NEW INFORMATION ON CRANIAL AND DENTAL FEATURES OF THE TRIASSIC ARCHOSAURIFORM REPTILE *EUPARKERIA CAPENSIS*

by PHIL SENTER

ABSTRACT. The course of the nasolacrimal duct, interdental plate morphology, and most details of tooth and denticle morphology have not previously been described in non-archosaurian archosauriform reptiles. Here I describe these details in the Triassic archosauriform *Euparkeria capensis*. The nasolacrimal canal opens orbitally via a pair of foramina between the lacrimal and prefrontal. The canal arches over the antorbital fenestra, as in archosaurs. The term 'interdental unit' is introduced for the unit composed of an interdental septum and its accompanying interdental plate. There is no demarcation between interdental plate and septum in *E. capensis*. The interdental units are heavily pitted on exposed surfaces. Like teeth, they are implanted in the dental groove and are separate from the surrounding bone and from each other. They are well positioned to serve as spacers between teeth, and to resist sagittal forces on teeth during prey capture. The teeth of *E. capensis* are labiolingually compressed, except for the nearly conical premaxillary teeth and mesialmost dentary tooth. Lateral teeth are serrated on mesial and distal keels. The denticles are low, rounded, and separated by grooves, and are slightly larger on the distal keel. Tooth morphology suggests carnivorous habits for *Euparkeria*.

KEY WORDS: Archosauriformes, Archosauromorpha, *Euparkeria*, dentition, interdental units, nasolacrimal canal, Reptilia.

EUPARKERIA CAPENSIS Broom, 1913 is an archosauriform from the *Cynognathus* Assemblage Zone of the Karroo system (Lower Triassic) of South Africa (Ewer 1965). This taxon occupies a phylogenetic position immediately basal to crown-group archosaurs (Benton and Clark 1988; Sereno 1991; Parrish 1993; Gower and Wilkinson, 1996). *E. capensis* is known from several specimens in which nearly every skeletal element is represented (Ewer 1965). Two of these specimens are preserved on UMZC T 692, a slab in the collection of the University Museum of Zoology at Cambridge (Text-fig. 1). This is the slab to which Ewer (1965) referred as R 527 or 'Watson's'. The slab is currently in four pieces, three of which contain parts of one skull (specimen A), the braincase of which was described by Ewer (1965) and Gower and Weber (1998). The fourth contains the left maxilla and dentary of a second specimen (specimen B).

UMZC T 692 reveals aspects of the osteology of *E. capensis* that have not yet been described. These include the course of the nasolacrimal duct, and the morphology of the interdental plates and teeth. Ewer (1965) described the tooth replacement pattern in *E. capensis*, but left most details of dental morphology undescribed.
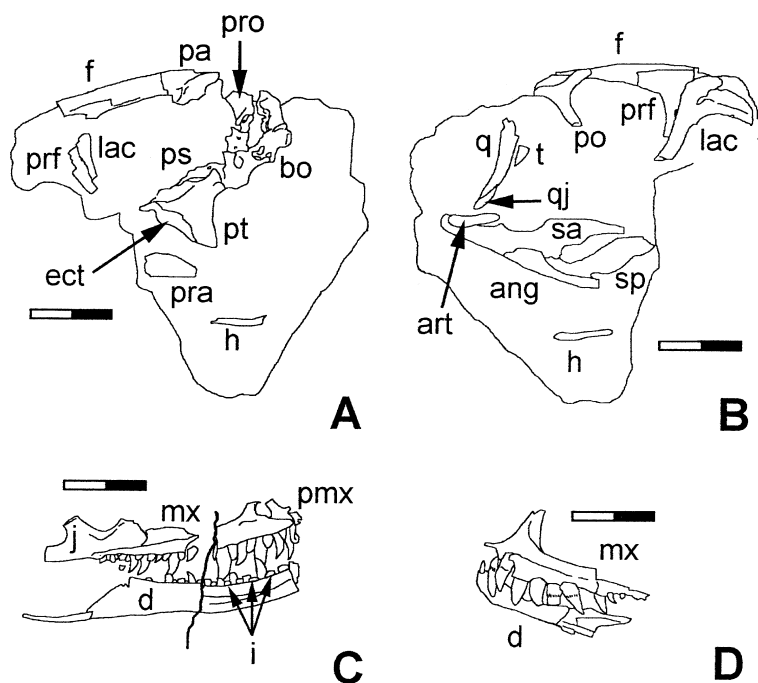
Institutional abbreviations. TTU, Texas Tech University, Austin, Texas; UMZC, University Museum of Zoology, Cambridge, UK; UUVP, Vertebrate Paleontology Collection, University of Utah, Salt Lake City, Utah.

