual cerebral internal carotid foramen (see description of medial aspect below). The prootic-parabasisphenoid suture can be detected just in front of this hole.

Further preparation from within the anterior end of the upper temporal fenestra of the left laterosphenoid and the ventral surface of associated dermal elements of the skull roof allow detail of this region to be added to existing descriptions. The anterolateral extent of the laterosphenoid makes contact with a depression on the ventral surface of the postfrontal, but it does not reach the postorbital. The dorsal part of the prootic is dorsoventrally crushed and partially doubled inwards, but a slender, subhorizontal, fractured bridge of bone can be seen dividing two foramina that are almost squeezed shut. A pair of openings here on each side in *S. robertsoni* were also described in BMNH R4787 by Walker (1961). Walker's (1961) original interpretation that the two openings were for the pas-

sage of different branches of the trigeminal nerve was later revised in favour of a hypothesis that the upper opening was for the middle cerebral vein (Walker, 1972: fig. 1(a), 1990: 88). Below the lower, trigeminal opening, the lateral surface of the prootic is relatively smooth, with no indication of a subhorizontal ridge such as that seen in some other Triassic archosaurs (e.g. Gower & Sennikov, 1996). The parietal dips down slightly, immediately above where the prootic and laterosphenoid make contact. The postorbital has become dislodged and pushed into the upper temporal fenestra. Unlike the larger specimens that formed the basis of Walker's (1961: 115) description of the postorbital of *S. robertsoni*, this element in the smaller MCZD 2 has an entirely smooth outer surface.

Medial aspect
Medially, the longitudinal fracture surface on MCZD 2-4 has exposed part of the endocranial cavity (Fig. 3).

Not many details are obtainable here, because a significant amount of dorsoventral crushing has occurred during preservation. However, information can be retrieved on several aspects that are unknown in other currently available specimens of *S. robertsoni*. This aspect of the specimen was only briefly described by Walker (1961: 126–127).

Posteriorly, the only exposed bone represents a fracture surface. Sutures (e.g. that between the basioccipital and parabasisphenoid) are not detectable on this surface. Recognizable landmarks include a window into the lower end of the metotic foramen and, in front of the ventral ramus of the opisthotic, part of the otic capsule immediately medial to the fenestra ovalis. From this point forwards, the endocranial cavity is more clearly exposed, but it also shows greater dorsoventral crushing. The ossified anterolateral margin of the vestibule of the otic capsule bulges into the cavity and, in front of this, the area of the trigeminal foramen can be detected, but the extent of crushing
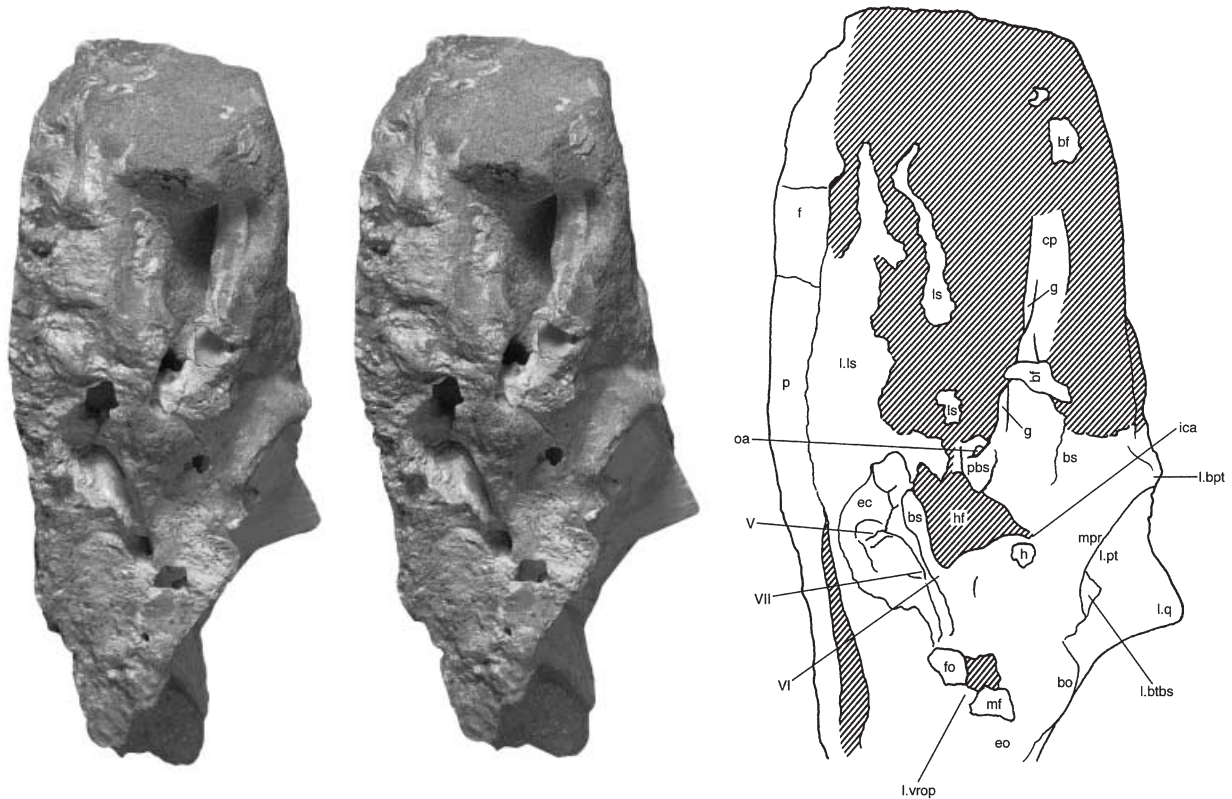

Figure 3. *Stagonolepis robertsoni* Agassiz. Medial view of left side of braincase of MCZD 2-4. The specimen has been longitudinally fractured close to the midline, revealing the cultriform process of the parabasisphenoid and the left side of the endocranial cavity. Areas of matrix are indicated by hatching. Anterior is to the top of the figure. For scale see Fig. 1. cp = cultriform process of parabasisphenoid; ec = endocranial cavity; g = groove; hf = hypophyseal fossa; ica = path of cerebral branch of internal carotid artery into hf; l.bpt = left basipterygoid process; l.btbs = left basal tuber of parabasisphenoid; l.ls = left laterosphenoid; l.vrop = left ventral ramus of the opisthotic; mpr = median pharyngeal recess; oa = foramen, possibly for orbital artery; pbs = prow of parabasisphenoid; V = position of foramen for trigeminal nerve; VI = position of path through floor of ec for abducens nerve; VII = position of depression, possibly leading to foramen for passage of facial nerve.

dictates that no actual opening is visible. Laterally, a small depression is positioned on the floor of the endocranial cavity, slightly overhung by the extreme anterior limit of the vestibule and behind the position of the trigeminal foramen. This seems too far posterior to be associated with the posteroventral lip of the trigeminal foramen and is instead possibly indicative of the position of the posterolateral passage of the facial nerve, through to the external foramen under the crista prootica. Approximately level with, and medial to this feature, an anteroventrally directed foramen pierces the subhorizontal floor of the endocranial cavity. This is interpreted as the channel for the left abducens (VI) nerve. It is notable in lying close to the midline (known from the block MCZD 2-2, which articulates with the front of block 2-4) and quite far back from the anterodorsal lip of the hypophyseal fossa. The floor of the endocranial cavity here appears to be formed by the parabasisphenoid. A bone fragment immediately in front of the hypophyseal fossa is probably a ventrally deflected piece of laterosphenoid.

