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The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia

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While the crocodyliform lineage extends back over 200 million years (Myr) to the Late Triassic, modern forms—members of Eusuchia—do not appear until the Cretaceous. Eusuchia includes the crown group Crocodylia, which comprises Crocodyloidea, Alligatoroidea and Gavialoidea. Fossils of non-crocodylian eusuchians are currently rare and, in most instances, fragmentary. Consequently, the transition from Neosuchia to Crocodylia has been one of the most poorly understood areas of crocodyliform evolution. Here we describe a new crocodyliform from the mid-Cretaceous (98–95 Myr ago; Albian–Cenomanian) Winton Formation of Queensland, Australia, as the most primitive member of Eusuchia. The anatomical changes associated with the emergence of this taxon indicate a pivotal shift in the feeding and locomotor behaviour of crocodyliforms—a shift that may be linked to the subsequent rapid diversification of Eusuchia 20 Myr later during the Late Cretaceous and Early Tertiary. While Laurasia (in particular North America) is the most likely ancestral area for Crocodylia, the biogeographic events associated with the origin of Eusuchia are more complex. Although the fossil evidence is limited, it now seems likely that at least part of the early history of Eusuchia transpired in Gondwana.

Keywords: Crocodyliformes; Eusuchia; Crocodylia; evolution; Cretaceous; Gondwana

1. INTRODUCTION

Crocodyliforms are the only non-avian archosaurs to have persisted through the Mesozoic and Cenozoic into modern times. With their stark appearance, it is often assumed that they have changed little in 200 million years (Myr) of evolution. Yet the morphological diversity that crocodyliforms display today represents only a fraction of that during the Mesozoic when several distinct suborders existed (Clark 1994). Only one of these suborders, Eusuchia, still exists.

Eusuchia includes all extant crocodyliforms: members of the crown group Crocodylia (Benton & Clark 1988). Crocodylia comprises Crocodyloidea (which includes extant species of *Crocodylus* and *Osteolaemus tetraspis*), Alligatoroidea (alligators and caimans) and Gavialoidea (the group that includes the Indian gharial, *Gavialis gangeticus*). The position of the Sunda or false gharial, *Tomistoma schlegelii*, floats between Crocodyloidea (morphological studies: e.g. Norell 1989; Salisbury & Willis 1996; Brochu 1997, 1999, 2004) and Gavialoidea (biochemical or molecular studies: e.g. Densmore & Owen 1989; Gatesy *et al.* 2003; Harshman *et al.* 2003).

Fossils that can be referred to each of the three superfamilies of Crocodylia are well known, extending

back to the Campanian (*ca* 80 Myr ago; alligatoroids and gavialoids) and late Maastrichtian (*ca* 67–65 Myr ago; crocodyloids; Brochu 1997, 2001). Fossils of more basal forms, however, such as the advanced neosuchian *Bernissartia* (Norell & Clark 1990), are much older (Hauterivian–lower Aptian; *ca* 130–120 Myr ago).

The transition between advanced neosuchians and crocodylians involved subtle but far-reaching changes to the entire body. Sir Thomas Huxley was the first to recognize these changes, regarding them as one of the strongest cases yet for Darwin's then recently published theory of evolution, and integrated them into the first formal classification of both fossil and living crocodyliforms (Huxley 1875). Huxley identified three main phases in the evolution of crocodyliforms: 'Parasuchia', 'Mesosuchia' and Eusuchia. His definition of Eusuchia was apomorphy-based, with referral to the group dependent on the combined possession of: (i) a fully developed bony palate, where the secondary choanae are fully enclosed medio-orally by ventral laminae of the pterygoids; and (ii) procoelous vertebrae, in which there are synovial, semi-spheroidal articulations between adjoining vertebral bodies (Salisbury & Frey 2001). Although these features are now known to have evolved independently in other crocodyliforms (Michard *et al.* 1990; Rogers 2003; Clark *et al.* 2004), the presence of both features in combination with a sagittally segmented paravertebral shield has thus far proven to be limited to eusuchians and, therefore, phylogenetically informative (Norell & Clark 1990; Clark & Norell 1992).

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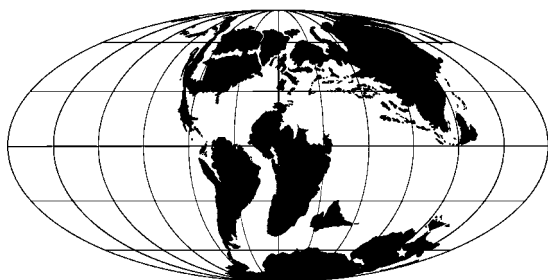


Figure 1. Mid-Cretaceous (latest Albian–earliest Cenomanian; 98–95 Myr ago) palaeogeographic map, (Mollweide projection, latitude and longitude lines at 30° intervals; after [Dettmann *et al.* 1992](#); [Scotese 2001](#)). White star indicates fossil locality.

Unfortunately, the transition itself—the point at which neosuchians become eusuchians, and eusuchians in turn become crocodylians—has been obscure, with the known fossils tending to be incomplete, badly preserved or undescribed ([Molnar 1980](#); [Clark & Norell 1992](#); [Buscalioni *et al.* 2001](#)). Consequently, the origins of Eusuchia and the subsequent emergence of taxa immediately ancestral to Crocodylia have remained one of the most poorly understood areas of crocodyliform evolution ([Huene 1933](#); [Benton & Clark 1988](#); [Norell & Clark 1990](#); [Clark & Norell 1992](#); [Brochu 1999](#)).

Herein we report on a new crocodyliform from Australia that provides new evidence on the transition from Neosuchia to Crocodylia during the Early Cretaceous. Among the material referred to, the new taxon is a complete skull and an almost complete, fully articulated skeleton—the earliest such example from a definitive basal eusuchian and the most complete crocodyliform fossil from Australia.

2. MATERIAL AND METHODS

The material described here has been accessioned to the Queensland Museum (QM), Brisbane, Australia. The phylogenetic position of the new taxon was assessed by scoring 45 crocodyliform taxa (including two outgroups) for 176 discrete morphological characters (see electronic supplementary material for character list, data matrix, analysis protocol and apomorphy list).

3. SYSTEMATIC PALAEOLOGY

Crocodyliformes ([Hay 1930](#))

Mesoeucrocodylia ([Whetstone & Whybrow 1983](#))

Eusuchia ([Huxley 1875](#)) (see electronic supplementary material for revised differential diagnosis).

Isisfordia duncani gen. et sp. nov.

