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Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar

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Phylogenetic analysis indicates that *Crocodylus robustus* Grandidier & Vaillant, 1872 is more closely related to the living African dwarf crocodiles (*Osteolaemus*) than to living *Crocodylus*. The type series cannot be identified, but the original description includes details consistent with known specimens that almost certainly pertain to the same species. It had a prominent triangular 'horn' on the posterolateral corner of each squamosal; near-exclusion of the nasals from the external naris; constricted supratemporal fenestral rims; a dorsoventrally deep snout; a constricted external mandibular fenestra in which the surangular–angular suture emerges from the posterior rather than posteroventral margin; and robust limb and limb girdle elements. It shares with *Osteolaemus*, and with several extinct crocodylids from the Neogene of Africa, a depressed surface of the pterygoid around the internal choana forming a choanal 'neck'. It cannot be referred to *Crocodylus* and a new praenomen, *Voay*, is established for its reception. *Voay* persisted into the Holocene and may have been extant when humans first settled Madagascar 2000 years ago, when it may have been a casualty of a megafaunal extinction event on the island. This is consistent with molecular data that suggest comparatively recent dispersal of *Crocodylus niloticus* to Madagascar from mainland Africa. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150**, 835–863.

ADDITIONAL KEYWORDS: Crocodylus – Osteolaeminae – phylogeny – Voay.

INTRODUCTION

Large fossil crocodiles have been known from the Quaternary of Madagascar for over a century (Grandidier & Vaillant, 1872). Although first thought to represent an extinct species (*Crocodilus robustus* Grandidier & Vaillant, 1872), they were later thought to represent older populations of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1786), currently found in Madagascar (Boulenger, 1889; Boettger, 1913; Fuchs, Mertens & Wermuth, 1974a). Cranial material clearly distinct from *C. niloticus* was later figured and referred to *C. robustus* (Barbour, 1918; Mook, 1921), but some authorities continued to view *C. robustus* as conspecific with *C. niloticus* (e.g. Wermuth, 1953; Fuchs *et al*., 1974a). As such, crocodiles have been said to be among the few large vertebrates to survive a major extinction phase coinciding with human settlement of the island over the past 2000 years (e.g. de Wit, 2003).

Recent phylogenetic analyses have found a close phylogenetic relationship between these fossils and the modern African dwarf crocodiles (*Osteolaemus tetraspis* and *O. osborni*; Brochu, 1997, 2000, 2006b). This is significant for two reasons. First, it suggests that crocodylians were among the victims of megafaunal extinctions that swept Madagascar and the western Indian Ocean region during the Late Quaternary (e.g. Peake, 1971; Dewar, 1984; MacPhee & Marx, 1997; Austin & Arnold, 2001). This increases the range of clades and, hence, the range of physiological and ecological characteristics, affected by this event.

Second, it reveals morphological characters also found in several crocodiles of Oligocene through Pliocene age from throughout Africa, but not in extant *Crocodylus*. *Osteolaemus* is among the smallest and least aquatic of extant crocodylians (Ross, 1998), but extinct relatives include animals outwardly resem-

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bling modern *Crocodylus*, such as *Rimasuchus lloydi* and '*C.*' *pigotti*, which probably played the ecological role currently played by *C. niloticus*. They also include *Euthecodon*, a long-snouted form resembling modern *Gavialis* or *Tomistoma*, and some molecular data would put the living African slender-snouted crocodile (*Mecistops cataphractus*) in this assemblage as well (White & Densmore, 2001; Gatesy *et al*., 2003; Schmitz *et al*., 2003; McAlily *et al*., 2006). There thus appears to have been a morphologically diverse endemic radiation of crocodylids in the African Neogene. An endemic radiation occurred in Australasia at approximately the same time (Willis, Molnar & Scanlon, 1993; Salisbury & Willis, 1996; Willis, 1997, 2001). The name Osteolaeminae has been established for the African clade (Brochu, 2003) and is defined as *O. tetraspis* and all crocodylians more closely related to it than to *C. niloticus*.

On the surface, our task with the extinct Malagasy crocodile appears straightforward – a new generic name should be established for it. Its morphology was described twice – once by Grandidier & Vaillant (1872) and again by Mook (1921) – and most of the features that distinguish it from other crocodylians are apparent in these references. But the situation is complicated by two problems – first, no holotype was ever designated for *C. robustus*, and the material described by Grandidier & Vaillant in 1872 cannot be located; second, another species name, *C. madagascariensis*, was coined independently by two different authors, and although both were based on modern Nile crocodile populations in Madagascar, some authorities considered *robustus* and *madagascariensis* to be the same, which led to the synonymy of *C. robustus* with *C. niloticus*. The reasons for the confusion are unclear, but the names *robustus* and *madagascariensis* have become linked in the literature.

This paper attempts to resolve these problems and to provide a diagnosis for the extinct Quaternary crocodile of Madagascar. It describes the extinct form in more detail, including those portions of the skeleton – the mandible and postcranium – not described in previous treatments of the form. It also reviews the morphological evidence for a close phylogenetic affinity between the fossil Malagasy crocodile and extant *Osteolaemus*.

Abbreviations

The following institutional abbreviations have been used: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; MCZ, Museum of Comparative Zoology, Cambridge, MA, USA; MNHN, Museum National d'Histoire Naturelle, Paris, France; SUI, University of Iowa Paleontological Repository, Iowa City, IA, USA; TMM, Vertebrate Paleontology Laboratory, Texas Memorial Museum, Austin, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UF, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA; USNM, United States National Museum of Natural History, Washington, DC, USA.

The following anatomical abbreviations have been used in the figures: 4t, fourth trochanter; aaf, articulation facet for astragalus on tibia; an, angular; art, articular; bo, basioccipital; bs, basisphenoid; ccr, medial wall of caviconchal recess; cf, coracoid foramen; cn, choanal neck; cor, coronoid; cr, caecal recesses on wall of caviconchal recess; d, dentary; dc, deltoid crest; dpc, deltopectoral crest; ear, anterior ramus of ectopterygoid; ect, ectopterygoid; emf, external mandibular fenestra; en, external naris; eoa, external otic aperture; eoc, exoccipital; f, frontal; fae, foramen aereum; fc, frontal crest; fic, foramen intermandibularis caudalis; fim, foramen intermandibularis medius; fm, foramen magnum; gf, glenoid fossa; hg, humeral groove on ulna; ic, internal choana; if, incisive foramen; ift, iliofibularis trochanter; itf, infratemporal fenestra; itf, iliofibularis internus scar; j, jugal; lac, lacrimal; lcf, lateral carotid foramen; lp, lingual process of angular; ls, laterosphenoid; lsb, laterosphenoid bridge; lsg, lateral squamosal groove; meu, median eustachian foramen; msA-D, muscle scars A and D of Iordansky; msB, 'muscle scar "B"' of Iordansky'; mx, maxilla; mx5, fifth maxillary tooth/alveolus; n, nasal; orb, orbit; pa, parietal; paf, articulation surface for pubis on ischium; palp, anterior palatine process; pfl, palatine flange within suborbital fenestra; pmx, premaxilla; po, postorbital; poc, preorbital crest; pos, preotic sinus; prf, prefrontal; pt, pterygoid; ptf, post-temporal fenestra; q, quadrate; qj, quadratojugal; s.b, broken surface; s.ect, sutural surface on maxiila for ectopterygoid; s.f, sutural surface on parietal for frontal; s.mx, sutural surface on maxilla for other maxilla; s.n, sutural surface on maxilla for nasal; s.pal, sutural surface on maxilla for palatine; s.pmx, sutural surface on maxilla for premaxilla; s.po, sutural surface on parietal for postorbital; s.qj, sutural surface on quadrate for quadratojugal; s.soc, sutural surface on parietal for supraoccipital; s.sq, sutural surface on parietal for squamosal; san, surangular; sdp, descending process of squamosal; sh, squamosal horn; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra; tmds, common insertion point for M. teres major and M. dorsalis scapulae; vf, vagus foramen; XII, exit foramen for 12th cranial nerve.

TAXONOMIC REVIEW

Crocodylus madagascariensis Grandidier, 1872

Grandidier (1872) and Gray (1874) independently based *C. madagascariensis* on recent material.

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Neither author specified a type. Grandidier (1872) did not include a figure, but Gray (1874) illustrated the material at his disposal, which is now housed at the Natural History Museum, London. Both descriptions suggest a rather gracile animal, with proportions much like those of *C. niloticus*.

Evaluation of the name is difficult because *C. madagascariensis* is a *nomen nudum* regardless of which description is used. Nevertheless, the animal figured by Gray (1874) is indistinguishable from *C. niloticus* currently found in the Malagasy Republic. The material described by Grandidier (1872) is also consistent with the living form. Boulenger (1889) and most subsequent authors regarded *C. madagascariensis* as a junior subjective synonym of *C. niloticus*.

Living crocodiles in Madagascar were later treated as a distinct subspecies (*C. niloticus madagascariensis*) based on scalation features said to distinguish Malagasy populations from those on the mainland (Fuchs *et al*., 1974a). Recent molecular work has found minimal genetic divergence between Malagasy and eastern African populations of *C. niloticus* (Schmitz *et al*., 2003; Hekkala, 2004), suggesting modern populations in Madagascar were established relatively recently.

CROCODYLUS ROBUSTUS GRANDIDIER & VAILLANT, 1872

Crocodylus robustus was established on the basis of fragmentary subfossil remains from Amboulisatre. No figures were included, and the material is probably now lost (see below). These authors described a rather broad-snouted crocodile with more 'robust' proportions than those of extant *C. niloticus*. In particular, they noted the wide angle of the mandibular symphysis relative to *C. niloticus* and the dorsoventral depth of the snout, which prevented extrusion of the dentary teeth through the premaxilla in mature specimens.

Grandidier & Vaillant (1872: 150) apparently did not have complete skulls or associated postcrania, but felt that some of the elements 'came from the most important parts of the skeleton to permit a complete understanding of the animal'. They listed six dentaries (right and left), two premaxillae, two maxillae, and among 'numerous other cranial bones', two 'mastoids' (squamosals) and some frontals. They also had three ilia, a fragmentary ischium, 'more than 40' vertebrae, and numerous osteoderms. No associations between specific elements were implied, but they stated that 'at least three individuals' were represented.

The diagnostic characters listed by Grandidier & Vaillant (1872) relate to robust build. The teeth and alveoli were described as 'enormous', and the snout as 'short' with a symphyseal angle of 49° and a large distance between the lateral borders of the maxillae. References were made, albeit not directly, to wide premaxillae and exclusion of the nasals from the external naris. Finally, they stated that the premaxillae lacked holes for reception of the anterior dentary teeth, a character known to vary ontogenetically in most crocodylians (Kälin, 1933).

The new crocodile was classified as *Crocodylus* on the basis of three characters. First, the enlarged fourth dentary tooth occluded in a notch between the premaxilla and maxilla, a character presently regarded as plesiomorphic at the level of Crocodylia (Willis, 1993; Brochu, 1999). Second, 'the frontoparietal opening [supratemporal fenestra], judging from the curvature of the internal border of the squamosal, was largely open'. Because it is unclear what the authors meant, it is difficult to compare this statement with the markedly constricted supratemporal fenestrae of material described here (see below). Finally, there were 19 upper and 15 lower teeth, a formula consistent with *Crocodylus* (Iordansky, 1973).

The earliest illustration of a fossil referred to *C. robustus* was a skull figured by Barbour (1918: plate 1; Fig. 1). Mook (1921) republished the same plate and added a more detailed description. The specimen, MCZ 1006, is consistent with what Grandidier and Vaillant wrote: the bones of the rostrum (especially the premaxillae) are broad, and although the nasals contribute to the narial rim (Mook, 1921; see below), their contribution is minimal, and it is easy to envision fragmentary material leading one to conclude that the premaxillae completely surround the nares.

This taxon differs from *C. niloticus* in numerous ways, the most obvious being the prominent squamosal 'horns' (Fig. 2). The squamosals generally become upturned late in ontogeny in most species of *Crocodylus*, most notably in *C. rhombifer* from Cuba and in *C. siamensis* from south-eastern Asia and Indonesia, but they are unusually tall in the extinct Madagascar form and are present in all known mature skulls. The only other crocodylian known to show such horns is the Palaeocene alligatoroid *Ceratosuchus burdoshi* (Schmidt, 1938; Bartels, 1984). Grandidier & Vaillant (1872) had isolated squamosals at their disposal, but they did not describe the presence of horns.

The skull of the extinct crocodile is broader and more robust than most *C. niloticus* and comes closest, in overall shape, to *C. palustris*. Snout shape varies widely within crocodylian species (e.g. Kälin, 1933, 1936; Hall, 1985; Hall & Portier, 1994), so much so that taxonomic judgements should be based on more than skull proportion. The skull of the extinct form is also dorsoventrally deep (Fig. 2) to a greater extent than in any living species of *Crocodylus*, but similar to that in *Osteolaemus*.