SYSTEMATIC PALAEONTOLOGY

Clade ARCHOSAUROMORPHA Huene, 1946
Clade ARCHOSAURIFORMES Gauthier, Kluge, and Rowe, 1988

Genus EUPARKERIA Broom, 1913

TEXT-FIG. 1. UMZC T 692, *Euparkeria capensis*. A, specimen A, rear block, left lateral view. B, specimen A, rear block, right lateral view. C, specimen A, anterior blocks, medial view of left side of snout; heavy line indicates break between the two blocks. D, specimen B, left lateral view. ang, angular; art, articular; d, dentary; ect, ectopterygoid; f, frontal; h, hyoid; i, interdental units; j, jugal; lac, lacrimal; mx, maxilla; pa, parietal; pmx, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; t, tooth; scale bar represents 2 cm.

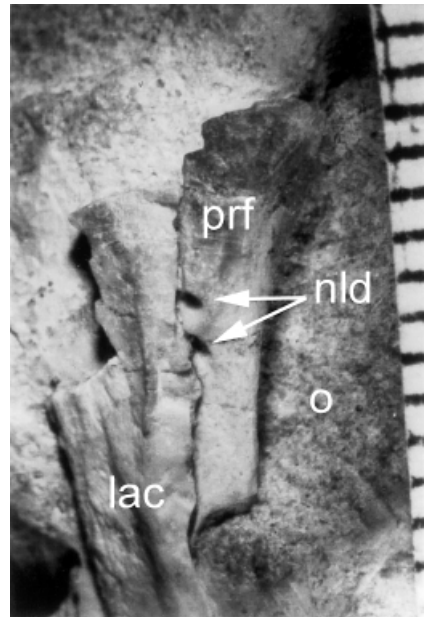## *Euparkeria capensis* Broom, 1913

Text-figures 1–7

Nasolacrimal canal

Description. The course of the nasolacrimal canal has not been described previously in a non-archosaurian archosauriform (Witmer 1997). The orbit of UMZC T 692 exhibits two nasolacrimal foramina, one above the other, between the prefrontal and lacrimal, at about the mid-height of the orbit. These foramina are clearly visible on the left side of specimen A (Text-fig. 2). On the right side, they are obscured by matrix. On the right side of specimen A, the lateral surface of the lacrimal bone is broken off dorsal to the antorbital fenestra. The course of the nasolacrimal canal can be seen inside the lacrimal bone (Text-fig. 3). The canal arches over the antorbital fenestra immediately dorsal to the contribution of the lacrimal to the antorbital fossa. The canal remains inside the lacrimal for the full length of the preserved portion of this bone.

Discussion. Dorsal passage of the nasolacrimal canal over the antorbital cavity in *E. capensis* and archosaurs supports the interpretation of the archosauriform antorbital cavity as a pneumatic feature (Witmer 1997).

The number of nasolacrimal foramina per orbit varies in sauropsids, with no clear phylogenetic trend (Text-fig. 4). The polarity of this character is therefore obscure. Taxa in which each orbit exhibits a single nasolacrimal foramen include *Trilophosaurus* (Gregory 1943), sphenodontians (Sues *et al*. 1994), non-varanid squamates (Estes *et al*. 1988), *Youngina* (Gow 1975), and the basal testudine *Proganochelys* (Gaffney 1990). Taxa in which each orbit exhibits a pair of nasolacrimal openings, as in *Euparkeria*,

TEXT-FIG. 2. Dual orbital opening of nasolacrimal canal of *Euparkeria capensis*, UMZC T 692, Specimen A. lac, left lacrimal; nld, foramina for nasolacrimal canal; o, orbit; prf, left prefrontal; scale bar in mm.


