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Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853

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ABSTRACT: Eusuchians with deep snouts and labiolingually compressed teeth are known from the Palaeogene of Laurasia. These are usually referred to Pristichampsinae, but the type species, *Pristichampsus rollinati*, is based on insufficiently diagnostic material and should be treated as a nomen dubium. At least two Lutetian species formerly referred to *Pristichampsus* can be recognised – *Boverisuchus magnifrons* in Germany and possibly elsewhere in Europe, and *Boverisuchus vorax*, new combination, in western North America. Material from the middle Eocene of Italy and Texas may represent distinct species. A phylogenetic analysis confirms their close relationship and also supports a relationship with two Asian forms – early Eocene *Planocrania datangensis* and Palaeocene *Planocrania hengdongensis*. The name Planocraniidae Li 1976 is applied to this group. A distinctive quadrate with a prominent dorsal peak between medial and lateral hemicondyles is known only in *Boverisuchus*, and although the teeth of *Planocrania* are flattened, they are not serrated. Planocraniids maintain a phylogenetic position as the sister group to Crocodyloidea + Alligatoroidea, but this part of the tree is unstable and discovery of older, more primitive planocraniids will help resolve conflicts on the phylogenetic relationships of extant crocodylian lineages.

KEY WORDS: *Boverisuchus*, Crocodylia, Crocodyliformes, *Planocrania*, Planocraniidae

Although most Cenozoic crocodyliforms closely resemble their living relatives, the ziphodont forms do not. Strictly speaking, the term "ziphodont" refers to the possession of labiolingually compressed serrated teeth (Fig. 1a; Langston 1975), but the term has come to include a suite of derived features often found in crocodyliforms with ziphodont dentition, including a mediolaterally compressed and dorsoventrally deep (altirostral) snout (Fig. 1c). At least some had blunt, hoof-like unguals (Fig. 1b), and they are sometimes seen as an archosaurian attempt to retain the terrestrial predator ecological roles cleared by the disappearance of non-avian theropods.

One such group is found in the Palaeogene of North America and Eurasia. These are referred to Pristichampsinae Kuhn, 1968 (Rossmann 1998; Brochu 2003) and, based on phylogenetic analyses, are part of a lineage basal within or closely related to Crocodylia (Salisbury & Willis 1996; Pol *et al.* 2009; Brochu *et al.* 2010). Although not known prior to the Palaeocene, the phylogenetic placement of the group implies a minimum time of origin in the Campanian.

Its phylogenetic position makes this group relevant to the controversy over higher-level crocodylian relationships. Morphological evidence draws the Indian gharial (*Gavialis gangeticus*) and its extinct relatives to the base of Crocodylia and supports a crocodylid affinity for the false gharial (*Tomistoma schlegelii*), but molecular data link *Gavialis* and *Tomistoma* together and root trees on the alligatorids (e.g., Densmore 1983; Norell 1989; Brochu 2003; Gatesy *et al.* 2003; Piras *et al.* 2010; Oaks 2011). Improved sampling from early-diverging groups such as this might help determine if morphological data are being misled by incorrect character state polarity optimisations.

At present, only one Laurasian species – *Pristichampsus vorax* (Troxell 1925) – has been included in phylogenetic analyses (Salisbury & Willis 1996; Brochu 1997, 1999, 2007; Delfino *et al.* 2008a; Pol *et al.* 2009; Martin 2010). This is one of the youngest and most morphologically derived of these forms. Expansion of our sample, especially from earlier in the history of the group, could limit the impact of phylogenetic overprinting of plesiomorphic traits and improve our ancestral state reconstructions at the base of Crocodylia.

To do this, we face several challenges. The first is a clear understanding of species-level diversity. Some argue that all known Eocene ziphodont eusuchians, including *P. vorax*, are referable to a single species, *Pristichampsus rollinati* (Gray 1831), and that differences between samples reflect intraspecific variation (Rauhe & Rossmann 1995; Rossmann 1998), but not all of the differences are within observed levels of variation among living crocodylian species. Indeed, some currently recognised species might include multiple diagnosable units.

The preservation of some holotypes complicates our assessment. Whether *P. rollinati* can be diagnosed is doubtful (Langston 1975) – the holotype is limited to teeth, postcranial remains, a partial dentary and something that is part of either a snout or a mandible (Fig. 2). This renders the term Pristichampsinae itself systematically problematic, in spite of its prominence in the literature.

This paper represents an initial reevaluation of the phylogenetic relationships of these forms based on first-hand examination of specimens from the United States, France, Germany, Italy and China. It also provides a revised taxonomy for some of these species. Hopefully, it will help guide further research the origins, biogeographic history and extinction of ziphodont crocodyliforms during the Age of Mammals.

Wann Langston coined the term "ziphodont," and his 1975 paper on *Pristichampsus vorax* stands as a model of descriptive morphology and taxonomic review. There isn't much hyperbole involved when I say I owe Dr. Langston my career – I may have absorbed my phylogenetic philosophy elsewhere, but much of what I am as a scientist was learned from him. Whatever good comes from this paper is dedicated to Dr. Langston. The shortcomings should be laid right on my feet.