(a) Etymology

The generic name refers to the shire of Isisford where the specimens were found ([figure 1](#)); the specific name honours Ian Duncan, who discovered the holotype.

(b) Holotype

QM F36211, a near complete, articulated skeleton ([figures 2 and 3](#)).

(c) Referred specimens

QM F44320 (paratype), a skull without the mandible ([figure 4a–d](#)); QM F44319 (paratype), a partial mandible

along with tooth crowns from the left maxilla ([figure 4e,f](#)); QM F34642, a partial, articulated skeleton.

(d) Locality and horizon

The holotype was found at field locality QM L1021, near the town of Isisford, central-western Queensland, Australia ([figure 1](#)). All the preserved portions of the holotype were found in close association, in adjoining portions of a large nodule of fluvial, volcanoclastic sandstone. Most of the holotype and QM F34642 were found during the mid-1990s, with the remaining portions discovered during 2001 and 2003. Other referred specimens were found in the same horizon, at sites in the vicinity of the type locality during University of Queensland expeditions between 2003 and 2005.

The horizon in which the specimens occur is part of the Winton Formation. This formation spans the transition between the Early Cretaceous and the Late Cretaceous (latest Albian–earliest Cenomanian; [Helby *et al.* 1987](#))—a time that we informally refer to as the ‘mid-Cretaceous’. The Winton Formation has previously produced the remains of titanosauriform sauropods ([Molnar & Salisbury 2005](#)), ceratodont lungfishes ([Dettmann *et al.* 1992](#)) and vertebrate microfossils referable to theropods, thyreophorans, turtles and possible mammaliaforms. Trackways also point to the presence of two types of theropod and at least two types of ornithopod ([Thulborn & Wade 1984](#)).

(e) Differential diagnosis

Isisfordia differs from other crocodyliforms in the following unique combination of traits (autapomorphies marked with an ‘a’): broad exposure of the exoccipital within the supratemporal foramen rostral to the rostral aperture of the posttemporal canal (a); maximum diameter of the caudal aperture of the cranioquadrate siphonium approximately one-third the mediolateral width of the foramen magnum, with the lateral wall of the siphonium formed exclusively by the quadrate (a); maximum mediolateral width of the secondary choanae exceeds the minimum mediolateral width of the palatines (symplesiomorphic for Neosuchia; in Crocodylia, the secondary choanae are considerably smaller); naris with a distinctly pear-shaped outline (a); caudal dentary teeth confluent and set in a shallow alveolar groove (shared with some alligatoroids); dentary and maxillary teeth flattened labiolingually at the base of the crown, but become conical towards the apex; cervical, thoracic and cranial-most caudal vertebrae weakly procoelous at maturity (a); caudal vertebra I weakly procoelous (a); sacral vertebra II with a low caudal condyle (a); distal extremity of ulna expanded transversely with respect to the long axis of the bone (shared with *Susisuchus* and *Theriosuchus pusillus*).

(f) Description

Compared with the majority of its modern-day counterparts, *Isisfordia* is a diminutive crocodyliform. Fusion of the neurocorporal suture on all the trunk vertebrae of the holotype ([figure 2](#)) suggests that it represents an adult individual ([Brochu 1994](#)) with a total length of approximately 1.1 m.

The lateral margins of the planar skull table of *Isisfordia* are gently convex. The frontoparietal suture enters the supratemporal foramen, so that the frontal prevents any