TEXT-FIG. 3. Right lacrimal of *Euparkeria capensis*, UMZC T 692, Specimen A, showing the course of the nasolacrimal canal (shaded). ao, antorbital fossa; is, internal surface; m, matrix obscuring right orbital openings of nasolacrimal canal; shading indicates matrix; heavy line indicates broken edge; scale bar represents 1 cm.
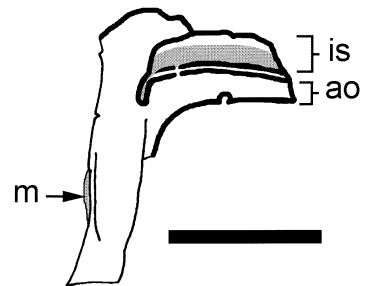
include rhynchosaurs (Benton 1983, 1990; Dilkes 1998), *Prolacerta* (Gow 1975), varanid squamates (Estes *et al*. 1988), *Petrolacosaurus* (Reisz 1981), *Bolosaurus* (Watson 1954), and *Eocaptorhinus* (Heaton 1979). The nasolacrimal ducts of *Sphenodon* and extant lizards are posteriorly forked, although in all but varanids the two posterior limbs of the duct are appressed closely enough to be accommodated by a single orbital foramen (Bellairs and Boyd 1950). To my knowledge, the functional significance of spacing between the posterior limbs of the nasolacrimal duct has not been explored.

The character polarity of the location of the orbital nasolacrimal foramen/ina is clearer than for the character polarity of the number of foramina per orbit (Text-fig. 4). Primitively, sauropsid orbital nasolacrimal foramina open into the lacrimal bone. This is the case in *Procolophon* (Carroll and Lindsay 1985), *Bolosaurus* (Watson 1954), captorhinomorphs (Fox and Bowman 1966; Heaton 1979), and *Proganochelys* (Gaffney 1990). It is also the case in the archosauromorph taxa Rhynchosauria (Benton 1983, 1990; Dilkes 1998), *Proterosuchus* (J. Welman, pers. comm. 2000), Crocodylomorpha, and Dinosauria (Witmer 1997). In contrast, the orbital nasolacrimal foramen/ina open between two bones in lepidosaurs (Bellairs and Boyd 1950; Sues *et al*. 1994), *Euparkeria*, Parasuchia, Stagonolepididae, and probably Ornithosuchidae (Witmer 1997). These two bones are typically the lacrimal and prefrontal in archosauromorphs (Witmer 1997). In some lepidosaurs, the lacrimal is absent, and the duct opens into the orbit between the prefrontal and maxilla (Bellairs and Boyd 1950; Sues *et al*. 1994). The distribution of the
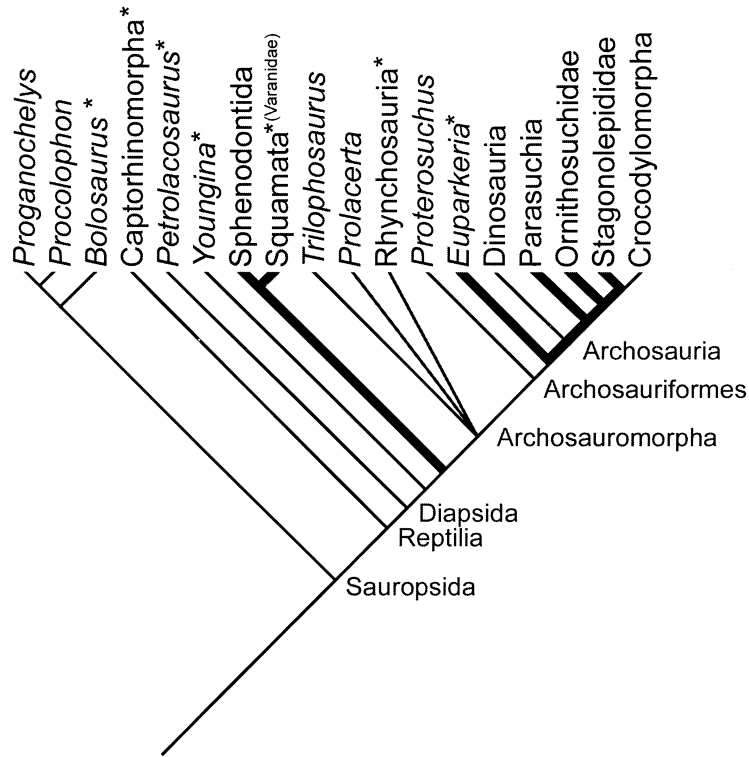
TEXT-FIG. 4. Distribution of character states relating to the nasolacrimal foramen in Sauropsida. Thin line indicates opening of the orbital nasolacrimal foramen in the lacrimal bone. Thick line indicates opening of the orbital nasolacrimal foramen between the prefrontal and the lacrimal or maxilla. Asterisk indicates dual orbital opening of the nasolacrimal canal. Phylogeny after Gower and Wilkinson (1996), Lee (1997), Dilkes (1998), and Berman *et al.* (2000).

location of the orbital nasolacrimal foramen/ina suggests that its opening between two bones is a synapomorphy for both Lepidosauria and *Euparkeria* + more derived archosauriforms. Reversal of this character appears to be a synapomorphy of both Crocodylomorpha and Dinosauria.

