The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians

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ABSTRACT

The Triassic reptile *Euparkeria* has been frequently given a pivotal position in interpretations of the evolution of archosaurs. Most recently, Welman (1995) has argued from braincase data that *Euparkeria* is more closely related to birds than are either theropod dinosaurs or crocodilians – a conclusion clearly at odds with the current orthodoxy. The braincase of a single specimen of *Euparkeria* is described in detail and compared with previous descriptions and with the braincases of other diapsids. Variations among the known specimens are documented. The homology of various braincase structures are reassessed in light of the study by Welman (1995). We argue that the braincase of *Euparkeria* has an undivided metotic fissure, an incompletely ossified medial wall of the otic capsule, a well-defined 'semilunar depression', and posteroventrally positioned foramina in the parabasisphenoid for the entrance of the cerebral branches of the internal carotid arteries. It lacks enclosure of the Eustachian system in bone, well-developed tympanic sinuses, or a well-defined recess for the lagena. A review of braincase morphology in extinct and extant diapsids suggests that braincase features of *Euparkeria* are largely plesiomorphic for Archosauria. The evolutionary relationships between *Euparkeria* and extant archosaurs (birds and crocodilians) are considered by reviewing braincase morphology in extant and extinct diapsids. No shared derived characters could be found that support the resolutions (crocodilians (*Euparkeria* + birds)) or (birds (*Euparkeria* + crocodilians)). Three derived characters shared by extant archosaurs support the resolution (*Euparkeria* (crocodilians + birds)), but only the presence of laterally positioned foramina in the parabasisphenoid for the entrance of the cerebral branches of the internal carotid arteries appears to represent strong evidence. The other two features are a degree of ossification (of the medial wall of the otic capsule) that exhibits some homoplasy among archosaurs, and an absence (of the 'semilunar depression'), and therefore do not represent particularly robust hypotheses of homology. Our interpretation of the braincase of *Euparkeria* is fully congruent with the consensus among recent explicit phylogenetic analyses that this taxon is close to, but not a member of, the archosaur crown group. Birds and crocodilians share a number of other derived similarities (subdivided metotic fissure, elongated and tubular cochlear recess, enclosed Eustachian system, extensive tympanic sinuses, quadrate-prootic articulation) that are probably not homologous because of their absence in a number of non-avian dinosaurs and crocodilian-line crown-group archosaurs.

Key words: *Euparkeria*, archosaurs, diapsids, birds, crocodilians, braincase, morphology, homology, phylogeny.

CONTENTS

I. INTRODUCTION

(1) General comments

Euparkeria capensis Broom is an early, non-crown-group archosaurian reptile known exclusively from the *Cynognathus* Assemblage Zone of the Beaufort Series of the South African Karoo basin. The *Cynognathus* Assemblage Zone has been considered (e.g. Charig & Sues, 1976; Anderson & Cruickshank, 1978; Sun, 1980) to be late Early Triassic (Scythian) in age, but more recently (Ochev & Shishkin, 1988; Shubin & Sues, 1991; Shiskin, Rubidge & Hancox, 1995) it has been interpreted as covering the Scythian–Anisian boundary. The *Euparkeria*-bearing sediments lie in the middle of three recently identified zones of the *Cynognathus* Assemblage Zone (Hancox *et al.*, 1995), and their precise age is unknown. Since Broom's (1913*a*, *b*) original description, a pivotal role has often been imposed on *Euparkeria* in reconstructions of the pattern of the early part of the archosaurian radiation. Broom (1913*b*) considered *Euparkeria* to be a member of the Pseudosuchia, a group he viewed as ancestors to dinosaurs and, separately, birds, and Heilmann (1926) discussed similarities between *Euparkeria* and *Archaeopteryx* that were instrumental in his pseudosuchian ancestry hypothesis for the origin of birds. Cruickshank (1979) initiated a new phase in the recognition of *Euparkeria* as a potential ancestor of later archosaur groups in the first of many ankle-only phylogenies (Thulborn, 1980, 1982; Brinkman, 1981; Chatterjee, 1982; Cruickshank & Benton, 1985; see Sereno, 1991*a*; Gower, 1996 for a more recent perspective). The most recent explicit analyses of basal archosaur phylogeny (Sereno & Arcucci, 1990; Sereno, 1991*a*; Parrish, 1993; Juul, 1994; Bennett, 1996) have reached a consensus (Gower & Wilkinson, 1996, although they did not include the analysis of Bennett, 1996) in recovering *Euparkeria* in a position outside the archosaurian crown group (the most recent

common ancestor of extant archosaurs – birds and crocodilians – and all of its descendants).

Although consensus has emerged on both the position of *Euparkeria* relative to other basal archosaurs, and the 'theropod hypothesis' for the origin of birds (see reviews by Witmer, 1991 and Padian & Chiappe, 1997, 1998), this has recently been challenged by Welman (1995). Welman (1995) argues, solely on evidence from braincase structure, that the two most recently favoured contenders for the closest relatives of birds (crocodylomorphs and theropod dinosaurs) are too derived to be considered as such. Welman (1995, p. 536) further suggests that *Euparkeria* belongs to 'the specific group of archosauromorphs from which birds evolved'. Welman (1995) thus resurrects the thecodontian (or pseudosuchian) ancestry hypotheses for avian origins of Broom (1913*b*) and Heilmann (1926), and more recently favoured by e.g. Tarsitano & Hecht (1980), but attempts to place it in a modern 'cladistic' framework by proposing braincase synapomorphies shared by *Euparkeria* and birds. Apart from brief mentions by e.g. Feduccia (1996, p. 408) and Carroll (1997, p. 308), Welman's unorthodox thesis has not yet been discussed or fully evaluated in even the most recent considerations of bird origins (e.g. Padian & Chiappe, 1997, 1998). Welman's (1995) study clearly reinforces Witmer's (1991, p. 438) suggestion that *Euparkeria* is 'among the most influential fossil evidence in the debate on avian origins'.

The braincase of *Euparkeria* has also been discussed briefly in a number of previous studies. Ewer (1965) was the first to consider braincase structure, but no specimens were adequately prepared at that time and comparative information was limited. Cruickshank (1970, 1972) figured and briefly described a newly acid-prepared specimen (SAM 7696), which was later compared with *Prolacerta* by Gow (1975) and Evans (1986). Clark *et al.* (1993) presented evidence for the presence of a laterosphenoid in *Euparkeria*, and described and figured this bone in SAM 7696. Brief comments on the
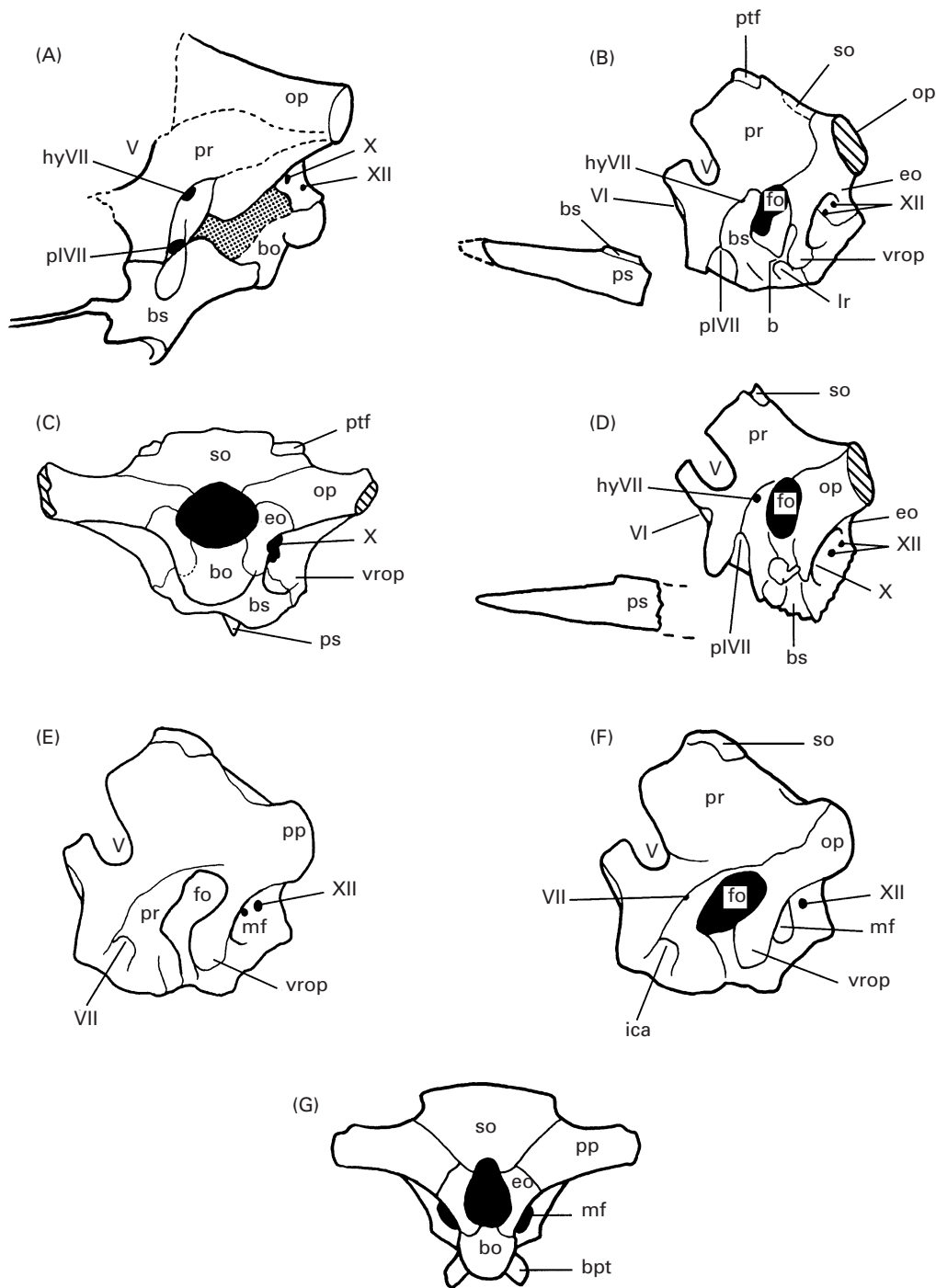
Fig. 1. Previously published figures and reconstructions of the braincase of *Euparkeria*. (A) Left lateral view of UMZC T692 redrawn from fig. 3 in Ewer (1965); (B) right (reversed) lateral view of SAM 7696 redrawn from fig. 2 in Cruickshank (1970); (C) occipital view of SAM 7696 redrawn from fig. 1 in Cruickshank (1970); (D) left lateral view of SAM 7696 redrawn from fig. 3d in Cruickshank (1972); (E) right (reversed) lateral view of SAM 7696 redrawn from fig. 7 in Evans (1986); (F) left lateral view redrawn from fig. 28a in Chatterjee (1991); (G) occipital view redrawn from fig. 40a in Chatterjee (1991). The standardised abbreviations (see section IX for list of abbreviations) match original equivalents, except for the bridge of bone 'b' which was unlabelled by Cruickshank (1970). The reader is referred to Welman (1995) for his nine detailed figures of the braincases of SAM 5867 and 7696.

braincase of *Euparkeria* have also been made in publications of a broader phylogenetic scope (e.g. Walker, 1990; Chatterjee, 1991; Gower & Sennikov, 1996*a*). Illustrations of the braincase of *Euparkeria* presented in these previous studies are shown in Fig. 1.

Despite this attention, the detailed osteology of the braincase of *Euparkeria* has yet to be documented. Here, we present a full description of the osteology of the braincase of a single specimen of *Euparkeria* and include comparisons with the other known specimens and with other diapsids. This forms the basis for a critical evaluation of the comparisons that Welman (1995) draws between *Euparkeria* and birds, and of the proposed synapomorphies that he presents as evidence for their close relationship. Finally, we reconsider how braincase structure in *Euparkeria* impacts on the understanding of archosaur phylogeny and the evolution of the braincase structures seen in birds and crocodilians. Much of the discussion focuses on the paper by Welman (1995) because it is the most detailed study of the braincase of *Euparkeria* to date, because it covers most of the previous interpretations that have been made, and because of the challenging nature of the conclusions that were reached.

(2) Materials and methods

Braincase structure is currently well exposed in three specimens of *Euparkeria*. The holotype (SAM 5867) skull formerly revealed data only on the occiput (e.g. Broom, 1913*b*; Ewer, 1965), but it has recently been mechanically prepared (Welman, 1995). The braincase of SAM 7696 was first isolated from a block of matrix containing associated elements, acid prepared, and described by Cruickshank (1970). The same braincase has since been figured and/or commented on a number of times with often differing interpretations (Cruickshank, 1972; Gow, 1975; Evans, 1986; Walker, 1990; Chatterjee, 1991; Clark *et al.*, 1993; Welman, 1995). The third specimen of *Euparkeria* currently revealing significant information on braincase structure is UMZC T692 (formerly D. M. S. Watson collection R527) and it is this third specimen that is the focus of the descriptive section of this paper.

UMZC T692 comprises several blocks of matrix preserving cranial and postcranial remains of *Euparkeria*. The part of the specimen displaying the braincase is represented by an incompletely prepared block of matrix (T692f) preserving the posterior part of a skull. The right side of the block shows the

lateral surface of the right surangular, angular and prearticular of the right mandible. This is essentially in natural position below the right side of the cranium, the lateral surface of which preserves the quadrate, the anterior part of the parietal, the postorbital, frontal, postfrontal, prefrontal, lacrimal, a fragment of the anterior of the jugal, the posterior end of the nasal, and an isolated tooth. The left side of the specimen (Fig. 2) is much less complete than the right with respect to the mandible and dermatocranium: the left quadrate, quadratojugal, postfrontal, postorbital, squamosal, and virtually all of the mandible are lacking. The posterior parts of the parietals, much of the supraoccipital, and the tips of the paroccipital processes are also absent. The left frontal, nasal, and anterior part of the parietal are in articulation with their counterparts, and small parts of the prefrontal and lacrimal are preserved. The lateral surface of the right side of the neurocranium has not been exposed by preparation, and remains embedded in matrix within the right lower temporal fenestra. As a result of the loss of most of the left dermal elements, much of the neurocranium and posterior part of the palate were able to be prepared from this side. Preparation appears to have been carried out in at least two phases.

Ewer (1965, fig. 3) depicted the posterodorsal part of the left side of the endocranium, and her description suggests that little else of this region was visible at that time. A combination of acid and mechanical preparation was subsequently undertaken in the early 1970s, as part of Cruickshank's (1970, 1972) investigation of early archosaur braincases (A. D. Walker, personal communication). This phase of preparation revealed the internal surface of the endocranium for the first time. The latest stage of preparation was undertaken by A. D. Walker (personal communication) in 1974 and was performed mechanically, by hand. This included clearing the right side of the occiput, part of the right orbit, details of the right inner endocranial surface, and much of the ventral surface of the parabasisphenoid.

Although the relative position of most of the elements remain undisturbed in UMZC T692, the braincase has been subject to some distortion and erosion during preservation and preparation. The area housing the endocranial cavity has been laterally compressed to some degree, and most of the supraoccipital has disappeared in concert with the loss of the hindmost part of the skull roof. A break runs subhorizontally through the left prootic and exoccipital, so that the area dorsal to this can be detached. The ventral ramus of the left opisthotic
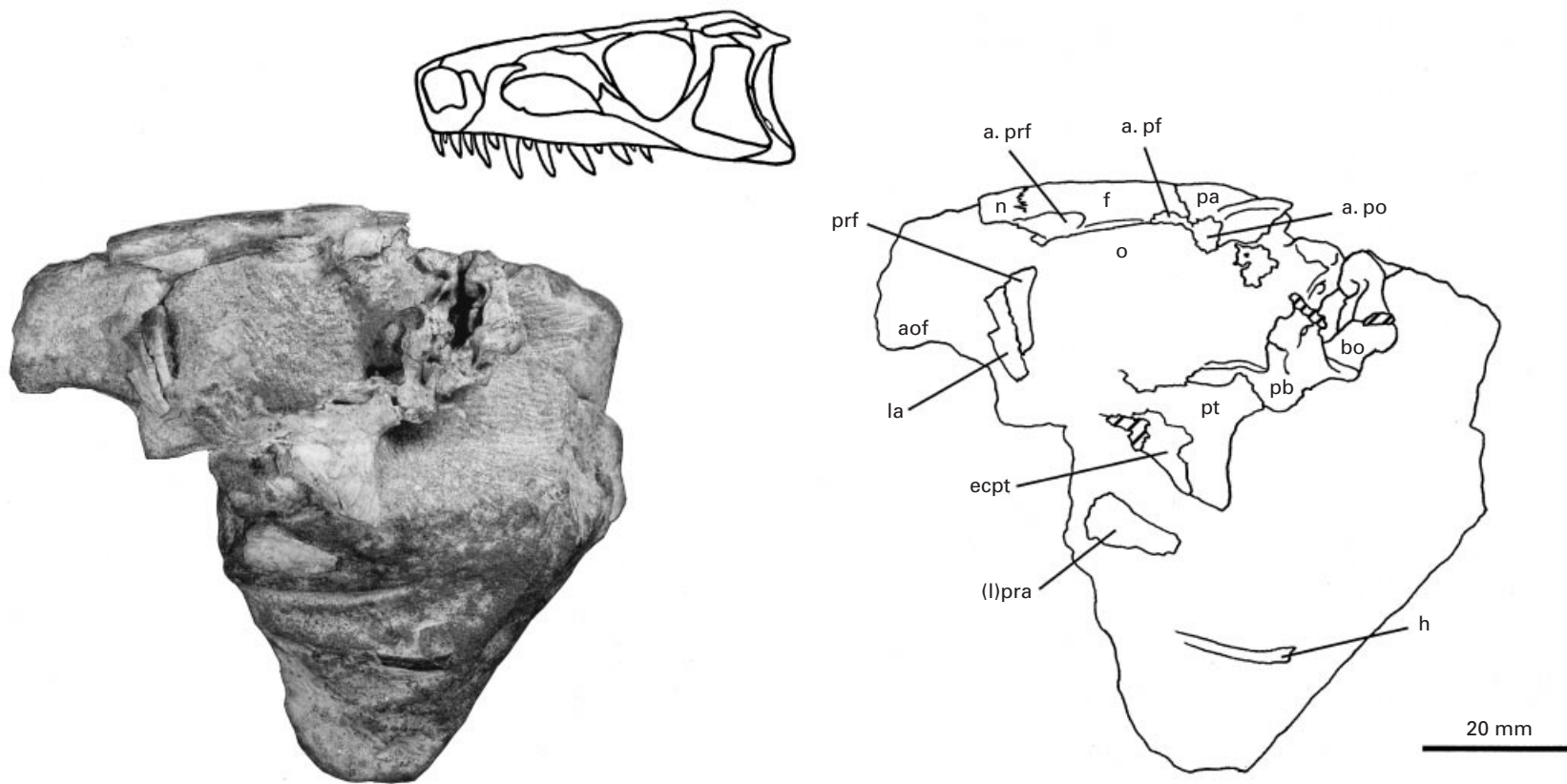
Fig. 2. UMZC T692, *Euparkeria capensis*. General view of single block (T692f) of the specimen, showing skull remains in left lateral view. See section IX for list of abbreviations.

has been lost, perhaps following the detachment of the dorsal part of the prootic and paroccipital process. Most of the left laterosphenoid has been worn away. The left basal tuber of the parabasisphenoid is shorter and more rounded than that of the right side. The left lateral side of the basioccipital is heavily pitted, perhaps as a result of acid preparation. The floor of the endocranial cavity is slightly laterally compressed and its surface appears to have been moderately overprepared. Both paroccipital processes are incomplete, and that on the right side has been almost completely hollowed out (it is not clear whether during preservation or preparation), leaving only an outer shell.

All specimen drawings were produced with the aid of a *camera lucida*. An explanation of the abbreviations used in the text and figures is given in section IX.

(3) Terminology

There are at least two definitions of each of the taxa Archosauria and Aves in current usage. Archosauria is employed here in its traditional sense (see Juul, 1994), with members of the Archosauria *sensu* Gauthier (1986) referred to as 'crown-group' archosaurs. Aves is used in the sense of the crown group, i.e. the most recent common ancestor of extant birds and all of its descendants. The clade composed of the most recent common ancestor of extant birds and *Archaeopteryx* and all of its descendants is referred to as Avialae (Gauthier, 1986). Our use of Aves differs to that preferred by e.g. Padian & Chiappe (1997, 1998), but it is closer to the concept of the taxon established by Linnaeus, as well as the implied or explicit meaning used in many (including modern) neo-ornithological studies. The terms 'birds' and 'crocodilians' are also employed here in the sense of their respective crown groups.

The definitions of certain anatomical terms also need to be clarified. Anterior and posterior are used rather than rostral and caudal, respectively, largely for ease of comparison with the majority of existing descriptions of the braincases of other reptiles, including early archosaurs. Where the metotic fissure of the chondrocranium persists as a single, undivided opening in the osteocranium it is here referred to as the metotic foramen (Walker, 1985, 1990 and Rieppel, 1985 have also made this distinction). The term 'vestibule' is applied to the major cavity of the osseus labyrinth of the inner ear (Baird, 1960, 1970). The parasphenoid+basisphenoid are together referred to as the parabasisphenoid, especially where no division is detectable. The term 'perilymphatic foramen' is used for the aperture transmitting the perilymphatic duct from the otic capsule into the metotic fissure/foramen. This aperture has sometimes been referred to as the 'fenestra cochleae' (e.g. Gaupp, 1900; Shiino, 1914), while the term 'perilymphatic foramen' has occasionally (e.g. Oelrich, 1956) been applied to the aperture through which a diverticulum of the perilymphatic sac extends medially into the cranial cavity. Where the metotic fissure remains undivided (i.e. where there is a metotic foramen), 'ventral ramus of the opisthotic' is used to refer to the part of the opisthotic that separates the fenestra ovalis from the metotic foramen. The meanings of the confused terms 'fenestra rotunda', 'fenestra pseudorotunda', 'recessus scalae tympani', and 'occipital recess' are discussed in section III.2.*a*.