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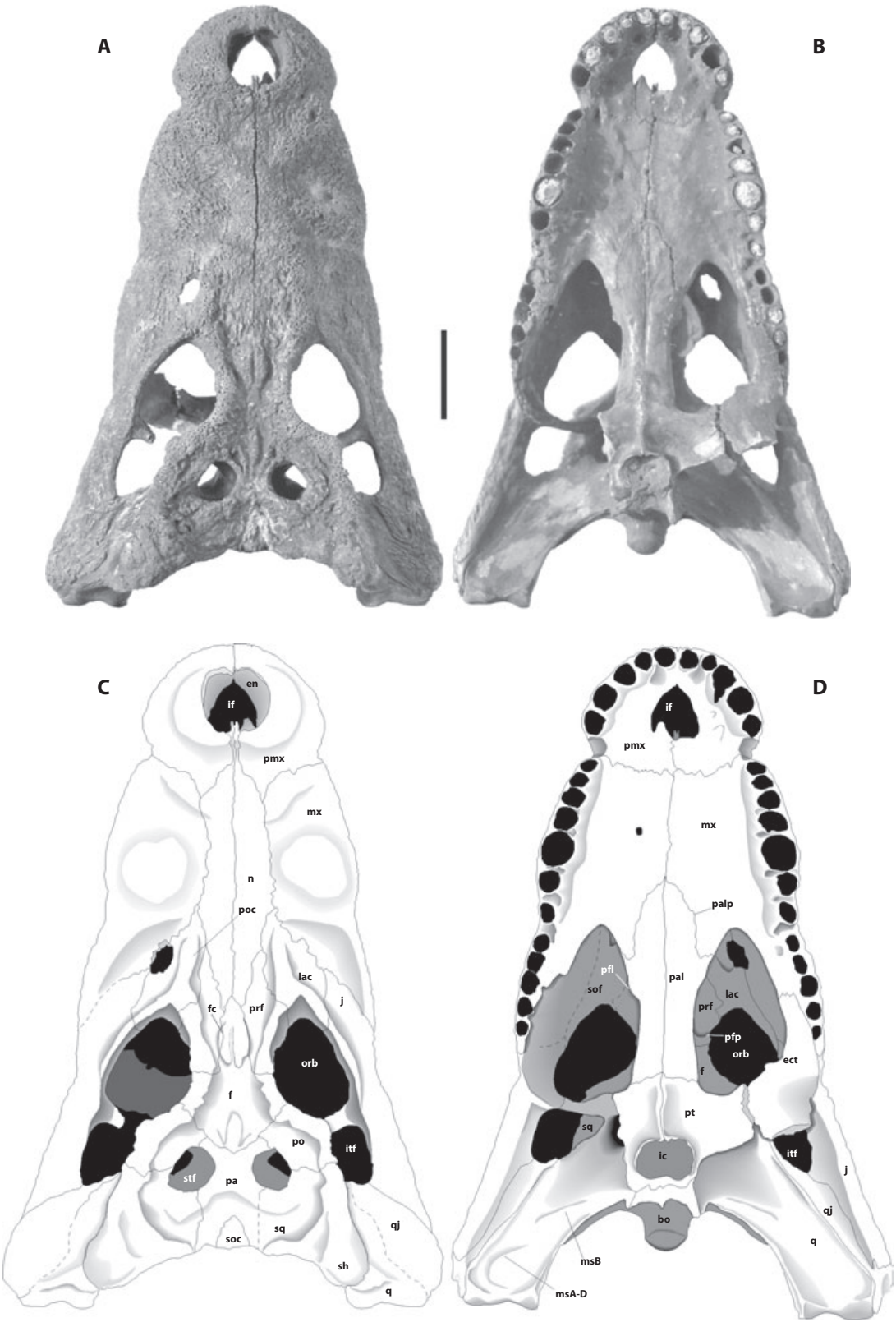

Figure 1. MCZ 1006, neotype, *Voay robustus*, dorsal (A, C) and ventral (B, D) views. Scale = 5 cm.

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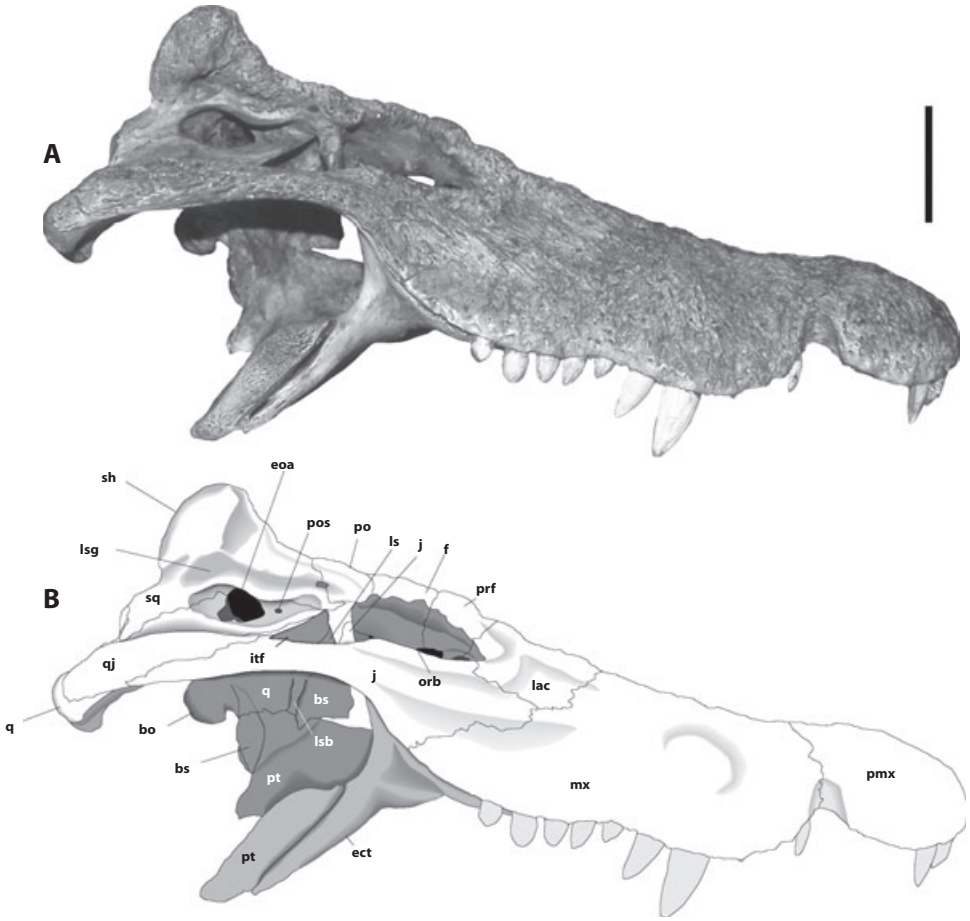

Figure 2. AMNH 3101, *Voay robustus*, skull, right lateral view. Scale = 5 cm.

Designation of a neotype: At the present time, *C. robustus* Grandidier & Vaillant, 1872 is a *nomen nudum*. The name has been used in various contexts (e.g. Bartels, 1984; Burness, Diamond & Flannery, 2001; Meers, 2002), and whatever its status from the standpoint of the ICZN, it has consistently referred to a recently extinct horned crocodile from Madagascar for the past several decades. The name has achieved a stable meaning. Conservation of *C. robustus* through designation of a neotype would preserve this stability.

A lectotype cannot be designated because the original material either no longer exists or cannot be identified from existing collections. Subfossil crocodylian specimens from Amboulisatre currently housed at the MNHN in Paris are congruent with the material described by Grandidier and Vaillant (C. A. Brochu, pers. observ.), but were collected after 1900. The original material might have been deposited in the Malagasy Academy in Antananarivo, but the building housing most of the Academy's collection was destroyed by fire in 1995, along with most of the collections (S. Goodman, pers. commun.).

Conservation of the name would promote clarification of the taxonomy of Quaternary Malagasy crocodiles. *C. robustus* has frequently been considered synonymous with *C. niloticus* (e.g. Boettger, 1913; Blanc, 1972, 1984; Fuchs *et al*., 1974a; Paulian, 1984). Reports of living *C. robustus* (Vaillant, 1883; Vaillant & Grandidier, 1910) that later turned out to be very old *C. niloticus* (Barbour, 1918) may have reinforced this view. It may also reflect confusion between *C. robustus* and *C. madagascariensis*.

The skull figured by Barbour (1918) and Mook (1921), MCZ 1006, is a good candidate for a neotype. It is clearly not *C. niloticus* – the prominent squamosal horns and anterior extent of the nasals are very different from *C. niloticus*, and the fact that other Malagasy subfossil skulls show this same combination of features argues against pathology. Concordance between what Grandidier & Vaillant (1872) described and what Barbour (1918) and Mook (1921) figured strongly suggests that they are conspecific.

The only conflict between the original description and the material described here concerns the

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supratemporal fenestra. It is unclear whether Grandidier & Vaillant (1872) simply meant that the fenestrae were open or that they were relatively large or wide; the former is common to all crocodylians except mature caimans and some *Osteolaemus*, and fossils later described as *C. robustus* actually have comparatively small fenestrae with caiman-like constricted dorsal rims. Comparatively large supratemporal fenestrae are more characteristic of longirostrine crocodyliforms (Langston, 1973), and *C. robustus* was not longirostrine. Constriction of the fenestrae may not have been apparent from isolated squamosals – the anteromedial corner of each squamosal is concave, forming part of the margin of the fenestra, which might have led Grandidier and Vaillant to conclude that the Malagasy form had open supratemporal fenestrae in comparison with the much more constricted features in *Osteolaemus*.

CROCODYLIA

CROCODYLIDAE

OSTEOLAEMINAE

VOAY ROBUSTUS (GRANDIDIER & VAILLANT, 1872)

Neotype: MCZ 1006, skull (Fig. 1).

Referred material: AMNH FR 3100, partial skull; AMNH FR 3101, skull (Figs 2, 3); AMNH FR 3102, skull; AMNH FR 3103, mandible; AMNH FR 3104, right mandibular ramus (Fig. 4); AMNH FR 3105, mandible; AMNH FR 3106, vertebrae; AMNH FR 3107, osteoderms; AMNH FR 17008, ribs; AMNH FR 17709, right ilium; AMNH FR 17010, right ulna; AMNH FR 17011, metacarpal, phalanx; AMNH FR 17012, right astragalus; BMNH R2001, osteoderms; BMNH R2002, teeth; BMNH R2026, skull and jaws; BMNH R2027, osteoderms, including articulated nuchal elements; BMNH R2081, squamosals and parietal; BMNH R2083, partial right dentary and left articular, surangular, angular; BMNH R2085, caudal and trunk vertebrae; BMNH R2086, right ilium; BMNH R2087, right femur; BMNH R2088, two femora; BMNH R2089, right ischium; BMNH R2090, left humerus; BMNH R2091, radius; BMNH R2093, metatarsal; BMNH R2097, left fibula; BMNH R2102, partial skull table and braincase; BMNH R2103, teeth; BMNH R2192, braincase and skull table; BMNH R2193, partial skull and jaws; BMNH R2194, teeth; BMNH R2195, vertebrae from at least two individuals; BMNH R2196, two left humeri; BMNH R2197, osteoderms; BMNH R2198, three ulnae; BMNH R2199, left fibula; BMNH R2200, left coracoid; BMNH R2201, calcaneum; BMNH R2202, three femora; BMNH R2203, two left ilia, one right ilium; BMNH R2204, partial skulls; BMNH R2205, partial right coracoid; BMNH R2206, ribs and caudal vertebrae; BMNH R2211, left fibula; BMNH R2218, vertebrae (trunk, sacral, caudal) and cervical rib; BMNH R2219, pathological dorsal vertebrae with fused centra; BMNH R2220, partial left femur, complete left femur; BMNH R2222, right radius; BMNH R2223, ribs; BMNH R2401, partial jaws; BMNH R2402, two cervical vertebrae; BMNH R3088, distal caudal vertebrae; MNHN 1906–16; MNHN 1932.80; MNHN 1908.5, postcranial material; MNHN 1932.80, partial skull.

Occurrence: Late Quaternary, Madagascar. The form is known from multiple sites across the island. The neotype was found near Antsirabe and described by Mook (1921: 26) as 'probably late Pleistocene'. Although most Quaternary deposits in Madagascar are Holocene, some of the radiocarbon dates reported from Antsirabe by Burney *et al*. (2004) are slightly older than 20 Ka. It is thus possible that MCZ 1006 is from the uppermost part of the Pleistocene.

Etymology: Voay, Malagasy, 'crocodile'. The name *robustus* refers to the robust construction of the skeleton.

Diagnosis: Osteolaemine crocodylid with a prominent triangular crest at the posterolateral corner of each squamosal and a pair of oval bosses on the frontal between the orbits. Supratemporal fenestrae constricted, with no dorsal fossae. Nasals form thin processes that penetrate the narial rim, but premaxillae approach each other closely behind external naris. Surangular–angular suture intersects external mandibular fenestra at the posteriormost end laterally and does not pass anteriorly along the ventral margin of the fenestra (reversal of derived feature in crocodylids). Circular boss on medial surface of splenial. Vaulted premaxillary and maxillary palate surfaces. Shares everted choanal margin (choanal 'neck') and lateral extension of squamosal on to quadrate ramus with other osteolaemines; shares broad supraacetabular buttress and altirostral skull with *Osteolaemus*.

Description

Primary cranial/mandibular openings: The circular external naris opens anterodorsally. The nasals enter the dorsal narial rim as a pair of thin processes. The narial chamber is comparatively deep, and the dorsal surface of the premaxillae is inflated around the narial rim.

The incisive foramen is subtriangular in shape, completely surrounded by the premaxillae, and nearly as large as the external naris.

The orbit is surrounded by the frontal, prefrontal, lacrimal, jugal, and postorbital. Because the skull is dorsoventrally deep, the orbits open laterally to a

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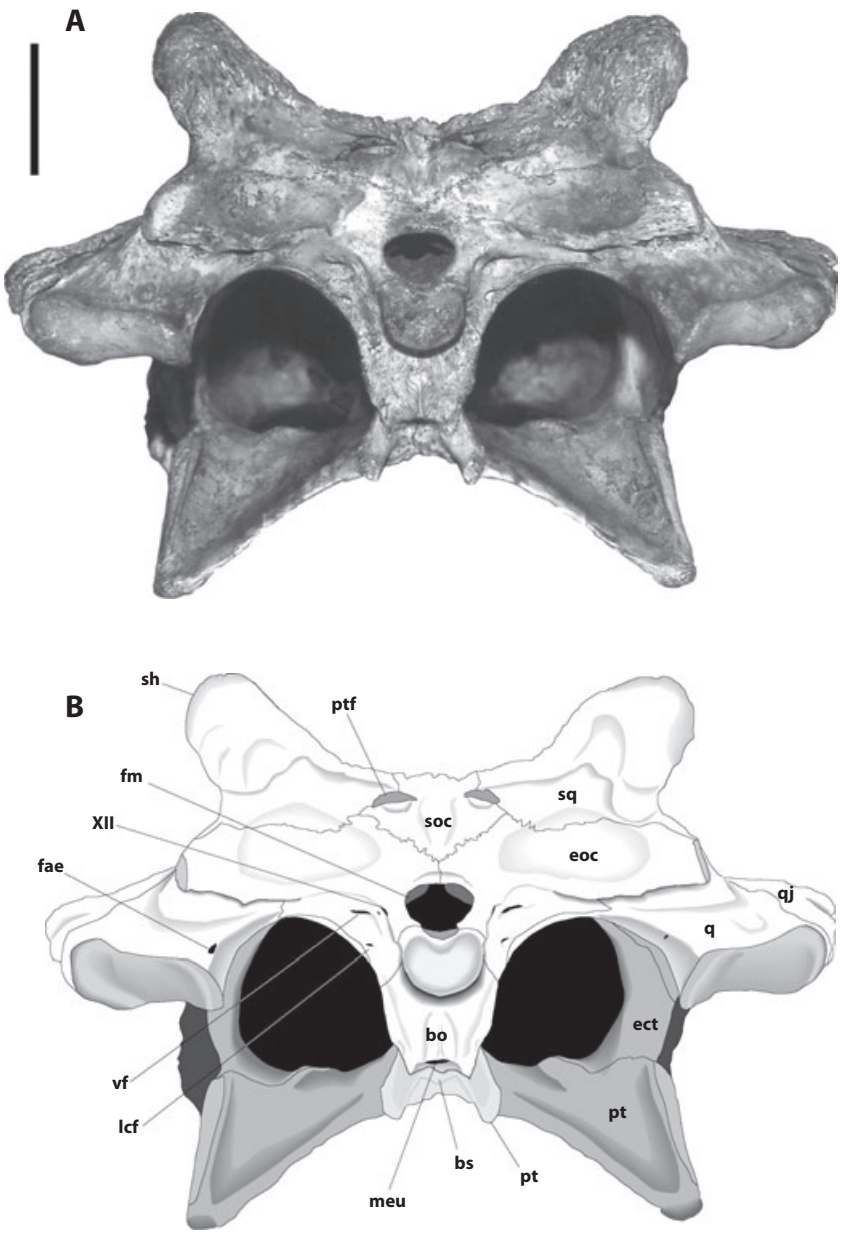

Figure 3. AMNH 3101, *Voay robustus*, skull, posterior view. Scale = 5 cm.

greater degree than in extant *Crocodylus*. Most of the orbital rim is upturned.