Given the above, the number of nasolacrimal foramina per orbit may be a more useful character in phylogenetic studies than is the location of these openings.

Interdental bone

Description. The lingual side of the premaxilla, maxilla, and dentary are visible on specimen A. Prominent interdental plates appear between the teeth on all three bones (Text-fig. 1). As in archosaurs (e.g. Chatterjee 1985; Currie 1995), the interdental plates in *E. capensis* are not discrete structures but are lingual expansions of the interdental septa. In conditions such as those described in *E. capensis*, it would be useful to refer to the interdental septum and plate as a single unit, as there is no clear demarcation between the two. I therefore propose the term 'interdental unit' (IDU) for the unit composed of interdental septum and plate. I also propose that IDUs be numbered from mesial to distal, with each IDU bearing the number of the tooth immediately mesial to it (i.e. the second maxillary IDU is that which occurs immediately distal to the second maxillary tooth).

The break that separates the blocks containing the anterior and posterior portions of the snout of specimen A exposes the distal ends of the third maxillary IDU and the seventh dentary IDU. Here one can clearly see that the IDUs are discrete units of bone, attached to the inside of the dental groove, and are not continuous with the bone of the tooth-bearing elements. They are, therefore, not outgrowths of the tooth-bearing elements, but are *de novo* ossifications. Here
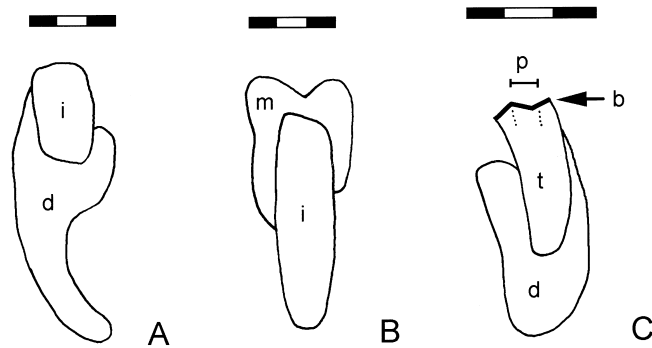
TEXT-FIG. 5. Transverse sections through tooth-bearing bones of *Euparkeria capensis*, UMZC T 692, specimen A, showing implantation of interdental units. A, seventh dentary interdental unit. B, third maxillary interdental unit. C, second dentary tooth, for comparison. b, broken edge; d, dentary; i, interdental unit; m, maxilla; p, pulp cavity; scale bar represents 3 mm.

one can also see that the IDUs are implanted in the dental groove at the same depth as the tooth roots (Text-fig. 5). IDUs are present between all tooth positions, even those for which the tooth has been shed. Unlike teeth, therefore, IDUs apparently were permanently attached to the interior of the dental groove.

Each IDU narrows gradually in the labial direction, with no distinction between interdental plate and septum, and without a labial expansion (Text-fig. 6). Each fully-erupted tooth contacts the IDUs that flank it (Text-fig. 6). The height of each IDU is roughly the same as that of the root-crown junction of adjacent teeth, and is roughly constant from lingual side to labial side. This shows up especially well on the distal maxillary IDUs and mesial dentary IDUs of specimen A.

The IDUs are coarsely pitted on exposed surfaces. This is especially clear in the first, third and fourth maxillary IDUs. Similar surface texture has been noted for the IDUs of archosaurs (Currie 1987, 1995).

Discussion. The wide separation between IDUs in *E. capensis* implies that these structures initially develop as separate units. Ewer (1965) interpreted them as once-continuous 'bone of attachment' in which resorption had taken place on the lingual side of each tooth. By 'bone of attachment', Ewer probably meant 'interdental bone', because the term 'bone of attachment' usually refers to cementum (Edmunds 1969). In any case, the IDUs of UMZC T 692 exhibit no evidence that they were once continuous. IDUs are fused lingually on the maxillae of many archosaurs, e.g. *Postosuchus* (TTU P 9000), *Ceratosaurus* (Madsen and Welles 2000), *Allosaurus* (UUVP 5427), and dromaeosaurids (Currie 1995). If the condition in *Euparkeria* is representative of the plesiomorphic state for archosaurs, then such fusion is a derived state.