The fracture exposing the left side of the endocranial cavity passes almost vertically through the hypophyseal fossa, which is still filled with matrix. The roof to the fossa, which is also the floor of part of the endocranial cavity, is thin. The posteroventral end of the fossa is close to a hole that breaks through to the lateral aspect of the specimen in the area where the entrance point of the cerebral branch of the internal carotid artery is expected to be. However, we do not think that this hole represents the actual foramen for this branch of the internal carotid artery. Instead, the matrix filled posteroventral corner of the pituitary fossa tapers to a fine channel that is seen to be passing to, or just beyond, the ventral edge of the hole (Fig. 3). This channel is interpreted as the actual path of the cerebral branch of the internal carotid artery. In addition, the hole in the specimen was slightly enlarged when bone was lost from its edge during preparation.

The anteroventral edge of the left laterosphenoid is visible above the hypophyseal fossa. The anterior process of this element was elongate and extended forward to articulate with the ventral surface of the frontal. Small fragments of adherent bone lie on the fracture surface, within what would be that part of the endocranial cavity enclosed by the anterior processes of the laterosphenoids. It is unclear whether these fragments originate from the left or right laterosphenoid. Below the hypophyseal fossa, the fracture through the specimen has exposed the left side of the midline ventral concavity that occupies the area between the basipterygoid process and basal tubera of the parabasisphenoid – the median pharyngeal recess *sensu* Witmer (1997a).

Immediately in front of the hypophyseal fossa, the cultriform process of the parabasisphenoid (Fig. 3) has been prepared from the right side to beyond the midline. It is the only part of the braincase for which the bone of both sides of the midline has been well preserved, so that a bilaterally symmetrical structure can be observed. Posteriorly, the parabasisphenoid sends up a subvertical prow of bone to demarcate the anteroventral border of the hypophyseal fossa. The prow is slightly more accentuated than indicated in Figure 3 because, during preparation, a small piece of bone was lost from its anteriormost point and it was not possible to replace it. A short distance from its base, the prow becomes abruptly narrow in transverse section, presenting a pair of longitudinal ledges either side of the midline that were perhaps closely associated with the passage of a nerve or blood vessel. The dorsal limit of the prow has not been exposed, but it extends to at least close to the anterodorsal end of the hypophyseal fossa.

Anteriorly, and close to either side of the midline, the base of the parabasisphenoid prow bears a pair of anterolaterally open foramina. The arrangement here, with a prow of bone at the anterior end of the hypophyseal fossa that is pierced by a pair of anterolateral foramina, bears a resemblance to the condition in the heron *Ardea cinerea* (pers. obs. of dried skull ZMUC CN.55). The function of these foramina in *S. robertsoni* is presently unclear. They are almost certainly too far forward, and are on the wrong side of the hypophyseal fossa, to be the external foramina for the abducens (VI) nerves, and they perhaps instead represent the exit route of the orbital arteries out of the hypophyseal fossa. The orbital artery (*sensu* Hochstetter, 1906) is present in adult crocodilians, birds and turtles, but only in early embryos of *Sphenodon* and lizards (see summary by Walker, 1990: 87). In those forms where it persists in adults, it branches from the cerebral branch of the internal carotid artery where this vessel anastomoses within the hypophyseal fossa. In the crocodile (Hochstetter, 1906), the orbital artery passes into the orbit in close association with the oculomotor nerve (III). Burda (1969): 370 describes in *Alligator* that 'Each internal carotid artery . . . sends off a fairly large orbital artery. The latter travels anteriorly a short distance and then emerges from the intracranial cavity by means of a special foramen at the anterior limit of the pituitary fossa.' It is unclear from this whether the special foramen lies within bone or unossified tissue, but Miall (1878: 15) describes the orbital artery as exiting the braincase through a membrane along with the oculomotor nerve. Otherwise, the literature is generally unclear regarding soft-tissue associations of variable (pers. obs.) foramina and notches in bone in the region of the hypophyseal fossa of crocodilians. The anatomy of the blood supply to the head

is poorly understood in extant archosaurs (Sedlmayr & Witmer, 2001), and further work is needed to ascertain whether the orbital artery has clear osteological correlates in crocodilians, and whether this can inform soft tissue reconstruction of this region in *S. robertsoni*. In birds, there are paired foramina for the exit of the orbital artery immediately in front of the hypophyseal fossa (e.g. Crompton, 1953; Baumel *et al.*, 1979). In reptile embryos (e.g. Bellairs & Kamal, 1981) and in birds (e.g. Crompton, 1953; Baumel *et al.*, 1979), this vessel is often termed the ophthalmic artery.

The slender part of the parabasisphenoid rostrum begins in front of the base of the prow. Preparation at this point is not complete enough to inform on the transverse section at the base, although here the lateral surfaces are sloped so that they face dorsolaterally, and the narrow dorsal edge bears a longitudinal groove either side of, and close to the midline. These dorsally open grooves taper as they travel forward a short distance in an anterolateral direction, maintaining contact with the dorsolateral edges of the rostrum. They are probably too far ventral to be associated with the foramina that are possibly for the orbital artery (which additionally extends laterally in *Alligator*, Burda, 1969) so that, if actually associated with a particular soft tissue, they were perhaps for attachment of part of the extrinsic musculature of the eyes. The left of these two grooves is damaged anteriorly, but the right groove dies out anteriorly at a point where the rostrum forms a dorsal gutter that gives the process a broad V-shaped transverse section. On the right dorsolateral edge, about 2 mm in front of

the end of the proximodorsolateral groove described above, a shorter, narrower groove passes out anterolaterally from the gutter to the dorsal edge of the rostrum. While it is possible that a small amount of bone may have been lost from the dorsal edge of this part of the rostrum during preparation, it seems unlikely that this is simply a continuation of the more posterior groove. The rostrum tapers but maintains its transverse section as it passes forwards to the anterior limit of the block MCZD 2-4, where it can be detected as a small V- to U-shaped section of bone within the matrix (Fig. 4).