II. DESCRIPTION OF THE BRAINCASE OF UMZC T692

(1) External surface

(a) Basioccipital

The basioccipital (Figs 3–5) forms the entirety of the hemispherical occipital condyle. The basal tubera of the basioccipital are a pair of simple, ventrally projecting tongues of bone separated by a median cleft that, in comparison with other earliest archosaurs (e.g. Gower & Sennikov, 1996*a*), are relatively long and slender. As a whole the basioccipital is a tall but antero-posteriorly short element. The ventral surface of the basioccipital, between the basal tubera, forms the posterodorsal limit of a well-defined posteroventral concavity. This continues onto the posterior surface of the parabasisphenoid, and the suture between the two elements can be seen towards the top of the fossa. Gower & Sennikov (1996*a*) referred to an equivalent concavity on the posteroventral surface of the braincases of other early archosaurs as the 'basioccipital-basisphenoid fossa'.

(b) Supraoccipital and epiotic

The supraoccipital (Fig. 6) is incomplete or perhaps absent in UMZC T692. There is a possibility that it is preserved in part on the left side (more of the left side of the specimen is preserved dorsally than the right), with uncertainty stemming from the imperfect preservation and preparation of the upper left side of the specimen, rendering the identification of fine details, such as sutures, difficult. Welman
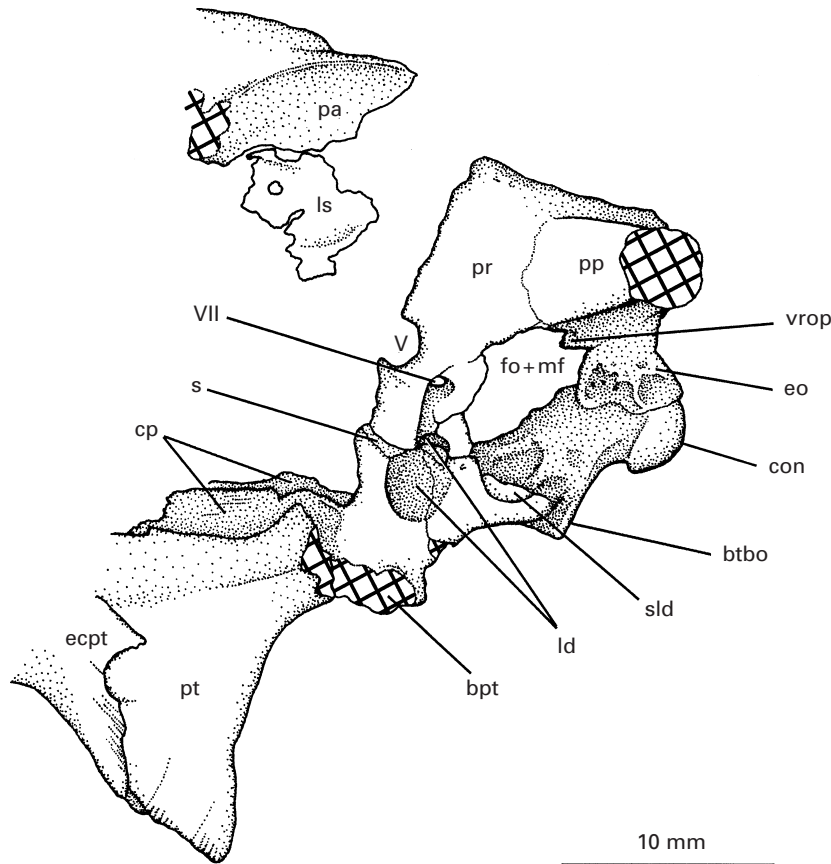
Fig. 3. UMZC T692, *Euparkeria capensis*. Braincase in left lateral view. See section IX for list of abbreviations.
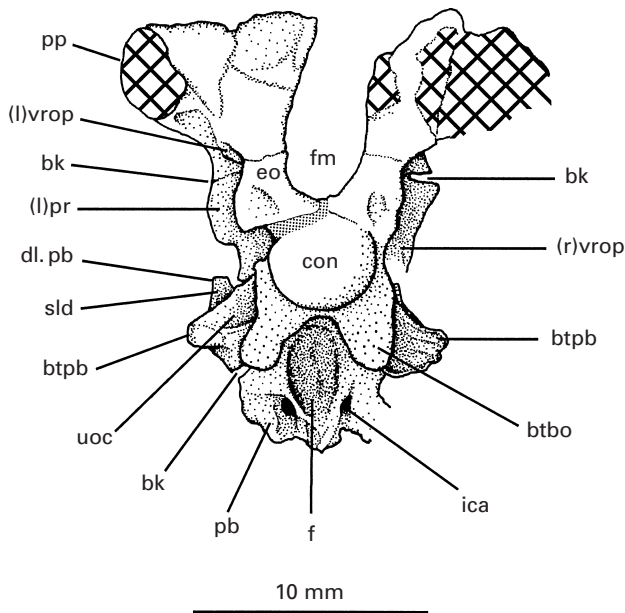
Fig. 4. UMZC T692, *Euparkeria capensis*. Occipital view of braincase. Incomplete lines on the right side of the specimen represent disappearance of bone into remaining matrix. See section IX for list of abbreviations.

(1995) also identified an epiotic ossification in SAM 5867 and 7696, in contrast with all previous studies of these specimens. No positive evidence can be found in UMZC T692 for the presence or absence of such an element.

(c) Exoccipital

No sutural distinction between the exoccipital and opisthotic (Figs 3–6) can be traced in UMZC T692. The two elements are described separately here, based on the assumption that the limit of the exoccipital and opisthotic resembles that of other basal diapsids, with the former element being restricted to the pillar separating the foramen magnum from the metotic fissure/foramen. The exoccipitals do not appear to meet along the midline to exclude the basioccipital from the ventral part of the foramen magnum, but this is not completely certain in UMZC T692 as a result of preparation and subsequent conservation. The exoccipitals of SAM 5867 (Ewer, 1965; Cruickshank, 1970; Welman, 1995) and perhaps SAM 7696 (Ewer, 1965; Welman, 1995) do not meet along the midline. The exoccipital pillar is tall in comparison with
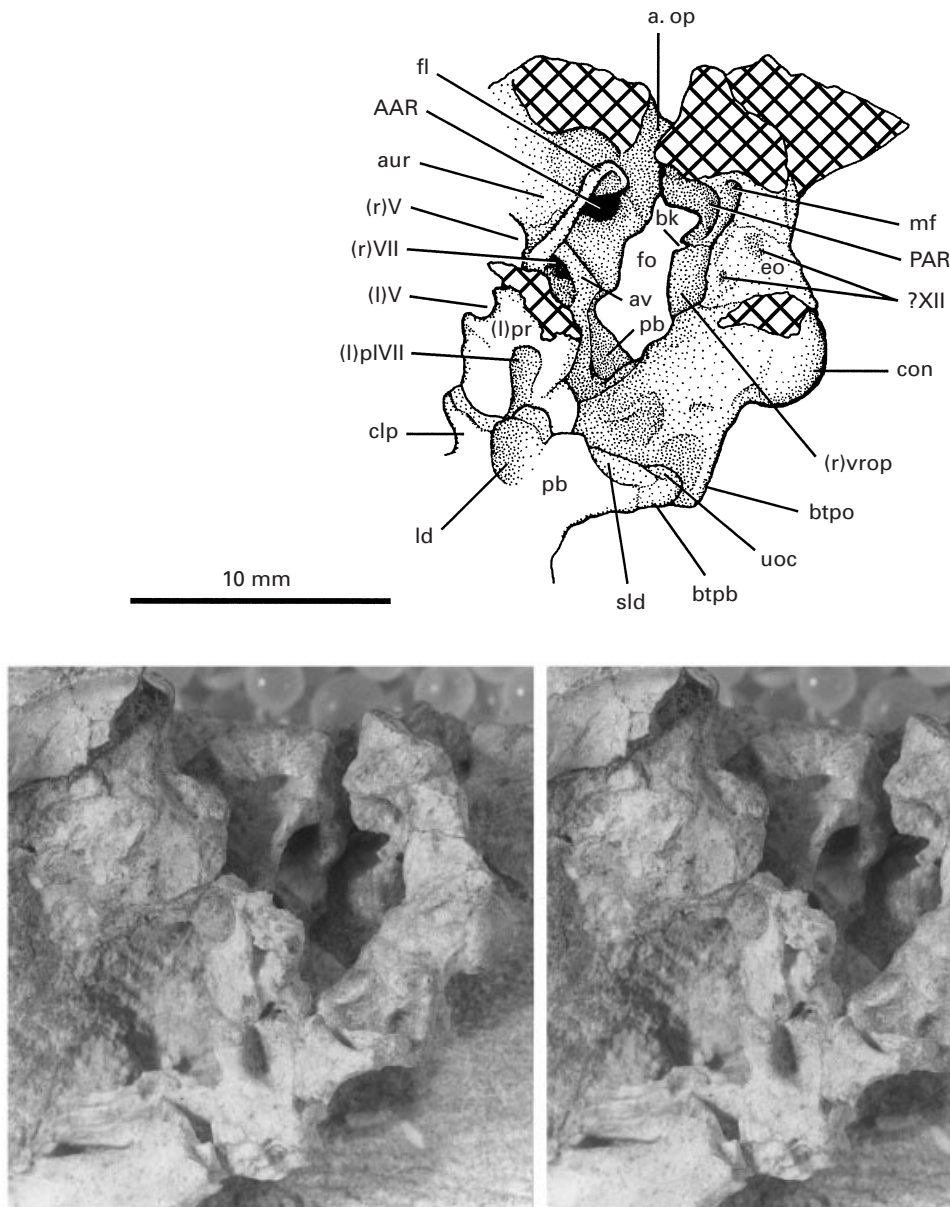
Fig. 5. UMZC T692, *Euparkeria capensis*. Drawing and stereo photographs of left lateral view of braincase. The dorso-lateral part of the left wall of the braincase has been removed to show the endocranial cavity and internal surface of the right side. The anterior of the right prootic disappears into matrix. See section IX for list of abbreviations.

those of other early archosaurs (Gower & Sennikov, 1996*a*), and its base does not have a posterior tongue that extends over the dorsal surface of the condylar part of the basioccipital. This means that the exoccipitals fail to contribute to the articulatory surface of the occipital condyle. The position and number of foramina for the branches of the hypoglossal nerves are difficult to detect with confidence, but two pits on the the medial surface of the right exoccipital (Fig. 5) are possible candidates. The external surface of the left exoccipital is now poorly preserved (perhaps as a result of acid

preparation since 1965), so that confirmation of Ewer's (1965, fig. 3) identification of two foramina here in this specimen is not possible. Ewer's (1965) identification of one of these foramina as an exit for the vagus nerve is here considered to be incorrect. Two hypoglossal foramina have been identified in SAM 7696 (Cruickshank, 1970; Evans, 1986; Welman, 1995), and there is currently no documentation of the number in SAM 5867. The metotic fissure shows no indication of any osteological subdivision, and the entire posterior margin of the metotic foramen is formed by the anterior edge of the
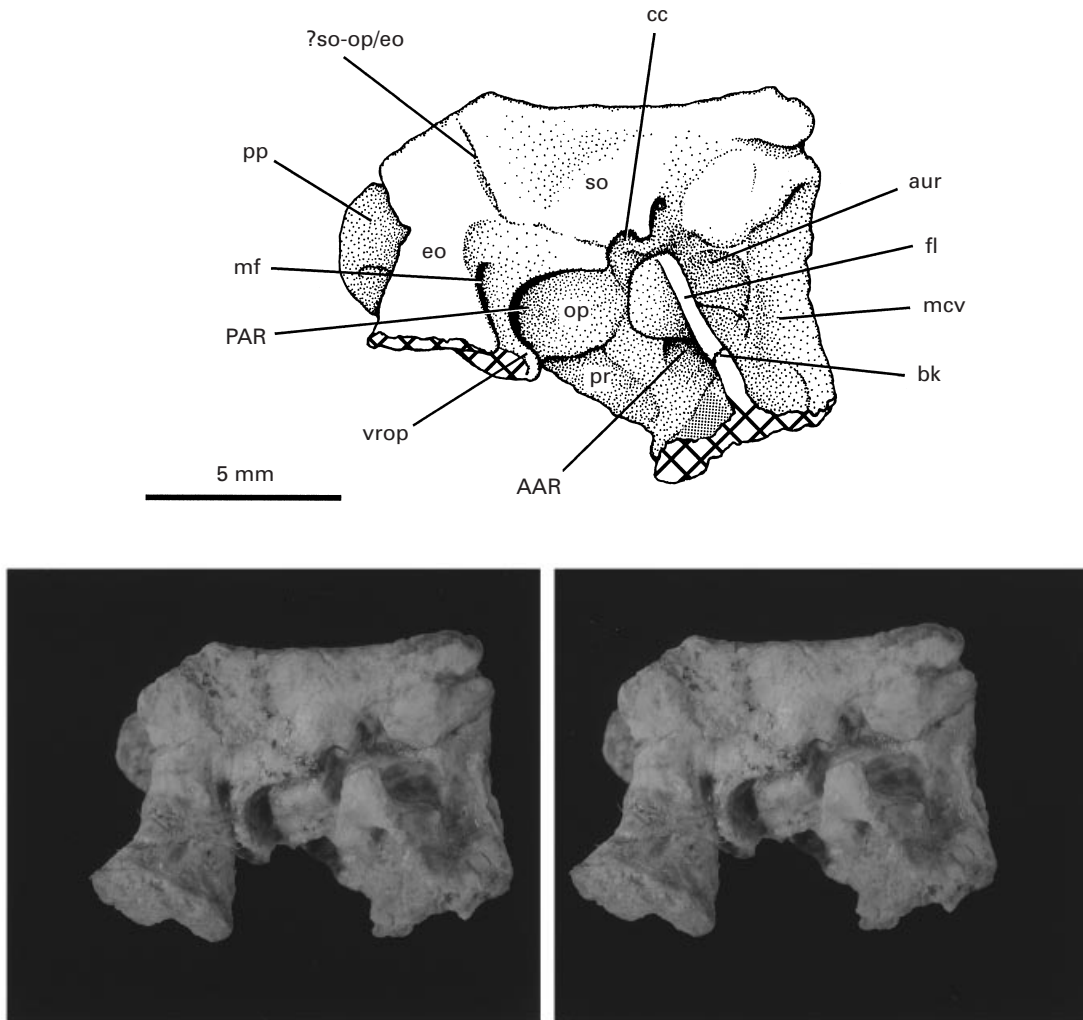
Fig. 6. UMZC T692, *Euparkeria capensis*. Internal surface of left dorsolateral wall of the braincase (the part removed in Fig. 5). The ventral part of the exoccipital pillar visible in the stereo photographs is removed in the drawing. See section IX for list of abbreviations.

exoccipital pillar, which bulges into the foramen in a manner superficially resembling *Sphenodon* (see Fig. 8).

(d) Opisthotic

The paroccipital processes of UMZC T692 are largely missing and the remaining proximal stumps are hollowed out. Despite their incompleteness, there is every indication that the paroccipital processes are similar to those of other earliest archosaurs, in being formed largely by the opisthotic with some antero-lateral overlap by the prootic at their bases. While the suture between opisthotic and prootic is not clear on the left side, these elements have been separated on the right (Fig. 5) during preservation. On the left side (Fig. 6), the dorsal surface of the prootic and opisthotic appear to be capped by part of the

supraoccipital, although evidence for sutures is absent on the external surface of the braincase.

The opisthotic possesses a well-defined ventral ramus that separates the fenestra ovalis, anteriorly, from the metotic foramen, posteriorly. Only the dorsalmost part of this ramus is preserved on the left side of UMZC T692 (Figs 3, 6). It is much more complete on the right side, although there is a break a third of the way down and the ventralmost tip is absent (Fig. 4). The ramus is robust and slightly thicker laterally than medially. It resembles that of *Prolacerta*, proterosuchids, and some erythrosuchids in being prominent and visible in lateral and posterior views of the braincase (Gower & Sennikov, 1996a). Other specimens (SAM 5867 and 7696; e.g. Evans, 1986; Welman, 1995) show that the distal end of the ventral opisthotic ramus has a clubbed tip that rests on the basioccipital-parabasisphenoid

commissure. A gap exists between these three elements that has been the subject of various interpretations (see sections III.2.a and IV.5).

The incompleteness of the distal ends of the ventral rami of the opisthotics of UMZC T692 means that the presence or absence of a delicate bridge of bone connecting the opisthotic to the dorsal wing of the parabasisphenoid (Cruickshank, 1970, 1972; Welman, 1995) cannot be assessed.

(e) Prootic

The prootic (Figs 3–6) forms a large part of the lateral wall of the braincase. A broad anterior notch forms the posterior half of the trigeminal foramen, while the lateral surface of the prootic bordering it is fairly flat and featureless (perhaps slightly over-prepared), so that Gower & Sennikov's (1996a) scoring of *Euparkeria* for the presence of a horizontal ridge below the trigeminal foramen in UMZC T692 can be considered something of an overinter-pretation.

The crista prootica is little developed, but forms a small free edge that partly harbours a foramen for the exit of the facial nerve. This is clearly only a single opening in UMZC T692, with grooves leading away from it posterodorsally for the hyomandibular branch of the nerve, and ventrally for the palatine branch. While the former of these grooves is very short and weak, the latter is particularly well defined, and it continues ventrally to a point just before the ventral edge of the prootic, where it leads into the dorsal limit of a conspicuous and well-delineated fossa that expands down on to the lateral surface of the parabasisphenoid (Figs 3, 5). In contrast to the dorsal end of this depression in SAM 5867, as described by Welman (1995), there is no indication that the depression in UMZC T692 extends postero-ventrally into a cavity within the dorsal wing of the parabasisphenoid (= trabeculate cavity of Welman, 1995). Immediately posterior to the groove for the palatine branch of the facial nerve, the prootic terminates in a short free edge that borders the anterior of the fenestra ovalis and contacts the dorsolateral ramus of the parabasisphenoid.

The prootic is tall above the trigeminal notch, and would have made substantial contact with the laterosphenoid. Below the trigeminal notch the opposite prootics meet briefly along the midline, as in SAM 7696 (Gow, 1975, fig. 37b; Evans, 1986, p. 195; Welman, 1995, fig. 3b), to form the dorsal part of the hypophyseal (pituitary) fossa. Gower & Sennikov (1996a) differentiated between conditions

where the abducens nerves exit foramina are on a vertical (exit anteriorly) or a horizontal (exit ventrally) surface. In UMZC T692, the condition (not figured) certainly resembles e.g. *Erythrosuchus* rather than *Proterosuchus*, in that the abducens exit foramina lie on a vertical, upturned anterior surface. The abducens foramen on the right side is open (perhaps overprepared), but is not detectable on the left. Anteriorly, the prootic-parabasisphenoid suture is also not traceable with confidence, although there is nothing to suggest that the abducens nerve did not exit along the suture as in SAM 7696 (Gow, 1975, fig. 37b; Welman, 1995, fig. 3).

(f) Parabasisphenoid

The parabasisphenoid (Figs 3–5) is well preserved and exposed in UMZC T692. This is clearly not a horizontally aligned and plate-like element, but instead has a significant vertical dimension to it, with the basal tubera positioned some distance above as well as behind the basipterygoid processes.

In lateral view, the posterodorsal edge of the parabasisphenoid (more complete distally on the right side of UMZC T692) bears a well-defined, curved, and posterodorsally open gutter that extends anterodorsally and slightly medially from the lateral edge of the distal end of the tuber, to a point immediately below and outside the fenestra ovalis. Cruickshank (1970, fig. 2) and Evans (1986, fig. 7) figured this feature without referring to it in their texts, while it was omitted by Ewer (1965, fig. 3) and Chatterjee (1991, fig. 28a). Following Evans (1986), we refer to this groove as the 'semilunar depression', and suggest that it can be homologised with the similarly well-defined groove seen in *Vjushkovia triplicostata* (Gower & Sennikov, 1996a) and the less well-developed, but similarly positioned, grooves in *Prolacerta* (Evans, 1986) and several other early archosaurs (Gower & Sennikov, 1996a; Gower, 1997). Our hypothesis of homology is based on the observation that in all cases where we have recorded its presence (in *Prolacerta* and all observed protero-suchids and erythrosuchids) it is consistently positioned on the lateral surface anterior to the basal tuber, curving from a point below the fenestra ovalis and behind the exit of the facial nerve, back along to the tuber.

The part of the parabasisphenoid that forms the medial wall to the semilunar depression is trans-versely thin, and its medial surface forms the lateral wall to an approximately parallel channel (Figs 4, 5). This channel is much broader than the semilunar

depression and it extends anteromedially towards the base of the fenestra ovalis along the posterodorsal edge of the parabasisphenoid. As hinted at by the right side of UMZC T692, and seen in SAM 5867 and 7696 (Fig. 4; Welman, 1995), the distal surface of the ventral ramus of the opisthotic completed this channel by forming its roof. The suture between the parabasisphenoid and basioccipital lies on the floor of the channel. The channel (discussed below in sections III.2.a and IV.5) therefore lies between the parabasisphenoid, basioccipital and opisthotic.