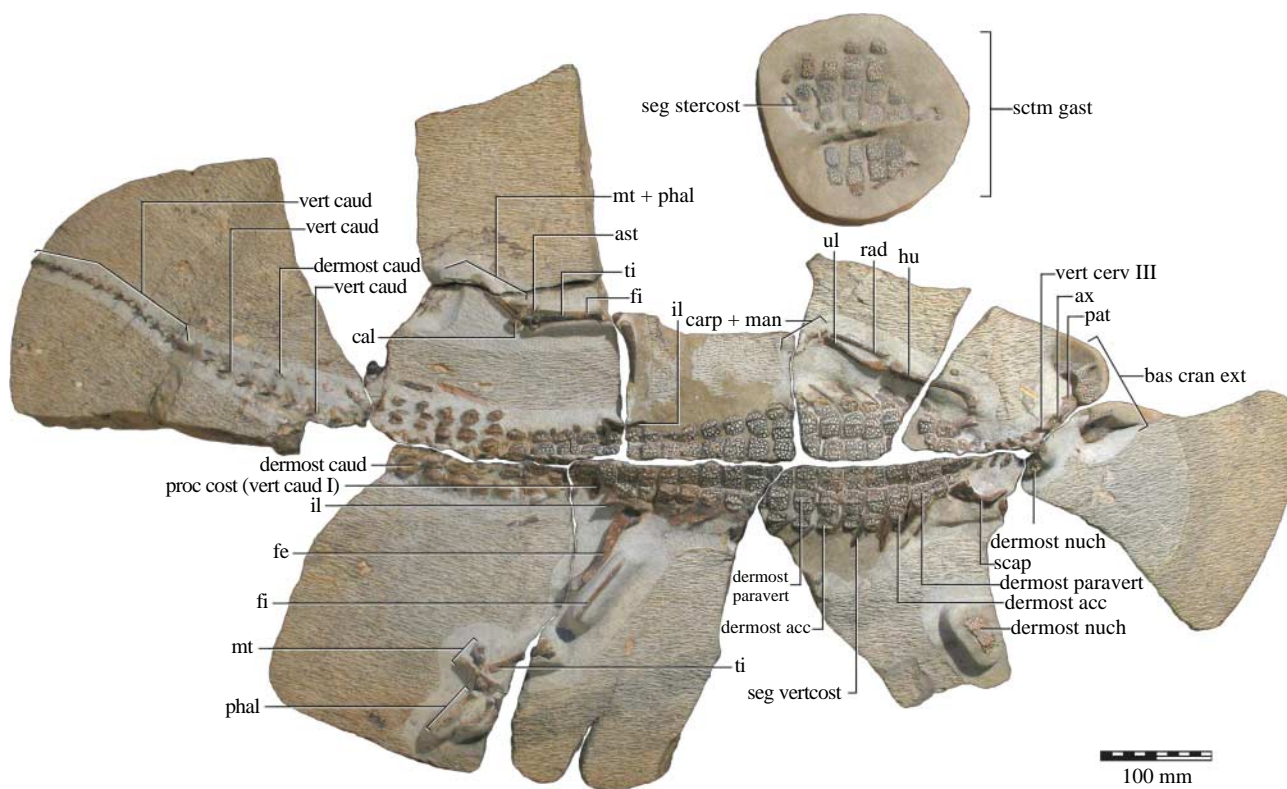


Figure 2. Skeleton of *Isisfordia duncani* gen. et sp. nov. (QM F36211, holotype) in dorsal aspect. The gastral shield is shown in external (ventral) aspect. Abbreviations: ast, astragalus; ax, axis; bas cran ext, external basicranium; cal, calcaneum; carp, carpus; dermost caud, caudal osteoderm; dermost acc, accessory osteoderm; dermost nuch, nuchal osteoderm; dermost paravert, paravertebral osteoderm; fe, femur; fi, fibula; hu, humerus; il, ilium; man, manus; mt, metatarsals; pat, proatlas; phal, phalanges; proc cost (vert caud I), costal process of caudal vertebra I; rad, radius; scap, scapula; sctm gast, gastral shield; seg sterco, sternal segment of a thoracic rib; seg vertcost, vertebral segment of a thoracic rib; ti, tibia; ul, ulna; vert caud, caudal vertebrae; vert cerv, cervical vertebra.

broad contact between the postorbital and the parietal. Unlike the condition in the advanced neosuchian *Susisuchus* (Salisbury *et al.* 2003a) and globidontan alligatoroids (except for basal-most forms such as *Brachychampsa*; Brochu 1999), the squamosal is separated from the parietal within the caudal part of the supratemporal foramen by the exoccipital and the quadrate. The condition seen in *Susisuchus* and some globidontans is also found in a number of remotely related crocodyliforms such as *Araripesuchus* (Price 1959) and dyrosaurids (Brochu *et al.* 2002). The caudolateral corner of the squamosal forms a short, but distinct prong, which is dorsal to a rugose paraoccipital process.

The occipital surface of the exoccipital is smooth, in contrast to *Hylaeochampsa* (Clark & Norell 1992) and *Allodaposuchus* (Buscalioni *et al.* 2001), in which this bone bears a prominent tubercle. In common with *Susisuchus* and crocodylians, the cranioquadrate siphonium is fully enclosed by the bones of the caudal otic region. However, the lateral wall of the siphonium is formed by the quadrate. In *Susisuchus* and crocodylians, the lateral wall of this siphonium is formed by the exoccipital. The diameter of the cranioquadrate siphonium of *Isisfordia* is also unusually wide in proportion to the size of the skull. The caudal margin of the otic aperture is continuous with the paraoccipital process, unlike that of most crocodylians and alligatoroids, where it is invaginated (Brochu 1999). The postorbital bar is inset from the rostralateral corner of the skull table and the lateral portion of the jugal. Similar to the condition in advanced neosuchians, the occipital

surface of the basicranium ventral to the basioccipital condyle slopes rostroventrally. This condition is comparable to that seen in immature crocodylians, regardless of clade (Brochu 2004). Work during the preparation of QM F44320 also revealed that there is a broad exposure of the basisphenoid immediately rostral to the basioccipital on the lateral wall of the braincase, slightly ventral to the caudal aperture of the carotid foramen. The full rostral extent of this exposure cannot be determined. This appears to differ from the condition seen in all mature crocodylians (except *Gavialis*) and *Hylaeochampsa*, where the basisphenoid extends caudoventrally as a thin lamina between the basioccipital and pterygoid, with the medial eustachian opening lying between the basioccipital and the descending lamina of the basisphenoid (Brochu 2004).

The paratype skull (QM F44320; figure 4a–d) shows that the secondary choanae are situated in the middle of the caudal part of the bony palate, in a position similar to that in *Bernissartia* and dyrosaurids such as *Dyrosaurus phosphaticus* (Buffetaut 1982). However, as in eusuchians, the ventral laminae of the pterygoids envelop the shared rostral margin of the secondary choanae, separating it from the palatines. The ventral laminae are united along the midline via a weakly serrated suture. In advanced neosuchians, such as *Bernissartia* and *Goniopholis*, the shared rostral margin of the secondary choanae is formed by the palatines, such that the ventral laminae of the pterygoids do not unite. The condition in other non-crocodylian eusuchians, such as *Hylaeochampsa*, is much more derived than in *Isisfordia*, with the ventral laminae of