The infratemporal fenestra is triangular and anteroposteriorly short, resembling its counterpart in *Osteolaemus*. The jugal forms the anteroventral and posteroventral corners, and the quadratojugal intersects the fenestral margin above the posteroventral angle. The quadratojugal terminates shortly below the dorsal angle of the fenestra, which is formed by the postorbital.

The supratemporal fenestrae are very characteristic. They are relatively small and set forward on the skull table. The roofing bones (parietal, postorbital, squamosal) lap over the fenestral rim, obliterating the dorsal fossa. The frontoparietal suture does not intersect the fenestral margin. A small, circular opening for the temporal canal lies on the posterior wall of the supratemporal fenestra, surrounded dorsally by the squamosal and parietal and ventrally by the quadrate.

The external otic aperture is clover leaf-shaped in outline and surrounded dorsally by the squamosal and posteriorly, ventrally, and anteriorly by the quadrate. The quadrate–squamosal suture extends dorsally along the posterior margin of the aperture.

The suborbital fenestra is an anteroposteriorly elongate oval surrounded medially by the palatine,

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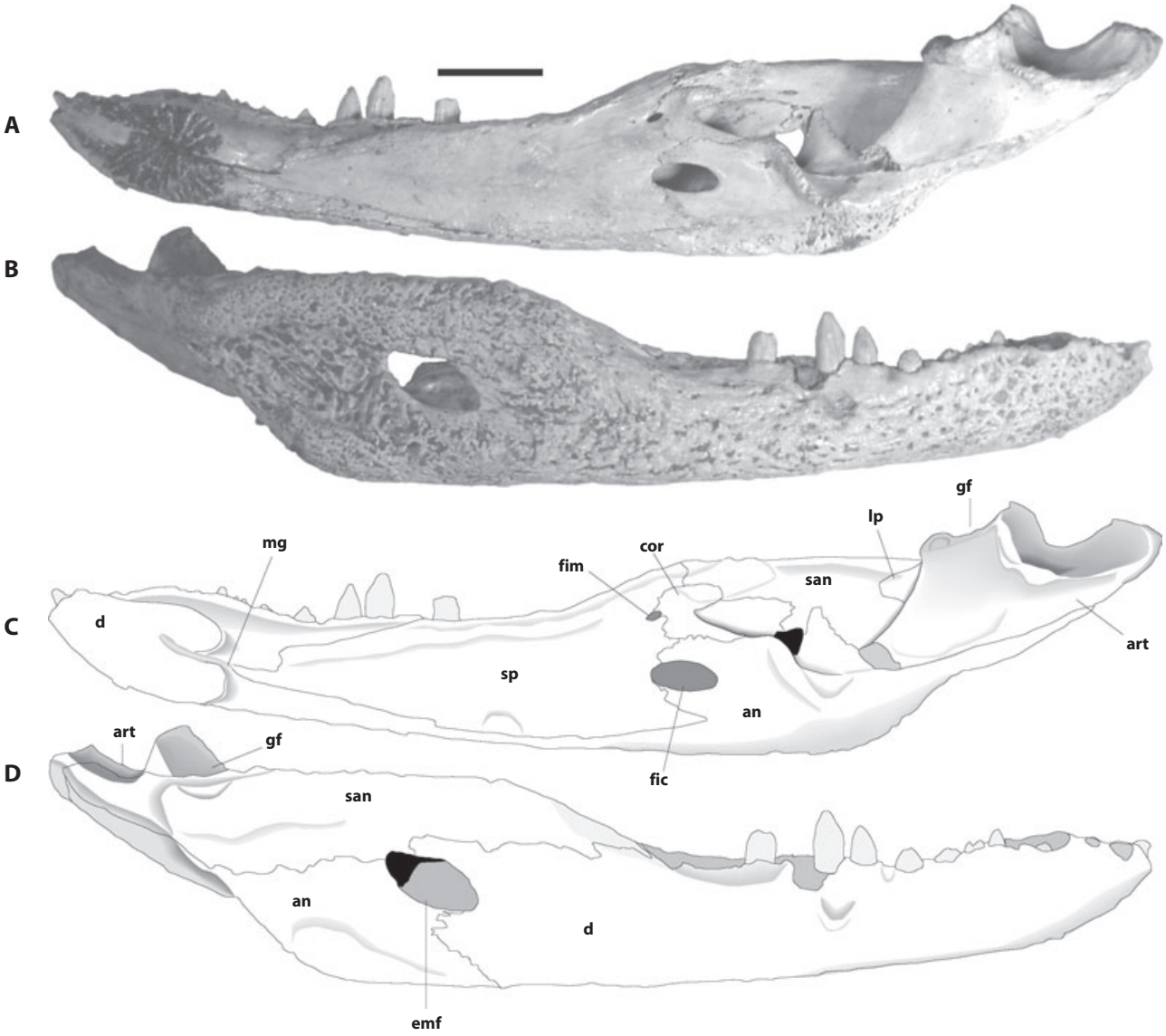

Figure 4. AMNH 3104, *Voay robustus*, right mandibular ramus, medial (A, C) and lateral (B, D) views. Scale = 5 cm.

posteriorly by the pterygoid, posterolaterally by the ectopterygoid, and anterolaterally by the maxilla. Their anterior limit lies at the level of a diastema between the seventh and eighth maxillary alveoli. Lateral processes of the pterygoids associated with the prefrontal pillars penetrate the fenestral space at approximately the level at which the palatine process diverges from the fenestral margin.

The circular internal choana is completely surrounded by the pterygoids and has the characteristic everted margin, or choanal 'neck', found in other osteolaemines (Fig. 5). It opens posteroventrally and although there is no evidence for a discrete midline septum, the dorsal roof of the nasopharyngeal duct bears a midline ridge that could have supported a septum.

The post-temporal fenestrae are small crescentic openings on the occipital surface. They are surrounded dorsolaterally by the squamosal and both ventrally and dorsomedially by the supraoccipital. The ventral floor projects posteriorly for a short distance as a semilunate process of the supraoccipital.

The foramen magnum is circular and lies at the centre of the occipital surface. It is bound dorsally and laterally by the exoccipitals and ventrally by the basioccipital. One or two small foramina for cranial nerve XII perforate the lateral wall of the foramen magnum.

The trigeminal foramen (foramen ovale) is a circular opening on the lateral braincase wall. Internally, it is ringed by the prootic. The prootic is not exposed

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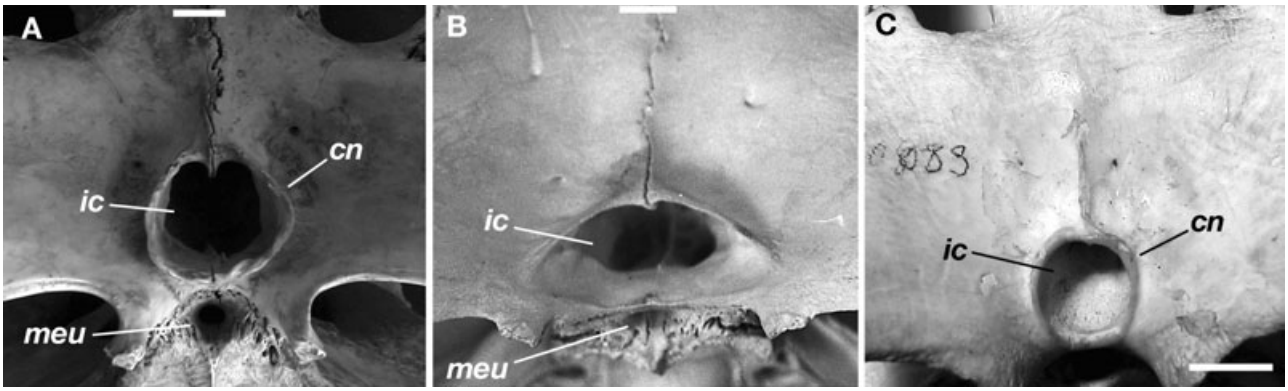

Figure 5. Internal choana, ventral view. A, AMNH 3101, *Voay robustus*. B, TMM m-1786, *Crocodylus niloticus*. C, AMNH 10083, *Osteolaemus osborni* (holotype). Scale = 1 cm.

broadly on the lateral braincase wall, and the trigeminal foramen is externally bound by the laterosphenoid anteriorly and quadrate posteriorly. A complete laterosphenoid bridge with no pterygoidal component forms a passage for the ophthalmic tract immediately anterior to the trigeminal foramen.

The vagus and lateral carotid foramina both lie within the exoccipital on the occipital surface. The lateral eustachian openings are small slits on the ventrolateral edge of the braincase, bound anterolaterally by the pterygoid and posteromedially by the basisphenoid, slightly dorsal to the median eustachian opening. The median eustachian opening lies at the ventralmost extent of the braincase behind the choana and is almost completely surrounded by the basisphenoid, although the basioccipital forms a small part of its posterior margin.

In lateral view, the external mandibular fenestra is bound anterodorsally by the dentary, posterodorsally by the surangular, and posteroventrally by the angular. The surangular–angular suture intersects the fenestra at its posteriormost extent and not along its posteroventral margin, as it does in other crocodylids.

The splenial is imperforate and there is no anterior foramen intermandibularis oralis, but the splenial forms the anterior margins of the foramen intermandibularis medius and foramen intermandibularis caudalis. The foramen intermandibularis medius is bordered posteriorly by the coronoid, and the foramen intermandibularis caudalis by the angular.

Skull: The premaxillae form most of the external narial rim. The naris opens anterodorsally because of the modest inflation of each premaxilla lateral and posterior to the narial aperture. On the dorsal surface, each premaxilla extends posteriorly as a short, but acute, process that terminates at approximately the level of the third maxillary alveolus. The palatal surface is vaulted relative to the alveoli. The premaxilla–maxilla sutures on the palate are nearly perpendicular to the sagittal plane and only barely concave anteriorly.

Each premaxilla bears five circular alveoli. The fourth is the largest and the second is the smallest, but differences in diameter are modest compared with most other crocodylians – the diameter of the second is more than half the diameter of the fourth, but it is usually less. The first alveolus is approximately the same size as the fifth. There is a modest diastema separating the third and fourth alveoli, with a large occlusal pit lying between and medial to these alveoli. Another large occlusal pit lies posteromedial to the first two alveoli.

The lateral margin of the rostrum is disrupted by a deep notch between the premaxilla and maxilla for reception of the fourth dentary tooth. The maxilla extends from its contact with the premaxilla rearward to meet the jugal and lacrimal dorsally and the palatine and ectopterygoid ventrally. It contacts the nasal medially and does not contact the prefrontal. A large circular boss is located dorsal to the position for the largest maxillary alveolus (the fifth). The dorsal surface is reflected laterally, giving the skull an altirostral appearance.

Each maxilla bears 12 circular alveoli divided into two laterally convex series – one containing the first to seventh and the other containing the eighth to 12th. The fifth is the largest. As with the premaxillae, the maxillary palate is elevated relative to the toothrow, especially adjacent to the first seven alveoli. Diastemata separate the sixth, seventh, and eighth alveoli, and the remaining alveoli are close together. Deep occlusion pits occur between the third to seventh alveoli.