MCZD 2-5, CAST OF NATURAL MOULD OF RIGHT OTIC REGION

One of the synthetic casts taken from the mould of the right otic capsule represented in MCZD 2-5 (Fig. 4) adds to the information on the otic region. In particular, the incomplete ventral ramus of the opisthotic is visible, situated in the furrow ('stapedial groove') between the lateral exoccipital ridge and the prootic/parabasisphenoid. The anterior edge of the cast portion of the opisthotic ramus ends in a small anteroventral spur, the natural mould of which was a little damaged in producing the cast. This spur forms the dorsal end of a smooth embayment toward the lower end of the cast part of the ramus. It is interpreted as representing the medial border of the perilymphatic foramen. This medial border was completely finished in bone, and incorporated with the observations of the lateral edge of the left opisthotic ramus of MCZD 2-4 (see above), it indicates that the perilymphatic fora-
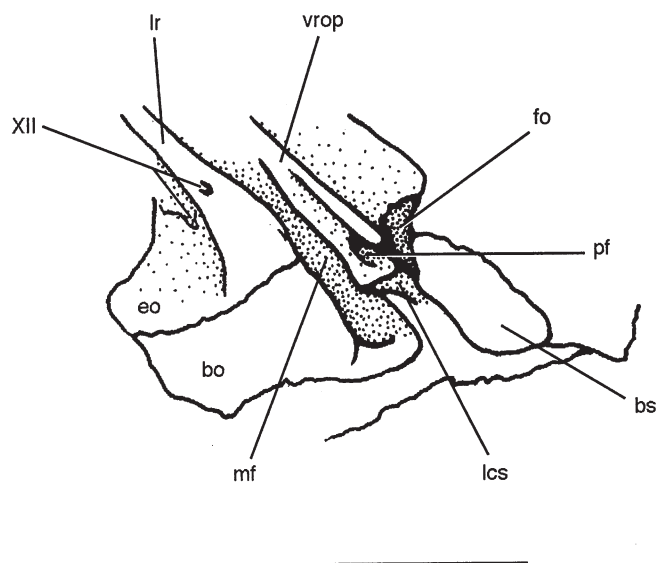

Figure 4. *Stagonolepis robertsoni* Agassiz. Incomplete synthetic cast of natural mould of right otic region in lateral view. Photograph and explanatory diagram not to same scale. Scale bar = 20 mm lcs = surface of loop closure suture.

men was surrounded by bone, rather than forming a medially open notch. The border of this foramen seems to have been formed entirely by the opisthotic. The ventral end of the cast of the opisthotic ramus ends abruptly at a flat surface that perhaps represents the position of the loop closure suture (Walker, 1990: 37, 111), where the opisthotic completes the border to the perilymphatic foramen by forming a suture with itself. Some of the fine details of this region were damaged through the loss of small pieces of matrix from the natural mould during the casting process. In addition, the surface of the synthetic cast made in 1979 has deteriorated. Thus some of the features described here were clearer than is now observable, as shown by detailed notes made by A.D.W. during preparation and casting.

The outer edge of the lateral exoccipital ridge is pierced by a small foramen (Fig. 4), probably for an anterior branch of the hypoglossal nerve, matching the condition on the left side. A further close correspondence is seen between the left and right otic regions in that they both indicate that the perilymphatic duct was transmitted in a posterolateral direction through the perilymphatic foramen, out of the otic capsule and into the base of the metotic foramen. Additionally, the cast is interpreted as indicating the dorsal end of the fenestra ovalis. As with the left side (Fig. 2), this opening would appear to lie medial to the lateral edge of that part of the ventral ramus of the opisthotic that separates it from the metotic foramen.

The larger, posterior opening for the main root of the hypoglossal nerve was isolated as a bar of matrix (that later broke away) during the removal of remnants of bone prior to casting of the mould. It passed straight through to the endocranial cavity well behind the medial opening of the metotic foramen, providing evidence that it was more probably for the hypoglossal nerve rather than being a distinct opening for the vagus nerve.

DISCUSSION

Previous descriptions of the braincase of *Stagonolepis robertsoni*

Walker (1985, 1990) interpreted the lateral ridge on the exoccipital pillar as an indication of 'some modest development of a subcapsular process' (Walker, 1985: 132). That the lateral exoccipital ridge might represent part of the subcapsular process in aetosaurians was followed by Parrish (1994: 200) for *Longosuchus meadei* and *Desmatosuchus haplocerus*. However, the details of the development of the embryonic subcapsular process of the crocodilian chondrocranium (Shiino, 1914) and its relation to ossified structures in the adult skull remain unknown (Walker, 1990: 33, 107). Gower & Weber (1998: 397) suggested that care must be taken not to associate fossilized structures with hypothetical chondrocranial structures purely through a common terminology. For that reason, the exoccipital ridge is here given a more neutral term and it is stressed that there is no intrinsic evidence that a subcapsular process *sensu stricto* had developed in embryonic *S. robertsoni*.

Walker (1985: 132) suggested that in *S. robertsoni* 'a secondary tympanic membrane was almost certainly present'. This interpretation was based on the posterolaterally opening, completely framed (with bone) foramen perilymphaticum and the development of a strong lateral exoccipital ridge. In extant crocodilians, these features are associated with a more laterally extensive part of the perilymphatic sac enclosed in bone, and a secondary tympanic membrane. Other suchian and noncrown-group archosaurs bear a closer resemblance in these hard-part features to *Sphenodon* (Walker, 1990: 111, Gower & Weber, 1998), which has an incompletely framed (with bone) and posteromedially directed perilymphatic foramen, and no specialized pressure relief window or membrane (e.g. Baird, 1960, 1970 and references therein). Gower & Weber (1998) argued that application of the term 'fenestra pseudorotunda', originally coined for the bony secondary tympanic window frame in crocodilians and birds (De Beer, 1937), requires evidence of a bony subdivision of the metotic fissure. This is lacking in *S. robertsoni* and in sphenosuchian crocodylomorphs such as *Sphenosuchus acutus* (Walker, 1990). The otic capsule of *S. robertsoni* clearly approaches that of crocodilians in terms of some derived features, including some of those structures closely associated with the secondary tympanic window and membrane of extant crocodilians. However, Walker's hypothesis that *S. robertsoni* possessed a secondary tympanic membrane is based on some possible osteological correlates, such as the lateral ridges surrounding the posterolateral exit for the perilymphatic duct, but not the probably most important correlate, namely the bony subdivision of the metotic fissure. It therefore pushes the limits of a level II inference *sensu* Witmer (1995a: 28), in which 'the soft tissue expected to occur in a fossil taxon is found in its extant sister group but not in any other [immediate] outgroups'. A secondary tympanic membrane may well have been present in a large range of extinct archosaurs, but inferring one with confidence is impeded by several immediate and interconnected problems. Finding unequivocal osteological correlates for this soft tissue structure in extant taxa is problematic. Although the metotic fissure becomes subdivided by a bony structure in all extant sauropsids in which a secondary tympanic membrane is present (unlike the situation in Triassic archosaurs), only *Sphenodon* among major groups lacks a secondary

tympanic membrane (and subdivided fissure). Furthermore, the use of extant phylogenetic brackets (Witmer, 1995a) must be carried out in a controlled way because at least lizards, crocodilians, and birds all seem to have independently evolved a secondary tympanic window (e.g. Rieppel, 1985; Gower & Weber, 1998), and perhaps membrane.