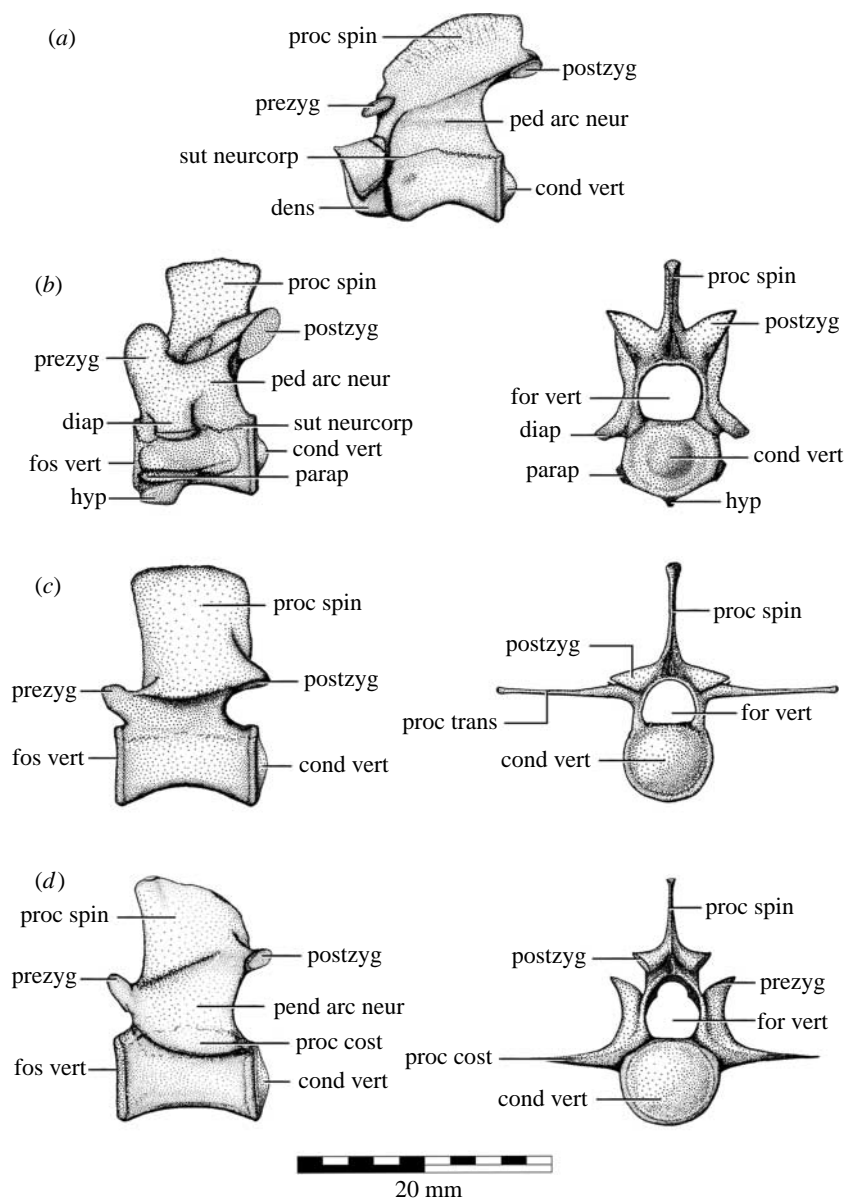


Figure 3. Axial osteology of *Isisfordia duncani* gen. et sp. nov. Schematic interpretations of selected vertebrae from QM F36211 (holotype): (a) axis in left lateral aspect; (b) cervical vertebra III in left lateral and caudal aspect; (c) lumbar vertebra III(?) in left lateral and caudal aspect; (d) caudal vertebra I in left lateral and caudal aspect. Abbreviations: cond vert, vertebral condyle; dens, dens; diap, diapophysis; for vert, vertebral foramen; fos vert, vertebral fossa; hyp, hypopophysis; parap, parapophysis; ped arc neur, peduncle of the neural arch; postzyg, postzygopophysis; prezyg, prezygopophysis; proc cost, costal process; proc spin, spinal process; proc trans, transverse process; sut neurcorp, neurocorpal suture.

the pterygoids being greatly expanded rostrocaudally. At least one atoposaurid (*Brillianceausuchus*; Michard *et al.* 1990) may also show the eusuchian-type condition and, therefore, this type of palate may have evolved independently at least twice within Mesoeucrocodylia.

The maxillary rostrum is long and broad (maximum length : minimum width ratio at the premaxillae is approximately 3 : 1), and flattened dorsoventrally (figure 4a–c), much resembling that of *Stomatosuchus* (Stromer 1925), *Susisuchus* and some Cenozoic alligatoroids. The nasals taper rostrally, but diverge slightly as they enter the distinctly pear-shaped naris. The teeth of the maxillary rostrum occlude labial to those of the mandible.

Unlike *Bernissartia*, but in common with crocodylians, the mandible bears an oval-shaped external mandibular fenestra, best preserved on QM F34642 and QM F44319 (figure 4e). The caudal-most dentary and maxillary teeth sit in a groove that lacks interdental septa (figure 4b,c,e), as

occurs in many alligatorids and *Hylaeochampsia*. Unusual for a platyrostral crocodyliform, however, and unlike alligatorids (where the teeth in these alveoli are bulbous), the dentary and maxillary teeth of *Isisfordia* are flattened labiolingually at the base of the crown, with a distinctly concave labial surface and a convex lingual surface (figure 4f). Putative eusuchian (Molnar 1980) and mesoeucrocodylian (Molnar & Willis 2001) remains from the Albian of New South Wales exhibit similar mandibular and dental characteristics but, unlike *Isisfordia*, interdental septa are present between what are believed to be the caudal-most teeth. The morphology of the caudal-most teeth in the alveolar groove of *Hylaeochampsia* is presently unknown.

All the vertebrae on the holotype are well preserved, and those of the neck, trunk and base of the tail are clearly exposed in the mid-sagittal break that extends through these parts of the specimen. There are 9 cervical, 15 trunk, 2 sacral, and at least 28 caudal vertebrae, all of them