The semilunar depression is bordered anteriorly and ventrally by a laterally compressed lamella which anterodorsally articulates with the postero-ventral edge of the prootic outside and below the fenestra ovalis. Anteroventral to this dorsal pro-jection of the parabasisphenoid is the conspicuous depression that dominates the lateral surface of the element. All of the margins of the depression are steep and well defined except posteriorly. Anteriorly, its border is formed by the posterior edge of the clinoid process of the parabasisphenoid. Antero-dorsally, the depression extends onto the ventral part of the prootic as described above. Although Welman (1995, fig. 5a) interpreted the (cerebral branch of the) internal carotid artery to have entered the para-basisphenoid within this depression in SAM 5867, the left side of UMZC T692 appears to be completely prepared here and there is no indication of any foramina within the concavity. Additionally, we identify the position of the internal carotid foramina to be in a posterior position on the parabasisphenoid. These differing interpretations are discussed in more detail in section III.2.d.

The left basipterygoid process and associated articulatory facet of UMZC T692 is damaged, while the right side is still embedded in matrix. Both pterygoids have moved relatively slightly forward from their life position, but ventrally the hooked part of the basipterygoid articulations (Ewer, 1965, p. 390) can be seen still in contact with the anterior part of the medial surface of the basispterygoid processes of the parabasisphenoid.

The posteroventral surface of the parabasi-sphenoid (Fig. 4) is dominated by the large fossa that extends down from the basioccipital. The ventral limit of this fossa is marked by ridges that extend down between a pair of foramina which are interpreted here as the point of entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid. Welman (1995) has inter-preted these foramina as the pharyngeal openings of lateral Eustachian tubes. Dorsally, a horizontal plate extending between the posteromedial surfaces of the basal tubera of the parabasisphenoid ('intertuberal plate' of Gower & Sennikov, 1996a) is absent. On the ventral surface of the parabasisphenoid, a low, longitudinal ridge separates the areas of the element that contact the left and right hooks of the basipterygoid articulations of the pterygoids.

Anteromedially, the clinoid processes of each side are in contact, and their anterior surfaces form the dorsum sellae at the back of the hypophyseal fossa. Dorsally, the clinoid processes meet the sub-tri-geminal processes of the prootic. There was clearly no articulation between the parabasisphenoid and laterosphenoids.

The cultriform process or rostrum of the parabasi-sphenoid, as scored by Gower & Sennikov (1996a, table 1), is not dorsoventrally tall at its base, but instead expands briefly before tapering. Its distal end is incomplete in UMZC T692.

(g) Laterosphenoid

As Clark et al. (1993) have discussed, a latero-sphenoid was long thought to have been absent in Euparkeria. The same authors presented the first evidence to the contrary, based on their reexam-ination of all three available specimens of Euparkeria that reveal braincase structure. Clark et al. (1993) also briefly described the form of the laterosphenoid of SAM 7696. We agree with Clark et al. (1993) that fragments anterior to the left prootic of UMZC T692 (Fig. 3) probably represent a poorly preserved laterosphenoid. Although Clark et al. (1993) reported laterosphenoids to be present and much better preserved in SAM 5867, Welman (1995) made no further mention of this element in com-parisons between the braincase of Euparkeria and other archosaurs. Because of the very poor pres-ervation of this element in UMZC T692, there is little useful information that can be presented.

(2) Internal surface

Fig. 5 shows the internal structure of the right side of UMZC T692, which appears to correspond very closely with that of SAM 7696 (Welman, 1995, fig. 3). The lowest part of the floor of the endocranial cavity lies a significant distance below the floor of the foramen magnum, a feature found in some other early archosaurs (e.g. Gower & Sennikov, 1996b). The sutural pattern on the floor of the endocranial cavity is not entirely clear but there is no evidence that it differs from SAM 7696 as depicted by

Welman (1995, fig. 3a). The basioccipital in UMZC T692 is certainly, as Cruickshank (1970, p. 684) described for SAM 7696, 'quite extensively exposed'. The parabasisphenoid is exposed in the centre of the anterior part of the floor, while in front of this the prootics meet in the midline (as Evans, 1986 describes for SAM 7696). There is therefore no contact between the anterior of the exoccipitals and the posterior of the prootics on the floor of the endocranial cavity, such as is seen in erythrosuchids (Gower & Sennikov, 1996*a*; Gower, 1997). The abducens foramen of the right side can be seen, but the equivalent area on the left is slightly compressed (transversely) and unprepared. The suture between prootic and parabasisphenoid is as depicted by Welman (1995, fig. 3a) for SAM 7696. The floor of the endocranial cavity of UMZC T692 is contoured, but seems to be poorly preserved and possibly attacked by acid preparation, and we are reluctant to identify detailed features. For example, an apparently over-prepared shallow pit on the right side, just inside the fenestra ovalis, does not match the left side of the same specimen and probably does not require further identification.

The medical wall of the otic capsule resembles that of *Erythrosuchus* (Gower, 1997) and other non-crown-group archosaurs (e.g. Gower & Sennikov, 1996*a*) in that it is not fully ossified, so that it lacks a complete bony 'otic pyramid' (Walker, 1990) and has a medially open 'tympanic bulla'. A strong internal flange of the prootic marks the anterior wall of the vestibule, but this crest does not extend far enough posteromedially to form the medial wall of the vestibule. A conspicuous hollow harboured by the most prominent part of the prootic flange is interpreted as housing the anterior ampullae, the anterior opening of the external (horizontal) semicircular canal, and the ventral opening of the anterior vertical semicircular canal. This is the anterior ampullary recess. The foramen for the exit of the facial nerve lies immediately posterior to the ventral end of the prootic flange, and is separated from the anteromedial corner of the vestibule by a ridge (perhaps slightly eroded on the right of UMZC T692), very similar to the condition in *Erythrosuchus* (Gower, 1997). No clear indication of the possible position of branches of the acoustic nerves can be located, probably as a result of the largely unossified medial wall of the otic capsule. One possible position of a branch of the acoustic nerve, a small notch on the medial edge of the left prootic flange (Fig. 6), could equally well be considered to be a small break, and the equivalent edge on the right side appears to

be slightly worn. The auricular (floccular) recess is seen as a well-defined concavity on the medial wall of the prootic, anterior to the flange that marks the anterior wall of the vestibule.

The posteromedial corner of the vestibule is demarcated by a low flange on the medial edge of the dorsal part of the ventral ramus of the opisthotic. This also forms the medial border to a postero-dorsally extending concavity (= posterior ampullary recess of Welman, 1995, fig. 3b) that is interpreted as housing the posterior ampulla, the posterior opening of the external semicircular canal, and the ventral opening of the posterior vertical semicircular canal. The incompleteness of the ossification of the vestibular border includes its floor, so that there is no bony division of the ventral end of the vestibule and the lagenar recess. Indeed, as in e.g. *Erythrosuchus* (Gower, 1997), there is no structure preserved that unequivocally indicates the exact position, orientation, or length of the recess for the lagena (but see section IV.5).

The supraoccipital is missing on the right side so that the dorsal part of the vestibule is unknown. We consider part of the supraoccipital to be preserved on the left side (Fig. 6), although confidently identifying sutures is problematic. The internal prootic flange, forming the anterior border of the vestibule, has been forced a short distance away (less than on the right side) from the anterior surface of the opisthotic immediately in front of the posterior ampullary recess. Just above where these two elements have become slightly separated during preservation, the inner wall of the presumed supraoccipital is slightly bulged and holds a ventrally directed opening. This is interpreted as the ventral limit of the osseus common crus – the union of the two vertical canals.

If the medial suture between the prootic and supraoccipital has been correctly identified, then the posterodorsal end of the floccular recess just extends onto the supraoccipital on the left of UMZC T692, and the broken surface exposed above the recess on the right side represents the prootic surface for articulation with the supraoccipital. A shallow groove on the left side immediately anterior to the floccular recess (Fig. 6) is interpreted as indicating the probable path of the middle cerebral vein.

III. INTERPRETATION OF THE BRAINCASE OF *EUPARKERIA*

(1) Variation among specimens

The following points represent possible instances of

differences in braincase structure among the known specimens of *Euparkeria capensis*.

(a) Common or separate openings for the palatine and hyomandibular branches of the facial nerve

UMZC T692 possesses a single opening in the prootic for the exit of the facial nerve. The separate opening for the palatine branch identified by Ewer (1965, fig. 3) in the same specimen represents the dorsalmost part of the large depression on the lateral surface of the parabasisphenoid and prootic – there is no opening positioned here. Cruickshank (1970, 1972) described the same arrangement as Ewer (1965), but for SAM 7696. Evans (1986, fig. 7) also identified this feature as representing the (apparently only) facial foramen in SAM 7696. Welman (1995) described the path of the palatine branch of the facial nerve as being enclosed for a short distance by the 'alaparasphenoid' (= dorsolateral extent of the parabasisphenoid) and indicates two separate openings on the left side of SAM 7696 in his fig. 4c. This represents a difference between UMZC T692 and Welman's (1995) documentation of SAM 7696, with the condition in SAM 5876 currently unclear.

(b) Trabeculate cavity

Welman (1995) describes the dorsal part of the lateral depression on the parabasisphenoid (interpreted by him as an anterior tympanic recess) as extending within the 'anterior part of the alaparasphenoid' and being confluent with a 'trabeculate cavity' that extends back into the basioccipital. In UMZC T692, there is no evidence that the lateral depression communicates with a cavity within bone. It is only seen in SAM 7696 (Welman 1995, fig. 4), possibly because the ventral part of the braincase has been broken away (and perhaps because the broken surface was subsequently exposed to acid during preparation).

(c) Perilymphatic foramen

The ventral ramus of the opisthotic is only preserved on the right side of UMZC T692. It carries no structure that might be interpreted as indicating the path of the perilymphatic duct into the metotic foramen, although this could be attributed to the loss of the distal end of the ramus. A small notch immediately below the posteromedial corner of the vestibule is associated with a fracture through the ramus (Fig. 5). On the right side of SAM 7696 however, the ventral ramus is notched (Cruickshank, 1970, fig. 1; Welman, 1995, figs 3c and 4b; personal observation of cast), potentially representing an incompletely ossified border to the perilymphatic foramen (as suggested by Walker, 1990, p. 111), similar to that seen in extant *Sphenodon*. It is also possible that a bony medial border to the foramen has been lost during preservation or preparation. Further comparisons within *Euparkeria* are currently not possible, but this also represents a potential instance of variation among specimens.

(d) Dorsal extent of parabasisphenoid

There has been disagreement about the position of the suture between the prootic and parabasisphenoid in the vicinity of the ventral border of the fenestra ovalis. Cruickshank (1970) identified the parabasisphenoid of SAM 7696 as forming the anterior and ventral margin of the fenestra ovalis and therefore also encompassing most of the dorsal extent of the lateral depression. Walker (1990, p. 100) also interpreted most of this region to be parabasisphenoid, but Evans (1986) identified the prootic as forming most of this area in the same specimen. Welman's (1995) interpretation represents something of an intermediate in that he identifies the anterior margin of the fenestra ovalis as being formed by the prootic and parabasisphenoid, with the dorsal limit of the depression lying entirely within the parabasisphenoid. Preservation of this area is not perfect in UMZC T692, but a horizontal fault line, where a dorsal section has moved posteriorly and slightly medially in relation to a ventral block, appears to lie, at least anteriorly, along the prootic-parabasisphenoid suture (Fig. 3). This leads us to identify most of the anterior border of the fenestra ovalis and the anterodorsal border of the lateral depression to be formed by the prootic in UMZC T692, with a dorsal process of the parabasisphenoid forming the anteroventral and posterodorsal borders of the fenestra ovalis and lateral depression, respectively. This represents a further possible instance of variation among specimens of *Euparkeria*.

(2) Interpretive differences not based on variation among specimens

Here, we address ten interpretations of features of the braincase of *Euparkeria* that were made by Welman (1995) and are crucial for his phylogenetic conclusions, and with which we disagree. Our

counterarguments are largely presented in the form of alternative hypotheses of homology that we consider to be better supported by the available evidence, but also include questioning of the significance that certain similarities might have for the proposal that *Euparkeria* is relevant to the immediate ancestry of Avialae.

(a) *Fenestra rotunda, fenestra pseudorotunda, and the path of the perilymphatic duct*

In *Euparkeria*, two lateral openings of disputed homology are present behind and below the fenestra ovalis (see section II.1; Welman, 1995, figs 3, 4). The more posterior opening (our metotic foramen) is separated from the fenestra ovalis by the ventral ramus of the opisthotic and was termed 'fenestra pseudorotunda' by Welman (1995). Welman (1995) additionally interpreted the ventral opening, lying between the distal end of the ventral ramus of the opisthotic, the basioccipital, and the parabasisphenoid, to represent a 'fenestra rotunda'. Welman's (1995) suggestion that *Euparkeria* – in contrast to all other amniotes – possesses both a fenestra pseudorotunda and rotunda is considered here to be puzzling and highly problematic (and might even be considered to imply the presence of a tertiary tympanic membrane!). Crucial for the understanding of Welman's (1995) arguments, and for our rejection of them, are the precise meanings of a number of the employed terms, such as metotic fissure, fenestra rotunda, fenestra pseudorotunda, recessus occipitalis and recessus scalae tympani. Before discussing Welman's (1995) hypotheses of homology, we draw upon a recent review (Rieppel, 1985) as a framework for clarifying certain issues of nomenclature.

(i) *The situation in recent sauropsids*

The metotic fissure is a gap between the otic capsule and basicranium of the chondrocranium which can persist undivided throughout life (where in adult skulls it is then probably best termed metotic foramen) as in e.g. *Sphenodon*, or it can become divided into two openings during ontogeny as in e.g. extant squamates and archosaurs. The anterior opening that results from a subdivision of the metotic fissure has been variously termed fenestra rotunda, fenestra pseudorotunda, foramen cochleare or apertura lateralis recessus scalae tympani, while for the posterior opening the terms jugular or vagal foramen are commonly used. We will not discuss the confusing nomenclature of these openings further here (see also Gauthier, Kluge & Rowe, 1988, p. 153), but it suffices to point out that the term 'fenestra pseudorotunda' was introduced by de Beer (1937, pp. 263, 431) simply to distinguish the anterior opening in crocodilians and birds from the analogous/non-homologous opening in mammals, which is formed during ontogeny by a somewhat different subdivision of the metotic fissure (de Beer, 1937, pp. 263, 431).

The vagal and glossopharyngeal nerves, as well as the jugular vein, pass through the metotic fissure/ foramen. In recent groups with a subdivided metotic fissure, the vagus nerve and jugular vein (unless reduced) pass through the vagal/jugular foramen, and the glossopharyngeal nerve variably through either this opening, its own opening, or through the anterior opening of a subdivided fissure. The perilymphatic duct of all Recent amniotes exits the otic capsule through a foramen (foramen perilymphaticum) and invades the metotic fissure/ foramen. Contrary to Welman (1995, p. 536), we understand that Whetstone & Martin (1979) were not emphasizing the invasion of the metotic fissure by the perilymphatic duct in certain archosaurs, but were rather (as also interpreted by Walker, 1985, p. 132) contrasting the condition where the duct passes into the fissure (whether subdivided or not) by taking a direct posterolateral route, as in crocodilians and birds, with that where an initially more posteromedial route occurs, as in *Sphenodon*. The extracapsular part of the perilymphatic duct is frequently termed saccus perilymphaticus. In recent amniotes exhibiting a subdivision of the metotic fissure, the perilymphatic sac is associated with the anterior opening (i.e. the fenestra rotunda/ pseudorotunda) where it forms the secondary tympanum together with the mucous membrane of the middle ear (cavum tympanicum).

Hasse (1873) introduced the term 'recessus scalae tympani' for the extracapsular space lying between the otic capsule and basicranium, and filled by the perilymphatic sac. Rieppel (1985) has pointed out that Hasse's (1873) term strictly applies only to those instances where the metotic fissure has become subdivided during ontogeny [because Hasse (1873) was describing the skulls of adult birds], where the space in question communicates with the otic capsule (*via* the perilymphatic foramen), with the middle ear (*via* the apertura lateralis recessus scalae tympani = fenestra rotunda/pseudorotunda) and with the cranial cavity (*via* the apertura medialis recessus scalae tympani). Confusion has arisen when the term

recessus scalae tympani has been transformed from Hasse's (1873) original meaning and applied to a space defined by the soft tissues that it holds (or is hypothesized to have held, in fossils) or by simply being the space immediately extracapsular and ventral to the perilymphatic foramen. This allows the term to be applied even in those instances where the metotic fissure is not subdivided (e.g. for *Sphenodon* by de Beer, 1937, p. 240; lizards by Baird, 1960; *Hyperodapedon* by Benton, 1983; *Sphenosuchus* by Walker, 1990; and for turtles by Gaffney, 1972). Welman (1995) is not explicit about how he understands and employs the term, but recessus scalae tympani remains largely superfluous to our discussion, because the homology of 'spaces' is solely determined by the homology of the (not only bony) structures that delineates those spaces.

(ii) Ventral opening (Welman's fenestra rotunda) in Euparkeria

The gap between the distal end of the ventral ramus of the opisthotic, the basioccipital and parabasisphenoid of *Euparkeria* has been argued by Welman (1995, p. 536) to represent a fenestra rotunda, on the basis that the cavity immediately medial to the opening 'corresponds in position with the recessus scalae tympani of *Youngina*, which in turn seems approximately homologous with the occipital recess of lizards and *Sphenodon*'. We reject this proposed homology for four main reasons.

Firstly, there is no indication whatsoever (as described above) that the metotic fissure in *Euparkeria* was subdivided by an ossified commissure. This might not necessarily mean that a secondary tympanic membrane was absent, but simply that there is no evidence of a separate opening that can be homologized with (or referred to as) either a fenestra rotunda or pseudorotunda, and no space that can be strictly termed the recessus scalae tympani.

Secondly, the fenestra rotunda of extant squamates and archosaurs, as well as the analogous fenestra of mammals, represents a bony frame to which a secondary tympanic membrane (at the distal end of the perilymphatic duct) is attached, acting as a pressure-relief window. Welman (1995, p. 536) concedes that, in *Euparkeria*, the space immediately posterior to the ventral ramus of the opisthotic (our metotic foramen, Welman's fenestra pseudorotunda) – and not the space immediately medial to the opening in question – would in all probability have received the perilymphatic duct.

The opening in question in *Euparkeria* lies beneath the distal end of the opisthotic ramus, immediately below the fenestra ovalis, while the fenestra rotunda (and analogous fenestrae) variably present in other diapsids lies posterior to the opisthotic ramus, at the anterior end of a subdivided metotic fissure. The strong likelihood that the perilymphatic duct did not communicate with the opening in question in *Euparkeria*, and the absence of topological correspondence between the position and structure of this opening and the fenestra rotunda of other diapsids, argues strongly against their proposed homology.

Thirdly, the occipital recess of adult lizards (Oelrich, 1956) does not (*contra* Rieppel, 1985) directly represent or correspond to the recessus scalae tympani. Oelrich (1956, pp. 15, 17, fig. 13) clearly describes the occipital recess as a feature confined to a region external to the fenestra rotunda, i.e. the fenestra rotunda lies between the recessus scalae tympani and the occipital recess. Welman's (1995) identification of either a recessus scalae tympani (*sensu* Hasse, 1873) or an occipital recess (*sensu* Oelrich, 1956) in *Youngina* and *Sphenodon* is highly problematic because the metotic fissure of these taxa is apparently (Evans, 1987) or clearly (see Fig. 8) undivided, respectively.

Fourthly, we consider that a more convincing alternative to Welman's (1995) hypothesis is the interpretation of the ventral opening in *Euparkeria* as an unossified gap. Gower & Sennikov (1996*a* – where the gap was referred to as a 'pseudolagenar recess' because of its form in *Vjushkovia triplicostata*) identified a similar gap in *Prolacerta* and a number of the earliest archosaurs, where (as in *Euparkeria*) it consistently appears between the free edges of a number of elements. While accepting that this gap is well defined in *Euparkeria*, we see no reason for invoking non-homology with, or different soft-tissue and functional relations to, similar gaps (see section IV.5) in extant forms.

While the opening in question in *Euparkeria* is comparable with the unossified gaps of forms that have no ossified division of the metotic fissure (e.g. *Sphenodon*, basal archosauromorphs), it differs in the presence of a slender bridge defining its anterolateral border (Fig. 1B, D). Cruickshank (1970, 1972) was the first to recognize the delicate bridge of bone connecting the distal end of the ventral ramus of the opisthotic to the dorsal wing of the parabasisphenoid, closing the lateral border of the gap between the opisthotic, basioccipital, and parabasisphenoid. Cruickshank labelled this slender bridge as basisphenoid (Cruickshank, 1970) and opisthotic

(Cruickshank, 1972). It was omitted by Evans (1986, fig. 7 – followed by Chatterjee, 1991, fig. 28a), but it was indicated by Welman (1995), who identified it as a process of the opisthotic, but in using dotted lines (his fig. 4b, c) was apparently uncertain about the line of contact with the parabasisphenoid. The bridge is also identified by Welman (1995, fig. 5a) on the apparently incompletely preserved/prepared left side of SAM 5867. The incompleteness of the distal end of the opisthotic of UMZC T692 means that the presence or absence of this bridge cannot be judged in this specimen.