Walker (1990: 111) reported that the lagenar region of *S. robertsoni* was imperfectly preserved in the available material, but considered that it 'does not appear to have been significantly elongated'. 'Significantly' here means with respect to the relatively short lagenar region of, for example, noncrown-group archosaurs (Walker, 1990; Gower & Sennikov, 1996; Gower, 1997; Gower & Weber, 1998) and the relatively elongate lagenar recess of *Sphenosuchus acutus* (Walker, 1990) and crocodilians (with the associated development of a cochlea). The lagenar region of *S. robertsoni* remains unknown in detail, but reconsideration and further comparison with other fossil archosaurs suggests that it is premature to remark on the probable length or form of this particular feature. For example, the close association between a recess for the lagena and an incompletely ossified region between the distal end of the ventral ramus of the opisthotic and the basal tubera of basioccipital and parabasisphenoid in as wide a range of taxa as *Sphenodon*, erythrosuchids, *Euparkeria capensis*, *Batrachotomus kupferzellensis*, crocodilians and birds (Walker, 1990; Gower & Sennikov, 1996; Gower & Weber, 1998; Gower, 2002b), suggests that determining the length of the lagenar/cochlear recess from external proportions can be problematic. Additionally, the medial view of MCZD 2-4 (Fig. 3) shows that some matrix remains in place at the anteroventral end of the ventral ramus of the opisthotic. This might be plugging the dorsal end of the lagenar recess, but it has been left in place in order to protect the delicate opisthotic ramus and perilymphatic foramen. Even if it was removed, some distortion in this region (as seen in lateral view) means that it might not be feasible to trace a recess that originally may only have been a gap between elements.

Walker (1961: 125) suggested that the channel transmitting the cerebral branch of the internal carotid into the hypophyseal fossa also transmitted the palatine branch of the facial nerve plus the palatine artery. However, a Vidian canal like that of extant squamates, where a bony channel transmits the palatine artery plus the palatine ramus of the facial nerve, is absent in noncrown-group and crurotarsan archosaurs. Thus, like the situation in *Sphenodon* (Säve-Söderbergh, 1947) and that reconstructed for the archosaurs *Erythrosuchus africanus* (Gower, 1997) and *S. acutus* (Walker, 1990: fig. 49), the palatine ramus of the facial nerve (plus palatine artery, if present) of *S. robertsoni* passed forwards to

the base of the cultriform process of the parabasisphenoid along an unenclosed channel between the basipterygoid processes, on the ventral surface of the parabasisphenoid. The palatine artery is absent in extant crocodilians (Shindo, 1914).

COMPARISON WITH OTHER AETOSAURIANS

Parrish (1994) figured and described the braincase of a single specimen (lectotype TMM 31185-84B) of the aetosaurian *Longosuchus meadei*. This material has been reexamined by one of us (D.J.G.) and we largely concur with Parrish's description and figures. However, no suture could be discerned between the laterosphenoid and 'orbitosphenoid'. Instead, all of the structure labelled 'ls' and 'os' in Parrish's figure 5 is here interpreted as laterosphenoid, with the 'os' component simply representing an elongate laterosphenoid anterior process. The subvertical ridge depicted (Parrish's figs 4, 5) as lying between laterosphenoid and orbitosphenoid is probably homologous with the ridge on the capitate process of the laterosphenoid recognized in a wide diversity of basal archosaurians (e.g. Clark *et al.*, 1993; Gower & Sennikov, 1996; Gower, 1997). The basis for other claims of such additional ossifications in suchians, and perhaps crurotarsans as a whole, needs to be reviewed (see also Gower, 2002b). The lack of compelling evidence for the presence of a supernumerary ossification in front of the laterosphenoid in *L. meadei* may have implications for Parrish's (1994: 204–205) discussion of functional aspects of the aetosaurian skull. Clack's (1997: 206–207) interpretation that Parrish's (1994) braincase description indicates that 'the fenestra vestibuli [ovalis] and metotic foramen are only barely separated, while the pressure relief [secondary tympanic] window is confluent with the latter' is perhaps intended to reconcile the lack of any observable structure that represents a secondary tympanic window with the implied assumption that a secondary tympanic membrane was present.

Overall, the braincase, and especially the otic region, of *L. meadei* closely matches that of *S. robertsoni*. There is a strong ridge on the anterolateral edge of the exoccipital pillar, the metotic fissure appears not to have been subdivided, and the ventral ramus of the opisthotic is recessed relative to the crista prootica and lateral edge of the exoccipital.

The braincase of *Desmatosuchus haplocerus* (= *D. spurensis* following Gregory, 1953) was described by Case (1922), and an endocranial cast of the same taxon was described and interpreted by Case (1921, 1922) and Hopson (1979). Walker (1961: 180) stated that Case's description indicates that the braincase of *D. haplocerus* 'is extremely like that of *Stagonolepis*, but shorter'. Following his (now revised – see above) interpretation of the situation in *S. robertsoni*, Walker

went on to interpret two pairs of foramina in the hypophyseal fossa region of the parabasisphenoid of *D. haplocerus* (Case, 1922: 31) as representing openings for the cerebral branches of the internal carotid arteries and the palatine branches of the facial nerves plus the palatine arteries. However, the probable absence of true Vidian canals in archosaurs (see above) means that Hopson's (1979: fig. 9) interpretation of the upper pair of foramina being for the abducens nerves is here deemed more probable.

Parrish (1994: 200) described a prominent lateral exoccipital ridge in the *D. haplocerus* specimen UCMP A269 131056, and Walker (1990: 111) noted that the part of ventral ramus of the opisthotic separating the fenestra ovalis and metotic foramen appears to be more prominent than that of *S. robertsoni* based on Case's (1922) figure 7. Case also figured the parabasisphenoid as possessing a dorsal prow at its base. This appears to be less dorsally extensive than that described for *S. robertsoni* here, but neither of us has directly observed the *D. haplocerus* material figured by Case, and it is unclear if this region is completely preserved.

Sawin (1947: 208–210) included the braincase of *Typothorax meadei* (referred to *L. meadei* by Hunt & Lucas, 1990) in his description of that taxon, but sutures were not observed in the material he studied. Parrish (1993: fig. 2B) figured a sketch of the braincase of '*Stagonolepis robertsoni*' to illustrate the path of the cerebral branch of the internal carotid artery through the parabasisphenoid. It might be noted that the specimen forming the basis of this diagram (UCMP 27414, from the Chinle Formation of Arizona) has been referred to *S.* (= *Calyptosuchus*) *wellesi* by Long & Murry (1995), and that the taxonomy of this material is a matter of debate (e.g. Heckert & Lucas, 2000: 1555).