The IDUs of *E. capensis* may have functioned as spacers, keeping the teeth at an optimal distance from each other. The positions of the IDUs of *E. capensis* also suggest a function in resistance to sagittal forces on teeth during prey capture. The IDUs may have been less effective at resisting transverse forces on teeth, because they do not extend lingually around the teeth (Text-fig. 6). The head motions of *E. capensis* during prey capture may therefore have been directed predominantly along a sagittal axis. In contrast, lingual fusion between IDUs of the aforementioned archosaurs creates a medial wall around the teeth, which suggests better resistance of transverse forces.

Dental morphology

Description. The maxillary and dentary teeth of *E. capensis* are serrated on both the mesial and distal keels. The denticles are low and rounded, and closely resemble those of the theropod *Richardoestesia gilmorei* (Currie *et al.* 1990, fig. 8.4I) (Text-fig. 7). Apical denticles are more worn than those near the base. Mesial denticles are slightly smaller than distal denticles. In specimen B, denticle density is nine per mm on the mesial keel, and seven per mm on the distal keel. In specimen A, denticle density is nine per mm on the mesial keel, and eight per mm on the distal keel. These serration densities are constant among teeth.
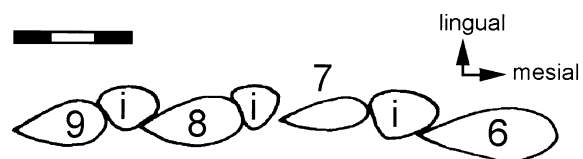
TEXT-FIG. 6. Frontal section through maxillary teeth and interdental units of *Euparkeria capensis*, UMZC T 692, specimen A, at the level of the dental root-crown junction. Tooth 7 is not fully erupted, and does not contact the interdental unit posterior to it. 6–9, sixth through ninth maxillary teeth; i6–i8, sixth through eighth interdental units; scale bar represents 3 mm.
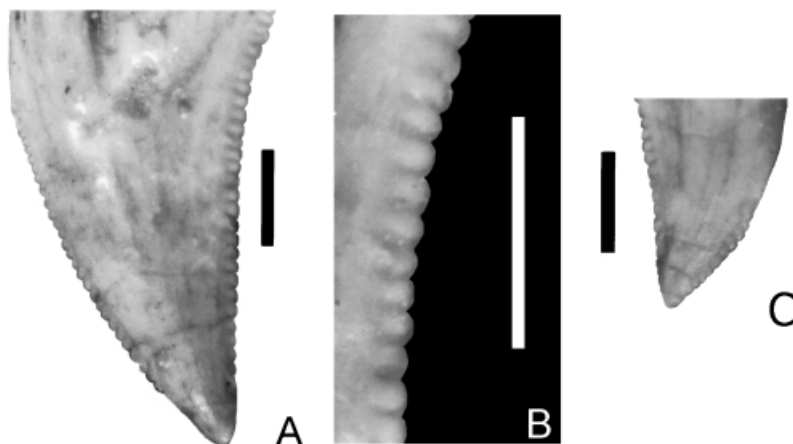
TEXT-FIG. 7. Teeth of *Euparkeria capensis*, UMZC T 692; note the difference in the relative length of the unserrated part of the mesial keel between the first maxillary tooth and the eighth maxillary tooth. A, first maxillary tooth, specimen B. B, denticles of distal keel of first maxillary tooth, specimen B. C, eighth maxillary tooth, specimen A. Scale bar represents 1 mm.

The tip of an isolated tooth is present in the right infratemporal fenestra of specimen A. Denticle density is nine per mm on the mesial keel and eight per mm on the distal keel of this tooth. Its serrations exhibit the same morphology as those of specimens A and B, and it is probably a tooth of *E. capensis*. There is no evidence that the tooth came from an individual other than specimen A.

Denticle density is constant along the length of a given tooth (except for the first dentary tooth; see below), except on the proximal end of the mesial keel, where serrations are absent. The distal keel is serrated along its entire length. The proximal unserrated length (PUL) of the mesial keel relative to tooth crown height (TCH) is not constant. The PUL/TCH ratio varies from 0·43 to 0·83, with no clear trend in this value along the tooth row (Table 1). Nor is there a clear trend in the value of PUL/FABL (fore-aft basal length), which varies from 0·69 to 1·5, along the tooth row (Table 1). The extent of the proximal unserrated portion of the mesial keel, therefore, cannot be used to infer tooth position in an isolated tooth.