We conclude that the metotic fissure of *Euparkeria* was undivided by bone, and therefore that there is no opening that can be interpreted as forming a separate secondary tympanic window frame (and termed fenestra rotunda), or any space that can be strictly termed recessus scalae tympani. *Euparkeria* possesses an unossified gap beneath the end of the ventral ramus of the opisthotic that is similar to that seen in various extant and fossil diapsids. The interpretation and possible phylogenetic significance of unossified gaps in the otic region of extant and extinct diapsids are discussed further in section IV.5.

(iii) *Posterior opening* (Welman's *fenestra pseudorotunda*) *in* Euparkeria

According to Welman (1995, p. 536), the lateral opening immediately posterior to the ventral ramus of the opisthotic in *Euparkeria* corresponds to a 'metotic fissure invaded by the perilymphatic duct, forming an incipient fenestra pseudorotunda, homologous to advanced archosaurs such as *Sphenosuchus* and *Syntarsus*'. As mentioned in the preceding paragraphs, *Euparkeria* lacks a bony subdivision of the metotic fissure and therefore has no separate opening homologous to the fenestra pseudorotunda of birds or crocodilians. Furthermore, the metotic fissures of both *Sphenosuchus* and *Syntarsus* have also been described as undivided, by Walker (1990) and Raath (1985), respectively.

It might be noted that while Walker (1990) has presented morphological evidence that argues for the presence of a secondary tympanic window in *Sphenosuchus*, he also recognized that the metotic fissure remains undivided in this form. Strictly, therefore, there is no opening in this taxon that can be fully homologized with the fenestra pseudorotunda of crocodilians. Similarly, there is no true recessus scalae tympani in *Sphenosuchus* (see above).

In summary, the historically confused terms 'fenestra rotunda' and 'fenestra pseudorotunda'

both describe an anterior lateral opening of a subdivided metotic fissure that forms an ossified frame for a secondary tympanic membrane. We reiterate that *Euparkeria* resembles *Sphenodon* in lacking any ossified subdivision of the metotic fissure, and therefore that *Euparkeria* must lack an opening that can be termed fenestra rotunda or pseudorotunda. The presumed passage of the perilymphatic duct from the otic capsule into the metotic foramen in *Euparkeria* is without further immediate significance here because this is the plesiomorphic amniote condition.

(b) *Metotic process*

Welman (1995, p. 535) identifies a 'metotic process' in *Euparkeria*, located on the 'dorso-medial edge of the ventral process of the opisthotic' and considers it to be homologous with the lateral of two *Anlagen* of the metotic cartilage in extant birds. Among the literature cited by Welman (1995), only Engelbrecht (1958) has described the development of the avian metotic cartilage from two separate *Anlagen*, and this is in *Euplectes* (= *Pyromelana*), a member of the derived neognath Passeriformes. The metotic cartilage is seen as a single indivisible condensation from its earliest appearance in most bird embryos (Toerien, 1971), including all described palaeognaths. More importantly, because the process of the opisthotic of *Euparkeria* referred to by Welman (1995) is on the medial (inner ear) rather than lateral (middle ear) edge of the ventral ramus of the opisthotic, we consider his hypothesis of homology with the avian metotic process to be strongly contradicted by a lack of topological correspondence between the structures. Additionally, the metotic cartilage of birds is ossified by the exoccipital rather than the opisthotic (e.g. Müller, 1963). Furthermore, what Welman (1995) refers to in birds as the 'metotic process' is clearly (Welman, 1995, fig. 2) the ossified structure that subdivides the metotic fissure into a vagal foramen and a fenestra (pseudo)rotunda, but the metotic fissure of *Euparkeria* is not subdivided. As we discuss in section IV.3.b.v, the bony structure dividing the avian metotic fissure might not bear a direct ontogenetic relationship to the metotic cartilage of the avian chondrocranium and should preferably not be termed 'metotic process'.

As Welman (1995, p. 536), in his 'evolutionary changes' section, recognizes, the 'metotic process' he identifies in *Euparkeria* is a structure readily homologized with the medial wall of the posterior end of the
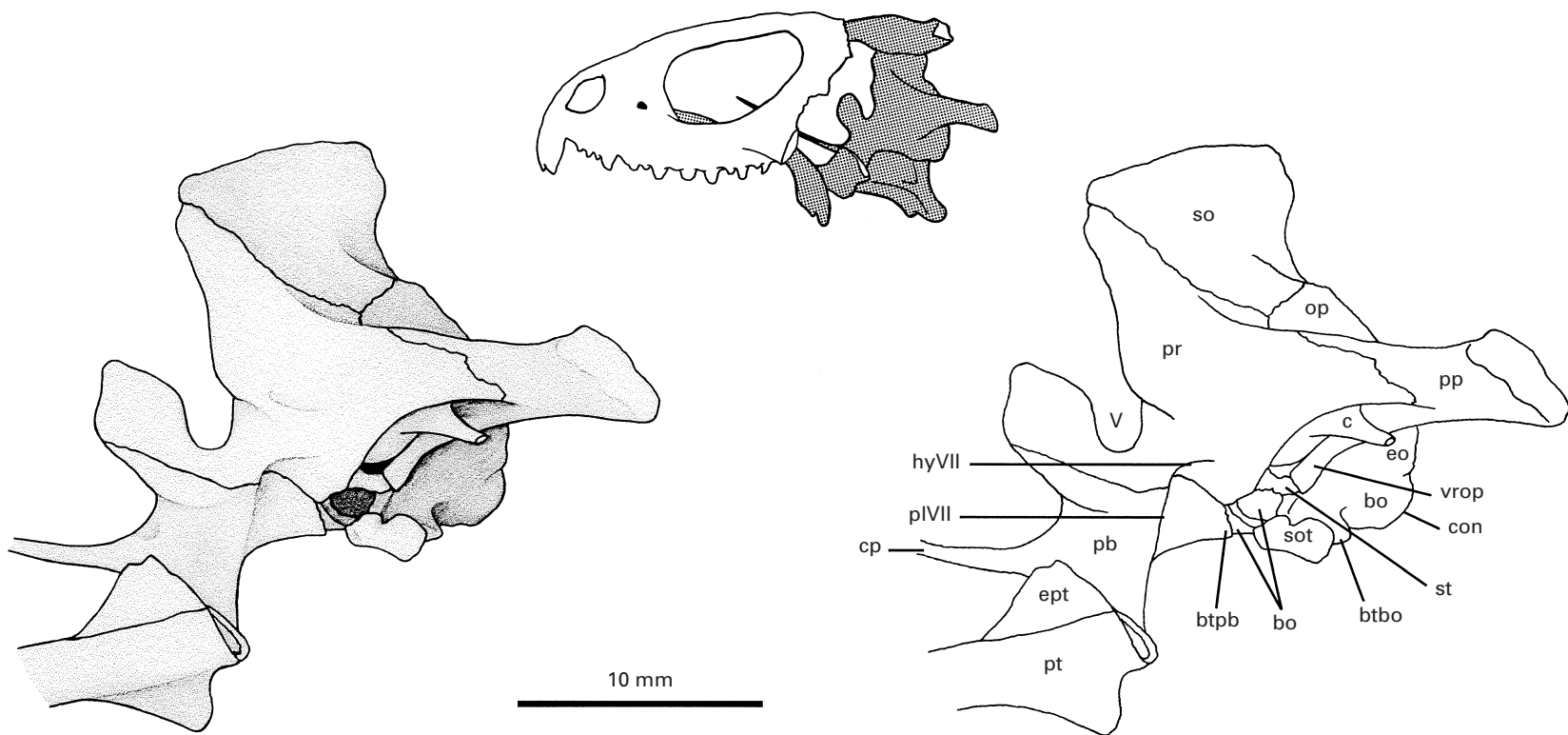
Fig. 7. *Sphenodon*. Braincase in left lateral view. The ventral part of the soft tissue covering the aperture of the unossified gap has been cut away, as has the tip of the left basal tuber of the parabasisphenoid. Most of the left epipterygoid and part of the left pterygoid have also been cut away, although the remainder still obscures the left basiptergoid processes. The columella is incomplete distally. The skull (shown top centre to aid orientation of braincase view) has had much of the left cheek cut away to reveal the braincase. See section IX for list of abbreviations.

otic capsule of other forms, and, as such, *Euparkeria* is no different to other earliest archosaurs or e.g. *Sphenodon*. Extant taxa such as birds, crocodilians and *Varanus* only differ in this respect from the condition in *Euparkeria* or *Sphenodon* in that the medial wall of the otic capsule is more extensively ossified – so that the part of the opisthotic equivalent to that in *Euparkeria* which Welman (1995) identifies as a 'metotic process' extends further anteromedially to meet the prootic and form the medial wall of the vestibule. It is particularly important that the structure in question in *Euparkeria* is more readily homologized with the ossified structure that partly or completely encloses the posteromedial wall of the canalicular part of the inner ear in at least all diapsids (including birds) – because birds have both a bony structure dividing the metotic fissure (= 'metotic process' of Welman, 1995) and a posteromedial wall of the canalicular part of the otic capsule, so that any attempt to homologize these structures fails the test of conjunction.

(c) Morphology of the basicranium

Welman (1995) argues that the basicranium of *Euparkeria* and birds, in contrast to that of crocodylomorphs and theropod dinosaurs, is horizontal, plate-like, and similarly subdivided. However, that the parabasisphenoid of *Euparkeria* is not a horizontal plate was described by Ewer (1965, p. 391): 'from its union with the basioccipital it slopes downwards and forwards'. UMZC T692 (Fig. 3) supports this, and confirms Gower & Sennikov's (1996*a*) observation that the basal tubera of the parabasisphenoid are significantly above, as well as behind, the basipterygoid processes, with the posteroventral edge of the element being strongly concave in lateral view. In this respect, *Euparkeria* resembles e.g. *Sphenodon* (Figs 7, 8) and erythrosuchids (Gower & Sennikov, 1996*a*; Gower, 1997) rather than *Prolacerta* (Gow, 1975; Evans, 1986), and the non-crown-group archosaurs *Proterosuchus* and *Fugusuchus* (Gower & Sennikov, 1996*a*) which have flat, horizontal parabasisphenoids. A consideration of even these few taxa immediately implies some homoplasy among diapsids in the shape of the basicranium.

Welman's (1995) subdivision of the ventral surface of the basicranium of birds into pretemporal and basitemporal platforms is problematic. In most neognath birds (e.g. Laridae), this apparent division of the ventral surface is exaggerated by a V-shaped edge that represents the anterior limit of the attachment of the musculus rectus capitis ventralis.

The subdivision is less clear when this edge is less well developed (e.g. the inconspicuous crista in *Sula*) or where the Eustachian tubes do not open at the junction between these areas, but in a more posterolateral position, as in palaeognaths.

Welman (1995) correlates areas of the parabasisphenoid of *Euparkeria* with terms (e.g. alaparasphenoid, sellaparasphenoid) that refer to distinct centres of ossification in birds (Jollie, 1957) that cannot (or have yet to) be determined in *Euparkeria*. Some of the similarities (and homologies) Welman (1995) proposes between *Euparkeria* and birds are biased by the use of this terminology. For example, the interpretation of the semilunar depression of *Euparkeria* as the site of the tympanic cavity opening of the lateral Eustachian tube is intimately related to Welman's (1995) understanding that this point lies between the 'basiparasphenoid' and 'alaparasphenoid'. There is an element of circularity in considering *Euparkeria* to be closely enough related to birds *a priori* to share a similar ontogeny of the parabasisphenoid, before using topology to correlate areas of the parabasisphenoid of *Euparkeria* and birds, and then citing similarities based on these correlations as evidence that *Euparkeria* is closely related to birds. We stress that such a subdivision of the avian parabasisphenoid is based on data from early ontogenetic series such as are unknown for *Euparkeria* – where the parabasisphenoid is a single recognizable ossification in all currently known specimens. There are no intrinsic data indicating whether the parabasisphenoid of *Euparkeria* more closely resembled that of birds, in having many separate centres of ossification (up to seven in the parasphenoid alone: Jollie, 1957), or that of crocodilians and lepidosaurs (three centres forming the parasphenoid: de Beer, 1937; Bellairs & Kamal, 1981).

(d) Path of internal carotid arteries

Welman (1995, p. 534) argues that the internal carotid arteries of *Euparkeria* would have resembled those of birds, rather than those of *Sphenosuchus* or *Syntarsus*, in converging (when seen in ventral view) anteriorly at a wide angle, instead of following a 'more or less parallel' course. Further, Welman (1995) suggests that, in lateral view, the internal carotid arteries of *Euparkeria* and birds follow a straight path, in contrast to the S-shaped route in *Sphenosuchus* and *Syntarsus*. In the following discussion it should be borne in mind that it is only proposed reconstructions that can be compared when
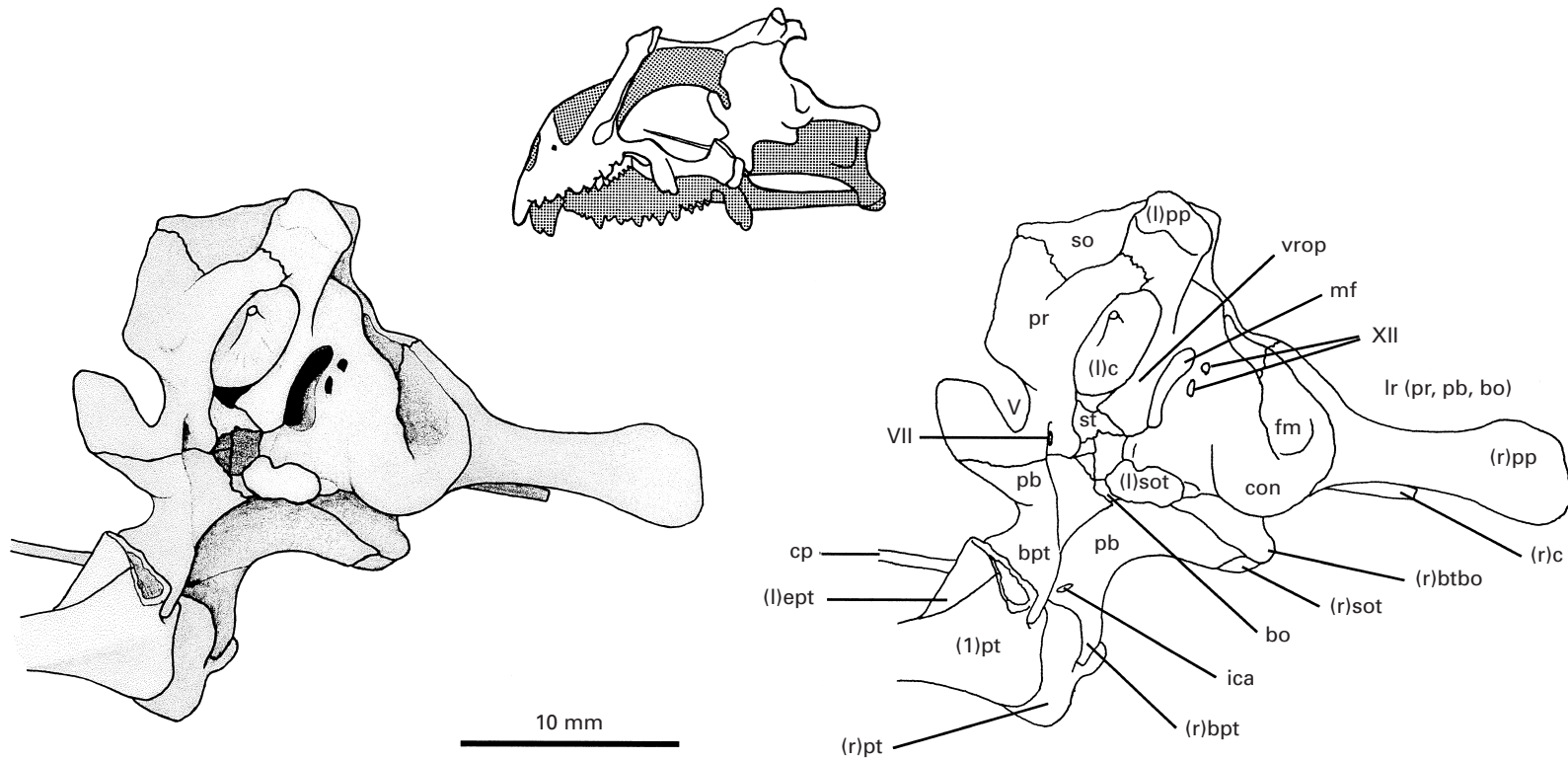
Fig. 8. *Sphenodon*. Posteroventral view of the left lateral side of the braincase. See section IX for list of abbreviations.

discussing the position of soft tissues in most fossils. It might also be pointed out that what Welman (1995) is referring to, and what are discussed below, are actually one of the two main divisions of the internal carotid arteries, the cerebral branches.

There is a fundamental disagreement between our and Welman's (1995) identification of ossified structures that indicate the course of the cerebral branches of the internal carotid arteries in *Euparkeria*. Welman (1995) interprets the cerebral branch of each side as running along the lateral surface of the parabasisphenoid, being partly enclosed by (his) 'parasphenoid'. In Welman's (1995) fig. 5a, the artery is depicted as entering the lateral surface of the parabasisphenoid, within the lower part of the depression immediately posterior to the clinoid process (the base of Welman's 'alaparasphenoid'), as has also been interpreted by Chatterjee (1991, fig. 28a). This does not seem to be compatible with the position of the artery depicted in Welman's fig. 1, where it is shown as passing forward from the posterior end of the semilunar depression ('gaci' in Welman's fig. 1) to a point immediately behind the basipterygoid process. In contrast, we hypothesize that the arteries entered the parabasisphenoid *via* a pair of foramina [interpreted by Welman (1995) as the pharyngeal openings of the Eustachian tubes] on the posteroventral surface of that element (Fig. 4) before passing anterodorsally through bone and into the base of the hypophyseal fossa. Palatine branches of the arteries (= palatine arteries) may have branched off from this course outside the posteroventral foramina and continued their path forward outside bone, between the basipterygoid processes along with the palatine branches of the facial nerves as they do in e.g. *Sphenodon* (O'Donoghue, 1920; Säve-Söderbergh, 1946, 1947).

We cite the following points in preferring our hypothesis: (1) nobody (including Welman, 1995) has described explicitly the presence of a foramen within the depression on the lateral surface of the parabasisphenoid in *Euparkeria*, or of a channel passing from any such foramen into the hypophyseal fossa. (2) There is no foramen within the lateral depression or within the semilunar depression of UMZC T692. Welman (1995, p. 534) seems to consider the semilunar depression to represent a gap between what he considers to be the 'alaparasphenoid' and 'basiparasphenoid', with both the internal carotid artery and lateral Eustachian tube passing through here. This interpretation is based on a subdivision of the parabasisphenoid that we believe to be indeterminable in *Euparkeria*, rather than on

observable anatomical features (see section III.2.*c*). (3) Our hypothesis that the paired foramina on the posteroventral surface of the parabasisphenoid are for the cerebral branches of the internal carotid arteries is partly based on the direct observation of their communication *via* ossified channels with the hypophyseal fossae in e.g. *Erythrosuchus* (Gower, 1997, fig. 4) and rhynchosaurs (personal observation of GPIT specimen of '*Cephalonia lotziana*' described by Huene, 1942, p. 262). This agrees with the identifications made for a range of early archosauromorphs (Chatterjee, 1974; Benton, 1983; Evans, 1986, 1990; Dilkes, 1995, 1998; Gower & Sennikov, 1996*a*). (4) While the arteries enter the lateral, rather than posteroventral primary surface of the parabasisphenoid in crown-group archosaurs (Parrish, 1993) in an equivalent position to that interpreted for *Euparkeria* by Welman (1995), and in extant squamates such as *Varanus*, a posteroventral entrance is not unknown in living diapsids, as demonstrated by *Sphenodon* (Fig. 8; Säve-Söderbergh, 1947).

The mistaken identification (e.g. Chatterjee, 1991; Welman, 1995) of a lateral position of the carotid foramina in *Euparkeria* can perhaps be explained by the fact that they are positioned here in crown-group archosaurs (Parrish, 1993; Gower & Sennikov, 1996*a*) and in Recent lizards (e.g. *Varanus*). Similar misidentifications have occurred for other archosauromorph taxa (e.g. for *Xilousuchus*, see Gower & Sennikov, 1996*a*). The presence of depressions on the lateral surfaces of the parabasisphenoid probably contributes to such instances of misidentification in fossil material, where foramina on the posteroventral surface can initially be overlooked when considering the entrance point of the internal carotid arteries. The evidence presented above, combined with the fact that no early archosauromorph has been described or figured with genuine foramina on both the posteroventral and lateral surfaces of the parabasisphenoid, suggests that foramina located in the posteroventral position might initially be considered to have transmitted the cerebral branches of the internal carotid arteries.

Concerning the angle between the path of the arteries seen in ventral view, we agree with Welman (1995) in observing a strong anterior convergence in birds and *Euparkeria*. We disagree however with the claim that the path in *Sphenosuchus* is 'more or less parallel'. In this taxon, the anterior part of the parabasisphenoid holding the hypophyseal fossa is much narrower, transversely, than the posterior of the parabasisphenoid (see the strong V-shape of this

element in ventral view depicted by Walker, 1990, fig. 20a), and this is true for an extremely wide range of archosaur taxa. In Recent crocodilians, the path of the carotid arteries is known and this is clearly strongly convergent anteriorly. We have not observed material of *Syntarsus*.