This brief review of the small amount of comparative data available for other aetosaurian taxa suggests that there was a conserved pattern in at least some aspects of braincase structure within the clade. Although these data are far from comprehensive, they do pertain to what are currently considered both relatively earlier (*Stagonolepis*) and later (*Longosuchus*, *Desmatosuchus*) branching lineages, and thus it can be tentatively hypothesized that the groundplan of the last common ancestor of at least non-*Aetosaurus* aetosaurians possessed a combination of features that are plesiomorphic (e.g. an undivided metotic fissure) and apomorphic (e.g. lateral exoccipital ridge anterior to the external foramina for the hypoglossal nerve) for suchians.

Future examination of braincase structure in aetosaurians lying outside the clade formed by all descendants of the last common ancestor of the three genera discussed here (*Stagonolepis, Desmatosuchus, Longosu-*

chus) will be informative regarding the groundplan condition for the radiation as a whole. Obvious target taxa are *Aetosaurus (*sister-taxon to all other aetosaurian genera in the consensus phylogeny of Harris *et al*., 2002) and perhaps the yet to be described 'carnivorous aetosaur' (Murry & Long, 1996). The latter taxon might be expected to lie outside a clade comprising other known aetosaurians by virtue of its plesiomorphic dentition, although it is from the Upper Triassic and therefore not among the oldest known aetosaurians.

Although known aetosaurian braincases exhibit similar overall structure, it is currently uncertain whether there are clear braincase synapomorphies for the whole clade or a subset of its constituent taxa. Parrish (1994: character 14) proposed that, among aetosaurian genera, *Longosuchus* and *Desmatosuchus* share a 'deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basipterygoid processes'. The same character could not be scored for six of the other included genera, and the remaining genus, *Stagonolepis*, was scored as exhibiting the plesiomorphic state of lacking this feature. The 'fontanelle' described by Parrish is the median pharyngeal recess of Witmer (1997a). A recess in the posteroventral surface of the parabasisphenoid is possibly present in at least all Triassic archosaurs, including noncrown-group taxa (e.g. Gower & Sennikov, 1996; Gower & Weber, 1998), so that it can only be the particular form of this fossa that might be a synapomorphy of a more restricted clade within Aetosauria. The parabasisphenoid of all aetosaurians, where known, shows a condition in which the basipterygoid processes are not much below the level of the basal tubera and a large median pharyngeal recess occupies the central region between these structures. More taxa need to be assessed in greater detail before aetosaurian braincase synapomorphies can be confirmed. Sutural details, in particular, remain very poorly known.

IMPLICATIONS FOR SUCHIAN PHYLOGENY

There are several derived (for Suchia) braincase features shared by crocodylomorphs and aetosaurians which are absent in other major crurotarsan groups such as rauisuchians (*sensu* Gower, 2000) and phytosaurs: perilymphatic foramen entirely bordered by bone with an associated loop closure suture in the ventral ramus of the opisthotic; posterolateral rather than posterior/posteromedial path of route of perilymphatic duct out of otic capsule; external foramina for hypoglossal nerve posterior to a lateral exoccipital ridge. Additional, potentially shared derived braincase features of aetosaurians and crocodylomorphs (that need further consideration) are a lack of midline contact of
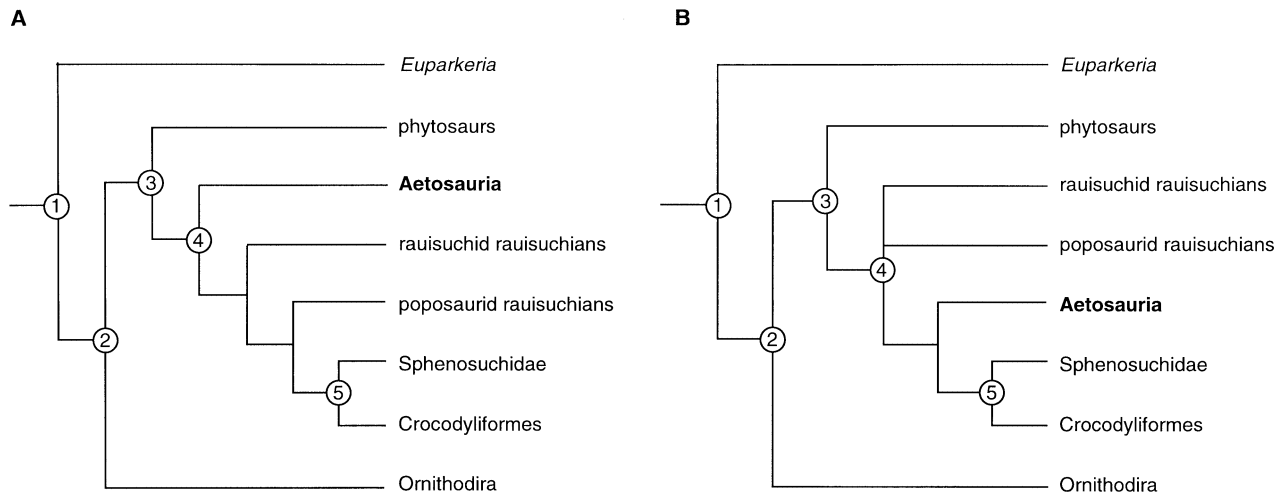
Figure 5. Alternative hypotheses of phylogenetic relationships of aetosaurians to other major clades of Crurotarsan archosaurs. (A) Currently orthodox hypothesis based on the five most recent numerical cladistic analyses (see Gower & Wilkinson, 1996; Benton, 1999) in which aetosaurians are more distantly related to Crocodylomorpha than are at least some rauisuchians. (B) Currently unorthodox hypothesis forwarded here for further consideration, in which aetosaurians are the major archosaurian clade most closely related to Crocodylomorpha. Sphenosuchia may not be monophyletic (e.g. Clark *et al.*, 2001). Some taxa of uncertain affinity are not shown here including Ornithosuchia and *Gracilisuchus stipanicicorum*. Labelled nodes: (1) Archosauria (2) crown-group archosaurs = Avesuchia (Benton, 1999) (3) Crurotarsi (4) Suchia (5) Crocodylomorpha.

the exoccipitals on the floor of the endocranial cavity, and the relatively elongate region comprised of that part of the exoccipitals and basioccipital posterior to the metotic foramen. These shared derived features (for more detail and a broader phylogenetic context, see Gower, 2002b) provide evidence that aetosaurians and crocodylomorphs are more closely related to one another than either clade is to other major crurotarsan groups (Fig. 5B). Additionally, there seem to be no braincase features that contradict this relationship (see Gower, 2002b). Although there is little consensus regarding the interrelationships of the major suchian clades (see Gower & Wilkinson, 1996; the subsequent archosaur phylogeny presented by Benton, 1999), there have been no proposals that crocodylomorphs and aetosaurians are each others' closest relatives, in a cladistic sense. Instead, it has been consistently hypothesized, since Gauthier (1986) and Benton & Clark (1988), that crocodylomorphs are more closely related to poposaurid rauisuchians (in the guise of *Postosuchus kirkpatricki*) than to aetosaurians (Fig. 5A). Although there is some consensus on the currently orthodox view, the trees forwarded by individual analyses are not particularly robust (Gower & Wilkinson, 1996). Thus, we propose that the hypothesis suggested from our interpretation of braincase structure, that Aetosauria and Crocodylomorpha are sister taxa among the major crurotarsan groups, merits closer examination and testing against other characters.