As with all crocodyliforms, the maxilla is inflated laterally by a pneumatic caviconchal recess. The medial wall of the recess in *Voay* is smooth and lacks the linear row of blind pits characteristic of *Crocodylus* (Fig. 6). The posterior opening into the recess itself

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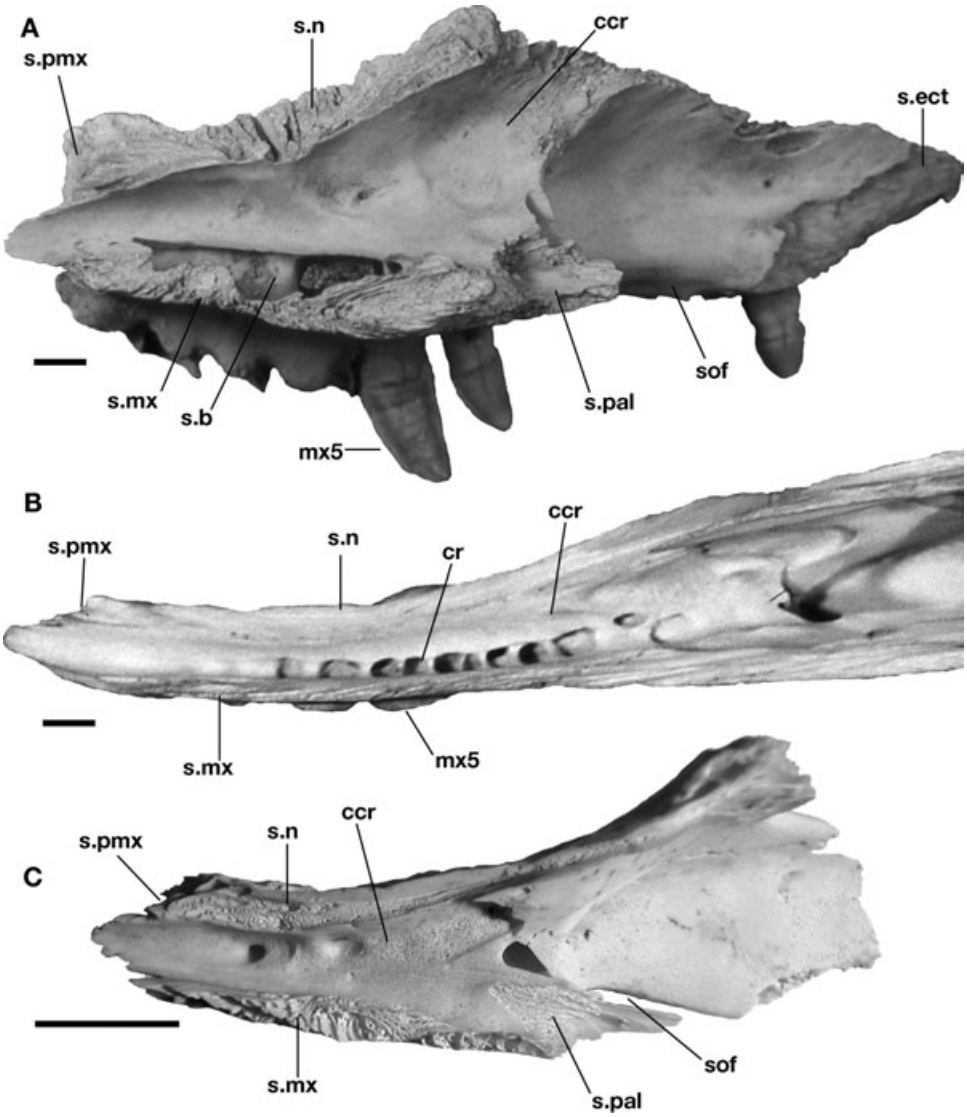

Figure 6. Right maxillae, medial view, showing medial wall of caviconchal recess (ccr). A, BMNH r2193, *Voay robustus*. B, UCMP 140795, *Crocodylus niloticus*. C, UF 34784, *Osteolaemus tetraspis*. Scale = 1 cm.

is circular and lies anteroventral to the maxillolacrimal contact.

The nasals enter the external naris dorsally and project for a short distance within the narial space, but they become extremely narrow posterior to the narial opening, and their narial entry is not very distinct (Mook, 1921). The premaxillae approach each other very closely behind the naris, and one could easily conclude from disarticulated cranial material that they actually met. Alternatively, the premaxillae might actually make contact variably in some individuals, including those seen by Grandidier and Vaillant, although in all material available for this study, the premaxillae did not make contact behind the naris.

The nasals extend behind the naris as a pair of slender elements to approximately the level of the fifth premaxillary alveolus, behind which they expand to form a pair of broad, thin plates. The lateral margins of the nasals are generally linear and parallel with each other, although in some individuals (e.g. Fig. 1) they may be slightly concave laterally. Their lateral width diminishes as they reach the lacrimals and prefrontals, and they terminate as they meet the frontal anterior to the orbit.

The broad anterior ramus of the jugal is in contact anterodorsally with the maxilla and dorsomedially with the lacrimal. This forms the lateral margin of the orbit. A large circular siphonial opening pierces its medial surface. The ascending process forming the ventral half of the postorbital bar is slender and offset from the lateral surface by a shallow anteroposterior sulcus. The jugal becomes dorsoventrally thin behind

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the postorbital bar, although it maintains a flattened, sculptured lateral surface along the ventral margin of the infratemporal fenestra.

The lacrimal is approximately triangular in dorsal view, with a sharply convex sutural contact with the prefrontal. It extends forward to approximately the level of the seventh maxillary alveolus. The anterolateral margin is not disrupted by a posterior process of the maxilla, and the maxilla does not extend posteriorly between the lacrimal and the nasal. The lacrimal duct foramen is a circular opening on the anterior margin of the orbit.

The prefrontal is also triangular, but with a concave sutural contact with the lacrimal. It extends forward to the level of the eighth or ninth maxillary alveolus and forms the anteromedial margin of the orbit. The prefrontal pillars are anteroposteriorly broad at their dorsalmost extent and contact the pterygoids ventrally, and each bears a thin medial process approximately halfway between the pterygoid and the roof of the rostrum.

The frontal bears a stout anterior process that passes for a short distance between the nasals. The anterior merges abruptly with the main body of the frontal. The posterior margin of the frontal, in contact with the postorbitals and parietal, is posteriorly concave. Its ventral surface bears a deep anteroposterior trough for the olfactory tract.

The postorbital comprises a dorsal corpus and slender descending process forming the dorsal half of the postorbital bar. The dorsal surface of the corpus is upturned anterolaterally and forms the anterolateral margin of the supratemporal fenestra. The descending process is columnar dorsally and is inset medially from the skull table. It flattens ventrally and passes medial to the ascending jugal process. A large vascular foramen pierces the postorbital on its lateral surface dorsal to the descending process. The postorbital does not contact the quadrate on the ventral surface of the skull table.

The parietal lies between the supratemporal fenestrae, forming their medial walls. The interfenestral bar is flat dorsally. Its sharply concave contact with the frontal is completely excluded from the fenestrae. Most contact with the postorbitals is abrupt, and the parietal–postorbital suture approximates a vertical plane with a thin lamina of the parietal underlying the postorbital corpus. The parietal contacts the laterosphenoids and quadrates ventrally on the braincase wall, and the parietal is excluded from the ventral margin of the temporal canal by the quadrate. The parietal also contacts the squamosals behind the fenestrae and has a deeply convex posterior margin for contact with the supraoccipital on the skull table.

The squamosal forms the posterolateral corner of the supratemporal fenestra. It contacts the postorbital anteriorly, passing below the postorbital and terminating immediately dorsal to the postorbital bar. It extends laterally over the clover-shaped otic aperture to form a deep otic recess, and the squamosal forms the dorsal roof of the aperture itself. The squamosal contacts the parietal behind the supratemporal fenestra and dorsal to the temporal canal, and the squamosal does not make external contact with the supraoccipital.

Several aspects of the squamosal are remarkable, the most notable being the upturned triangular 'horn' on the posterolateral corner. The morphology of the horn is consistent among available specimens; it is triangular in lateral view and bears a dorsoventrally elongate sulcus on its lateral surface immediately above the otic aperture. It projects dorsolaterally and, in many cases, there is no distinct cut-off between horn and dorsal skull table surface, resulting in a U-shaped skull table in posterior view. The surface of the horn is rugose.

Like most crocodylians, the squamosal of *Voay robustus* bears a lateral groove for the ear flap musculature. In most cases, the dorsal and ventral margins of the groove project laterally to a similar extent, resulting in a groove with a symmetrical U-shaped cross-section. In this case, the dorsal margin of the groove appears inflated and overhangs the ventral margin.

The squamosal extends posterolaterally against the paroccipital process of the exoccipital, as in all crocodylians, but its relationship to the dorsal surface of the quadrate ramus seems to vary among individuals. In some (e.g. Fig. 7), the descending lamina extends anteriorly over the quadrate. A similar configuration is seen in *Osteolaemus* (Fig. 8C), *Euthecodon*, *Rimasuchus*, and *'C.' pigotti*. But other specimens (e.g. Fig. 8B) share the condition found in other crocodylids, in which the descending lamina is limited to the anterior surface of the paroccipital process (Fig. 8A).

The quadratojugal lies between the quadrate and the jugal. Anterodorsally, it is a slender process forming the posterior margin of the infratemporal fenestra, although it neither extends all the way to the dorsalmost extent of the fenestra nor contacts the postorbital or the squamosal. A short process on the posterior margin of the fenestra represents a short dorsally projecting quadratojugal spine. The quadratojugal expands laterally behind the infratemporal fenestra, becoming thin again as it approaches the posterior end of the quadrate ramus. It does not contribute to the mandibular condyle.

The quadrate forms the floor and part of the posterior margin of the otic aperture. A circular preotic foramen is present in most specimens anterior to the otic aperture. Anterior to the preotic foramen, the

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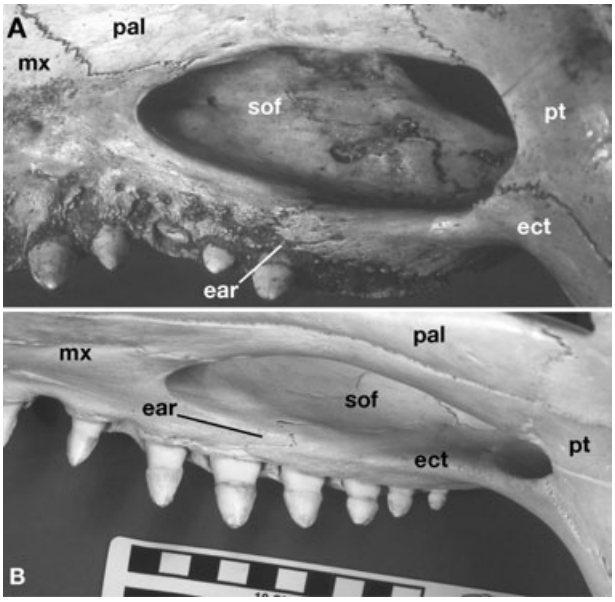

Figure 7. BMNH r2193, *Voay robustus*, right quadrate ramus showing condition of descending lamina of squamosal (dLs). Scale = 1 cm.

quadrate contributes to the posterior margin of the infratemporal fenestra.

The quadrate rami project behind the occipital surface to a lesser extent than in extant *Crocodylus*. Each bears a low circular protuberance on the ventral surface, close to the quadrate condyle, corresponding with the 'A' and 'D' scars of Iordansky (1973). An elongate muscle attachment crest, corresponding with scar 'B' of Iordansky, is present anterior to the A–D protuberance. The foramen aereum is located dorsomedially. The cranioquadrate canal opens between the quadrate and the paroccipital process of the exoccipital lateral to the occipital condyle. The medial hemicondyle is larger and dorsally expanded than its lateral counterpart, but because the medial hemicondyle is also reflected laterally, it looks smaller in Figure 1.

The quadrate extends ventrally from the temporal canal and behind the laterosphenoid to form the posterolateral side of the braincase wall. The quadrate–laterosphenoid suture extends ventrally below the trigeminal foramen until the quadrate makes contact with the pterygoid immediately ventral to the laterosphenoid bridge. Posteriorly, the quadrate also

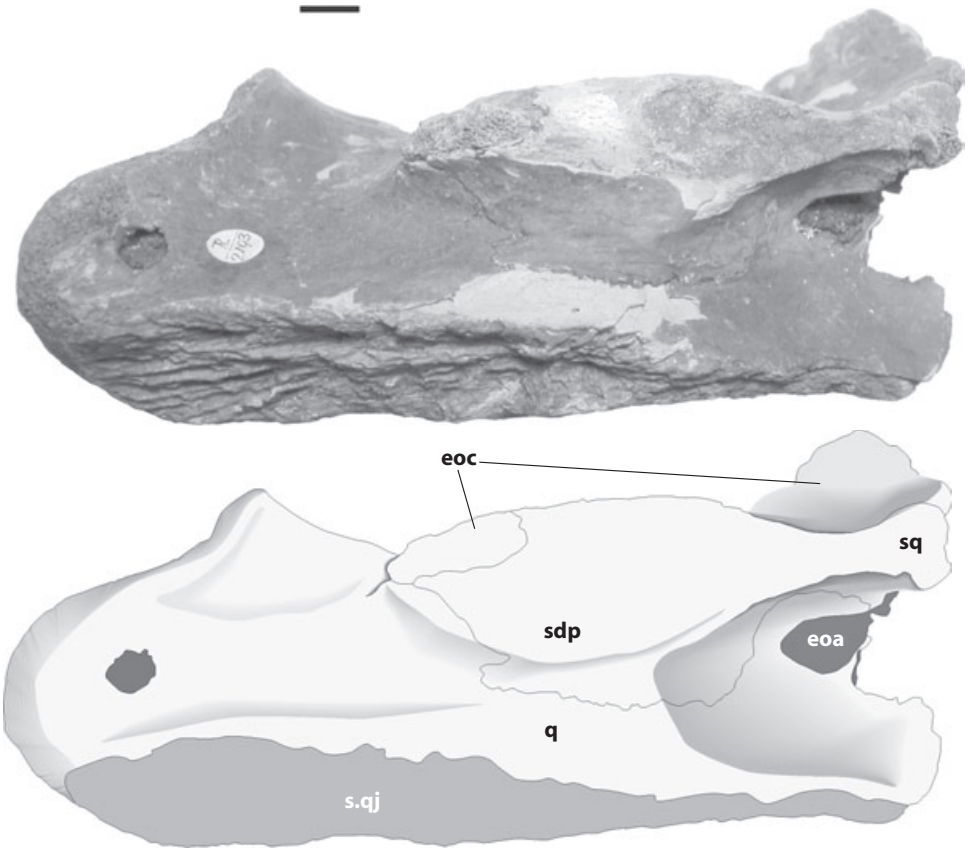

Figure 8. Right external otic recess and aperture, illustrating condition of descending squamosal lamina. A, TMM m-1786, *Crocodylus niloticus*. B, AMNH 3101, *Voay robustus*. C, AMNH 10082, *Osteolaemus osborni* (holotype). Scale = 1 cm.

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forms the anterodorsal border of the posterolateral basisphenoid exposure.

The palatines form the lateral walls and floor of the nasopharyngeal duct between the suborbital fenestrae. They contact the pterygoids close to the posteriormost limit of the fenestrae. The palatines extend forward between the maxillae to form a broad U-shaped palatine process that terminates at the level of the seventh maxillary alveolus. Thin laminae project laterally within the fenestral space anterior to the prefrontal pillars.