The presence of an S-shaped path of the carotid artery seen in lateral view is a character whose phylogenetic importance has perhaps been over-emphasized. Firstly, the degree of sinuosity is very much open to interpretation, as demonstrated by the incompatible views of Welman (1995), who suggests that birds and *Euparkeria* exhibit an almost straight path while in *Sphenosuchus* and *Syntarsus* it is S-shaped, and Walker (1972, 1990, p. 85), who has suggested a similarity between the S-shaped paths of the carotid artery in birds and crocodylomorphs. This discrepancy begs the questions: is the course of the artery S-shaped or not in birds, what is the course in *Euparkeria*, and how phylogenetically informative is the course?

Examination of the skull of a petrel macronettes indicates that the very shallow S-shape to the course of the artery is amplified by the view depicted in Walker's (1972) fig. 1c. Such a flat or extremely shallow S-shape is found in all birds whatever the extent of enclosure of the arteries, and is clearly associated with the rather flat parabasisphenoid. In *Euparkeria*, there is only evidence for the enclosed route of the arteries, between the foramina on the posteroventral surface of the parabasisphenoid and the hypophyseal fossa, and this is most probably rather straight. Unlike the condition in crocodilians and many birds, the carotid arteries were not enclosed in bone behind this point of entrance into the para-basisphenoid, so that additional hypotheses are required for the reconstruction of their position posterior to this. It could be argued that the vertical component to the shape of the parabasisphenoid of *Euparkeria* (see section III.2.c above) suggests that the arteries did follow a somewhat sinuous course, extending anteroventrally from near the cranio-vertebral joint to the ventral surface of the para-basisphenoid before turning dorsally through bone into the hypophyseal fossa (as depicted in *Sphenodon* by Säve-Söderbergh, 1947). Welman's (1995) reconstruction of a straight path in *Euparkeria* is perhaps partly a consequence of his understanding that the parabasisphenoid is flat and horizontal in this taxon.

Problems exist in using variation in the path of the carotid arteries as an independent character for archosaur phylogeny because of its close association with other characters (including the degree of enclosure of the arteries, the form of the parabasi-sphenoid, and even the angle between the plane of the foramen magnum and that of the basicranium, see Saiff, 1974, p. 235, 1981, p. 209), the difficulty of identifying homologous degrees of sinuosity, and because of the necessary reliance on hypothesized reconstructions of the path of the arteries in taxa where, for much of their path, they would not have been enclosed in bone.

In conclusion, the foramina for the entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid are in a posteroventral, not lateral, position in *Euparkeria*. These arterial branches are anteriorly convergent in crocodylo-morphs as well as in *Euparkeria* and birds. The full course of the cerebral branches of the arteries in *Euparkeria* is not known, but might have been sinuous in lateral view. The degree of sinuosity can only be hypothesized for most fossil taxa in which the arterial course lay outside bone, and it remains a character that has yet to be understood fully across Archosauromorpha.

(e) Eustachian system

Welman (1995) asserts that the Eustachian tubes in *Euparkeria* are enclosed in bone and that, as in birds, they form only a lateral system – lacking the connection with a medial system that is present in crocodilians and (as Welman states) theropod dinosaurs. We suggest that *Euparkeria* completely lacks any bony indication of the route of the Eustachian system and that it remained entirely unenclosed.

In the *Euparkeria* specimen SAM 7696, the feature identified by Welman (1995, fig. 4) as the tympanic cavity opening of the Eustachian tube corresponds to the anterodorsal end of the 'semilunar depression' (it is not clear why this structure is shown as a groove in Welman's fig. 4a but apparently as an enclosed channel in his Fig. 4b). In SAM 5867, Welman (1995, fig. 1) identifies pharyngeal openings of the Eustachian tubes on the posteroventral surface of the parabasisphenoid. Welman (1995) does not explicitly describe the existence of a channel passing through bone between these two points, and none exists in UMZC T692. We have described the semilunar depression as a closed groove in UMZC T692 and argued that it is readily homologized with similar structures in other early archosauromorphs (section II). Furthermore, strong evidence exists that the posteroventral foramina in *Euparkeria* that Welman (1995) interprets as the pharyngeal

openings of the Eustachian tubes are for the cerebral branches of the internal carotid arteries (see section III.2.*d*). Neither in our examination of UMZC T692, nor in published figures of the additional specimens can we identify any ossified structure that would indicate the path of the Eustachian tubes. We conclude that, as in living diapsids other than crocodilians or the adults of most birds (although not in some neognaths, e.g. Sulidae), the Eustachian tubes of *Euparkeria* traversed the short distance between the middle ear and the pharynx lateral to the parabasisphenoid and were unenclosed in bone.

Welman (1995, p. 534) states that the lateral Eustachian tubes of *Euparkeria* lie medial to the path of the cerebral branches of the internal carotid arteries. In birds, however, the situation is more complex, with the Eustachian tubes lying ventral to the arteries, being more lateral to them at the posterior end, and more medial anteriorly.

Welman's (1995, p. 533) statement that *Syntarsus* and 'primitive dinosaurs' possessed a 'secondarily modified median Eustachian system' requires substantiating. Witmer (1997) has argued that the 'median Eustachian system' of crocodilians is better termed a 'median pharyngeal system' because it is not a true auditory tube derived from the first pharyngeal pouch. While a connection between a median recess and the true Eustachian tubes has yet to be fully documented for *Syntarsus*, such a system is known among theropods (e.g. Larsson, 1996), but any proposition of homology with the similar communication in crocodilians must explain its absence in a number of other theropods and, where present, different topological relationships to other braincase structures (H. C. E. Larsson, personal communication). The possibility that the median pharyngeal recess of crocodilians and/or theropods bears some relation to Rathke's pocket of embryonic birds remains to be fully explored. Recesses on the posterior or posteroventral surface of the parabasisphenoid or basioccipital of *Euparkeria* and other early archosaurs might also be homologous with the pneumatic median pharyngeal recess of crown-group archosaurs.

(*f*) Exit of facial nerve

Welman (1995, p. 534) claims that the facial nerve in some bird embryos and *Euparkeria* passes through the vestibule on its way out of the braincase, that in most birds it exits between the labyrinthine and cochlear parts of the otic capsule (and is later enclosed in the anterior capsule wall), and that the

condition in *Sphenosuchus* and *Syntarsus* is much derived compared to this in that the facial nerve exits anterior to the otic capsule rather than passing between its two parts. Several points need to be made.

The borders of the vestibule are incompletely defined in *Euparkeria* as a result of the incomplete ossification of the medial wall of the otic capsule. This includes almost all of the ventral limit of the vestibule, and there is no clearly ossified differentiation between the canalicular and cochlear parts of the inner ear. Despite this, there is no evidence that the facial nerve of *Euparkeria* actually passed through the vestibule. Part of the anteroventral limit of the vestibule can be detected in *Euparkeria* as a sub-horizontal ridge in UMZC T692, on the medial surface of the braincase immediately above the facial foramen (Fig. 5). This is similar to the condition in *Erythrosuchus* (Gower, 1997), in which the medial wall of the otic region is also incompletely ossified. Thus, the facial nerve of *Euparkeria* can be strongly argued to have exited the braincase immediately anteroventral to the vestibule, which is the usual condition in Recent reptiles (e.g. Oelrich, 1956; Iordansky, 1973; Bellairs & Kamal, 1981).

The facial nerve of bird embryos passes out of the chondrocranium *via* a notch in the anterior margin of the otic capsule, approximately at a point between its cochlear and canalicular regions. Because the notch is in the anterior border of the capsule the nerve itself remains extracapsular (e.g. personal observation of *Larus ridibundis*). During ontogeny, a prefacial commissure develops and encloses the facial nerve between itself and the anterior border of the capsule. The avian condition is therefore essentially the same as the reptilian one. A review of the literature (Sonies, 1907; Crompton, 1953; Lang, 1956) that Welman (1995) cites in support of his statement that the facial nerve of some bird embryos passes through the vestibule, shows that in these embryos the facial fissure might be positioned more in the canalicular (and therefore vestibular) part of the anterior margin of the capsule than between the two regions, but it never passes through the vestibule itself. Crompton's (1953, p. 138) summary statement that 'in early development the facial nerve passes through the cavity of the auditory capsule, but later it is enclosed in a cartilaginous canal' is not in itself entirely clear (e.g. the use of the term 'cavity'), particularly when every other statement on the ontogeny of the path of the facial nerve in the descriptive part of the same publication documents a normal exit of the nerve, e.g. 'the facial nerve passes upwards through

the cochleocanalicular fissure' (Crompton, 1953, p. 87On the same page, Crompton (1953) quotes Brock's (1937) description of the similar course in the ostrich *Struthio*.

The condition in birds is therefore the same as in crocodilians and other reptiles, in that the facial nerve exits the chondrocranium *via* a notch between the anterior border of the two regions of the otic capsule that eventually becomes closed off by the prefacial commissure. A difference seen in at least some birds is that, in concert with a low basicranium, the long axis of the cochlea extends anteroventrally rather than ventrally, so that the facial nerve lies anterodorsal rather than anterior to the cochlear part of the capsule. The notch itself, however, still lies in the margin of the capsule and the nerve remains extracapsular. In direct opposition to Welman's (1995, p. 534) statement, the condition in some birds is thus derived relative to that in *Sphenosuchus* and *Syntarsus* (and extant reptiles) and not *vice versa*.

(g) Orientation of the cochlea

Welman (1995, p. 535) suggests that the cochlea of birds and *Euparkeria* 'probably had the same orientation', and cites a groove in SAM 5867 along with 'a mass of rounded calcitic crystals' discovered on the floor of the endocranial cavity during specimen preparation as evidence.

Several questions must be addressed before the crystals discovered in SAM 5867 can be 'considered to be homologous with the statolithic mass of the avian cochlea' (Welman, 1995, p. 535). Do the crystals represent granular material that was present in life? If so, can it be known that they originate from the macula lagenae and not from the macula sacculi? Can it be certain that the preserved crystals represent their life position? These crystals aside, there are also problems with a comparison of the orientation of the avian cochlea and that reconstructed by Welman (1995) for *Euparkeria*. The orientation of the cochlea is variable in birds (personal observation) being at a low angle to the horizontal in e.g. *Larus* and almost vertical in e.g. *Tetrao urogallus*. While extending anteroventrally or ventrally, the cochlea of birds never (to the best of our knowledge) extends posteroventrally, as seems to be indicated in Welman's (1995, fig. 3a) reconstructed cochlear orientation in *Euparkeria*. A further point is that the basioccipital forms much of the area that Welman (1995, fig. 3a) interprets would have housed the lagena in *Euparkeria*, and is therefore more similar to the recess of *Sphenosuchus* and *Syntarsus* than birds, in terms of the contrast emphasized by Welman (1995, p. 536).

The area labelled as the lagenar recess by Welman (1995) for *Euparkeria* lies just lateral to a median 'notochordal ridge', and might also be considered to be positioned too far medially within the endocranial cavity to have held the lagena/cochlea. The far from complete ossification of the floor of the vestibule and the absence of a clearly differentiated recess certainly demand caution when attempting to hypothesize the position, length, and orientation of the lagena/ cochlea in *Euparkeria*. Identifications of the position and form of the 'lagenar recess' (Welman, 1995) or 'base of the lagenar recess' (Walker, 1990, p. 100) in *Euparkeria* based on a groove in the floor of the endocranial cavity need to be substantiated. We suggest that there is no intrinsic, unambiguous evidence that the lagena of *Euparkeria* was more similar to that of birds and crocodilians, where an elongated and tubular cochlea is present, than that of lepidosaurs, which have a sac-like and strongly tapered lagena. Among archosauromorphs, clearly differentiated and elongate cochlear recesses are currently known with certainty only in birds, crocodylomorphs and some dinosaurs (Walker, 1990, p. 111). The potential correspondence between the position of the lagena/distal end of the cochlea and an unossified gap in the lateral wall of the braincase is discussed in section IV.5.

(h) Posterior ampullary and tympanic recesses

Welman (1995) considers the posterior ampullary recess (PAR) of *Euparkeria* to be a homologue of part of the posterior tympanic recess (PTR) of birds. As evidence, Welman (1995, p. 535) states that both the posterior ampulla and path of the posterior semi-circular canal lie inside the posterior tympanic recess of birds and inside the posterior ampullary recess of *Euparkeria*. Supporting evidence is forwarded by Welman's (1995) understanding that in both taxa these recesses open 'into the dorsal end of the metotic fissure'.

We here understand the term 'posterior ampullary recess' to refer to an ossified concavity in the canalicular part of the inner ear (= posterior osseus ampulla of Baird, 1970), in the region where the posterior vertical, and external (horizontal) semi-circular canals meet, and where the soft-tissue posterior ampulla is positioned in at least all living diapsids. Based upon this definition, we fully agree with Welman's (1995) identification of the position

of this structure in *Euparkeria*, but reject his proposed homologizing of this structure with any part of the posterior tympanic recess of birds.

Firstly, we contest Welman's (1995, p. 535) statement that the path of the posterior semicircular canal of *Euparkeria* and birds lies 'inside' the posterior ampullary recess and posterior tympanic recess, respectively. We suggest (as described above) that the condition in *Euparkeria* is the same as in extant reptiles, where the posterior ampullary recess holds the posterior ampulla and the ventral opening of the posterior vertical canal. The path of the posterior vertical canal does not therefore lie inside the recess, but rather opens into it and curves anteriorly and dorsally from it to the osseous common crus. The arrangement of the canal system in birds is essentially the same as in reptiles, with the posterior vertical and external semicircular canals opening into an ossified hollow (PAR) where the posterior ampulla is held (e.g. Retzius, 1881–84). The posterior (caudal) tympanic recess of birds extends from the tympanic (middle ear) cavity in a posterior direction before soon branching into a proximal and distal chamber (Witmer, 1990). The proximal chamber continues in a medial direction and 'is bounded approximately by the caudal [posterior] semicircular canal, horizontal [external] semicircular canal, utriculus and caudal [posterior] wall of the paroccipital process' (Witmer, 1990, p. 341). In adult birds in which tympanic pneumatization is extensive, the posterior tympanic recess may therefore reach and surround part of the ossified canalicular part of the otic capsule. To the best of our knowledge, however, there are no instances where the soft-tissue posterior ampulla does not lie in an ossified posterior ampullary recess. The posterior ampulla sits in a concavity that is always separated from the posterior tympanic recess – by the chondral bone that forms the ampullary recess. Because birds possess a posterior ampullary recess and a posterior tympanic recess, any attempt to homologize the PAR of *Euparkeria* with the PTR of birds fails the test of conjunction.

Welman (1995, p. 535) cites the opening of the PAR of *Euparkeria* and the PTR of birds into the 'dorsal end of the metotic fissure' as support for his homologizing of these two structures. The PTR of birds does open into the metotic fissure early in ontogeny and eventually opens into the columellar recess, a concavity in the middle ear that also houses the fenestra ovalis and secondary tympanic window (Witmer, 1990). Importantly, the PAR of *Euparkeria* 'opens' into the <u>medial</u> side of the metotic foramen,

i.e. it is an inner, not a middle, ear recess. This fundamental dissimilarity between the position of the two structures again counts strongly against their homology. Furthermore, the PAR of *Euparkeria* only appears to 'open' into the dorsal end of the metotic foramen because the incomplete ossification of the posteromedial wall of the otic capsule means that the vestibule is not closed off from it by bone.

The PAR of *Euparkeria* is also directly comparable with that of extant crocodilians. This region appears different at first glance only because the medial wall of the otic capsule is more extensively ossified in the extant group, forming a completely bony medial border to the vestibule. The incompletely ossified medial otic capsule wall of *Euparkeria* is more comparable with the condition in e.g. the early archosaurs *Erythrosuchus* (Gower, 1997) and *Vjushkovia triplicostata* (Gower & Sennikov, 1996*a*), and Recent turtles and *Sphenodon* than with the condition in birds, crocodilians, and e.g. *Varanus*. The more extensive ossification of the medial wall of the otic capsule in *Sphenosuchus* and *Syntarsus* does not (*contra* Welman, 1995) in itself explain the absence of the PTR in these two taxa, because similar ossification of the capsule wall occurs in birds. It might also be noted that a recess has been described in the middle ear of the crocodylomorph *Dibrothrosuchus* (Wu & Chatterjee, 1993) that is in an approximately comparable position to the PTR of birds.

In conclusion, the posterior ampullary recess of *Euparkeria* is homologous with the posterior ampullary recess of birds and at least all other diapsids, and *Euparkeria* appears to lack any cavity which can be putatively homologized with the avian posterior tympanic recess.

(i) *Anterior tympanic recess*

Welman (1995) argues that *Euparkeria* possesses an 'incipient' anterior tympanic recess (ATR) homologous with that of birds. We are currently reluctant to endorse this hypothesis of homology, partly because of the lack of an extension of the lateral depression into the parabasisphenoid of UMZC T692 and the fact that the presence of a 'trabeculate cavity' has only been identified in a single, broken and acid-prepared specimen, but largely because of the many problems that currently exist in assessing the homology of pneumatic cavities (particularly of the middle ear) in archosaurs (e.g. Witmer, 1990). In addressing the potential phylogenetic significance, particularly with regard to avian origins, of such a feature it might also be noted that similar

depressions, with varying degrees of excavation, are seen in a diverse range of other archosaurs; that a bony ATR is (presumably secondarily) absent in some birds (e.g. Sulidae); and that the ATR does not extend into the basioccipital of birds, contrary to the situation apparent from Welman's (1995, fig. 4) illustration of the 'trabeculate cavity' in the *Euparkeria* specimen SAM 7696.

(j) Basipterygoid processes

Welman (1995, p. 536) suggests that the shape and orientation of the basipterygoid processes of *Euparkeria* resembles those of palaeognath birds, 'while those of *Syntarsus* and *Sphenosuchus* are horn-shaped and pneumatic respectively'. We disagree with the suggestion that there is a close similarity between the basipterygoid processes of palaeognaths and *Euparkeria*, with the more or less transversely elongate processes of palaeognaths being one obvious difference.

(3) Synapomorphies of *Euparkeria* + *Archaeopteryx*?

Welman (1995) draws many comparisons between the braincase of *Euparkeria* and birds (most of which are discussed above), and then lists four proposed synapomorphies for *Euparkeria* + *Archaeopteryx*.

(a) Form of the basicranium

Welman (1995, p. 536, citing a personal communication from M. A. Raath) suggests that a previously problematic bone in the London specimen of *Archaeopteryx* represents the basicranium, and that it 'closely corresponds in shape and size' to the basicranium of *Euparkeria*. We do not find a close correspondence between the *Archeopteryx* 'basicranium' (Welman, 1995, fig. 5b), with its straight posteroventral edge, and the strongly arched basicranium of *Euparkeria* seen in lateral view (Fig. 3). Moreover, Welman's (1995) proposal is in contrast to Walker's (1985, p. 129) conclusion that this element represents a quadrate, an interpretation that has recently been endorsed by Chatterjee (1991, p. 318), Elzanowski & Wellnhofer (1996, p. 86) and L. M. Witmer (personal communication). We have not examined the specimen in question, but suggest that the uncertainty of identification, and the lack of a description of the plesiomorphic condition of the basicranium by Welman (1995), further weaken the credentials of this proposed synapomorphy.

(b) Anterior tympanic recess

Welman's (1995) second proposed synapomorphy is the shared position and structure of the anterior tympanic recess. Some problems associated with homologizing such features have been outlined above (section III.2.i). The depression in question in *Euparkeria* might be pneumatic, but the presence of similar depressions is widespread among archosaurs and homologies have yet to be established, particularly for taxa that might lie outside the crown group. It is worth repeating two of the comments made by Witmer (1990, 1991) following his detailed studies of tympanic pneumaticity in archosaurs: '…the homology of many sinuses has yet to be demonstrated. Until these homologies are determined, one should remain cautious about any phylogenetic conclusions' (Witmer, 1991, p. 449); 'At present, it seems unwise to use any pneumatic characters to link birds with any particular group of archosaurs' (Witmer, 1990, p. 370).

(c) Posterior ampullary and tympanic recesses

The basis for the third of Welman's (1995) synapomorphies, the PAR of *Euparkeria* and PTR of *Archaeopteryx* is discussed in detail above (section III.2.h), where it is shown that a hypothesis of homology of the respective concavities can be rejected on the grounds of their lack of topological correspondence and a failure to pass the test of conjunction. The PAR of *Euparkeria* is an inner ear feature, while the PTR of *Archaeopteryx* (Walker, 1985; Witmer, 1990) opens into the tympanic cavity of the middle ear. Additionally, the PAR of *Euparkeria* can be readily homologized with the PAR of birds and at least all other diapsids, thus representing a more convincing alternative hypothesis.

(d) Large fenestra ovalis

The final synapomorphy listed by Welman is the 'large' fenestra ovalis in both *Archaeopteryx* and *Euparkeria*. It is not specified whether this largeness is absolute or relative, a discrete state is not described, and no outgroup comparison is made. Clack (1997, 1998) has argued that a large fenestra ovalis is plesiomorphic for tetrapods, and that this condition is retained in early diapsids such as *Youngina* and *Euparkeria*. In extant amniotes, the middle ear (including the fenestra ovalis) is negatively allometric with respect to body mass (Schwartzkopff, 1957; Nummela, 1997) – so that a relatively large

fenestra ovalis in *Euparkeria* and *Archaeopteryx* might be explained simply by scaling, rather than an especially close phylogenetic relationship. We do not consider this character to be of phylogenetic significance in the given context.