A full reanalysis of crurotarsan phylogeny based on data from all regions of the skeletons of these taxa is beyond the scope of this contribution, but two details of cranial osteology that support a crocodylomorph–aetosaurian sister-group relationship are discussed briefly here. Among crurotarsans, Witmer (1997b: 16) recognized two basic types of palatine morphology with respect to the extent of the dorsal fossa for attachment of the dorsal part of the pterygoideus muscle. In one type, the dorsal fossa extends far anteriorly, up to the pila postchoanalis. This is present in, for example, the non-crown-group archosaur *Erythrosuchus africanus* (Gower, 2002a), phytosaurs (Witmer, 1997b), the ornithosuchian *Ornithosuchus longidens* (Walker, 1964; Witmer, 1997b), and the rauisuchians *Batrachotomus kupferzellensis* (Gower, 1999) and *Saurosuchus galilei* (Alcober, 2000). The dorsal fossa is more restricted in the other type, in that it does not extend very far anteriorly along the upper surface of the palatine. This is seen in crocodylomorphs (e.g. *Sphenosuchus acutus*, Walker, 1990; Witmer, 1997b) and aetosaurians (e.g. *S. robertsoni*, Walker, 1961; Witmer, 1997b; *L. meadei*, *D. haplocerus*, Witmer, 1997b). Witmer (1997b: 16) suggested that the first type mentioned here, found outside of aetosaurians and basal crocodylomorphs, was widespread among archosaurs and that it 'may well be the primitive condition'.

A feature currently interpreted to be a synapomorphy of sphenosuchian plus crocodyliform crocodylo-

morphs (e.g. Clark *et al.*, 2001), is a prefrontal with a ventromedial process that projects into the antorbital cavity (e.g. Iordansky, 1973; Walker, 1990; Witmer, 1997b). Walker (1961: 115, 1990: 102) described a descending near-midline process on the prefrontal of *S. robertsoni*, and Witmer (1997b: 16) believed that a 'prefrontal flange' is 'somewhat developed' in *D. haplocerus* and *L. meadei*. Parrish (1994) described the flange in *L. meadei* (TMM 31185-84B) as being formed by the lacrimal, but it may be mostly prefrontal (D.J.G., pers. obs.). Thus, although developed to differing degrees, aetosaurians and crocodylomorphs share the derived presence of a ventromedial prefrontal process. Witmer (1997b) interpreted a foreshortened dorsal palatine fossa and a prefrontal ventromedial process as osteological correlates of the position of the anterior end of the dorsal pterygoideus muscle. The prefrontal process might be associated with the posterior end of the cartilaginous nasal capsule, and it dictates that the pterygoideus was restricted to the ventral part of the postnasal fenestra (*sensu* Witmer, 1995b, 1997b).

Assuming that the noted shared features are homologous, palatine and prefrontal morphology provides evidence of a sister-group relationship of crocodylomorphs plus aetosaurians, exclusive of other major crurotarsan clades. As with the possible braincase synapomorphies discussed above, these are features that have not been included in recent numerical cladistic analyses of the phylogeny of Mesozoic archosaurs, and they certainly merit further study for that reason alone. If rauisuchians such as *B. kupferzellensis, P. kirkpatricki,* and *S. galilei* are more closely related to crocodylomorphs than are aetosaurians, then the distribution of derived braincase, palatine and prefrontal characters shared by crocodylomorphs and aetosaurians will need to be explained as homoplasy. It might be noted that some of the derived braincase characters outlined here have probably evolved independently in the ancestry of squamates and the ancestry of birds, so that the possible phylogenetic signal certainly needs to be investigated further. Important caveats for the current proposal, beyond the restricted number and range of characters considered, are the lack of braincase data for possibly important crurotarsan taxa such as *Gracilisuchus* and Ornithosuchia.

Walker did not previously use an explicitly cladistic approach in considerations of phylogeny, but instead adopted a more traditional consideration of possible ancestor-descendent relationships. Thus, while advocating that among 'thecodontians', aetosaurians came closest to crocodylomorphs in terms of derived braincase features (Walker, 1990: 111), the clear monophyly of Aetosauria precluded any aetosaurian from being considered to be the direct ancestor of any crocodylo-

morph. Walker's (1985, 1990) ideas have been developed and here presented in a cladistic context to both propose the hypothesis that Aetosauria and Crocodylomorpha are sister taxa, and to explore the consequences this has for the interpretation of braincase evolution.

IMPLICATIONS FOR SUCHIAN BRAINCASE EVOLUTION

Walker (1985, 1990) recognized derived similarities among crocodylomorph and *S. robertsoni* braincases, especially with regard to the otic region. However, in addition to not considering a cladistic phylogenetic hypothesis of relationships, Walker did not explicitly consider character optimization on a tree as a basis for interpreting suchian braincase evolution. A more explicit phylogenetic approach enables derived similarity in crocodylomorph and aetosaurian braincases to be interpreted as synapomorphies – derived characters that were present in the last common ancestor of the two clades (and that provide evidence that the two clades are each others' closest relative).

Walker's (1972, 1985, 1990) documentation of variation in the otic region of crocodylomorphs and various other archosaurs formed the basis of a scenario hypothesizing how the distinctive crocodilian otic region evolved from that of a more generalized diapsid condition. The main derived features of the crocodilian otic region explained by this scenario are the presence of a secondary tympanic membrane and window (fenestra pseudorotunda), the lateral exoccipital/basioccipital ridge, and the formation and orientation of the perilymphatic foramen. Walker's scenario proposed that the gradual changes that these structures underwent were the formation of a completely ossified border to the foramen perilymphaticum (and the development of a loop closure suture), its rotation to a more posterolateral rather than posteromedial exit from the otic capsule, and the addition of bone to the lateral edge of the exoccipital ridge. These changes may have all been correlated with the increased lateralization of the perilymphatic duct, a perilymphatic sac that is supported by/enclosed in bone for a greater lateral distance away from the otic capsule, and perhaps the formation of a secondary tympanic membrane.