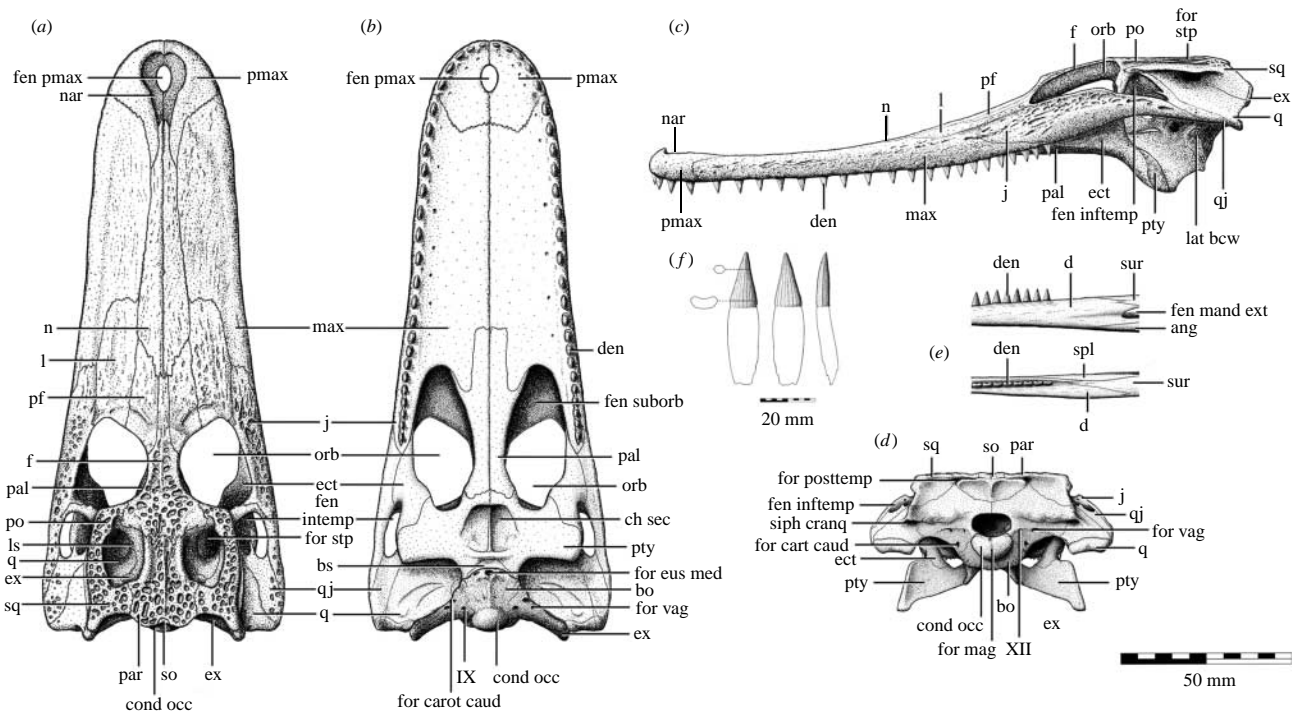


Figure 4. Cranial and mandibular osteology of *Isisfordia duncani* gen. et sp. nov. Schematic interpretation of the skull (QM F44320; paratype) in (a) dorsal, (b) palatal, (c) left lateral and (d) occipital aspect; (e) schematic interpretation of the mid-caudal portion of the left mandibular ramus (QM F44319; paratype) in lateral and dorsal aspect; (f) caudal dentary tooth in labial, lingual and mesial aspect. Abbreviations: ang, angular; bo, basioccipital; bs, basisphenoid; ch sec, secondary choanae; cond occ, occipital condyle; d, dentary; den, tooth; ect, ectopterygoid; ex, exoccipital; fen intemp, infratemporal fenestra; fen mand ext, external mandibular fenestra; f, frontal; fen pmax, fenestra premaxillaris; fen suborb, suborbital fenestra; for carot caud, caudal aperture of the carotid foramen; for eus med, median eustachian foramen; for posttemp, caudal aperture of the posttemporal foramen; for vag, foramen vagi; j, jugal; l, lachrymal; lat bcw, lateral braincase wall; ls, laterosphenoid; max, maxilla; n, nasal; nar, naris; orb, orbit; pal, palatine; par, parietal; pf, prefrontal; pmax, premaxilla; po, postorbital; pty, pterygoid; q, quadrate; qj, quadratojugal; siph cranq, caudal aperture of the cranioquadrate siphonium; so, supraoccipital; sp, splenial; sq, squamosal; sur, surangular; XII, foramen for cranial nerve XII.

except the sacrals being weakly procoelous (figure 3). The degree of procoely decreases in a cranial to terminal direction within the tail, which is typical for eusuchians (Salisbury & Frey 2001). There is also a decrease in the size of the condyle on the cervical vertebrae, such that it occupies only the central half of the otherwise flat caudal articular surface (figure 3a,b). There is no indication of a rugose depression in the centre of the vertebral condyle, as in *Theriosuchus* (Salisbury & Frey 2001), *Pachycheilosuchus* (Rogers 2003) and some of the crocodyliform vertebrae from the Albian of New South Wales (listed but not discussed in Molnar 1980). Caudal vertebra I is gently procoelous (figure 3c), and sacral vertebra II has a low caudal condyle. Both of these features are diagnostic of *Isisfordia*, whereas in all other eusuchians, along with *Bernissartia* and *Pachycheilosuchus*, caudal vertebra I is strongly biconvex and sacral vertebra II has a shallow caudal fossa.

The scapular blade flares dorsally, and the sharp cranial crest continues onto the coracoidal articular surface. The ilium has a prominent cranial process, and the iliac blade is dorsally convex, with a slight dorsal indentation caudally. The fore- and hindlimbs are approximately of the same length and, similar to *Borealosuchus* (Brochu 1999) and several advanced neosuchians, the stylopodial and zeugopodial elements are proportionately much more gracile than they are in other eusuchians. In common with *Susisuchus* and *Theriosuchus*, the distal extremity of the

ulna is expanded transversely with respect to the long axis of the bone.

The dermal skeleton of *Isisfordia* is typical of non-gavialoid eusuchians (Salisbury & Frey 2001). The nuchal shield is separated from the dorsal shield, and comprises at least four overlapping pairs of osteoderms. The dorsal osteoderms form a tetraserial paravertebral shield and on either side of this, from trunk vertebrae III–VIII, there is a single longitudinal row of transversely contiguous accessory osteoderms (figure 2). There are nine transverse rows of four paravertebral osteoderms each, from caudal vertebrae I–X. From caudal vertebrae II–XVII, two longitudinal rows of accessory osteoderms indicate the position of the double scale-crest. The gastral shield comprises at least eight transverse rows of up to eight contiguous square osteoderms (figure 2).

4. DISCUSSION

(a) Phylogenetic relationships

The results of the phylogenetic analysis place *Isisfordia* as the sister taxon to *Hylaeochampsia* and *Crocodylia* (figure 5a). *Susisuchus* and *Bernissartia* form successive sister taxa to the clade formed by *Isisfordia*, *Hylaeochampsia* and *Crocodylia*. The relationships of crocodylian taxa considered in the analysis are consistent with those of previous morphological analyses, with the exception of a weakly supported sister-group relationship between *Borealosuchus* and Gavialoidea.