The lectotype preserves only part of the left ectopterygoid, but other specimens preserve both complete ectopterygoids. The anterior ramus reaches the level of the tenth maxillary alveolus and forms the medial wall of the 12th and, sometimes, 11th alveoli. The tip of the anterior ramus is not deeply forked (Fig. 9). An acute ascending process projects for a short distance along the medial surface of the postorbital bar. The ectopterygoidal margin of the suborbital fenestra is convex, resulting in a constricted posterior outline to the fenestra. The posteroventrally projecting descending ramus lies on the ventrolateral surface of the pterygoid wing, and the pterygoid–ectopterygoid suture intersects the suborbital fenestra at approximately the posteriormost limit of the fenestra, with a modest lateral process of the pterygoid passing along the posterior fenestral margin anterior to the ectopterygoid. The ectopterygoid does not extend to the posteroventralmost tip of the pterygoid wing.

The pterygoids form the roof of the nasopharyngeal duct dorsal to the palatines between the suborbital fenestrae, extending anteriorly to contact the prefrontal pillars. The pterygoids completely enclose the duct behind the suborbital fenestrae. The interpterygoid suture is visible between the palatines and the internal choana. The broad, triangular pterygoid wings have dorsoventrally expanded lateral margins adjacent to the ectopterygoid. Short posterior processes extend behind the wings lateral to the median eustachian foramen and the basisphenoid. The pterygoids extend along the posterolateral braincase wall, bordered anteriorly and posteriorly by the basisphenoid, to contact the quadrate and the laterosphenoid.

The laterosphenoids meet at the midline, at least in large individuals, with a gap dorsally for the olfactory tract and ventrally for the optic nerve. A shallow sulcus extends parallel to the anterior margin of the supratemporal fossa on the anterolateral surface. Each laterosphenoid contacts the basisphenoid ventrally lateral to the pituitary fossa, the pterygoid ventrally ventral to the trigeminal foramen, and the quadrate posteriorly. A complete laterosphenoid bridge (with no pterygoid contribution) encloses a channel for the ophthalmic branch of the trigeminal nerve anterior to the trigeminal foramen, and the bridge extends the ventral limit of the laterosphenoid posterior to the basisphenoid.

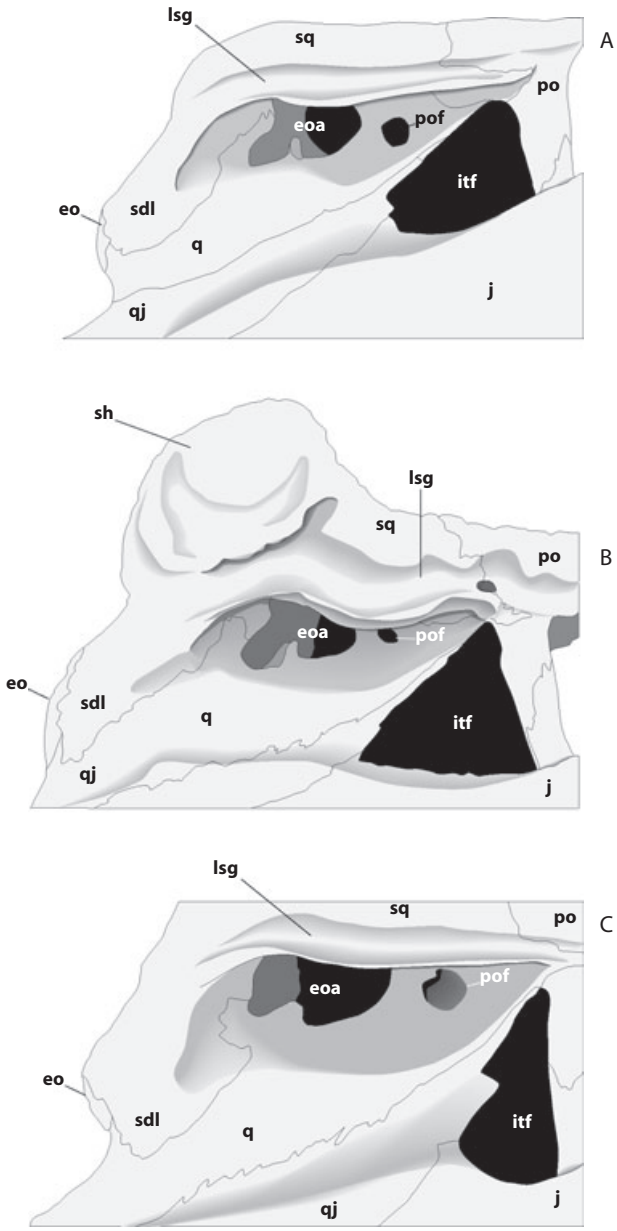

Figure 9. Right suborbital fenestra, lateral oblique view, showing condition of the anterior ramus of the ectopterygoid (ear). A, BMNH uncategorized, *Voay robustus*. B, TMM m-1786, *Crocodylus niloticus*. Scale = 1 cm.

The supraoccipital is exposed as a midline triangular element on the posterior margin of the skull table. The parietal–supraoccipital suture is not always visible on the skull table, especially on large individuals, but an isolated parietal (Fig. 10) bears a large V-shaped indentation on the posterior margin where the supraoccipital would have been, suggesting that the absence of a suture is an ontogenetic variant. The

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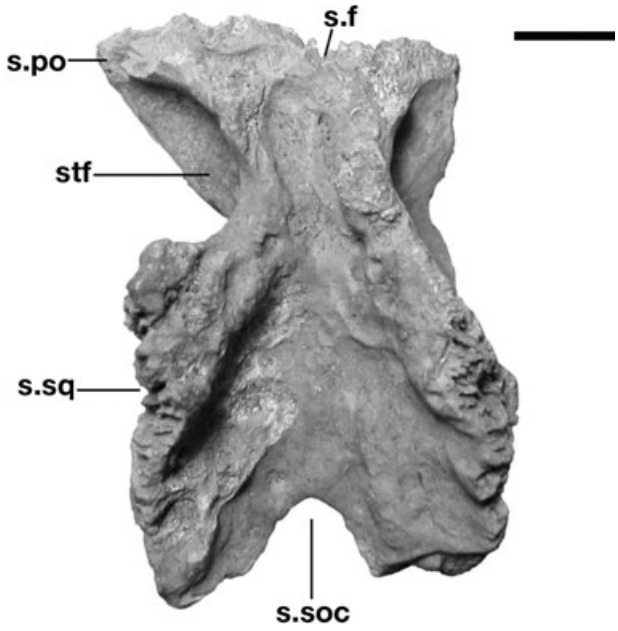

Figure 10. BMNH r2081, *Voay robustus*, parietal, dorsal view. Scale = 1 cm.

supraoccipital expands to form a broad triangle on the occipital surface, where it floors the post-temporal fenestrae. A broad sagittal crest expands the surface of the supraoccipital posteriorly between the fenestrae. The supraoccipital does not contribute to the margin of the foramen magnum.

The exoccipitals meet at the midline dorsal to the foramen magnum. Small openings for cranial nerve XII – usually one, sometimes two or three – perforate the lateral wall of the foramen magnum. Lateral to these openings, on the occipital surface, is a larger oval depression with the vagus foramen. The lateral carotid foramen is directly ventral to the vagus foramen on the short, blunt descending lamina lateral to the occipital condyle. The occipital surface of the paroccipital process is concave and rugose ventrally lateral to the cranioquadrate canal.

The basisphenoid is broadly exposed in three places – on the anterolateral braincase wall ventral to the laterosphenoid, on the posterolateral braincase wall between the quadrate and the pterygoid, and as a short, thin sheet ventral to the basioccipital tubera. A short cultriform process is preserved in AMNH 3101, and it has a vertically orientated anterior margin. As with other crocodyloids, the lateral surface of the basisphenoid immediately behind the pituitary fossa is smooth and lacks the deep sulcus found in other crocodylians, and the anterolateral exposure of the basisphenoid is broad, extending approximately to the level of the trigeminal foramen. The posterolateral exposure is semilunate and ventral to the level of the lateral carotid foramen, and the linear quadrate–pterygoid suture intersects it anterodorsally. The posteroventral basisphenoid lamina is short and broad, not extending significantly below the median eustachian foramen.

The basioccipital forms the hemispherical occipital condyle and the floor of the foramen magnum. Ventral to the occipital condyle, the occipital surface of the basioccipital bears a prominent, dorsoventrally elongate sagittal crest and less prominent crests along the lateral margins. The basioccipital borders the median and lateral eustachian openings posteriorly.

Mandible: Most preserved dentaries have 15 alveoli, but AMNH 3104 has 14. Alveolar counts can vary by one or two alveoli in most living species (Kälin, 1933; Wermuth, 1953; Iordansky, 1973), so this is not remarkable. The largest is the fourth, which is not confluent with the third. The largest behind the fourth is the 11th, and there is a broad sulcus in the dorsal outline of the dentary between the fourth and the tenth alveoli. Alveoli are circular, and the teeth are not mediolaterally compressed. The dentary symphysis extends to the level of the seventh alveolus. A shallow, dorsoventrally narrow Meckelian groove runs along the medial surface posterior to the symphysis.

The splenial is a flat plate medial to the dentary, forming the medial wall of the Meckelian channel. The splenials do not meet at the midline; each extends to approximately the level of the eighth dentary alveolus dorsal to the Meckelian channel and, as a slender process, almost to the level of the seventh alveolus ventral to the channel. There is no foramen intermedialis oralis, but the anterior tip of the splenial is sometimes notched where a foramen would ordinarily be in a more basal crocodyloid. The splenial is mediolaterally expanded along its dorsal margin, and it forms the medial wall of the posteriormost three dentary alveoli. It contacts the surangular, coronoid, and angular posteriorly, almost encircling the foramen intermandibularis medius and forming the anteriormost margin of the foramen intermandibularis caudalis. The splenial projects posteriorly ventral to the foramen intermandibularis caudalis as an acute process within the angular.

There is a circular rugose area on the medial surface of the splenial. In most cases, the rugosity is near the ventral margin of the splenial and at the level of the posteriormost two dentary alveoli. In at least one case it is at the level of the tenth and forms a protuberance.

The coronoid lies against the medial surface of the splenial anteriorly and forms the medial wall of the Meckelian fossa posteriorly. The posterodorsal ramus is broad and shorter than the posteroventral ramus, which contacts the angular and passes lateral to the angular within the Meckelian fossa. The coronoid

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itself is imperforate and forms the posterior margin of the foramen intermandibularis medius.

The surangular extends behind the dentary and lies lateral to the articular, forming the lateral wall of the glenoid fossa. The surangular suture within the fossa is deeply concave laterally. The surangular forms the dorsal half of the jaw behind the dentary. The anterior surangular processes are long, but the superior process is much longer than its inferior counterpart. The dorsal surface is flattened anterior to the glenoid fossa, and the surangular forms the anterolateralmost portion of the fossa itself. It is expanded laterally along its dorsal margin posterior to the external mandibular fenestra. A concavity runs along the dorsal margin of the smooth medial surface. Behind the fossa, the surangular is a flat plate lateral to the articular, with modest exposure on the dorsal surface of the retroarticular process, and extending nearly to the posteriormost tip of the retroarticular process.

The angular lies below the surangular and forms the ventral margin of the external mandibular fenestra. The angular–dentary suture emerges from the fenestra ventrally, with a short (and, in AMNH 3104, a dorsoventrally broad) process of the dentary passing along the lateral surface of the angular. The angular extends behind the fenestra along the ventrolateral surface of the retroarticular process. The lateral surface is laterally expanded to form a lamina parallel to the ventral surface behind the external mandibular fenestra. In medial view, the angular forms the ventromedial surface of the Meckelian fossa and bears a broad anterior process with a deep anterior concavity to form the posterior margin of the foramen intermandibularis caudalis. A shallow sulcus depresses the medial surface immediately posterior to this process. The angular is constricted posteriorly below the articular.

The articular bears a deep hourglass-shaped glenoid fossa bordered laterally by the surangular. The articular–surangular suture is deeply bowed and concave laterally within the glenoid fossa. The mediolaterally elongate lateral hemifossa is larger than the medial hemifossa, but both hemifossae are of approximately the same depth. The medial hemifossa is expanded anteroposteriorly and extends further anteriorly. The posterior wall of the glenoid fossa extends dorsally to form a short wall separating the fossa from the retroarticular process.

Below the glenoid fossa, the main body of the angular is triangular and passes anteroventrally against the medial surface of the surangular. A thin lamina of the articular passes anteriorly along the medial surface of the surangular dorsal to the lingual foramen, and the foramen is on the surangular–articular suture. The anterior surface of the main articular body bears a shallow dorsoventrally elongate sulcus, and the lateral surface flares medially as it approaches the retroarticular process.

The triangular retroarticular process is medially thin and dorsally concave in medial or lateral view. A broad ridge runs along the dorsal surface from the distal tip along the lateral half of the dorsal surface, dividing the dorsal surface into a pair of concavities, although the ridge becomes indistinct anteriorly. The articular foramen aereum is on the dorsal surface close to the anteromedial margin, but is inset and not on the margin itself.

Postcranial skeleton: What is known of the axial skeleton is consistent with that of other crocodylids – the first caudal vertebral centrum is biconvex; the remaining caudal, dorsal, and cervical centra are procoelous, and there are two sacral vertebrae with stout sacral ribs. Cervical vertebrae bear ventral hypapophyseal keels, but the number of anterior dorsal vertebrae with such structures is unknown; nor is it known whether the first postaxial centrum bore a keel. The atlas–axis complex was not observed.

Because articulated limbs have not been reported, we cannot estimate relative proportions between limb bones. In most morphological details, the appendicular skeleton of *Voay robustus* is like that of other crocodylids. Nevertheless, individual bones tend to be relatively robust (Grandidier & Vaillant, 1872; Meers, 2002), and muscle attachment features are more prominent than in living crocodiles.

The flat scapular blade flares dorsally from a body that expands anteroposteriorly and tapers anteriorly along its contact with the coracoid (Fig. 11G). The deltoid crest is slender and lies on the anterodorsal surface of the scapular body. Articulated scapulocoracoids are not known, but the overall shape of the coracoid (Fig. 11H) suggests a comparatively shorter dorsoventral expanse. The coracoid blade also flares anteroposteriorly, and the coracoid body is pierced by a circular coracoid foramen. The deltopectoral crest of the humerus (Fig. 11A, B) is comparatively thick, with a prominent common attachment scar for M. teres major and M. dorsalis scapulae on the dorsal surface opposite the crest. The amount of proximal flare of the ulna compared with the distal end appears greater than in extant crocodylians; the proximal surface is triangular and bears a broad groove for articulation with the humerus. The degree of flare is slightly exaggerated in Figure 11C, D because the distal tip is damaged, making it appear more gracile. The radius (Fig. 11E, F) is linear with a rectangular proximal articular surface and a rounded distal surface.