IV. PHYLOGENETIC IMPLICATIONS

(1) Historical perspective

Several statements have been made on the phylogenetic implications of braincase structure in *Euparkeria* in addition to the work by Welman (1995). Cruickshank (1970) considered the braincase of *Euparkeria* to be surprisingly underived for an archosaur, citing similarities with *Proterosuchus*, *Sphenodon* and even *Captorhinus*. This was partly based on the understanding at that time that a laterosphenoid was absent in *Euparkeria*, a view recently corrected by Clark *et al.* (1993). Gow (1975, p. 121) interpreted the braincase of *Euparkeria* to be 'considerably more primitive than that of Phytosaurs and Aetosaurs though somewhat advanced over that of the Proterosuchids'. Evans (1986) followed Cruickshank (1970) in considering the braincase of *Euparkeria* to be plesiomorphic for archosaurs, but made no specific phylogenetic statements. Walker (1990) clearly considered the braincase of *Euparkeria*, particularly the otic region, to be plesiomorphic – suggesting that it 'presumably represents the ancestral archosaurian pattern' (p. 111), and is 'closely similar to that of *Sphenodon*' (p. 97). Walker's (1990) view was based on the observation in both *Sphenodon* and *Euparkeria* of e.g. an undivided metotic fissure, an incompletely ossified medial wall of the otic capsule, and an unelongated lagenar region. Walker (1972, 1974, 1985, 1990) additionally drew attention to derived (and potentially homologous) features shared by crocodylomorph and avian braincases that he considered (Walker, 1990) to be absent in *Euparkeria*. Chatterjee (1991) has also considered the braincase of *Euparkeria* to be generally plesiomorphic for archosaurs, stating that 'the structure of the otic capsule is primitive' (p. 334). Gower & Sennikov (1996*a*) included *Euparkeria* as part of a small range of the earliest archosaurs in a preliminary numerical parsimony analysis of only braincase data. The most parsimonious representation of Gower & Sennikov's (1996*a*) data places *Euparkeria* outside the crown group, although the result is not particularly robust.

Aside from Welman's (1995) radical hypothesis, all other considerations of the phylogenetic position of *Euparkeria* based on braincase structure are
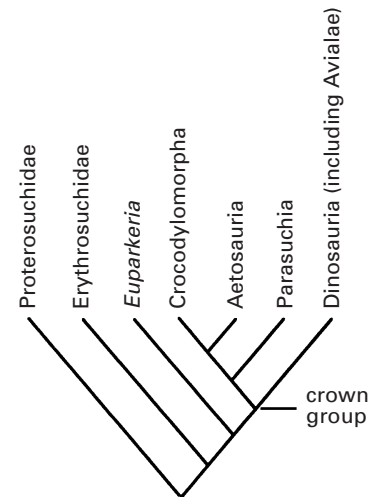

Fig. 9. Semi-strict reduced cladistic consensus found by Gower & Wilkinson (1996) of four recent (Sereno & Arcucci, 1990; Sereno, 1991*a*; Parrish, 1993; Juul, 1994) explicit analyses of archosaur phylogeny, depicting *Euparkeria* outside the crown group. As well as the taxa pruned by Gower & Wilkinson (1996) (Ornithosuchidae, *Saurosuchus*, *Ticinosuchus*, *Prestosuchus*), other taxa excluded are those included in only a single analysis, as well as Proterochampsidae and Pterosauria (because of disagreement on their position in a recent study by Bennett, 1996).

therefore congruent with the consensus (Fig. 9) reached by recent explicit analyses (Sereno & Arcucci, 1990; Sereno, 1991*a*; Parrish, 1993; Juul, 1994; Bennett, 1996) that *Euparkeria* lies outside the currently recognized limits of the crown group, i.e. birds and crocodilians are more closely related to one another than either is to *Euparkeria*.

(2) Welman's (1995) hypothesis

Welman (1995) has proposed that birds (+*Archaeopteryx*) and *Euparkeria* are more closely related to each other than either is to theropods or crocodylomorphs. Although Welman (1995) did not present a tree, we have reconstructed a graphic representation of his hypothesis (Fig. 10). Welman's (1995) proposal is more precise than many previous proposals that birds derived from the paraphyletic 'thecodontians' (which have been criticized for this lack of precision, see Witmer, 1991; Padian & Chiappe, 1997, 1998 for reviews), but there are a number of aspects of the formulation of his hypothesis that require discussion in addition to the empirical evidence.

Welman (1995, p. 533) claims that 'the braincase structures of the dinosaurs [*Syntarsus* and
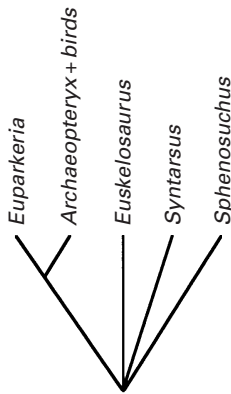
Fig. 10. Graphic representation of Welman's (1995) phylogenetic hypothesis. Although noting similarities between *Sphenosuchus* and *Syntarsus*, Welman (1995) does not make a specific statement about a possible sister-group relationship between these taxa so that this tree is not fully resolved.

Euskelosaurus] and *Sphenosuchus* are too specialized for these groups to be the sister group of birds'. The same author elsewhere states that theropods and crocodylomorphs are 'too specialized…to be ancestors of birds' (p. 536) and e.g. that it 'is impossible to derive the parabasal canals seen in birds from the condition in *Syntarsus* or *Sphenosuchus*…' (p. 534). These statements relate to two different kinds of phylogenetic hypothesis – one citing shared derived characters in support of sister-group relationships, and the other an ancestor-descendant formulation. Being 'too specialized' (autapomorphic) argues against a group being a plausible ancestor, but does not refute hypotheses of sister-group relationships.

The main, comparative section of Welman's (1995) paper does not specify whether the interpreted similarities of *Euparkeria* and birds are actually being forwarded as putative synapomorphies in support of his phylogenetic hypothesis, and limited outgroup comparison leaves it unclear whether these similarities might alternatively be considered plesiomorphic for archosaurs as a whole. These uncertainties are compounded by the fact that Welman (1995) listed only four synapomorphies of *Euparkeria* + *Archaeopteryx* (and, presumably, birds), despite proposing many similarities.

While it is commendable that Welman (1995) has largely restricted his more detailed interpretations to material that he has been able to observe directly, the limited taxonomic range of comparative data means that alternative explanations to many of his proposals were not explored. The reigning orthodoxy

(see Witmer, 1991; Padian & Chiappe, 1997, 1998) favours the hypothesis that birds are nested within Theropoda, but it has more exactly proposed that Avialae is nested within coelurosaurian theropods. Welman has rejected the 'theropod hypothesis' on the basis of comparisons with *Syntarsus*. However, there seems to be agreement (Gauthier, 1986; Rowe, 1989; Rowe & Gauthier, 1990; Russell & Dong, 1993; Holtz, 1994) that *Syntarsus* is a basal theropod (possibly a ceratosaur), quite removed from the derived coelurosaurians (whether or not this includes Avialae). Witmer (1990, p. 370) has stressed that theropods are 'an extremely diverse group', so that comparisons between the braincases of birds and a single theropod might be considered insufficient to reject the 'theropod hypothesis' as a whole.

Welman (1995, p. 536) regards *Euparkeria* as 'an early member of the specific group of archosauromorphs from which birds evolved', but does not comment on the extent of the membership of this specific group, or mention the implications of his hypothesis for the understanding of braincase structure in, and the phylogenetic position of, other basal archosaurs such as proterosuchids, erythrosuchids, proterochampsids and parasuchians (phytosaurs).

A final point on the general formulation of Welman's (1995) phylogenetic hypothesis concerns phrases suggesting that scenarios derived from a phylogenetic hypothesis (that has not been explicitly proposed) are cited as evidence supporting that particular phylogenetic hypothesis. For example, Welman (1995) claims that certain structures are 'approximately homologous', transitional series of morphologies are used to support proposed homologies, and synapomorphies are stated to have been 'identified' (p. 533) rather than forwarded as putative homologies to be tested. We consider nothing fundamentally wrong in putting forward the strongest case possible for any particular hypothesis (particularly a radical, provocative one), as long as it is recognized that this may not include detailed testing, or consideration of alternative explanations. Our study is partly an attempt to provide tests of Welman's (1995) hypotheses of homology and phylogeny, and explore alternatives. The problems we have outlined above concerning the formulation of Welman's (1995) hypothesis should not wholly be taken as criticism of the overall approach employed – clearly it is not possible to cover every archosaurian taxon or potentially important aspect of morphological data in comprehensive detail, and Welman's (1995) study has been important in prompting this reconsideration of the evidence.
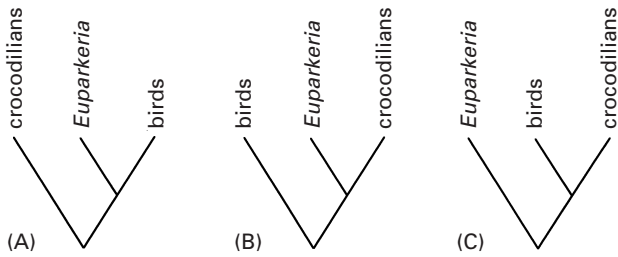
Fig. 11. The three possible dichotomous resolutions of the cladistic relationships of *Euparkeria*, crocodilians and birds.

(3) Reassessment

Synthesizing data on the braincases of all archosauromorphs is beyond the scope of this study. In the following section, we reassess the implications that braincase morphology in *Euparkeria* has for the understanding of basal archosaur phylogeny by focusing our discussion on evidence relevant to resolving the interrelationships between *Euparkeria*, birds and crocodilians. Derived braincase characters were sought that potentially offer support for any of the three possible dichotomous resolutions of this three-taxon problem (Fig. 11).

(a) Evidence potentially supporting (crocodilians (birds + Euparkeria)) or (birds (crocodilians + Euparkeria)) (Fig. 11 A, B)

We can find no apomorphic braincase characters that unite *Euparkeria* and birds to the exclusion of crocodilians, or that unite *Euparkeria* with crocodilians to the exclusion of birds.

(b) Evidence potentially supporting (Euparkeria (birds + crocodilians)) (Fig. 11 C)

Several derived features of the braincases of birds and crocodilians, that are absent in *Euparkeria*, can be forwarded as synapomorphies. A few of these appear to stand up to the test of congruence, some are equivocal, and others apparently non-homologous on the basis of incongruent distributions. These are discussed below, often with reference to the currently understood limits of the crown group, and consensus on basal archosaur phylogeny (Fig. 9).

(i) Entrance into parabasisphenoid of cerebral branches of the internal carotid arteries

Parrish (1993) considered a lateral, rather than a posterior or posteroventral, entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid to be a synapomorphy of the crown-group archosaurs. The condition in extant archosaurs (birds and crocodilians) is further derived in that the paths of the arteries have become extensively enclosed in bone (see section IV.3.*b.vii*) so that they now have a more posteriorly positioned entrance. However, the 'primary' entrance (i.e. the entrance into the chondrocranium) of the arteries into the parabasisphenoid of birds and crocodilians still lies on the lateral surfaces. In non-crown-group archosauromorphs, the entrance of the arteries into the parabasisphenoid is posterior/posteroventral (Parrish, 1993; Gower & Sennikov, 1996*a*). While the condition is currently unclear in proterochampsids (Parrish, 1993, p. 289), the lateral position appears to be one of the few derived characters of the braincase shared by crocodilians and birds that is both homologous and represents evidence that these extant archosaurs are more closely related to one another than either is to *Euparkeria*.

(ii) Ossification of the medial wall of the otic capsule

In adult birds and crocodilians, the medial wall of the vestibule is almost completely closed by bone, and the perilymphatic foramen has an entirely ossified border. This is not the case in *Euparkeria* (Figs 5, 6), undisputed non-crown-group archosauromorphs (e.g. Benton, 1983; Evans, 1986; Gower & Sennikov, 1996*a*; Gower, 1997), or more basal diapsids such as *Youngina* (Evans, 1987), where much of this region remains unossified. Among extant reptiles, the medial wall of the vestibule is usually fully ossified in adult lizards (e.g. Oelrich, 1956) and snakes (e.g. Rieppel, 1979, 1980), but not in turtles (although the unossified area, the 'hiatus acusticus', can be reduced in certain forms: Gaffney, 1972, p. 26) or *Sphenodon*. The condition in many extinct crown-group archosaurs is unclear, although the presence of the derived state in the parasuchian *Machaeroprosopus* (Camp, 1930) might indicate that extensive ossification of the medial capsular wall is a synapomorphy of the archosaurian crown group – to the exclusion of *Euparkeria*. Problems might be encountered in distinguishing the incompletely ossified condition from cases where preservation is incomplete, and in formulating a character for phylogenetic analysis because of difficulties in identifying putatively homologous degrees of ossification. Additionally, the absence of a fully ossified medial wall in certain crown-group archosaurs, such as some sauropods (L. M. Witmer, personal com-

munication), suggests that this feature is also prone to homoplasy.

(iii) Absence of semilunar depression

Crocodilians and birds seem to lack any structure that can be compared with the semilunar depression (Evans, 1986; Gower & Sennikov, 1996a, 1997) of the parabasisphenoid of *Euparkeria* (Figs 3, 5; section II), *Prolacerta* (Evans, 1986), proterosuchids (Gower & Sennikov, 1996a, 1997), and erythrosuchids (Gower & Sennikov, 1996a; Gower, 1997). An equivalent is also unknown among other crown-group archosaurs. It is difficult to assess the probability of the homology of the absence of features using similarity criteria because comparisons are limited, but a semilunar depression can currently be excluded from a reconstruction of the braincase of the most recent common ancestor of birds and crocodilians (the *Grundplan* of the crown group). If the absence of this feature is synapomorphic in birds and crocodilians, its presence in *Euparkeria* supports the exclusion of that taxon from the crown group.

(iv) Subdivided metotic fissure

Crocodilians and birds both have a metotic fissure that becomes subdivided during ontogeny (e.g. de Beer, 1937; Rieppel, 1985; Gauthier et al., 1988), with a foramen for the vagus nerve separated from the lateral aperture (= fenestra pseudorotunda) of a recessus scalae tympani. The earliest archosauromorphs, including proterosuchid and erythrosuchid non-crown-group archosaurs, have an undivided metotic fissure (e.g. Evans, 1986; Gower & Sennikov, 1996a), resembling *Sphenodon* and chelonians (Rieppel, 1985). The metotic fissure is also apparently undivided in basal crocodilian-line, crown-group archosaurs such as parasuchians (Camp, 1930, fig. 37; Chatterjee, 1978, fig. 5), aetosaurs (Walker, 1961; Parrish, 1994), at least one 'rauisuchian' (personal observation of SMNS 80260), and even the sphenosuchid crocodylomorph *Sphenosuchus* (Walker, 1990). The fissure has been interpreted as divided in many dinosaurs, including ornithischians (e.g. *Zephyrosaurus*: Walker, 1985, p. 133; *Lesothosaurus*: Sereno, 1991b) and saurischians (e.g. *Sellosaurus*: Galton & Bakker, 1985), but apparently not in e.g. the basal theropod *Syntarsus* (Raath, 1985, p. 224). The presence of the plesiomorphic condition in basal crocodilian-line archosaurs, and perhaps some dinosaurs, suggests that the derived, subdivided fissure might have been independently acquired in crocodilians and birds – assuming Avialae lies within Dinosauria. A subdivided metotic fissure also appears to have evolved several times in other tetrapod clades (Rieppel, 1985; Gauthier et al., 1988). The non-homology of the subdivision of the avian and crocodilian metotic fissure implies the non-homology of the space (recessus scalae tympani) and window (fenestra pseudorotunda) that result from this subdivision. In light of the non-homology of the avian and crocodilian fenestra pseudorotunda, de Beer's (1937) coining of the term fenestra pseudorotunda to satisfy a distinction of the window in birds and crocodilians from the non-homologous fenestra rotunda of mammals appears rather ironic, and the meaning of de Beer's (1937) term must be called into question. Non-homology of the subdivision of the avian and crocodilian metotic fissures would mean that the absence in *Euparkeria* of a subdivided metotic fissure is not unequivocal evidence that that taxon can be excluded from the currently understood limits of the crown group (i.e. that birds and crocodilians are more closely related to each other than either is to *Euparkeria*).

(v) Metotic cartilage and subcapsular process

In assessing the potential homology of the subdivision of the avian and crocodilian metotic fissure, recent authors (Rieppel, 1985; Gauthier et al., 1988) have compared the structures that realise this division in the chondrocrania of the two recent groups: the avain metotic cartilage and the crocodilian subcapsular process. It has been suggested that the two structures are (de Beer, 1937), might be (Walker, 1985, p. 133, 1990, p. 98), or are more probably not (Rieppel, 1980; Gauthier et al., 1988) homologous. Here, we argue that it has yet to be convincingly demonstrated that it is the avian metotic cartilage that actually subdivides the metotic fissure; that care should be taken to avoid oversimplified and misleading correlations between the metotic cartilage of the avian chondrocranium and any particular area of the osteocranium; and that the subdivisions in the avian and crocodilian metotic fissures are similar (although not necessarily homologous).

The avian metotic cartilage (Sonies, 1907) arises in the chondrocranium from one (or possibly two: Engelbrecht, 1958) separate condensation(s) before attaching to the otic capsule. It then extends

ventrally, enclosing the cavum metoticum between itself and the capsule, and contacting the basal plate and occipital arch in the general vicinity of the prevagal commissure – a cartilaginous bar that separates a foramen for the vagal nerve from the lateral opening of the recessus scalae tympani (= fenestra pseudorotunda). Importantly, there is no clear evidence that it is the metotic cartilage that consistently forms the prevagal commissure. While Brock (1937), for example, has described the commissure as being formed by the metotic cartilage in *Struthio*, Crompton (1953, pp. 91–92, figs 10–12) reported that the foramen for the vagus nerve is formed entirely by the basal plate in *Spheniscus*. Careful observation of thin sections (see material described by Weber, 1990) of the chrondrocranium of *Larus* found it impossible to detect a clear line of contact of histological differentiation between the basal plate, occipital arch, and metotic cartilage in this region of the chondrocranium. A similar condition in other birds may be responsible for differences between existing documentations. Later in bird ontogeny, the basal plate is ossified in the region in question by the basioccipital/basisphenoid, while the exoccipital ossifies both the occipital arch and at least the ventral part of the metotic cartilage, and thus forms the bony prevagal commissure in the adult osteocranium. Two important points need to be made. Firstly, the extent of the metotic cartilage in the avian chondrocranium and whether it participates in the prevagal commissure can be difficult to determine, and a consistent pattern has yet to be documented. Secondly, the precise limits of the contribution of the metotic cartilage to the osteocranium are not determinable. The often cited (e.g. Rieppel, 1985; Gauthier *et al.*, 1988; Chatterjee, 1991, p. 332) statement that the metotic cartilage subdivides the metotic fissure in birds has therefore, in our opinion, yet to be convincingly demonstrated, and might even be untrue for at least some birds.

Contrary to Baumel & Witmer (1993, p. 84), a separate ossification ('os metoticum') does not develop in birds from the metotic cartilage. This mistake may reflect the pitfalls of correlating a cartilage of the chondrocranium with a precise area of the osteocranium. The ossified and laterally extensive prevagal commissure of fossil members of Avialae has similarly been considered to represent an ossification of the metotic cartilage, termed e.g. 'metotic strut' (Witmer, 1990). This has been extended to fossil archosaurs (e.g. *Dromaeosaurus*: Currie, 1995), implying that a metotic cartilage homologous with that of birds was present in these extinct forms. The metotic cartilage is an apomorphic structure that can be reconstructed for the chondrocranium of the *Grundplan* of birds (crown group) on the basis of its presence in the chondrocrania of neognaths and palaeognaths (Weber, 1990), but it cannot be inferred with certainty in taxa lying outside the Extant Phylogenetic Bracket (Witmer, 1995) of its known existence, i.e. outside Aves (crown-group birds). We suggest that where the chondrocranium is unknown for non-avians, the ossified structure separating the vagal foramen from the secondary tympanic window should be termed e.g. 'prevagal strut' to avoid confusion or uncorroborated homologization with the metotic cartilage. The term 'metotic' should perhaps be avoided when referring to structures of the osteocranium (e.g. 'metotic process'). Welman's (1995) study includes a similar, unjustified correlation of areas of the chondrocranium with precise areas of the osteocranium when he essentially attempts (p. 535) to homologize a condensation in the chondrocranium of the Recent weaver bird *Euplectes* with a process of the osteocranium of *Euparkeria*.

The subcapsular process (Shiino, 1914) of the chondrocranium of crocodilians arises from 'the outer aspect of each occipital arch and extends forwards beneath the otic capsule and anterior part of the metotic fissure' (Bellairs & Kamal, 1981, p. 238). The details of the ossification of this process are currently unknown (Walker, 1990, pp. 33, 107), although the term 'subcapsular process' has also been freely applied to the osteocranium – to the area of bone dividing the fenestra pseudorotunda from the vagal foramen, and flooring the recessus scalae tympani. Walker (1990, p. 33) has viewed a strong lateral ridge on the exoccipital of the crocodylomorph *Sphenosuchus* as evidence that the crocodilian subcapsular process 'had developed to some extent…' in this taxon, and subsequently refers to this ridge as the 'subcapsular buttress'. As with the avian metotic cartilage, however, the subcapsular process cannot be inferred to have been present with any certainty in the chondrocrania of any taxon lying outside the crocodilian crown group, and it is problematic to correlate this cartilaginous process of extant crocodilians with an area of the osteocranium of a non-crown-group crocodylomorph.