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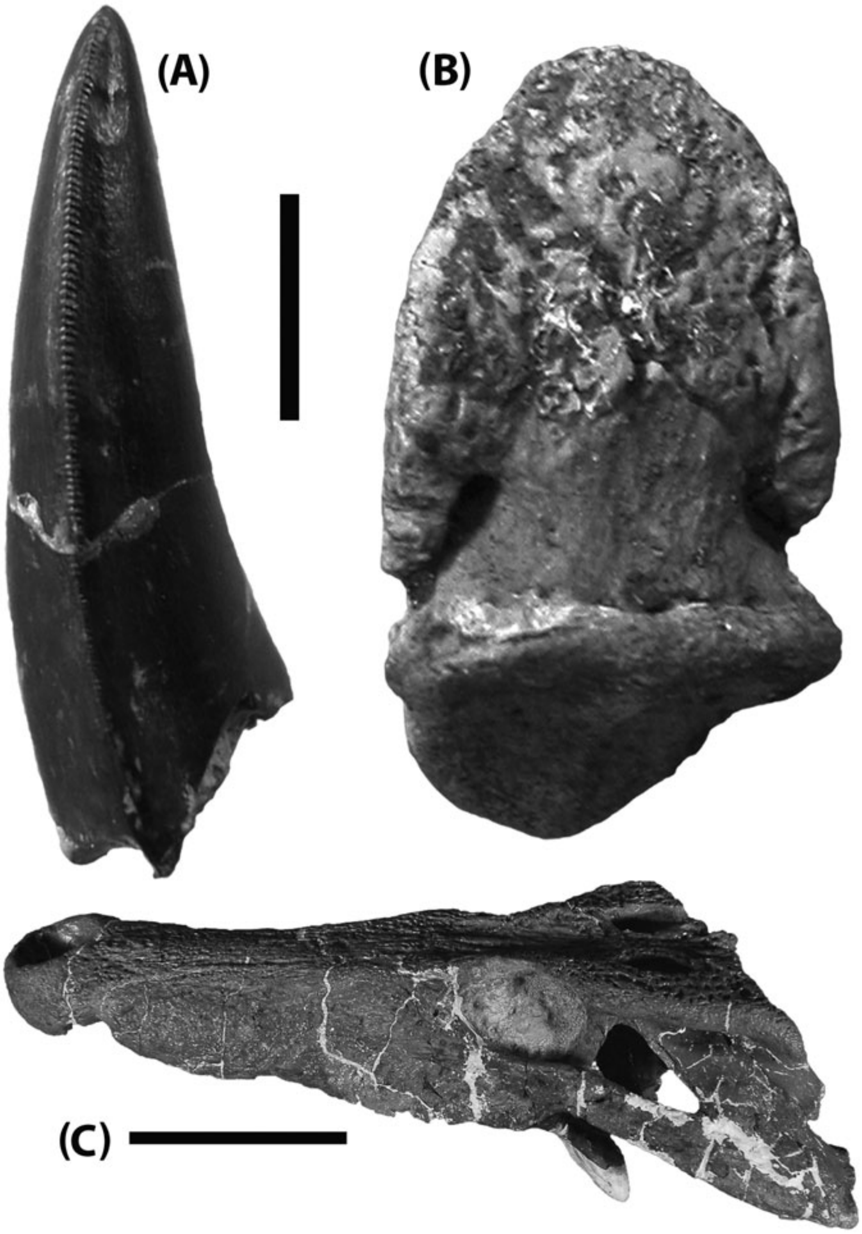

Figure 1 Morphological features characteristic of ziphodont eusuchians: (A) labiolingually compressed, serrated teeth (AMNH 2090, *Boverisuchus vorax*); (B) hooflike unguals (GM Tr I Leo, *B. magnifrons*, ventral view); (C) altirostral snout (FMNH PR399, *B. vorax*, left lateral view). Scale bars = 1 cm (A, B); 10 cm (C).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, NY; Field Museum of Natural History, Chicago, Illinois, USA; GM, Geiseltalmuseum, Martin Luther Universität, Halle, Germany; HLMD, Hessisches Landesmuseum, Darmstadt, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Museum of Natural History of Los Angeles County, Los Angeles, CA; MGPD, Museo di Geologia e Paleontologia, Università di Padova, Padua, Italy; MNHN, Museum National d'Histoire Naturelle, Paris, France; MNHT, Musée d'Histoire Naturelle de Toulouse, Toulouse, France; NHMUK, Natural History Museum, London; PU, Princeton University, Princeton, NJ (collections now at YPM); TMM, Texas Memorial Museum, Austin, TX; UCM, University of Colorado Museum of Natural History, Boulder, CO; UCMP, University of California Museum of Paleontology, Berkeley, CA; USNM, United States National Museum of Natural History, Washington, DC; YPM, Peabody Museum of Natural History, Yale University, New Haven, CT.