The ilium (Fig. 12B) comprises most of the acetabulum and a broad, robust posterior process that lacks the dorsal constriction, or 'wasp waisting', characteristic of the ilium of extant *Crocodylus* (Fig. 12A;

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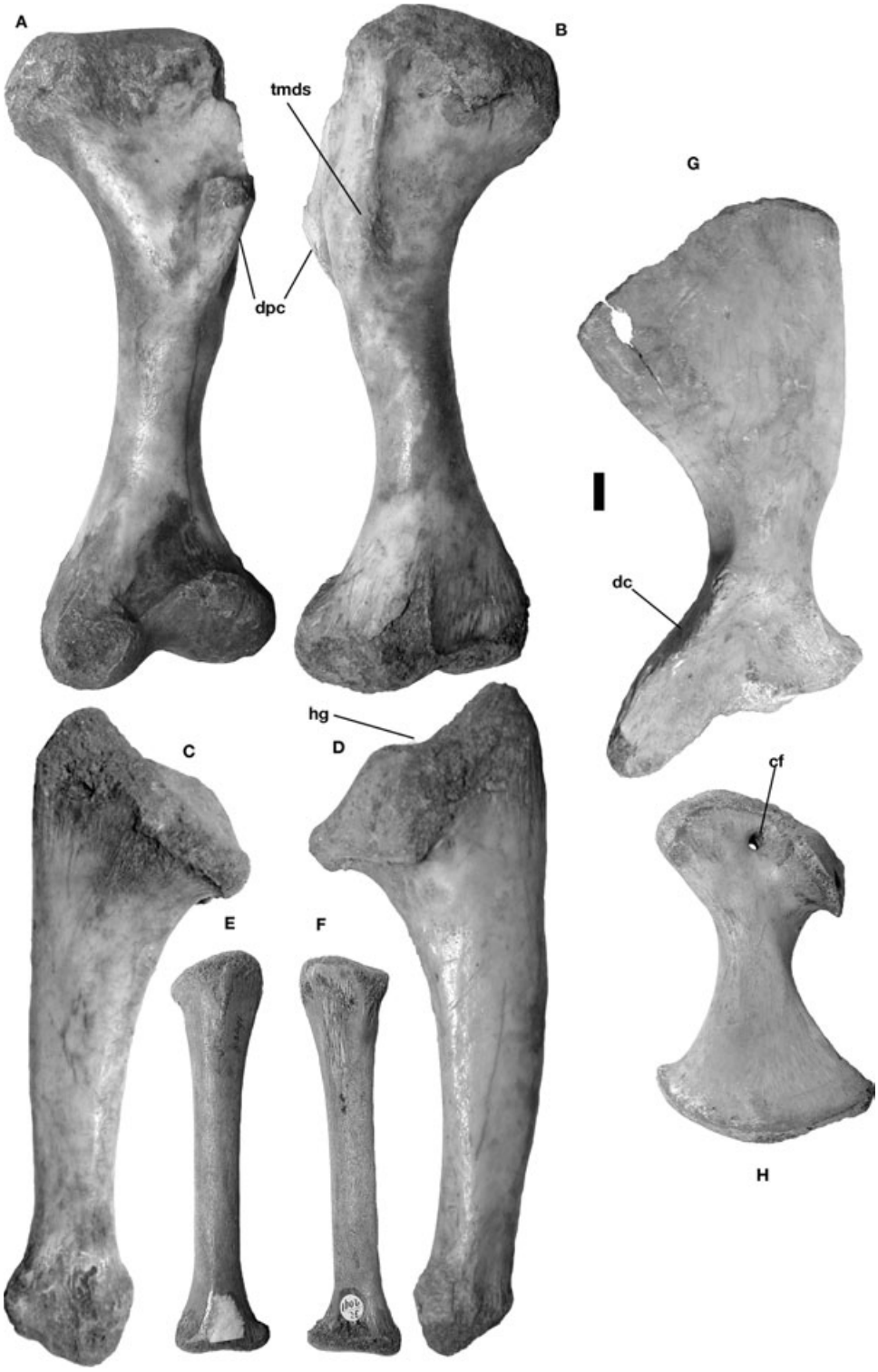

Figure 11. Left pectoral and forelimb skeleton of *Voay robustus*: humerus in ventral (A) and dorsal (B) views; ulna in medial (C) and lateral (D) views; radius in dorsal (E) and ventral (F) views; scapula, lateral view (G); coracoid, lateral view (H). Scale = 1 cm, but elements not from the same individual. The radius is BMNH r2091; the remaining bones are currently BMNH uncategorized.

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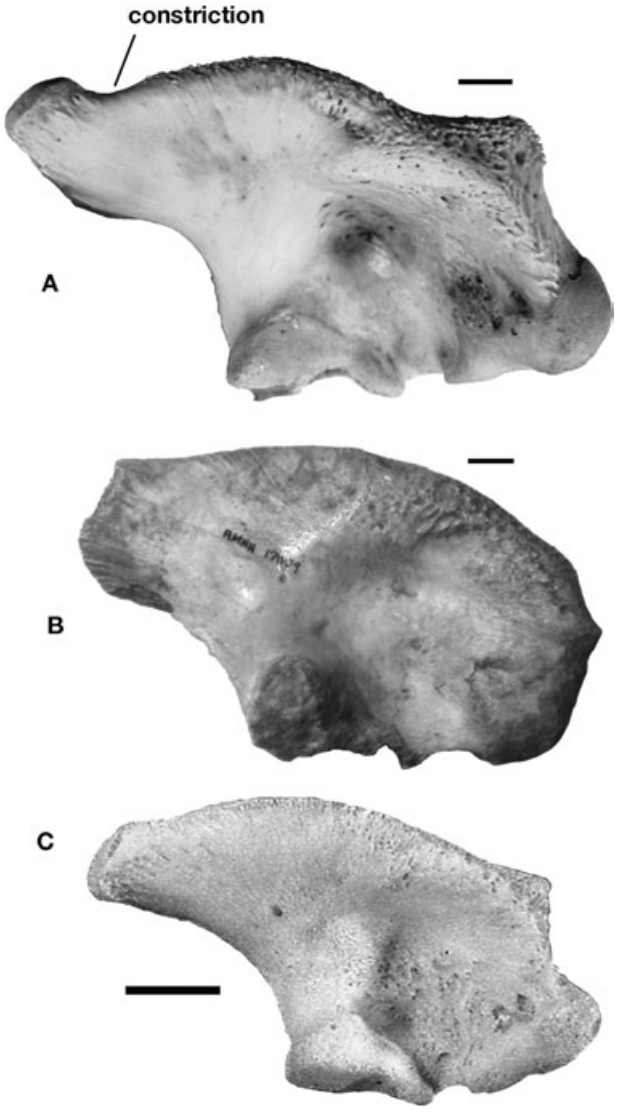

Figure 12. Right ilium, lateral view. A, *Crocodylus acutus*, USNM 211278. B, *Voay robustus*, AMNH 17008. C, *Osteolaemus tetraspis*, USNM 194448 (left element, image reversed). Scale = 1 cm.

Brochu, 2000). The anterior process is either very short or absent completely. The supra-acetabular crest is dorsoventrally thick and passes below an oval depression at the dorsally highest point of the iliac blade. The ischium (Fig. 13A) is consistent with that of other crocodylians, consisting of a flattened distally flaring blade with a long axis orientated anteromedially and prominent attachment scars for the flexor tibialis internus musculature proximally. The ischium contacts the ilium in two places, excluding the pubis from the acetabulum. The pubis flares distally, but to a lesser extent than in most other crocodylians (Fig. 13B).

Preserved hindlimb elements are generally similar to those of other crocodylids, although (as with the forelimb) they are relatively robust. The fourth trochanter and associated attachment scars for the caudofemoralis musculature on the sigmoid femur are especially prominent, and the trochanter itself takes the form of an acute crest rather than a low prominence (Fig. 14A). Muscle attachment scars are also prominent on the stout tibia and more slender fibula (Fig. 14C–F). In particular, the iliofibularis trochanter on the fibula is dorsoventrally more expansive than in extant crocodylians.

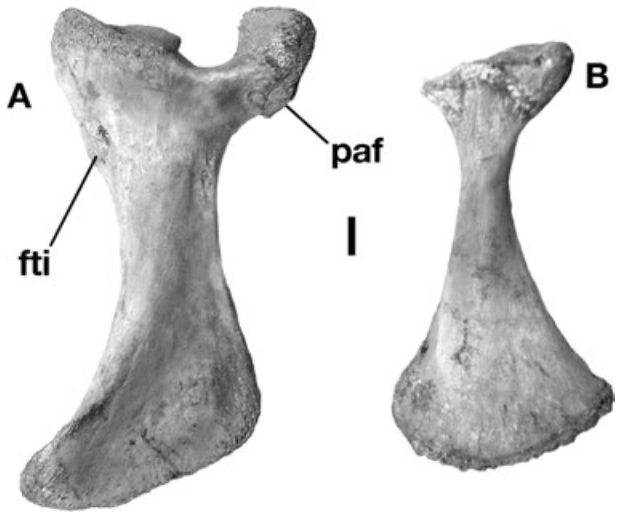

Figure 13. BMNH uncategorized, *Voay robustus*. A, right ischium, lateral view. B, right pubis, lateral view.

In some cases, pairs of nuchal osteoderms have been preserved in articulation (Fig. 15). These consist of thick, dorsally pitted plates with an abrupt lateroventral reflection. A tall, stout keel runs anteroposteriorly along the line of the bend. The margins of each osteoderm are irregular, suggesting tight articulation with osteoderms on all sides.

Osteoderms presumably from the dorsal shield (Fig. 16) are also dorsally pitted and are approximately square in outline or form rectangles with a slight mediolateral expansion. Putative laterally placed osteoderms are more nearly square with slightly shorter lateral than medial margins. Most bear smooth dorsal surfaces along their anterior margins for articulation with succeeding osteoderms. They also bear prominent keels, but unlike the keels of the nuchal osteoderms (which are simple, albeit robust, blades), these are complex structures with acute ridges extending medially or laterally away from the dorsal apex. The result is a division of the dorsal surface into discrete sulci. It is unknown whether ventral osteoderms were present, but nearly all preserved osteoderms have keels, suggesting that most come from the dorsal shield and that ventral armour was absent.

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Figure 14. Hindlimb skeleton of *Voay robustus*: BMNH uncategorized, right femur, ventral (A) and dorsal (B) views; MNHN 1908–5, left tibia, anterior (C) and posterior (D) views; BMNH uncategorized, right fibula, medial (E) and lateral (F) views. Scale = 1 cm.

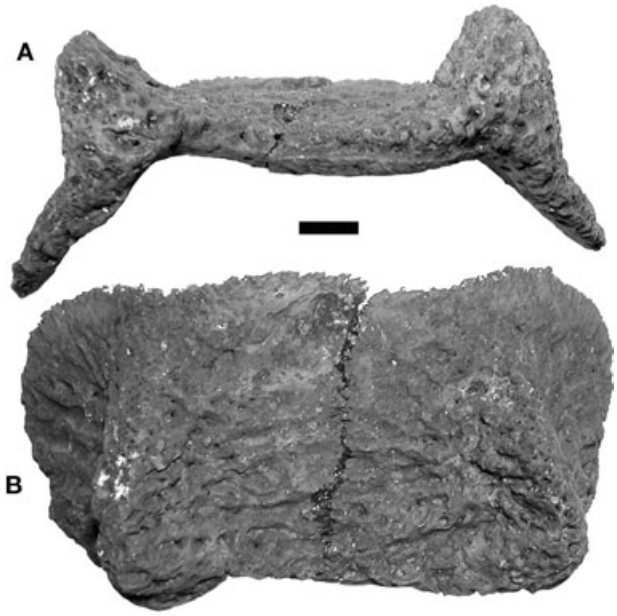

Figure 15. BMNH r2027, *Voay robustus*, sutured nuchal osteoderms, posterior (A) and dorsal (B) views. Scale = 1 cm.

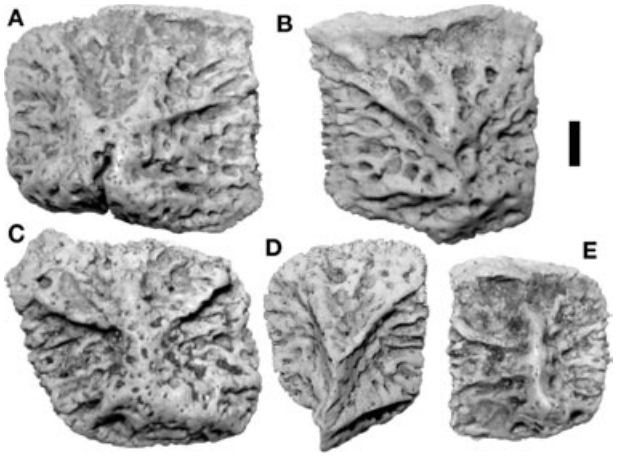

Figure 16. BMNH r2197, osteoderms from dorsal shield. Scale = 1 cm.

PHYLOGENETIC ANALYSIS

METHODS

A matrix based on 166 discrete morphological characters (Brochu, 1997, 1999, 2000, 2004, 2006a, b) was subjected to a maximum parsimony analysis using PAUP* 4.10b (Swofford, 2002). A few typographical errors involving *Voay* and closely related forms were caught and corrected during this analysis, as indicated in the Appendix. The analysis included 59 ingroup taxa and two outgroups (*Hylaeochampsa vectiana* and *Bernissartia fagesii*). Multistate characters were left unordered and all characters had equal weight. Five hundred separate heuristic searches were conducted with the starting order of ingroup taxa randomized in each iteration.