A true equivalent of the avian metotic cartilage is apparently absent in crocodilians, although the chondrocranium in both groups exhibits a prevagal commissure. While there appear to be some differences (e.g. possible contribution of metotic cartilage to prevagal commissure in the bird chon-

drocranium) these are not entirely clear, and there remains an underlying similarity in the subdivision of the avian and crocodilian metotic fissure of the chondrocranium by a prevagal commissure. The possible homology of the bird and crocodilian condition has perhaps prematurely been considered as (negatively) resolved in the wake of the currently favoured 'theropod hypothesis' of avian origins, and the rejection of de Beer's (1937) process-laden hypotheses of homology (Rieppel, 1985). However, if the theropod hypothesis is accepted, and if e.g. parasuchians (which lack an ossified subdivision of the metotic fissure) lie within the crown group, then the ossified prevagal commissure of birds and crocodilians is likely to have been acquired independently. If so, the lack of an ossified subdivision of the metotic fissure of *Euparkeria* cannot be taken as unequivocal evidence that this taxon lies outside the crown-group.

(vi) *Elongated, tubular cochlear recess*

While the plesiomorphic diapsid lagenar recess (as seen in *Sphenodon* and squamates) is relatively short and strongly tapered, birds and crocodilians share an elongated, tubular recess in concert with the development of the cochlea. While the long axis of the crocodilian cochlear recess is geniculate, that of *Sphenosuchus* (Walker, 1990) is straight, as in birds. Walker (1990, p. 111) has discussed the distribution of an elongated recess among extinct crown-group archosaurs, suggesting that it is restricted to crocodylomorphs, some dinosaurs, and birds. In non-crown-group archosaurs, the lagenar recess is not a clearly defined bony structure and would probably have been relatively short (e.g. *Erythrosuchus*, where there is only a short distance between the floor of the endocranial cavity and where the floor of the vestibule would have lain: Gower, 1997). In at least some crown-group archosaurs, e.g. parasuchians (Case, 1928; Camp, 1930), the recess is also relatively short, suggesting that (if crocodilians are more closely related to parasuchians than to birds) elongation was perhaps acquired independently in the evolution of the two extant groups (or became reversed during the evolution of parasuchians). The form of the lagenar/cochlear recess has yet to be described in detail in most extinct archosaur groups, but presently the lack of a well-defined, elongated recess in *Euparkeria* does not unequivocally indicate that it lies outside the crown group.

(vii) *Enclosure in bone of the Eustachian system*

While birds and crocodilians both have Eustachian systems at least partly enclosed in bone, birds have isolated lateral tubes that lack any connection with a median pharyngeal recess (Witmer, 1997), such as is seen in crocodilians. Other extant reptiles lack any such bony enclosure and this clearly represents the plesiomorphic condition. Some theropods apparently have a connection between the true Eustachian tubes and a median pharyngeal recess (e.g. Larsson, 1996), but possible homology with that of the crocodilian condition has yet to be explored in detail (Witmer, 1990, p. 369). However, the absence of any bony enclosure of the Eustachian system of basal crocodilian-line archosaurs such as parasuchians (Camp, 1930; Chatterjee, 1978) and aetosaurs (Walker, 1961; Parrish, 1994), and the incomplete enclosure in *Sphenosuchus* (Walker, 1990) suggests that the derived state (enclosure) evolved independently in birds and crocodilians – if Avialae lies within Theropoda. The presence of the plesiomorphic state in *Euparkeria* is therefore not unequivocal evidence that it lies outside the crown group. Enclosure of the internal carotid arteries is closely associated with enclosure of the Eustachian system, and a similar taxonomic distribution of this feature is observable.

(viii) *Tympanic sinuses*

Birds and crocodilians have extensively pneumatized tympanic cavities. The pneumatic tympanic sinuses in extinct archosaurs are currently rather poorly understood. Increasing present knowledge will probably require active feedback between an existing phylogenetic framework and assessments of homology of the sinuses that might modify this phylogeny. We agree with Witmer (1990, 1991) in recommending caution in the use of pneumatic structures as independent phylogenetic data until greater understanding is reached on the distribution and variation of pneumatic recesses in extinct archosaurs. The lack of extensive recesses in non-crown-group archosauromorphs and taxa such as parasuchians, aetosaurs, and at least some rauisuchians suggests that some of the similarities between birds and crocodilians have been convergently acquired (if Avialae lies within Theropoda), and that the potentially plesiomorphic condition in *Euparkeria* is therefore not unequivocal evidence that it lies outside the archosaur crown group.

(ix) *Quadrate-prootic articulation*

Contact occurs between the quadrate and the lateral surface of the prootic in both birds and crocodilians. The lack of such contact in parasuchians, aetosaurs, rauisuchians, ornithischian and basal saurischian dinosaurs, and in all non-crown-group archosauromorphs indicates that this contact arose independently in the two extant lineages (if the currently favoured hypothesis of avian origins is accepted). Walker (1985, p. 132, 1990, p. 84) has supported this hypothesis of non-homology by noting a difference between crocodilians and birds in the relation of the anteriorly extended quadrate head to the course of the stapedial artery. Walker (1985, 1990) also notes other features that may have arisen in unison with the anterior shift of the quadrate in each lineage. The probable non-homology of the avian and crocodilian condition means that absence of this condition in *Euparkeria* does not necessarily exclude this taxon from the archosaur crown group.

(x) *Ossification of the pila antotica*

Ossification of the pila antotica of birds and crocodilians is largely achieved by the basisphenoid and laterosphenoid, with these elements making contact anterior to the prootic in the osteocranium. The same condition is found in a number of extinct crown-group archosaurs, e.g. *Sphenosuchus* (Walker, 1990) and *Tyrannosaurus* Molnar, 1991). In *Euparkeria*, the laterosphenoid does not contact the parabasisphenoid and the pila antotica was therefore only ossified by the laterosphenoid and prootic. The latter condition is also found in perhaps all non-crown-group archosaurs (e.g. Clark *et al.*, 1993; Gower & Sennikov, 1996*a*) – the taxa exhibiting the earliest known occurrences of a laterosphenoid (Clark *et al.*, 1993) – and therefore might be considered the plesiomorphic condition for Archosauria. That the derived condition is a synapomorphy of crown-group archosaurs, and therefore homologous in birds and crocodilians, is questioned by the presence of the *Euparkeria*-like condition in a number of crown-group taxa, including the basal sauropodomorph dinosaurs *Sellosaurus* (Galton & Bakker, 1985) and *Massospondylus* (Gow, 1990), the hypsilophodontid dinosaur *Zephyrosaurus* (Sues, 1980), and the theropod dinosaur *Syntarsus* (Raath, 1985). Thus, the crocodilian and bird condition might not be homologous, and its absence in *Euparkeria* is not necessarily evidence that the latter lies outside the archosaur crown group.

It might be noted that Evans (1986, p. 194) recognized a distinction between the condition in the early archosaurs *Euparkeria* and *Proterosuchus*, where the base of the pila antotica is mainly ossified as prootic, and a lepidosaur condition, where the base of the pila antotica is ossified as prootic and basisphenoid, a situation more similar to that of birds and crocodilians.

(xi) *Enclosure of abducens nerves*

In birds and crocodilians, the abducens nerves exit the braincase *via* foramina that are enclosed within the parabasisphenoid, while in *Euparkeria* the abducens foramina lie between the parabasisphenoid and the prootic. In non-archosaurian archosauromorphs, the usual conditions are that the abducens exits are marked by barely closed grooves on the anterodorsal surface of the parabasisphenoid or by foramina enclosed between parabasisphenoid and prootics (e.g. rhynchosaurs: Benton, 1983; *Prolacerta*: Gow, 1975; Evans, 1986). In non-crown-group archosaurs, the position of the abducens exit varies (Gower & Sennikov, 1996*a*), with the foramina lying either between prootic and parabasisphenoid or entirely within the prootic. The abducens foramina lie between prootics and parabasisphenoid in parasuchians (Camp, 1930; Chatterjee, 1978), suggesting that the condition in birds and crocodilians might have arisen independently (assuming, for example, that crocodilians are more closely related to parasuchians than to birds).

The exit of the abducens nerves relative to the prootics and parabasisphenoid might not be independent of patterns of ossification in the base of the pila antotica or sutural contacts. For example, the erythrosuchid condition occurs in concert with extensive midline contact between the opposite prootics on the floor of the endocranial cavity (Gower & Sennikov, 1996*a*; Gower, 1997).

Of the above 11 features, there is currently strong evidence that only one – the lateral entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid – is homologous in birds and crocodilians, and absent in *Euparkeria*. Two further characters, extensive ossification of the medial wall of the otic capsule, and absence of a parabasisphenoid 'intertuberal plate', are possibly synapomorphic for birds + crocodilians to the exclusion of *Euparkeria*, but satisfactory assessment of their possible homology is much more problematic. The other eight derived braincase features discussed above

would seem to represent convergences in the bird and crocodilian condition, but more data are required to substantiate character optimizations. These proposed convergences depend to an extent on whether birds are nested within Theropoda. Even if birds are more closely related to crocodilians than to theropod dinosaurs, the available evidence is still best explained by birds and crocodilians being more closely related to one another than either is to *Euparkeria*. While three possible bird-crocodilian braincase synapomorphies (two of which are not particularly robust) are not compelling evidence that *Euparkeria* lies outside the crown group, we can find no braincase characters that are incongruent with this interpretation.

(4) Relationships of the non-crown-group archosaurs

In as much as the braincase of *Euparkeria* suggests that this taxon lies outside the crown group, is there any evidence for shared derived braincase features with the crown group that are absent in other non-crown-group archosaurs such as proterosuchids and erythrosuchids? In other words, is there any evidence from the braincase that supports the consensus found by Gower & Wilkinson (1996) and the result of the preliminary numerical analysis of braincase data by Gower & Sennikov (1996 a) that *Euparkeria* occupies a more crownward position than do proterosuchids and erythrosuchids? We can find only a single potential synapomorphy – the absence of the 'inter-tuberal plate' (Gower & Sennikov, 1996 a), a crista seen on the posterior of the parabasisphenoid of many basal archosauromorphs (see also Parrish, 1992). This character was also responsible for the recovery of *Euparkeria* in a more crownward position than proterosuchids and erythrosuchids in Gower & Sennikov's (1996 a) numerical parsimony analysis. While crocodilians, birds and other crown-group archosaurs lack the 'intertuberal plate', the phylogenetic significance of the absence of this feature is difficult to assess at present. This is partly because of problems associated with absence characters, but also because the plate is much reduced in the non-crown-group archosaur *Erythrosuchus* (Gower, 1997) and is absent in the non-archosaurian archosauromorphs, rhynchosaurs (personal observation), indicating that homoplastic reduction or loss has occurred elsewhere in early archosauromorph evolution. We can find no new braincase characters that are incompatible with the hypothesis that *Euparkeria* and the archosaurian crown group are more closely
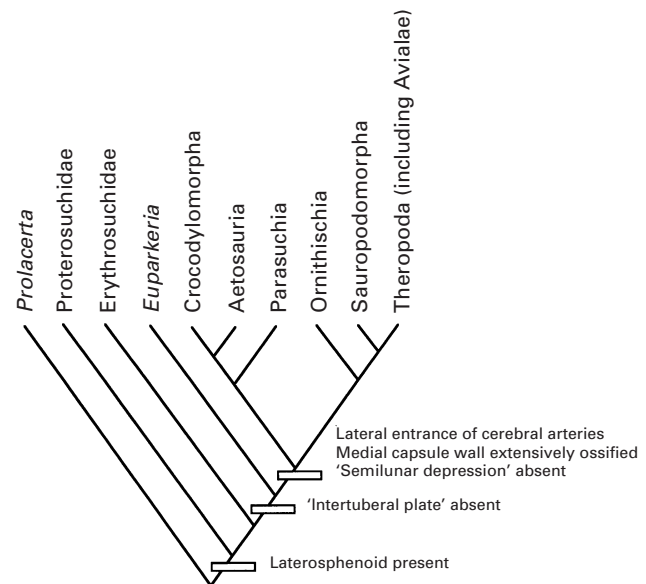

Fig. 12. Annotated basal archosaur phylogeny indicating sequence of acquistion of those braincase synapomorphies discussed in the text. Topology based on Gower & Wilkinson (1996), with dinosaurian relationships from e.g. Gauthier (1986).

related to each other than either is to proterosuchids or erythrosuchids. Proterochampsids have not been considered here because we have not examined any proterochampsid braincase material, and detailed accounts have yet to be published. A consensus archosaur phylogeny, including some of the taxa discussed above and annotated with the acquisition of putative braincase synapomorphies, is shown in Fig. 12.

(5) The morphology of unossified gaps

We have suggested in sections II and III that the opening in the lateral surface of the braincase of *Euparkeria* that lies between the distal surface of the ventral ramus of the opisthotic, the posteroventral edge of the prootic, and the dorsal edge of the parabasisphenoid is not (*contra* Welman, 1995) a fenestra rotunda, but rather an unossified gap that was probably covered by cartilage in life. Here, we provide a fuller account of how we have visualized such gaps, and a brief discussion of the possible significance of comparisons that might be made between taxa. Our observations and interpretations are based on the examination of a handful of specimens of skulls of extinct and extant diapsids. In the absence of a fuller survey, we are largely ignorant of the variability of gaps during ontogeny or among individuals of the same, or different taxa, even for extant forms. An important distinction is made in

5 mm
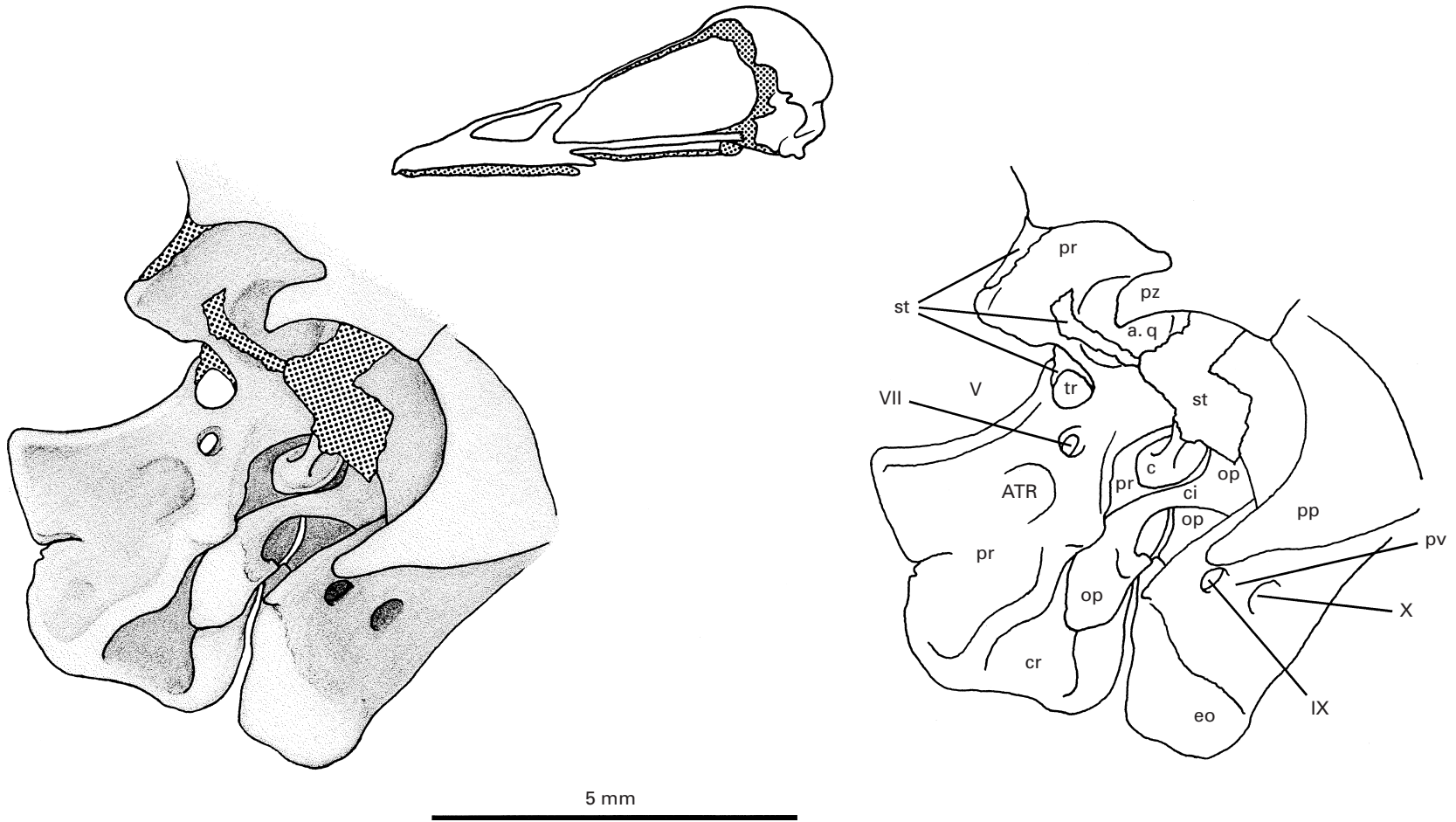
Fig. 13. *Somateria mollissima* (common eider). Ventro(antero)lateral view of part (basioccipital and parabasisphenoid removed) of the left side of the braincase of pullus. The columella is attached to a piece of soft tissue and its footplate sits in the fenestra ovalis. The secondary tympanic window (fenestra pseudorotunda) lies immediately posterior and ventral to the crista interfenestralis, which separates it from the fenestra ovalis. The presence of a separate foramen for the glossopharyngeal nerve is a derived character found in adults of most birds. See section IX for list of abbreviations.

the following discussion of the morphology of 'gaps', a term we use in a general sense to describe unossified areas. We recognize apertures, which we view as essentially two-dimensional gaps, and channels, which are a continuation of apertures in a third dimension.

The most obvious gap that might be observed in the lateral surface of the otic region of the braincase of diapsids lies between the edges of several of the elements that meet in this area, possibly including the opisthotic, exoccipital, basioccipital, parabasisphenoid and prootic. In *Sphenodon*, there is a large aperture in this region, between the distal surface of the ventral ramus of the opisthotic, the anterodorsal edge of the basioccipital, the posteroventral edge of the prootic, and the posterodorsal edge of the parabasisphenoid (Figs 7, 8). This aperture is confluent with the ventral part of the fenestra ovalis and is covered with cartilage. Säve-Söderbergh (1947) also depicted this unossified aperture, and similar windows have been described for the extinct sphenodontid *Clevosaurus* (Fraser, 1988; Wu, 1994). A large channel lies immediately inside (medial to) this unossified aperture in *Sphenodon* and communicates with the otic capsule – it is the lagenar recess. There is therefore a continuous gap between opisthotic, parabasisphenoid and prootic consisting of a lateral aperture covered in cartilage, and a medial channel (floored by basioccipital) that holds the lagena. A gap appears to be absent here in adult extant squamates, and the laterodistal wall of the lagenar recess is fully ossified (e.g. *Ctenosaura*: Oelrich, 1956; *Tupinambis*: Barberena, Gomes & Sanchotene, 1970; *Varanus*: personal observations).

Gower & Sennikov (1996a) described unossified gaps in a number of non-crown-group archosaurs, where they are often visible on the latero-occipital surface of the braincase between opisthotics, basioccipital and parabasisphenoid. In some early archosaur taxa (e.g. *Erythrosuchus*, *Shansisuchus*), these gaps are absent (Gower & Sennikov, 1996a; Gower, 1997). The gap in *Vjushkovia triplicostata* extends anterodorsally onto the floor of the endocranial cavity and, because it emerges in the lagenar region, was referred to by Gower & Sennikov (1996a) as a 'pseudolagenar recess'. The gaps in *Sphenodon* and in *Prolacerta* (as figured by Gow, 1975 and Evans, 1986) are different from those in the non-crown-group archosaurs described by Gower & Sennikov (1996a), and in the extinct sphenodontid *Clevosaurus* (as figured by Fraser, 1988 and Wu, 1994). In the former taxa, the ventral ramus of the opisthotic fails to contact the parabasisphenoid, while in the latter,

opisthotic-parabasisphenoid contact separates the gap from the margin of the fenestra ovalis.

Unossified gaps can also be observed in bird osteocrania prior to the fusion of elements and obliteration of sutures. There is an aperture between exoccipital, basioccipital, parabasisphenoid and prootic, and the lateral wall of the cochlear recess (a dorsomedial channel) is unossified (Fig. 13; Walker, 1985, 1990, fig. 52). This is broadly equivalent to the situation in *Sphenodon* except that, in this taxon, the aperture lies in a plane approximately perpendicular to the long axis of the lagenar recess. The situation in *Somateria mollissima* (Fig. 13) differs slightly to that in e.g. *Daption* (Walker, 1990, fig. 52b) because the cochlear recess lies within the prootic, with no exoccipital contribution. Walker (1990, p. 95) has described the presence of an unossified area at the laterodistal end of the cochlear recess in birds: 'the lateral wall of the cochlear recess closes in development from the top downwards, so that an unossified, cartilage-filled cleft persists for a time at the lower end between prootic and opisthotic + metotic [= exoccipital] or, in later stages, between prootic and metotic'. The situation we have observed in our small sample of young birds is closely matched in crocodilians that we have examined (Fig. 14), where a gap may exist between parabasisphenoid, basioccipital, exoccipital, prootic and opisthotic (although this is closed in the adult *Osteolaemus* figured by Walker 1990, fig. 52a), and the laterodistal wall of the cochlear recess is unossified. The similarity between *Crocodylus niloticus* (Fig. 14) and *Somateria mollissima* (Fig. 13) is particularly close because in both cases the exoccipital does not participate in the cochlear recess. While the condition in birds and crocodilians appears to be similar (compare Figs 13 and 14), a difference might exist in that the lateral wall of the distal end of the crocodilian tubular cochlear recess appears to remain unossified into adulthood (Walker, 1985, p. 130; personal observation).