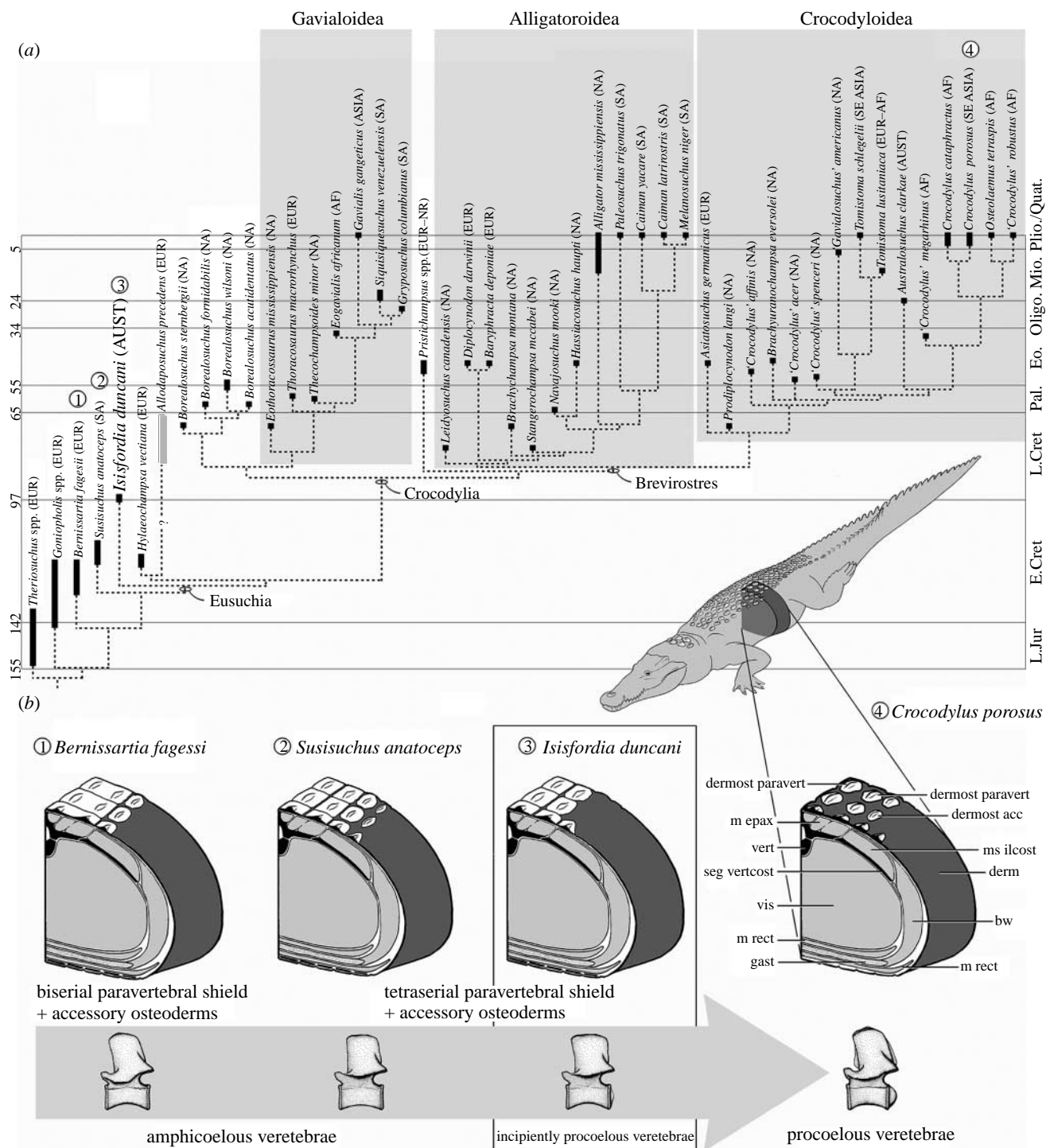


Figure 5. Hypothesized phylogenetic relationships of *Isisfordia duncani* and key postcranial transformations that occurred during the origin of eusuchian crocodyliforms. (a) Stratigraphically calibrated strict consensus of six equally optimal trees resulting from parsimony analysis of 176 characters in 45 taxa (46 if *Allodaposuchus* is included). Thick solid lines represent known minimal ranges (see Brochu 1997 and references therein), while the abbreviations above the names denote the area in which the taxon occurs (AF, Africa; ASIA, Asia; AUST, Australia; EUR, Europe; NA, North America; SA, South America; SE ASIA, Southeast Asia). See electronic supplementary material for character list, data matrix, analysis protocol, apomorphy list and bootstrap support indices. (b) Key postcranial transformations (sagittal segmentation of the paravertebral shield and the acquisition of procoelous vertebrae) that took place during the evolutionary transition from advanced neosuchians (represented by *Bernissartia* and *Susisuchus*) to basal eusuchians (*Isisfordia*) and, finally, crocodylians (represented by *Crocodylus porosus*). Abbreviations: bw, body wall musculature; derm, dermis; dermost acc, accessory osteoderm; dermost paravert, paravertebral osteoderm; gast, gastral rib; m epax, epaxial musculature; m rect, musculus rectus abdominalis; ms ilcost, myoseptum of the musculus iliocostalis; seg vertcost, vertebral segment of a thoracic rib; vert, vertebra; vis, viscera.

Our results strongly supported the inclusion of *T. schlegelii* within Crocodyloidea to the exclusion of *G. gangeticus*. Constraining the matrix such that *T. schlegelii* is the sister taxon to *G. gangeticus* requires an

additional 40 steps, and decreases the consistency index from 0.47 to 0.43.

Synapomorphies that unite *Isisfordia* with *Hylaeochampsia* and Crocodylia include procoelous cervical, thoracic and

lumbar vertebrae, and secondary choanae enclosed medio-orally by ventral laminae of the pterygoids. The combined presence of these characters has long been considered a hallmark of Eusuchia (Huxley 1875; Huene 1933; Benton & Clark 1988; Norell & Clark 1990; Clark & Norell 1992; Brochu 1999; Buscalioni *et al.* 2001; Salisbury & Frey 2001). However, the poor preservation of many putative basal eusuchian and advanced neosuchian taxa has meant that pinpointing the phylogenetic transition from Neosuchia to Eusuchia, and then from Eusuchia to Crocodylia has been difficult to establish. To ease this problem, Brochu (1999) proposed a node-based definition of Eusuchia that relies on the placement of *Hylaeochamps* as the sister taxon to Crocodylia. The phylogenetic position of *Isisfordia* in the present analysis shows that the acquisition of key eusuchian characteristics occurred prior to the appearance of *Hylaeochamps*. Given both the historical and biomechanical significance (see below) attached to the features used to diagnose Eusuchia, we believe its status as a purely apomorphy-based taxon should be retained (see electronic supplementary material for a revised differential diagnosis of Eusuchia). In this light, *Isisfordia* can be considered the most basal member of the group.

With most of its morphology well represented, *Isisfordia* fills an important gap in terms of fossil evidence for one of the major anatomical transitions in the evolution of crocodyliforms (figure 5*b*). In almost all respects, *Isisfordia* neatly conforms with Huxley's 1875 model for the gradual evolutionary transformation of crocodyliforms, possessing the morphology expected for a basal eusuchian (Huxley 1875).

(b) Anatomical changes associated with the emergence of Eusuchia

Postcranially, the key changes that occurred during the transition from Neosuchia to Eusuchia involved the sagittal segmentation of the paravertebral shield (*Bernissartia* to *Susisuchus*) and the acquisition of procoelous vertebrae (*Susisuchus* to *Isisfordia*) (figure 5*b*); whereas, in the skull, the pterygoids became incorporated into the bony secondary palate (*Bernissartia/Susisuchus* to *Isisfordia*) (figure 4*b*).

Sagittal segmentation of the paravertebral shield meant that large-angle lateral flexion of the trunk could be achieved without compromising the width necessary for stabilization against the mechanical loads encountered during high-walking (Salisbury & Frey 2001). A greater capacity for lateral flexion in forms such as *Susisuchus* would have increased the efficiency of aquatic locomotor modes that incorporate lateral undulation of both the trunk and the base of the tail, such as axial and hybridized swimming (Frey & Salisbury 2001). Yet the capacity to sustain high-walking in *Susisuchus* would still have been restricted to animals with a mass less than approximately 50 kg since there is no anatomical mechanism in place to counteract excessive shear loading at the intercorporeal articulations between adjoining vertebrae. This mechanical constraint may explain the small adult size of *Susisuchus* (and *Isisfordia*) relative to most crocodylians. (For comments on the possible sagittal segmentation of the dorsal osteoderms in *Gobiosuchus*, *Simosuchus* and *Notosuchus*, see electronic supplementary material.)