A fuller investigation of early suchian braincase evolution is presented by Gower (2002b), and a brief summary is given here. Interpretation of character evolution depends on the particular phylogenetic hypothesis used as a framework. In the present case, there are two alternative interpretations to consider. If the orthodox (Fig. 5A; see Gower & Wilkinson, 1996) view of suchian phylogeny is correct, then the derived similarity shared by aetosaurians and crocodylomorphs has either evolved convergently, or was present in
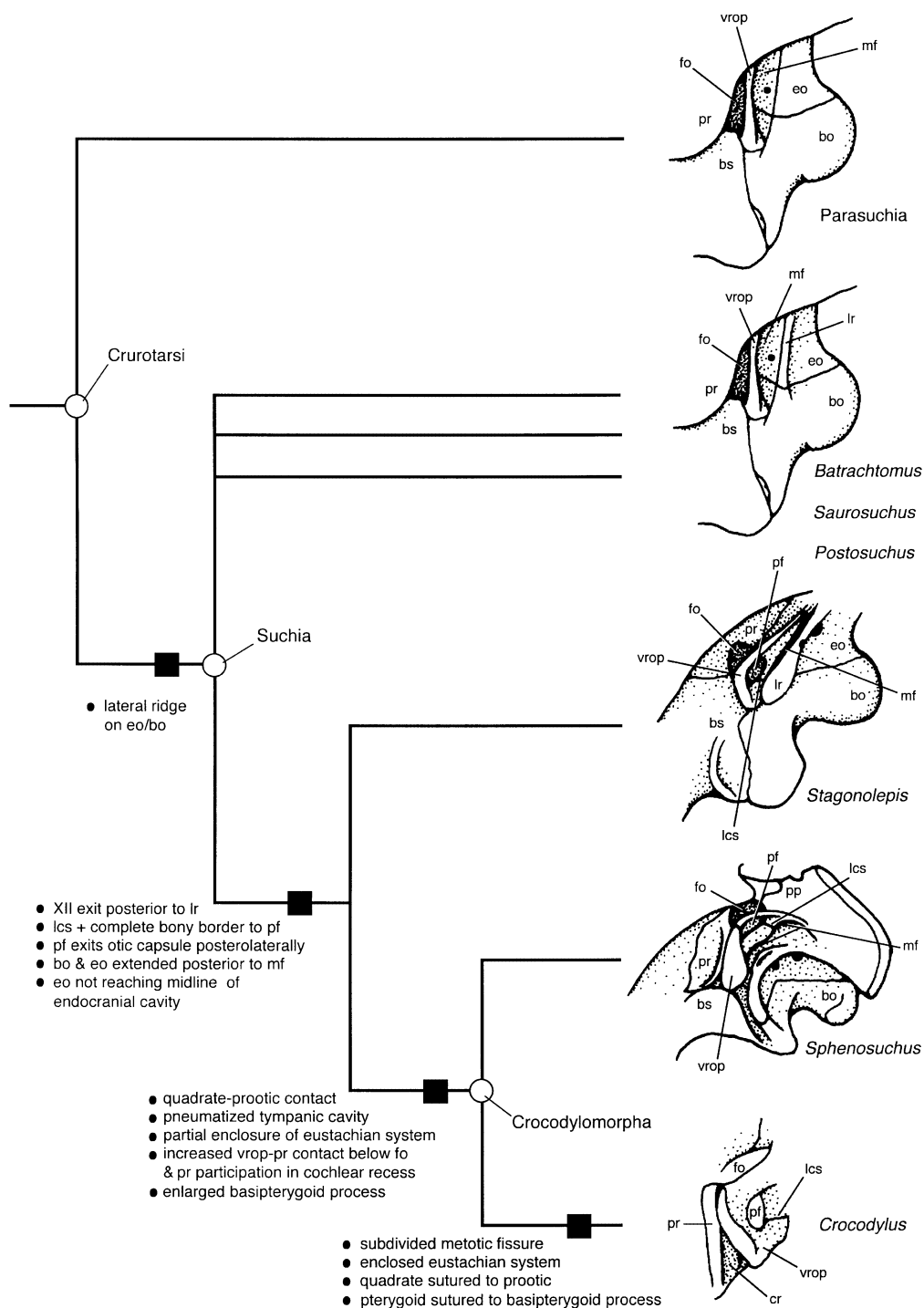
Figure 6. Summary of hypothesis of suchian braincase evolution, based on phylogeny presented in Fig. 5B and morphological and phylogenetic evidence presented in text. Key caveats include the omission of ornithosuchians and *Gracilisuchus stipanicicorum* from consideration. Schematic figures depict the left otic region in lateral view. Some proposed braincase synapomorphies are shown on some branches – for a broader context and consideration of more characters, see Gower (2002b). *Sphenosuchus* redrawn from Walker (1990), *Crocodylus* redrawn from Gower & Weber (1998). For *Crocodylus*, only the detail of the ventral ramus of the opisthotic is shown. The metotic foramen does not exist because the metotic fissure is subdivided so that the external foramina for the vagus nerve (X) lies far posterior to the ventral ramus of the opisthotic. External foramina for the hypoglossal nerve (XII) are indicated by solid black dots. cr = cochlear recess; lcs = loop closure suture of ventral ramus of the opisthotic; pr = prootic. Diagrams not drawn to scale.

their last common ancestor and subsequently lost in those taxa more closely related to crocodylomorphs. Alternatively (Fig. 5B), if aetosaurians are more closely related to crocodylomorphs than are rauisuchians (or at least those rauisuchians for which braincase structure is adequately known, if the group is not monophyletic – see Gower, 2000), then shared derived braincase features among suchians can be interpreted as homologies. This second alternative is explored here, and braincase character evolution is mapped onto a tree in which Aetosauria and Crocodylomorpha are sister taxa (Fig. 6).

The braincase of the ancestral crurotarsan had an undivided metotic fissure, a short and/or poorly demarcated lagenar region, a posterior or posteromedially opening perilymphatic foramen with an incompletely ossified border, and lacked a lateral ridge on the exoccipital/basioccipital. The ancestral suchian differed from this pattern in that it had evolved a lateral exoccipital ridge posterior to the external foramina for the hypoglossal nerve, and a longer and more clearly demarcated lagenar region. Changes in the perilymphatic foramen, and in the relative position of the exoccipital ridge and external foramina for the hypoglossal nerve characterize braincase evolution that occurred on the internal branch leading to the last common ancestor of aetosaurians and crocodylomorphs. The ancestral crocodylomorph further evolved tympanic cavity pneumatization and partial bony enclosure of the eustachian tubes, quadrate-prootic articulation, enlarged basipterygoid processes and an increased association between the prootic and the ventral ramus of the opisthotic plus the cochlear recess. Characters subsequently acquired by the last common ancestor of crocodilians include enclosure of the eustachian tubes, sutural contacts between quadrate and prootic and between pterygoid and basipterygoid process, and a bony subdivision of the metotic fissure (and thus development of a true fenestra pseudorotunda).

As stressed throughout, the interpretations presented here require further testing through the addition of braincase data for other taxa, especially *Gracilisuchus* and ornithosuchians, but also additional rauisuchians, aetosaurians, and crocodylomorphs. In addition, the phylogenetic framework used to investigate character evolution needs further independent evaluation.

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REFERENCES

Alcober O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology* **20:** 302–316.