Little attention has been paid to these unossified areas in previous studies of braincase morphology in extant and extinct diapsids (but see Clack, 1997, 1998, for reviews of tetrapod otic structures, including gaps). Walker (1985, p. 130) described the distal end of the cochlear region in *Archaeopteryx* as 'laterally notched' and compared this with the condition in juvenile birds and adult crocodilians. An unossified 'cleft' was also described by Walker (1990) for *Sphenosuchus*, and furthermore this was compared with the unossified region in *Sphenodon* (Walker, 1990, p. 100). Fraser (1988, p. 140) com-
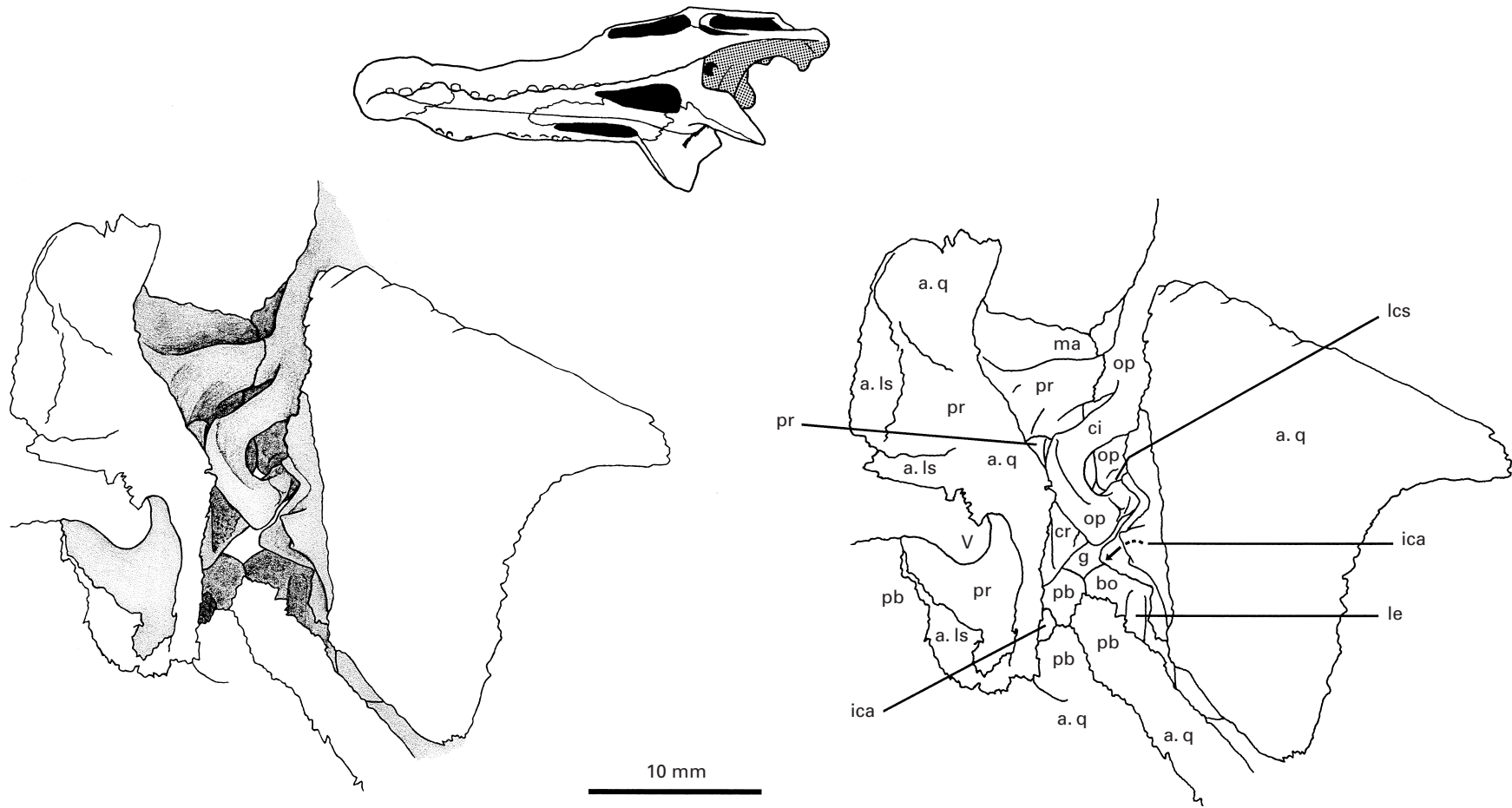
Fig. 14. *Crocodylus niloticus*. Anteroventrolateral view of left otic region with left quadrate removed. The fenestra ovalis lies immediately above the crista interfenestralis (ci) of the opisthotic. Immediately below this crista lies the fenestra pseudorotunda and, positioned more deeply, the perilymphatic foramen. The metotic fissure is subdivided, with the vagus nerve exiting the braincase *via* a separate foramen (not shown). The unossified gap is slightly larger than in life, because of disarticulation and reassembly of the prepared specimen. See section IX for list of abbreviations.

pared the unossified gap in sphenodontids with the condition in crocodilians, while Gower & Sennikov (1996*a*) suggested, incorrectly, that similar gaps were absent in crown-group archosaurs, and used this information in an exploratory parsimony analysis.

We propose that the lateral opening between opisthotic, parabasisphenoid and basioccipital in *Euparkeria* (Welman, 1995, fig. 4) represents an unossified area (potentially equivalent to those in other diapsids) that would probably have been covered by cartilage in life. In *Euparkeria* there is a space between the opisthotic and the posterodorsal edge of the parabasisphenoid (also seen in *Sphenodon*, Fig. 8) that is bridged by a slender piece of bone (it is unclear whether this is parabasisphenoid or opisthotic) separating the aperture of the gap from the margin of the fenestra ovalis (Welman, 1995, fig. 4). This unossified aperture continues medially as a channel communicating with the inner ear region. If the positional relationship between the lateral aperture and the cochlear/lagenar recess in birds, crocodilians, and *Sphenodon* is broadly consistent throughout diapsids, then the unossified channel immediately medial to the aperture in *Euparkeria* represents, at least in part, the lagenar recess. Referring to Welman's (1995) fig. 3a, the possible position of the lagena would therefore be where 'rst' is labelled, i.e. just ventromedial to the fenestra ovalis, rather than (as Welman interprets) close to the midline of the endocranial cavity. Potential support therefore exists for Cruickshank's (1970, fig. 2) labelling of the channel immediately medial to the unossified aperture as a lagenar recess. However, the possible relationship (also suggested by Fraser, 1988, p. 140) between unossified gaps and the lagenar recess, and the position and form of the recess in other early archosaurs, remains to be fully explored.

The ossification of braincase elements from *Anlagen* within the chondrocranium means that, at least early in the development of the osteocranium, there must be unossified regions lying between certain ossifying elements. If the focus for comparison is a particular gap, then comparisons are essentially between ontogenetically and phylogenetically conserved, plesiomorphic features of the skull. This would be similar to focusing on the hole when attempting to understand the homology of secondary tympanic windows (Gauthier *et al.*, 1988, p. 153). A more fruitful approach might be to putatively homologize derived aspects of how these unossified gaps are bordered. As we have pointed out (section III.2.*a*) with respect to the recessus scalae tympani,

the homology of spaces is determined by the homology of the (not only bony) structures defining those spaces. For example, the similarity of the morphology of this region in crocodilians and birds is clearly derived over that seen in *Euparkeria* and the non-crown-group archosaurs studied by Gower & Sennikov (1996*a*), although whether this yields phylogenetic information independent of the morphology of e.g. the elongate cochlear recess (which might not be homologous in crocodilians and birds – see discussion above) is as yet unexplored.

V. DISCUSSION

We have argued that the similarities that Welman (1995) has proposed as existing between *Euparkeria* and birds are not demonstrably derived, are demonstrably invalid, or are less well supported than alternative hypotheses of homology. We have also argued that the four apomorphies that Welman (1995) proposes are shared by *Euparkeria* + *Archaeopteryx* do not represent convincing *a priori* hypotheses of homology and/or are formulated from features that are currently poorly understood among archosaurs. We have proposed three braincase apomorphies that support the hypothesis that birds are more closely related to crocodilians than they are to *Euparkeria*, and we can find no putative braincase synapomorphies that might support the other two alternative resolutions of the relationships of *Euparkeria*, crocodilians and birds. We conclude that there are currently no new braincase data that challenge the recently reached consensus that *Euparkeria* lies outside the archosaurian crown group, although the limited evidence does not make this hypothesis overwhelmingly compelling as yet.

Witmer (1991, p. 457) proposed that, until it is comprehensively discredited or challenged by a better corroborated hypothesis, the analysis of Gauthier (1986) should be regarded as the benchmark hypothesis for avian origins (see also Padian & Chiappe, 1998), and we believe this still to be the case. We do not consider Welman (1995) to have forwarded a well-supported alternative to the 'theropod hypothesis', but we do welcome his study as a clear indication of the depth of work that needs to be carried out before the patterns of morphological evolution across Archosauria as a whole are as fully understood as possible, whichever phylogenetic hypothesis is ultimately favoured.

Welman (1995, p. 536) forwarded the notion that 'the braincase structure of *Euparkeria* represents a

model from which that of primitive birds may be directly derived'. Our interpretation is concordant with this, not because of shared derived similarities between *Euparkeria* and birds, but for the reason that braincase features of *Euparkeria* are largely plesiomorphic with respect to crown-group archosaurs. The plesiomorphic nature of many features lends the braincase of *Euparkeria* to detailed comparison not only with crown-group archosaurs but also with such distantly related taxa as *Sphenodon* (corroborating the observations of Walker, 1990) and squamates. *Euparkeria* is the known archosaur that most closely approximates to the *Grundplan* (ancestor) of crown-group archosaurs. In terms of the braincase, there is only a single possible autapomorphy that precludes *Euparkeria* from being directly ancestral to crocodilians and birds – the small bridge of bone forming the ventral border of the fenestra ovalis (Cruickshank, 1970, 1972; Welman, 1995; Fig. 1B, D). In all other respects, the braincase of *Euparkeria* represents an appropriate (and currently the best available) actual model for the braincase of the most recent common ancestor of birds and crocodilians. *Euparkeria* is a small, carnivorous 'thecodontian' with apparently very few skeletal autapomorphies, so that it is unsurprising that it has frequently been viewed as a pivotal taxon in studies of archosaur evolution.

That it is possible to compare and homologize many detailed structures of braincases across a very wide range of taxa perhaps underlies the belief (e.g. Currie, 1996, 1997) that braincases are conservative, and therefore a source of relatively more informative phylogenetic data (e.g. Parrish, 1993, Currie, 1996). Clearly, certain features of the braincase must be conservative if we can homologize them across disparate taxa, but, for example, the likelihood that many of the derived similarities shared by bird and crocodilian braincases were independently evolved suggests that viewing braincases as a whole as conservative is misleading. Braincases can perhaps be considered similar to other comparative units of data such as the skull as a whole or molecules – where conservative aspects may allow us to homologize (putatively) many features, but not all details can be homologized because of extensive variation. Parts of molecular sequences can sometimes be aligned across taxa even if it is clear that single sites within such sequences are highly variable. Similarly, it is not difficult to 'align' ossified elements, or openings such as the orbit, external naris and foramen magnum of the skull across Tetrapoda, but while the presence of these features is conservative,

invoking evolutionary conservatism for the skull as a whole would contradict what we know to be true. The observations and comparisons made in this study are compatible with Gower & Sennikov's (1996*a*) findings from their rudimentary quantitative analysis that there is little evidence to support the belief that braincase data as a whole are phylogenetically especially informative. It might be noted that assessing conservatism and phylogenetic informativeness are not the same thing – Gower & Sennikov (1996*a*) measured only the informativeness of the characters they formulated and selected for the taxa that they chose to include. Numerical methods can measure the performance of certain selected characters under a particular analytical regime, but quantitatively measuring conservatism is a far more complex issue. Finally, conservative features of an organism are by definition plesiomorphic and therefore often less informative in, and largely removed *a priori* from, phylogenetic analyses – so that it is mistaken to consider phylogenetic informativeness as an indicator of conservatism or *vice versa*. Clearly, conservatism is a relative rather than absolute condition and its relationship to phylogenetic informativeness is complex.

Welman (1995) formulated putative homologies and cited these as evidence against particular phylogenetic hypotheses. We have argued against the power of Welman's (1995) approach (and against several statements of similarity) because explicit 'testing' of putative homologies was not presented. We do not, however, subscribe to the currently pervasive view that discovery of homology can be essentially reduced to a rigid two-stage process (e.g. Rieppel, 1988; dePinna, 1991; see also Brower & Schawaroch, 1996) of forwarding putative homologies that pass similarity tests, and then testing them by congruence with other characters. If Welman's (1995) statements of similarity (character formulations) were preliminarily accepted and analysed, it is not inconceivable that these supposed similarities would be congruent with a phylogeny indicating a close relationship between *Euparkeria* and birds. It is clearly possible to force the interpretation of the braincase of *Euparkeria* into a framework based on avian anatomy. Considering alternative possible phylogenetic positions of *Euparkeria* during the process of character formulation, however, forces the investigator to compare a range of competing possible homologies that will inform decisions of character formulation and possibly lead to a better supported hypothesis of (putative) homology. Thorough character formu-

lation is still the most important part of phylogenetic analysis of morphological data, because it determines the results of analyses, and it is one that we believe does not (and possibly cannot) best take place in a phylogenetic vacuum. The methodology of a two-step test is flawed because rather than restricting congruence to testing hypotheses of homology, a consideration of congruence (with a range of possible phylogenies) increases the information available while formulating the homology hypotheses that are to be 'tested'. What have been called 'alternative conjectures of similarity' (Rieppel, 1996, p. 1397) are alternative formulations of characters from the same source of data. In order to consider alternative character formulations and to inform the decision of which one(s) will be forwarded, a range of possible phylogenies that these characters might produce and be mapped onto needs to be imagined. Thus, a satisfactory formulation of a particular character might benefit from the consideration of a phylogeny that the character itself will eventually provide evidence for. It is sometimes suggested that phylogeny should not be considered when homology is being assessed if circular reasoning is to be avoided (e.g. Rieppel, 1994). Two points can be cited in response. Firstly, even with the rigid two-stage method 'a certain element of apparent circularity seems always to persist' (Rieppel, 1996, p. 1398). Secondly, rather than being viciously circular, the feedback between possible character formulations and possible phylogenies can instead be viewed as a hermeneutic spiral, an important tool in historical biological research (see Hoffman & Reif, 1988, 1990). Hermeneutic analysis operates by the process of reciprocal illumination ('wechselseitige Erhellung': Hennig, 1950) – such as between possible hypotheses of homology and phylogeny. The outcome of reciprocal illumination regarding the hypothesising of homology remains 'testable' (in terms of the extent to which available data are explained) by comparison with competing character formulations. Future studies might explore further the criteria that could be employed in choosing between competing formulations.

Following extensive comparative studies of the braincases of extant and extinct diapsids, Walker (1972, 1974, 1985, 1990) highlighted a number of similarities that exist between the braincases of birds and crocodilians, particularly their otic regions (compare also Figs 13 and 14 here). Walker (1972, 1974) initially drew the conclusion that birds were more closely related to crocodylomorphs than to other archosaurs. While the currently dominant 'theropod hypothesis' of the origin of birds rejects this, the similarities shared by crocodilians and birds noted by Walker remain incongruent data that are yet to be fully explored and explained. The detailed description and explicit reasoning provided in Walker's studies means that his primary data remain sound and useful despite shifting phylogenetic hypotheses. Similar studies on the braincases of other archosaurs, particularly dinosaurs, need to be carried out if the theropod hypothesis of avian origins is to be tested further, and if the apparent convergences in bird and crocodilian braincases are to be more completely understood.

VI. CONCLUSIONS

(1) Marked disagreement exists among current interpretations of the morphology of the braincase of the Triassic archosaur *Euparkeria*. This has implications for estimates of the evolutionary relationships and origins of birds and crocodilians, as well as for the interpretation of braincase evolution in Archosauria.

(2) The braincase of *Euparkeria* possesses an undivided metotic fissure, an incompletely ossified medial wall of the otic capsule, a well-defined 'semilunar depression', and posteroventrally positioned foramina for the entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid. It lacks enclosure of the Eustachian system in bone, well-developed tympanic sinuses, and a well-defined recess for the lagena. These features are plesiomorphic for archosaurs.

(3) Ten homologies of *Euparkeria* braincase structures proposed by Welman (1995) are argued to be not demonstrably derived, demonstrably invalid, or less well supported than alternative hypotheses of homology.

(4) Four apomorphies proposed by Welman (1995) to be shared by *Euparkeria* + *Archaeopteryx* do not represent convincing *a priori* hypotheses of homology and/or are formulated from features that are currently poorly understood among archosaurs.

(5) No shared derived braincase characters are found to support the resolutions (crocodilians (*Euparkeria* + birds)) or (birds (*Euparkeria* + crocodilians)).

(6) Of three shared derived characters supporting the resolution (*Euparkeria* (birds + crocodilians)), only the presence of a lateral entrance of the cerebral branches of the internal carotid arteries into the parabasisphenoid represents relatively robust evi-

dence. The absence of a 'semilunar depression' and the more complete ossification of the medial wall of the otic capsule are also derived features shared by birds and crocodiles, but they do not yet represent compelling hypotheses of homology.

(7) Despite exhibiting at least one putative braincase autapomorphy, a delicate bridge of bone connecting the ventral ramus of the opisthotic with the parabasisphenoid below the fenestra ovalis, *Euparkeria* represents the best known actual model for the ancestor of bird and crocodilian braincases.

(8) Data from braincase morphology are congruent with the recently reached consensus among explicit phylogenetic analyses that *Euparkeria* lies outside the archosaur crown group, and in a more crownward position than proterosuchids and erythrosuchids.

(9) Birds and crocodilians share a number of derived braincase characters (subdivided metotic fissure, elongated and tubular cochlear recess, enclosed Eustachian system, extensive tympanic sinuses, and quadrate-prootic articulation) that are apparently not homologous because of their absence in a number of non-avian dinosaurs and crocodilian-line crown-group archosaurs.

VII. ACKNOWLEDGEMENTS

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IX. EXPLANATION OF ABBREVIATIONS USED IN TEXT AND FIGURES

(1) Institutional

GPIT   Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany

SAM   South African Museum, Cape Town, South Africa

SMNS   Staatliche Museum für Naturkunde, Stuttgart, Germany

UMZC   University Museum of Zoology, Cambridge, U.K.

(2) Anatomical

a.   surface for articulation with…
aof   antorbital fenestra
AAR   anterior ampullary recess (anterior vertical canal and external canal open into this concavity)
ATR   anterior tympanic recess (= rostral tympanic recess of Witmer, 1990)
aur   auricular (floccular) recess
av   anteroventral limit of vestibule
b   bridge of bone below fo
bk   break in specimen
bo   basioccipital
bpt   basipterygoid process
bs   basisphenoid
bt   basal tuber of pb or bo
c   columella
cc   osseus common crus
ci   crista interfenestralis (part of ventral ramus of the opisthotic separating the fenestra ovalis from a secondary tympanic window)
clp   clinoid process of pb
con   occipital condyle
cp   cultriform process of pb
cr   cochlear recess
dl.   dorsolateral extension (of pb)
ecpt   ectopterygoid
eo   exoccipital
ept   epipterygoid
f   frontal
fl   internal flange of prootic
fm   foramen magnum
fo   fenestra ovalis
g   gap
h   probable part of hyoid apparatus
hyVII   groove foramen for hyomandibular branch of facial nerve
ica   foramen for cerebral branch of internal carotid artery
(l)   left
la   lacrimal
lcs   loop closure suture (see Walker, 1990, p. 37)

ld	lateral depression on pb	ptf	posttemporal fenestra
le	lateral Eustachian tube	PTR	posterior tympanic recess (= caudal tympanic recess of Witmer 1990)
lr	lagenar recess		
ls	laterosphenoid	pv	prevagal strut/bar (ossified prevagal commissure)
ma	mastoid antrum		
mcv	groove for middle cerebral vein	pz	zygomatic process of the squamosal
mf	metotic foramen	q	quadrate
n	nasal	(r)	right
o	orbit	s	surface exposed by shearing between pr and pb
op	opisthotic		
pa	parietal	sld	semilunar depression
PAR	posterior ampullary recess (fossa holding posterior ampulla and ventral opening of posterior vertical canal)	so	supraoccipital
		sot	spheno-occipital tuber
		st	soft tissue
pb	parabasisphenoid	tr	tympanic recess
pf	postfrontal	uoc	unossified channel
plVII	groove foramen for palatine branch of facial nerve	vrop	ventral ramus of op
		V	foramen/notch for exit of trigeminal nerve
po	postorbital	VI	foramen for exit of abducens nerve
pp	paroccipital process	VII	foramen for exit of facial nerve
pr	prootic	IX	foramen for exit of glossopharyngeal nerve
pra	prearticular	X	foramen for exit of vagal nerve
prf	prefrontal	XII	foramen for exit of hypoglossal nerve
ps	parasphenoid	?	identification uncertain
pt	pterygoid	-	suture between elements (e.g. so-op/eo)