The results of our phylogenetic analysis indicate that the transition from amphicoelous to procoelous vertebrae occurred from *Susisuchus* to Crocodylia, with *Isisfordia*

representing the intermediate condition (figure 5*b*). This transformation occurred after sagittal segmentation of the paravertebral shield, and may have resulted from the incipient exposure of the intercorporeal articulations between adjoining vertebrae to dorsoventral and transverse shear loads (Salisbury & Frey 2001).

The sagittal segmentation of the paravertebral shield in the transition from *Bernissartia* to *Susisuchus*, and the subsequent acquisition of procoelous vertebrae from *Susisuchus* to *Isisfordia*, characterized the emergence of the eusuchian-type bracing mechanism (Salisbury & Frey 2001), and saw crocodyliforms circumvent what can be regarded as a major biomechanical constraint. Unlike all the other crocodyliform-type bracing systems that preceded it (including the ones that existed in *Gobiosuchus*, *Simosuchus* and *Notosuchus*), the anatomical topography associated with the eusuchian-type provides effective stabilization against the mechanical loads encountered during sustained high-walking in animals with a mass greater than approximately 50 kg, combined with a capacity for extensive ventral and lateral flexion of the trunk and the base of the tail (Salisbury & Frey 2001). Crocodyliforms with this type of bracing system therefore not only had a more diverse locomotor repertoire than most of their Mesozoic counterparts, but also had the capacity to become much larger without forfeiting their terrestrial locomotor behaviour. This, in part, may explain the dramatic increase in the size of eusuchians post-*Isisfordia* as early as the Campanian (e.g. *Deimosuchus*, 8–10 m total length and 2500–5000 kg; Erickson & Brochu 1999), and the subsequent explosive radiation that the group underwent during the Late Cretaceous and early Tertiary.

The rapid diversification of eusuchians has also been linked to the acquisition of an extensive bony secondary palate (Langston 1973; Clark & Norell 1992; Busbey 1995). The contribution of the pterygoids to the bony secondary palate of *Isisfordia* is minimal when compared with crocodylians. The caudal pterygoidal plate is also considerably shorter rostroventrally than it is in the majority of derived crocodylians. In these respects, the palatal construction of *Isisfordia* is transitional between the condition seen in advanced neosuchians such as *Bernissartia* and basal crocodylians (such as *Borealosuchus* and *Albertochamps*). Even the palate of *Hylaeochamps*, with its extensive pterygoidal participation, is considerably more derived than the condition in *Isisfordia*.

Traditionally, it was assumed that the separation of the nasal passage from the oral cavity in crocodyliforms was associated with respiration and feeding behaviour, because it allows animals to breathe while prey is held in the mouth, and to open the mouth under water (Huxley 1875). The separation is achieved in part by the bony secondary palate, and in part by a fold of tissue, the urohyal valve, which forms a caudodorsal extension of the tongue.

More recently, it has been posited that the formation of the eusuchian-type palate relates to structural reinforcement of the skull associated with changes in feeding behaviour (Langston 1973; Clark & Norell 1992; Busbey 1995). Modifications to the crocodyliform skull such as increased platyrostry, more conical teeth, caudal deepening of the mandible and the development of large scarf joints are all thought to indicate a shift from 'bite-and-tear' to 'bite-and-hold' feeding behaviour (Langston 1973; Busbey 1995). In extant crocodylians, bite-and-hold

feeding behaviour may incorporate crushing as well as rolling, which is employed to either destabilize or dismember prey items. Rolling, in particular, results in an unequal distribution of forces across the facial skeleton, and places enormous torsional loading on the jaws, especially on the horizontal parts of the maxillary rostrum (Busbey 1995).

Finite-element modelling of the skull of *Alligator* by Daniel & McHenry (2001) has also shown that a bite at the tip or middle of the maxillary rostrum causes maximum tensile strain in the caudal part of the palate, particularly around the caudal end of the ventral laminae of the palatine bones (see Daniel & McHenry 2001; figures 4 and 5). Such loading occurs during both symmetrical (crushing) and asymmetrical (torsion-induced) bites. The transition between the caudal end of the palatines and the rostral end of the pterygoids is where the secondary choanae are positioned in most mesoeucrocodylians and neosuchians, making this area structurally weak. In eusuchians (including *Isisfordia*), tensile strain in this part of the skull is offset through the formation of a more extensive bony secondary palate. The structural tie across the caudal part of the palate is formed by sutural reinforcement between the pterygoid ventral laminae, rostral to the secondary choanae (as has been suggested by Langston 1973; Clark & Norell 1992; Busbey 1995).

Assuming that a urohyal valve existed in *Isisfordia*, enclosure of the secondary choanae by the ventral laminae of the pterygoids would have resulted in minimal respiratory advantage, given their position in the palate. Indeed, assuming the presence of a urohyal valve, the position of the secondary choanae in most neosuchians and many longirostrine mesoeucrocodylians is indicative of respiratory capabilities that are similar to those of extant crocodylians. It is hard to envisage how further caudal migration of the secondary choanae, commencing with *Isisfordia* and continuing into Crocodylia, would increase the efficiency of this system.

Structural reinforcement of the skull would therefore seem to be the most likely factor behind the progressive caudal migration of the secondary choanae in crocodyliforms, and the subsequent formation of an extensive bony secondary palate in eusuchians. In *Hylaeochampsia* and many crocodylians (in particular globidontan alligatoroids), further reinforcement of the pterygoid part of the secondary palate (through a rostrocaudal elongation of the ventral laminae of the pterygoids) may also relate to an increased capacity for the manipulation and crushing of prey in the caudal part of the jaws. This is suggested by the greatly enlarged caudal teeth (Clark & Norell 1992) and, at least in globidontans and extant taxa such as *Alligator sinensis* and *O. tetraspis*, by a shortening of the rostrum and an elevation of the jaw articulation (the shape of the rostrum in *Hylaeochampsia* is unknown). Bulbous caudal teeth were already present in advanced neosuchians such as *Bernissartia* (Clark & Norell 1992) and, similar to dyrosaurids, *Susisuchus* and eusuchians, the tooth row had moved caudally relative to the position in more basal forms such as *Goniopholis* and *Theriosuchus* (Clark & Norell 1992). Thus, the shift to processing food in the caudal part of the mouth may have preceded, and thereby facilitated, the formation of the eusuchian-type palate.