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Taxon sampling largely mirrored that of Brochu (1999, 2000, 2004, 2006a; Appendix). Alligatoroidea was limited to seven species (*Leidyosuchus canadensis*, *Diplocynodon darwinii*, *Brachychampsa montana*, *Stangerochampsa mccabei*, *Alligator mississippiensis*, *Caiman yacare*, *Palaeosuchus trigonatus*) and South American gavialoids reduced to one (*Gryposuchus colombianus*) to reduce computation time.

Results

The analysis recovered 344 972 equally optimal trees (length = 472, consistency index without uninformative characters = 0.408, retention index = 0.792). The strict consensus of these trees is consistent with all previous analyses using this matrix (Fig. 17).

As with previous analyses based on this matrix, *Voay* and *Osteolaemus* are sister taxa. Indeed, the clade including *Voay* and *Osteolaemus* is one of the few with significant bootstrap support (81%), and the relationship is stable in trees two steps longer than optimal. Also appearing closer to *Osteolaemus* than to *Crocodylus* are *Rimasuchus lloydi*, *'C.' pigotti*, and *Euthecodon*. This clade of African crocodylids forms the sister taxon to a group including *Crocodylus s.s.*

The closest living relative of *Crocodylus* in this analysis, the African slender-snouted crocodile (*Mecistops cataphractus*), is often considered to be a species of *Crocodylus*. In different analyses it is either basal to other *Crocodylus* or closer to *Osteolaemus* (McAlily *et al*., 2006; see below). Referral of the species to *Mecistops* Gray, 1844 renders the nomenclature consistent with any of the current phylogenetic hypotheses.

DISCUSSION

Morphological evidence for relationships of *Voay*

Voay lacks several derived features that characterize the crown genus *Crocodylus*. These are also absent from *Osteolaemus*. The maxilla lacks extensive development of blind recesses along the medial surface of the caviconchal recess (Fig. 6). The anterior ramus of the ectopterygoid forming the posterolateral margin of the suborbital fenestra is not deeply forked (Fig. 9). The posterior iliac blade is not constricted near its posterior tip (Fig. 12). The pterygoid of *Voay* is also tall ventral to the median eustachian foramen, exposing the basisphenoid as a broad sheet (Fig. 3); in all extant *Crocodylus*, the pterygoid is much shorter below the median eustachian foramen, limiting exposure of the basisphenoid. The condition seen in *Voay* is also found in *Osteolaemus* and *Mecistops* (Brochu, 2000).

The number of unambiguous synapomorphies for Osteolaeminae depends on how basal relationships within the group are resolved. If *Rimasuchus* is the basalmost osteolaemine or closely related to *'C.' pigotti* and *Euthecodon*, there are two – extension of the squamosal on to the quadrate ramus and prominent preorbital crests. The former is a subtle character state, and variation in *Voay* suggests its secondary loss within the group (see below), but it is unique to osteolaemines. The latter is not unique to osteolaemines; most crocodyloid skulls bear nearly parasagittal ridges on the lacrimal, and they become especially prominent in Indopacific species of *Crocodylus* (Brazaitis, 1973; Brochu, 2000). They are also anteroposteriorly short in extant *Osteolaemus* and, in both *Osteolaemus* and *Voay*, contiguous with the line along which the lateral surface of the snout is ventrolaterally reflected.

Extension of the squamosal beyond the paroccipital process is unambiguously present in Osteolaemus and the specimens used to code *Euthecodon*, *'C.' pigotti*, and *Rimasuchus*. The specific shape of the descending lamina of the squamosal varies in all crocodylian species, but its extension does not vary in *Osteolaemus*. Nevertheless, variation in this feature in *Voay* calls utility of this feature into question. Unfortunately, because the other three osteolaemines are each based on single specimens, variation cannot be assessed.

A third character unambiguously diagnoses Osteolaeminae if *Rimasuchus* is closer to *Voay* and *Osteolaemus* – a distinct choanal neck (Fig. 5). The surface of the pterygoid anterior and lateral to the choana is depressed in most crocodyloids, but this condition is elaborated in osteolaemines such that the choana appears to open at the end of a short tube or 'neck'. Choanal necks are also seen in some alligatoroids, but these result from deeper depressions lateral and posterior to the choana. This condition is observable in *Osteolaemus* at all stages of posthatching ontogeny.

This feature is ambiguous because the palate is incomplete in the specimen used to code *Rimasuchus lloydi* in this study (BMNH r14154) and in the holotype (Fourtau, 1920), both of which are from the same Burdigalian site in Egypt. Skulls from several sites in Africa have been referred to *Rimasuchus lloydi* (Tchernov, 1986; Pickford, 1994, 1996, 2000; Leakey *et al*., 1996; Llinás Agrasar, 2004), including one that appears to preserve a choanal neck (Storrs, 2003: 146). However, there is considerable variation in the overall shapes of these skulls (Tchernov, 1986; C. A. Brochu, pers. observ.) and they derive from several horizons throughout the Miocene and into the Pleistocene. Pending a more complete review of all of this material the condition of the choana in *Rimasuchus* will remain unknown.

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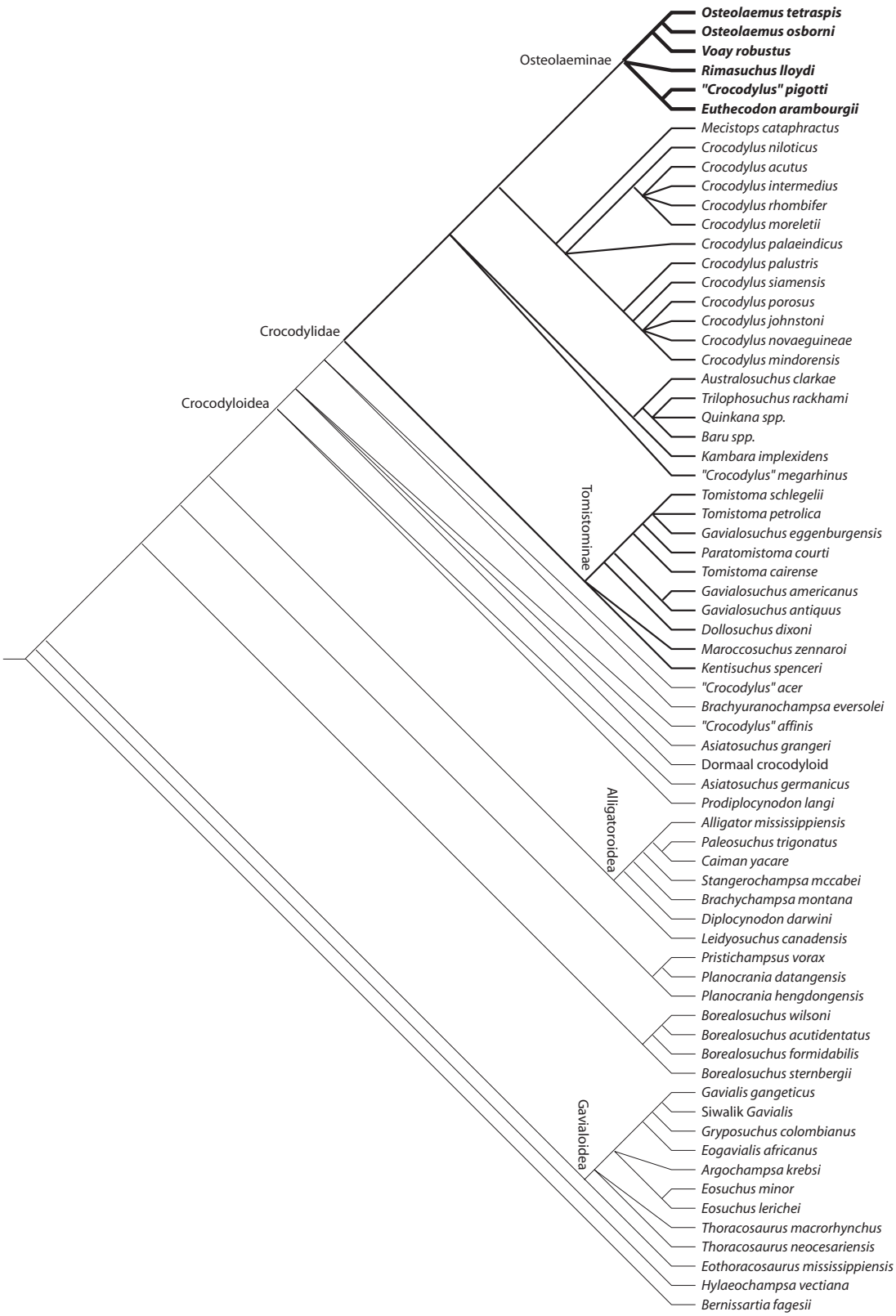

Figure 17. Strict consensus of 344 972 equally optimal trees (consistency index = 0.408, retention index = 0.794, length = 472); maximum parsimony analysis, 66 ingroup taxa, 166 morphological characters (see the Appendix).

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The choana is not preserved in *Euthecodon arambourgii* (Ginsburg & Buffetaut, 1978; C. A. Brochu, pers. observ.). More complete specimens of other species of *Euthecodon* not included in this study clearly show a strongly depressed pterygoid around the choana (Tchernov, 1986; Storrs, 2003). Given the distribution of this feature in other crocodylids, its presence in *Euthecodon arambourgii* is predicted.

Two character states unambiguously unite *Voay* and *Osteolaemus* – a short palatine process that does not extend far beyond the anterior margins of the suborbital fenestrae and constricted supratemporal fenestrae. Both might be related to snout shape – in both cases, the skull is dorsoventrally deep relative to snout length (see below). In addition, *Voay* and *O. tetraspis* (but not *O. osborni*) have short flanges that extend from the lateral margins of the palatines into the suborbital fenestra, another feature that might reflect overall skull shape.

Osteolaemine diversity

The set of most-parsimonious trees supports a clade of crocodylids restricted to Africa and Madagascar during the Neogene. This group minimally includes *Osteolaemus*, *Euthecodon*, *Rimasuchus*, *'C.' pigotti*, and *Voay*. At the present time, its known stratigraphic range extends from the Early Miocene through the Holocene.

Several additional taxa may belong to this assemblage. One is *Aldabrachampsus dilophus*, a poorly known, but distinctive, crocodylid from the Quaternary of Aldabra Atoll (Brochu, 2006b). The phylogenetic placement of *Aldabrachampsus* is unclear – positions close to *Voay* and to an extinct species of *Crocodylus* (*C. palaeindicus*) are equally parsimonious, largely because known material of *Aldabrachampsus* is so incomplete. *Aldabrachampsus* is also a horned crocodile, although the horns are less acute and located further forward on the skull table. It also occurs in fissure-fill deposits formed shortly after a time when Aldabra Atoll was completely submerged, strongly indicating that *Aldabrachampsus* was a postemergence immigrant and not truly endemic to that island. There is no record of *Aldabrachampsus* from anywhere else, but it comes from deposits on Aldabra older than any found in the Quaternary of Madagascar.

Many more extinct osteolaemine taxa may be known, but have gone unrecognized as such because few crocodiles from the Neogene of Africa have been examined in a phylogenetic context. Most are of Miocene age, including *C. checchiai* Maccagno, 1948 from Libya (Maccagno, 1952; Hecht, 1987) and *C. gariepensis* Pickford, 2003 from Namibia. Llinas Agrasar (2003, 2004) illustrated several unnamed crocodylids that might pertain to the group. In addition, many Miocene and Pliocene fossils from several African localities have been referred to *Rimasuchus lloydi* or one of the living African crocodylids (*Osteolaemus*, *C. niloticus*, *Mecistops cataphractus*) on the basis of overall similarity and skull dimensions (e.g. Tchernov, 1986; Aoki, 1992; Pickford, 1994, 1996, 2000). All of this material should be re-evaluated.

Some DNA sequence data support a closer relationship between *Mecistops cataphractus* and *Osteolaemus* than between *Mecistops* and living *Crocodylus* (White & Densmore, 2001; Gatesy *et al*., 2003; Schmitz *et al*., 2003; McAlily *et al*., 2006). Morphology does not support this arrangement, but *Mecistops* assumes a placement outside *Crocodylus* (Brochu, 2000). Molecular data not specifically aligning *Mecistops* with *Osteolaemus* nevertheless posit a substantial distance between *Mecistops* and *Crocodylus* (Densmore, 1983; Densmore & White, 1991). More work is clearly needed to resolve the position of *Mecistops* relative to other crocodylids, but it might be another living representative of an African endemic radiation.

Some members of Osteolaeminae have derived skull configurations (Fig. 18B). *Euthecodon* is a longirostrine crocodile outwardly resembling *Tomistoma* or *Gavialis*, and it was traditionally classified as a tomistomine, although Ginsburg & Buffetaut (1978) argued instead for a closer relationship with *Crocodylus*. There is no morphological evidence to support a close relationship between *Euthecodon* and *Mecistops*; if the latter is an osteolaemine, the derived slender snout may have appeared twice independently within the clade. This suggests an unusually high diversity of longirostrine crocodylians in the Neogene of Africa – in addition to *Euthecodon* and *Mecistops* and its putative extinct relatives, tomistomines and gavialoids are also both known from the Miocene of Africa (Fourtau, 1920; Müller, 1927; Arambourg & Magnier, 1961; Pickford, 1994; Vignaud *et al*., 2002; Storrs, 2003).

Osteolaemus and *Voay* also have derived skull shapes. In both cases, the snout is comparatively short and deep and the supratemporal fenestrae are reduced in relative size. *Voay* and at least some *Osteolaemus* also have lateral palatine flanges within the suborbital fenestra. These modifications are typically associated with crocodylian taxa that generally do not exceed 2 m in total body length, such as the living dwarf caimans (*Palaeosuchus*). The same is true for the Miocene mekosuchine *Trilophosuchus rackhami* Willis, 1993, known from a single partial skull from an animal that would have fallen within this size range. *Osteolaemus* is small at maturity, but larger skulls of *Voay* indicate animals reaching at least 3 m. Moreover, *Voay* lacks some of the derived features commonly seen in dwarf taxa, such as the comparatively short quadrate rami.