Between every two adjacent denticles is a groove that is perpendicular to the margin of the keel. The groove is slightly longer than the length of a denticle. Similar grooves are known in the teeth of theropods and several other taxa of extinct vertebrates with serrated teeth (Abler 1992).

The distal two premaxillary teeth are present in specimen A. These teeth are labiolingually compressed, but less so than the maxillary teeth. No serrations are visible on the premaxillary teeth in specimen A, but this may be due to being obscured by matrix. Serrations are present on the premaxillary teeth of other specimens of *E. capensis* (Ewer 1965).

The mesialmost dentary tooth is present on specimen B. This tooth is smaller than the other dentary teeth. As Ewer (1965) noted, it is nearly conical, whereas the others are labiolingually compressed. Serrations are present on the distal keel of the mesialmost dentary tooth. Its position prevented measurement of serration density with vernier calipers. However, the denticles are seen to decrease in size and increase in density toward the tooth's tip. No mesial denticles are visible on this tooth, but this may be a result of being obscured by matrix. The rest of the teeth are labiolingually compressed, particularly on their distal halves and apically. The mesial half of each tooth is transversely bulbous near the base (Text-fig. 5).

TABLE 1. Tooth measurements in *Euparkeria capensis*, UMZC T 692. FABL, fore-aft basal length (mm); TCH, tooth crown height (mm); PUL, length of proximal unserrated part of mesial keel (mm); e, estimated.

		TCH	FABL	PUL	PUL/TCH	PUL/FABL
Specimen A						
Premaxilla	1	–	–	–	–	–
	2	–	–	–	–	–
	3	4·4	1·5	–	–	–
	4	3·2	1·8	–	–	–
Maxilla	1	–	–	–	–	–
	2	2·2	1·6	–	–	–
	3	6·6e	2·7	–	–	–
	4	–	–	–	–	–
	5	6·8e	2·0	–	–	–
	6	–	–	–	–	–
	7	3·4	2·0	–	–	–
	8	2·4	1·8	2·0	0·83	1·1
Dentary	1	–	–	–	–	–
	2	–	–	–	–	–
	3	4·1	2·3	2·0	0·49	0·87
	4	–	–	–	–	–
	5	–	1·6	–	–	–
	6	1·6	1·3	–	–	–
	7	–	–	–	–	–
	8	2·2	1·6	1·6	0·73	1·0
	9	–	–	–	–	–
	10	–	1·6	1·5	–	0·94
Specimen B						
Maxilla	1	6·3	3·9	2·7	0·43	0·69
	2	–	3·5	5·4	–	1·5
	3	–	3·7	3·7	–	1·0
	4	–	3·5	–	–	–
	5	6·0	3·1	–	–	–
	6	–	–	–	–	–
	7	–	2·5	3·0	–	1·2
	8	–	–	3·0	–	–
	9	–	–	–	–	–
Dentary	1	3·8	1·2	–	–	–
	2	6·3	2·3	–	–	–

Discussion. Denticle-related characters are useful in identifying isolated theropod teeth to family, and often to genus (Currie *et al.* 1990). Such characters include denticle shape, density, and distribution. The same might be true for other archosauriforms with serrated teeth, but comparative studies have not been carried out for most taxa. Particularly unfortunate is the lack of published descriptions of denticle-related characters in close outgroups to Archosauria, for example proterosuchids, erythrosuchids, proterochampsids, and *Euparkeria*. These taxa are the most basal archosauriforms known to exhibit serrated teeth. Denticle characters in these groups might thus be able to shed light on the original morphology and function of serrations in Archosauriformes. Hopefully, the description of denticle morphology in *E. capensis* will prove useful for future comparative studies of denticle characters in basal archosauriforms.

Ewer (1965) suggested that *E. capensis* may have been insectivorous, omnivorous, or herbivorous. However, the teeth of *E. capensis* teeth exhibit low serrations, which are better for gripping than for slicing (Abler, 1992). This suggests that *E. capensis* was more likely to have been a carnivore than a herbivore. Among extant tetrapods, only certain varanid lizards (e.g. *Varanus komodoensis*) possess pointed, laterally

compressed teeth with fine serrations (Auffenberg 1981), as in *E. capensis*. Juvenile *V. komodoensis* are largely insectivorous, but adults are active predators upon animals that may match them in size (Auffenberg 1981). It is plausible that the same was true for *E. capensis*.

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