Accompanying an increased capacity for torsional feeding and a stronger bite for holding and crushing prey

in basal eusuchians, would be an increased need for more powerful adductor musculature. Owing to the confining nature of the crocodyliform temporal fossae, only two of the many adductor muscles—the musculus adductor pterygoideus anterior (MPTa) and the musculus adductor mandibular externus profundus (MAMEP)—are in positions that are amenable to size increases (Busbey 1989). Of these, the MPTa has been shown to play a dominant role during crushing and in the holding of prey during rolling (Busbey 1989). Moreover, Daniel & McHenry (2001) have been able to demonstrate that the amount of mechanical stress induced in the palate during symmetrical and asymmetrical bites is critically dependant on the degree to which the MPTa puts the caudal part of the palate into compression, while countering the tension that is induced during beam-like bending of the maxillary rostrum.

The number of parallel fibres that comprise the MPTa can be increased through a widening of the adductor arcade (the area enclosed by the pterygoids, the lateral braincase wall and the infratemporal bones; see figure 4c,d). In crocodylians, the diameter of the adductor arcade has been expanded, relative to the condition in *Isisfordia*, through verticalization of the basicranium and an increased ventral deflection of the pterygoid flanges (in advanced neosuchians the pterygoid flanges are short and directed sub-horizontally). Although the process of braincase verticalization has long been recognized in the transition from Neosuchia to Crocodylia (Tarsitano 1985; Brochu 2004), the reasons for this transformation have been unclear. Commencing with *Isisfordia* (see figure 4), a deepening and caudoventral expansion of the basioccipital has the dual effect of expanding the dorsoventral height of the adductor arcade, greatly expanding the pterygoid flanges caudoventrally, and elongating the pterygoid contribution to the bony secondary palate. The corollary of these transformations is further structural reinforcement of the bony secondary palate, the caudal migration of the secondary choanae, an increase in the size of the oral cavity, and an associated increased stabilization and deepening of the caudal part of the mandible. As has been suggested by Busbey (1995), the latter two changes probably help to resist medial traction of the mandibular rami produced by more medial orientation of the jaw musculature, along with any mediolateral movements of the mandible during active use of the jaws, in particular crushing and holding. They would also strengthen the caudal part of the palate against compression induced by contraction of the MPTa.

The anatomical changes associated with the emergence of *Isisfordia* thus signalled a new phase in the locomotor and feeding behaviour of crocodyliforms. Postcranially, sagittal segmentation of the paravertebral shield and the acquisition of procoelous vertebrae meant that later eusuchians could become large, efficient swimmers without forfeiting their capacity for high-walking on land. An option to take larger prey is associated with this increase in size. This option would have been facilitated in part through the participation of the pterygoids in the bony secondary palate. This combined shift in locomotor and feeding capability may have played a pivotal role in the rapid diversification of eusuchians during the Late Cretaceous and early Tertiary, and undoubtedly helped ensure their status as the world's largest and most dominant semi-aquatic ambush predators in regions where their physiology would allow it.

(c) Palaeobiogeographic implications

Optimized against phylogenetic models, the biogeographic occurrences of fossils unambiguously indicate that all three superfamilies of crocodylians originated in Laurasia, specifically North America, with a minimum divergence timing between Gavialoidea and Brevirostres during the Campanian (*ca* 80 Myr ago; Brochu 1997, 2001). The results of the present analysis (figure 5a) support a Laurasian origin for Crocodylia.

Previously, the occurrence of non-crocodylian eusuchians such as *Hylaeochampsa* and *Allodaposuchus* in Europe, along with advanced neosuchians such as *Bernissartia*, *Goniopholis* and *Theriosuchus*, has similarly pointed to a Laurasian origin for Eusuchia (Sill 1968; Brochu 1999; Buscalioni *et al.* 2001). The 'Glen Rose form', another animal often put forward as a non-crocodylian eusuchian (Benton & Clark 1988; Brochu 1999; see electronic supplementary material for further comments on this crocodyliform), is also from North America. However, there are two problems associated with a Laurasian origin for Eusuchia.

First, there is a paucity of fossil evidence documenting the distribution of advanced neosuchians and non-crocodylian eusuchians during much of the Cretaceous, particularly in Gondwanan provinces. The Cretaceous was one of the most tectonically active times during the Mesozoic, with the separation of most Gondwanan provinces occurring between 145 and 80 Myr ago (Scotese 2001). Indeed, Turner (2004) has shown that Gondwanan fragmentation affected non-neosuchian crocodyliform diversification during the mid-Late Cretaceous, particularly among South American–African groups (Early Cretaceous) and South American–Malagasy groups (Late Cretaceous).

Secondly, there are a number of putative non-crocodylian eusuchians and advanced neosuchian taxa from Gondwanan continents that were not considered when these biogeographic assessments for the Laurasian origin of Eusuchia were made. Foremost among these are *Stomatosuchus* (Cenomanian, Egypt; Stromer 1925), *Aegyptosuchus* (Cenomanian, Egypt; Stromer 1933) and *Dolichochoampsa* (Maastrichtian, Argentina; Gasparini & Buffetaut 1980). Unfortunately, all three taxa are either poorly known (*Stomatosuchus*) or represented only by fragmentary material (*Aegyptosuchus* and *Dolichochoampsa*), hence their relationships with other crocodyliforms have been (and remain) difficult to resolve (Norell & Clark 1990; Brochu 1999). Neither of these problems exists with *Isisfordia* and *Susisuchus*, and their occurrences in the Southern Hemisphere indicate that the biogeographic events associated with the origins of Eusuchia are more complex than was previously thought.

Optimization of the biogeographic occurrences of basal eusuchians in the cladogram shown in figure 5 suggests that, at the level of *Isisfordia*, resolving the point of origin for Eusuchia is ambiguous: eastern Gondwana (Australia) and Laurasia (western Europe) are equally likely. Yet there are growing indications that the scales may eventually fall on the southern side of the equator. Although most advanced neosuchians were Laurasian (e.g. *Goniopholis* and *Theriosuchus*), the one that is the sister taxon to Eusuchia, *Susisuchus*, is from South America. This fact, combined with the Australian provenance of the basal-most eusuchian, *Isisfordia*, may be cited as evidence that

the transition from Neosuchia to Eusuchia transpired in Gondwana, but the number of specimens and localities is too small at present to establish clear patterns. The phylogenetic position of *Dolichochoampsa* and *Stomatosuchus* may ultimately bolster this scenario, as could the discovery of additional Australian fossils from sites that are already producing material suggestive of susisuchid neosuchians (Aptian–Albian, Victoria; Salisbury *et al.* 2003b) and basal eusuchians (Albian, New South Wales; Molnar 1980).

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