Baird IL. 1960. A survey of the periotic labyrinth in some representative Recent reptiles. *University of Kansas Science Bulletin* **41:** 891–981.

Baird IL. 1970. The anatomy of the reptilian ear. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, *Vol. 2.* London: Academic Press, 193–275.

Baumel JJ, King AS, Lucas AM, Breazile JE, Evans HE. 1979. *Nomina Anatomica Avium*. London: W.B. Saunders Co.

Bellairs Ad'A, Kamal AM. 1981. The chondrocranium and the development of the skull in recent reptiles. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, *Vol. 11.* London: Academic Press, 1–263.

Benton MJ. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London B* **354:** 1423–1446.

Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods*, *Vol. 1.* Oxford: Clarendon Press, 295–338.

Burda DJ. 1969. Developmental aspects of the intracranial arterial supply in the alligator brain. *Journal of Comparative Neurology* **135:** 369–380.

Case EC. 1921. On an endocranial cast from a reptile, *Desmatosuchus spurensis*, from the Upper Triassic of western Texas. *Journal of Comparative Neurology* **33:** 133–147.

Case EC. 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. *Carnegie Institute of Washington Publication* **321:** 7–84.

Clack JA. 1997. The evolution of tetrapod ears and the fossil record. *Brain, Behavior and Evolution* **50:** 198–212.

Clark JM, Sues H-D, Berman DS. 2001. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology* **20:** 683–704.

Clark JM, Welman J, Gauthier JA, Parrish JM. 1993. The laterosphenoid bone of early archosauriforms. *Journal of Vertebrate Paleontology* **13:** 48–57.

Crompton AW. 1953. The development of the chondrocranium of *Spheniscus demersus* with special reference to the columella auris of birds. *Acta Zoologica* **34:** 71–146.

De Beer GR. 1937. *The Development of the Vertebrate Skull*. Oxford: Clarendon Press.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* **8:** 1–55.

Gower DJ. 1997. The braincase of the early archosaurian reptile *Erythrosuchus africanus*. *Journal of Zoology, London* **242:** 557–576.

Gower DJ. 1999. Cranial osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde B* **280:** 1–49.

Gower DJ. 2000. Rauisuchian archosaurs (Reptilia, Diapsida): an overview. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **218:** 447–488.

Gower DJ. 2002a. A revision of the South African early archosaur *Erythrosuchus africanus* Broom. *Annals of the South African Museum*, in press.

Gower DJ. 2002b. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. *Zoological Journal of the Linnean Society* **136:** 49–76.

Gower DJ, Sennikov AG. 1996. Morphology and phylogenetic informativeness of early archosaur braincases. *Palaeontology* **39:** 883–906.

Gower DJ, Sennikov AG. 1997. *Sarmatosuchus* and the early history of the Archosauria. *Journal of Vertebrate Paleontology* **17:** 60–73.

Gower DJ, Weber E. 1998. The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. *Biological Reviews* **73:** 367–411.

Gower DJ, Wilkinson M. 1996. Is there any consensus on basal archosaur phylogeny? *Proceedings of the Royal Society of London B* **263:** 1399–1406.

Gregory JT. 1953. Typothorax *and* Desmatosuchus. *Postilla* **16:** 1–27.

Heckert AB, Lucas SG. 2000. Taphonomy, phylogeny, biostratigraphy, biochronology, paleobiogeograhy, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie* **11–12:** 1539–1587.

Hochstetter F. 1906. Beiträge zur Anatomie und Entwickelungsgeschichte der Blutgefässsystemes der Krokodile. In: Voeltzkow A, ed. *Reise in Ostafrika*, *Vol. 4*. Stuttgart: E. Scheizerbart, 1–139.

Hopson JA. 1979. Paleoneurology. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, *Vol. 9*. London: Academic Press, 39–146.

Hunt AP, Lucas SG. 1990. Re-evaluation of '*Typothorax*' *meadei*, a late Triassic aetosaur from the United States. *Paläontologische Zeitschrift* **64:** 317–328.

Iordansky NN. 1973. The skull of the Crocodilia. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, *Vol. 4*. London: Academic Press, 201–262.

Long RA, Murry PA. 1995. Late Triassic (Carnian and Norian) tetrapods from the Southwestern United States. *Bulletin of the New Mexico Museum of Natural History and Science* **4:** 1–254.

Miall LC. 1878. The skull of the crocodile, a manual for students. *Studies in Comparative Anatomy* **1:** 1–50.

Murry PA, Long RA. 1996. A diminutive carnivorous aetosaur from the Upper Triassic of Howard County. *Texas. Journal of Vertebrate Paleontology* **16** (Suppl.to 3)**:** 55A.

Parrish JM. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* **13:** 287–308.

Parrish JM. 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. *Journal of Vertebrate Paleontology* **14:** 196–209.

Rieppel O. 1985. The recessus scalae tympani and its bearing on the classification of reptiles. *Journal of Herpetology* **19:** 373–384.

Säve-Söderbergh G. 1947. Notes on the brain-case in Sphenodon and certain Lacertilia. Zoologiska Bidragen tot de Anatomie 25**:** 489–516.

Sawin HJ. 1947. The pseudosuchian reptile *Typothorax meadei*. *Journal of Paleontology* **21:** 201–238.

Sedlmayr JC, Witmer LM. 2001. Homology and evolution of cephalic vasculature in Archosauria. *Journal of Morphology* **248:** 282.

Shiino K. 1914. Studien zur Kenntnis des Wirbeltierkopfes. I. Das Chondrocranium von *Crocodilus* mit Berücksichtigung der Gehirnnerven und der Kopfgefässe. *Anatomische Hefte* **50:** 257–382.

Shindo T. 1914. Zur vergleichenden Anatomie der arteriellen Kopfgefässe der Reptilien. *Anatomische Hefte* **51:** 267–356.

Walker AD. 1961. Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London B* **244:** 103–204.

Walker AD. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London* **B 248:** 53–134.

Walker AD. 1972. New light on the origin of birds and crocodiles. *Nature, London* **237:** 257–263.

Walker AD. 1985. The braincase of *Archaeopteryx*. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P, eds. *The Beginnings of Birds*. Eichstätt: Freunde des Jura-Museums Eichstätt, 123–134.

Walker AD. 1990. A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliott Formation (late Triassic or early Jurassic) of South Africa. *Philosophical Transactions of the Royal Society of London B* **330:** 1–120.

Witmer LM. 1995a. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason J, ed. *Functional Morphology in Vertebrate Paleontology*. Cambridge: Cambridge University Press, 19–33.

Witmer LM. 1995b. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology* **225:** 269–327.

Witmer LM. 1997a. Craniofacial air sinus systems. In: Currie PJ, Padian K, eds. *The Encyclopedia of Dinosaurs*. San Diego: Academic Press, 151–159.

Witmer LM. 1997b. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology, Memoir* **3:** 1–73.