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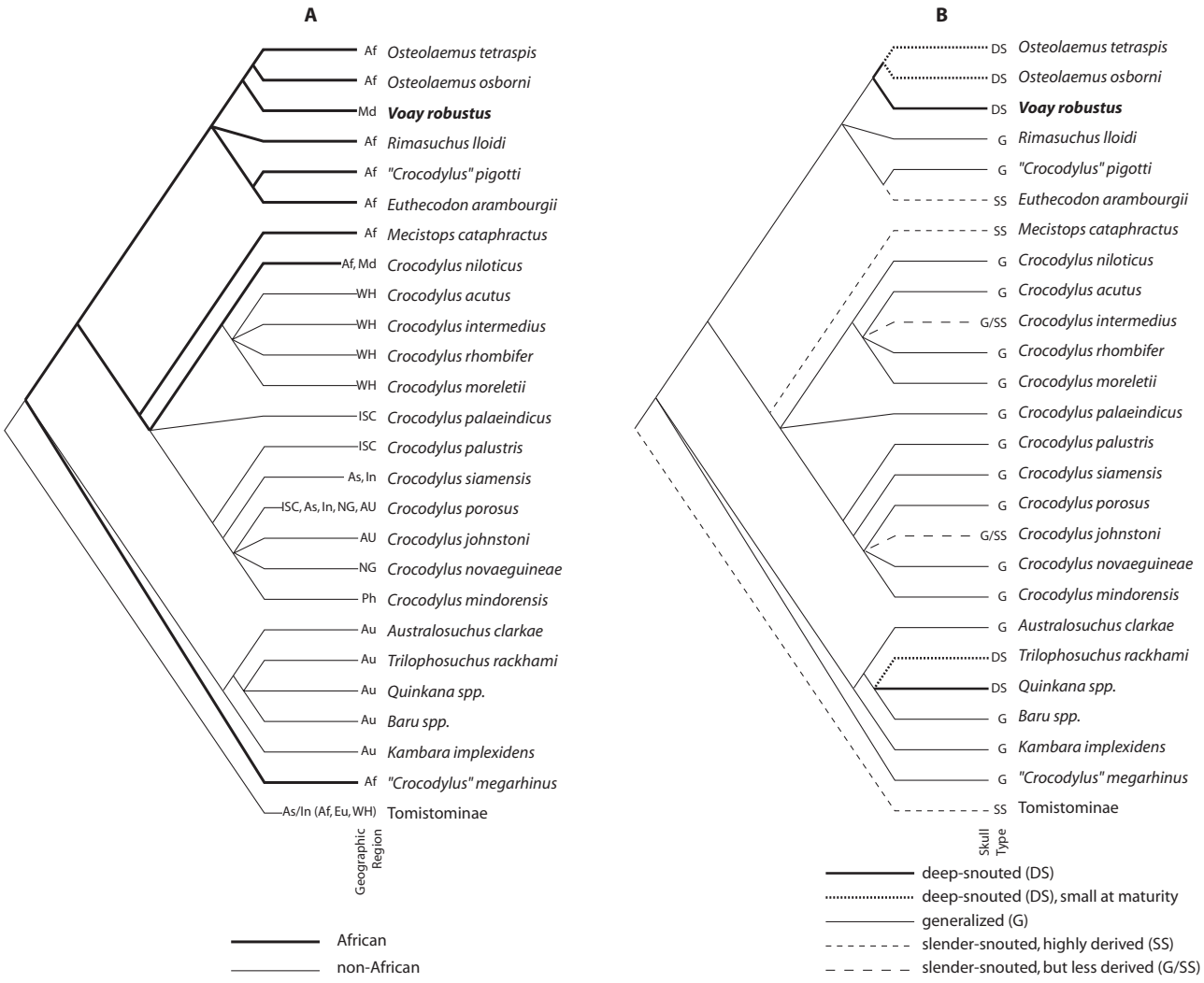

Figure 18. Phylogenetic patterns of biogeography (A) and the evolution of derived snout shapes and body size (B) for Crocodylidae. Af, Africa; As, mainland Asia; Au, Australia; Eu, Europe; ISC, Indian subcontinent; In, Indonesia; Md, Madagascar; NG, New Guinea; Ph, Philippines; WH, western hemisphere. Madagascar is optimized as part of Africa in (A).

It is thus not clear whether the derived similarities of the skulls of *Osteolaemus* and *Voay* reflect similar functional pressures.

Deep snouts are seen in the so-called 'ziphodont' crocodiles, such as the pristichampsines or the mekosuchine *Quinkana*. There are also similarities between the dorsal osteoderms of *Pristichampsus* from the Eocene of North America and Europe and those of *Voay* – they have prominent compound keels (Rossmann, 2000). It is unclear how these particular modifications to the dorsal osteoderms might relate to ecology, and the dental modifications that define the ziphodont condition (laterally compressed, serrated crowns) are not found in *Voay*.

A strict evolutionary reading of Figure 18B suggests that cranial modifications associated with 'dwarf' crocodylians sometimes arose before dwarfism, as none of the immediate sister taxa to *Osteolaemus* + *Voay* are small animals. In contrast, in alligatorids these conditions seem to have arisen among animals that were already small at maturity (Brochu, 2004). The pattern among mekosuchines is ambiguous in this analysis, but more comprehensive mekosuchine analyses suggest that the deep-snouted condition may have arisen multiple times within that clade (Salisbury & Willis, 1996); taxa presumed to have been small at maturity also occur throughout the clade, and so whether body size and skull shape are correlated is difficult to test among mekosuchines. Given the wealth of fossil information not yet included in phylogenetic analyses, including several Miocene fossils putatively representing *Osteolaemus*, any conclusions about the

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evolution of skull shape and body size among osteolaemines are tenuous at best.

Historical biogeography and Neogene crocodylian endemism

The crocodyline half of Crocodylidae (i.e. animals closer to *Crocodylus* than to *Tomistoma*) is ancestrally an African group (Fig. 18A). Osteolaeminae represents a radiation that remained endemic to Africa during the Tertiary. To date, nothing has been found from outside Africa or nearby islands that belongs to this assemblage. Similar radiations occurred in Australasia (Mekosuchinae; Willis, 1997) and South America (caimans; a clade of endemic gavialoids; and, outside Crocodylia, sebecosuchians; Buffetaut, 1982; Gasparini, Fernandez & Powell, 1993; Gasparini, 1996; Langston & Gasparini, 1997; Brochu & Rincon, 2004) during the Neogene. There is also tantalizing evidence for an endemic radiation in the Antilles at this time (Brochu *et al.*, 2007). In this sense, Africa is part of a global pattern of increased endemism in crocodylian faunas compared with the Palaeogene, when crocodylian clades were more cosmopolitan (Brochu, 2003).

In this context, *C. niloticus* is a puzzle. It is an ancestrally African lineage – its proximate sister taxa (*Mecistops*, Osteolaeminae) are African (Fig. 18A), and there is no reason on phylogenetic grounds to posit dispersal from elsewhere. However, unambiguous *C. niloticus* does not appear until the Late Miocene or Pliocene (Tchernov, 1986; Storrs, 2003). This suggests that *Crocodylus* radiated elsewhere and reinvaded Africa. This is an argument from negative evidence (*C. niloticus* has not yet been found in deposits older than the Late Miocene) and is thus speculative.

Madagascar was separated from Africa by the Jurassic (Martin & Hartnady, 1986) and from all other land masses by the Cretaceous (Storey *et al.*, 1995; Wells, 2003). Both tectonic events occurred long before the first appearance datum of Osteolaeminae in the Lower Miocene. Assuming post-Mesozoic divergences within Crocodylidae, the ancestor of *Voay* must have rafted or, more probably, swum across the Mozambique Channel from mainland Africa to Madagascar.

This crossing would have required survival on the part of the immigrants in seawater. *Osteolaemus* is more commonly found in forested settings and avoids saline or brackish water (Waitkuwait, 1989; Kofron, 1992; Riley & Huchzermeyer, 1999). Although this might argue against transoceanic dispersal, its absence in marginal marine habitats may reflect competitive exclusion by its larger sympatric relative, *C. niloticus*, which is regularly seen in such environments (Cott, 1961; Kofron, 1992; Lawson, 1993; Leslie & Spotila, 2000). Furthermore, Taplin & Grigg (1989) reported functional lingual salt glands in *Osteolaemus*. These glands, present in all crocodylids, help to maintain osmotic balance by secreting excess salt. *Osteolaemus* thus appears to have the anatomical apparatus required for survival in saltwater.

To date, *C. niloticus* has not been found in any deposit predating human arrival on Madagascar. Molecular data suggest minimal divergence between modern Malagasy and mainland African populations of *C. niloticus* (Schmitz *et al.*, 2003; Hekkala, 2004). This is consistent with a relatively recent crossing of the Mozambique Channel by *C. niloticus*. It is tempting to conclude that the extinction of *Voay* was related to the arrival of humans and that *C. niloticus* invaded Madagascar only after suitable habitats were cleared of competing forms, but there is simply not enough data to rule out alternative scenarios, including extinction of *Voay* resulting from the invasion of *C. niloticus*. This is yet another parallel with other parts of the world in which *Crocodylus* appears after endemic forms are either extinct or diminished in diversity (Willis, 1997; Brochu, 2003), but whether these are causally linked remains speculative.

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APPENDIX

Codings for morphological characters used in the phylogenetic analysis. For character descriptions, see Brochu (1999, 2006a) except character 166: teeth and alveoli of maxilla and dentary circular in cross-section (0); posterior teeth laterally compressed (1); all teeth compressed (2).

Previous analyses with this matrix used a single species of *Osteolaemus* (*O. tetraspis*). In this study, *Osteolaemus* was divided into two species: *O. tetraspis* Cope, 1861 and *O. osborni* (Schmidt, 1919). The latter is from the Congo Basin rather than western Africa and was formerly considered to be a monotypic genus (*Osteoblepharon* Schmidt, 1919) or a species of *Osteolaemus*, but differences between western African and Congolese specimens were dismissed as ontogenetic or intraspecific variation (Chabanaud, 1920). The two forms were later regarded as subspecies of *Osteolaemus tetraspis* (Wermuth & Mertens, 1961; Fuchs, Mertens & Wermuth, 1974b). In fact, differences between *O. tetraspis* and *O. osborni* are consistent among specimens from similar geographical regions and lie outside the range of variation for any extant crocodylian species (Inger, 1948; C. A. Brochu, pers. observ.). Regardless of how one applies concepts of character 'significance' to different ranks, samples from western Africa and the Congo are consistently different and should be treated as separate OTUs, and these are here treated as different species. Codings for *Osteolaemus* in previous analyses by this author are completely congruent with *O. tetraspis*, and differences are found only in codings for *O. osborni*.

This version also separates codings for two Neogene North American tomistomines – *Gavialosuchus antiquus* (Leidy, 1852) and *Gavialosuchus americanus* (Sellards, 1915). Codings for *G. antiquus* in this study are consistent with those for *G. americanus* in previous versions.

Codings for taxa not included in previous analyses (*Trilophosuchus*, *Baru*, *Quinkana*, *Maroccosuchus*, and both species of *Planocrania*) are based on direct observations of holotypes and additional specimens.

Bernissartia fagesii	??11?1210?010?0???0??0?0?0000??0001000100000????00100??????110???0?0000???0?00000??0?100301??0??00?0?000100?00?00??0?0??0??0?????????00???000000000?0?01???????00??0?0
Hylaeochampsa vectiana	??0100??1?0?000?01100?00110???0?000200?0000?00??0101???0??000?10000?0?0000?000000?00??????????0?000
Borealosuchus formidabilis	000001010011001??0?000000000100010000?200000000?010010?001001100000001100?0?020000001100300100200000000000000000000?021100?100000??000?101001100001 0?1001???????000?000
Borealosuchus wilsoni	???????10???0?1??????00000001???10000?20??102000010010?0???011?000000110000102001 00?110030010 02?000000000000?00?00000211??01????0??00001?1?011????1??1001???????000?000
Borealosuchus acutidentatus	????????????????????????0?????????????????????????????????????0000001????0?020?1000?10?3?01002?00?000000???0??0????2?????10???0??????1???011????1???001???????000?000
Borealosuchus sternbergii	000001?100110010011000000000100010 00???000000000010010000?001000000011000010100000010013001012?000000000000000000?000110010000001000 11?1?011000010010010??????000?000
Eothoracosaurus mississippiensis	??????????????1???????000??????00?00???0??30???0011?1??????0???????2?0100?01021?00?110004001?02?00?000000000000000???01000?0?0??????0?00???011000100???0????????00??000
Thoracosaurus neocesariensis	???1?1?1????0?1???1??????01?0???0000???0??30????01?11????????1?00?0200100001021?000110004001002?000000100000000000?01??000000000000?000?0?011000100?0000???????000?000
Thoracosaurus macrorhynchus	??11?1?1??0???1???1??????0??0???000???0??300??00111???????0?100000200100?0102100001110040010 02??000001000000000000?1010?000000?0?0?0000?0?011000100?1000???????000?000
Eosuchus minor	???1?1????0???1???1??00?0?100??000000??0?0300000011110?0??00?1?00?02?0100?0102101001100040010 02?00000?10000000031???0100000000??010000?0?0011000100?1?10???????000?100
Eosuchus lerichei	???0?1????????1???????????1???????0???????3????????11??????????????200100?0?021?2?0110004001002?00?00?100?000003?0?001000?0000????000?0?0?011000 10??1010???????0?0?100
Eogavialis africanus	?????1??????0?????11?????????????0?????0?030??10?1111??????1?1?000020010000102101101100040010 02?000000200000000010000100000?00?0?00000?000111000100?10100??????000?000
Argochampsa krebsi	??11??????01??1??????????01?????0?????????3????????11????????????????1100?0?021?10???1004?01002?0??000100?00?000????01???10000?00000000???0110001 0??1010???????0?0?0?0
Gryposuchus colombianus	??1?0?????00??1???????000??????????????0?030000001111100???001000002001001010210100111004001102?020000200000000?010000100000000000000000????121000100?1010???????000?000
Gavialis lewisi	????????????0?????????????????????????????30???0?1???????????1?0000200100?01?2?0?001??00?00??03??20?002000?000?010????00000??000??0000????111????00?1010???????000?000
Gavialis gangeticus	021101011000001000100000001001000 0?000000030000001111000010001000002001000010210100111004001103002000020000000001000010000000000000000?000111000100010100000000000000

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APPENDIX *Continued*

Pristichampsus vorax	?20001012?01?1?1?20?2000001112?0001072?1?111?????????1?2000007110070100000000010000300100120000001000000020700001000?1000?1?101010?2?01100001072100127????20007002
Planocrania hengdongensis	?????????????

Crocodylus megarhinus	???????0?????1?????????????