1. Taxonomic review and phylogenetic sampling

1.1. *Pristichampsus rollinati* (Gray 1831)

Pristichampsus rollinati (Gray 1831) is based on the "Crocodile des marnières d'Argenton" of Cuvier (1824). It consists of some teeth and bone fragments from the middle Eocene of Argenton in western France. Gray (1831) established *Crocodilus rollinati* from one of the teeth (MNHN AG 3) and vertebrae (MNHN AG 4) figured by Cuvier (1824). This was transferred to *Pristichampsus* by Gervais (1853).

Cuvier (1824) was struck by the flattened, serrated teeth associated with the Crocodile d'Argenton. They are sometimes compared with those of theropod dinosaurs (Langston 1975), but nonavian theropods being poorly understood in 1824, Cuvier compared them with the teeth of a monitor lizard (as have others, e.g. D'Amore & Blumenschine 2009). He interpreted two cranial elements as a partial maxilla preserving strongly compressed alveoli, and a piece of the rostrum preserving the anterior margin of the orbit. Based on the maxillary

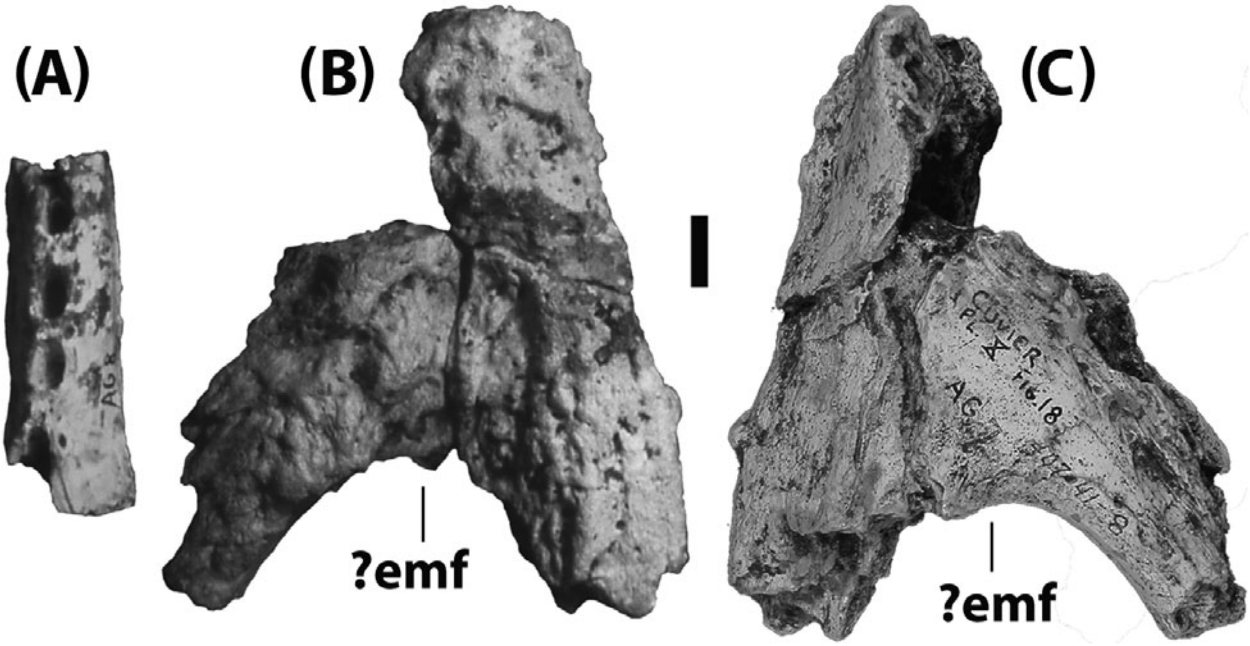

Figure 2 *Pristichampsus rollinati*, material referred by Cuvier (1824): (A) MNHN AG 8, partial dentary, dorsal view; (B–C) TMM 40741-8, cast of MNHN AG 7, fragment of skull or lower jaw in lateral (B) and medial (C) views. Scale bar = 1 cm. Abbreviation: ?emf = possible external mandibular fenestra.

fragment, Cuvier concluded that the snout was deep relative to that of a modern crocodile.

Although his assessment of comparative snout depth was eventually verified, this seems to be a case of drawing the right conclusion from the wrong evidence. What Cuvier identified as a partial maxilla is actually a partial dentary (Fig. 2a). The other skull fragment (Fig. 2b, c) does seem to preserve a sutural contact trending from the border of an opening, but there is no indication on what would be the ventral surface of either the lacrimal duct or the prefrontal pillar. The specimen is equally consistent with a partial surangular and angular posterior to the external mandibular fenestra, though this is also equally tenuous.

Fossils from elsewhere in Europe have been referred to *P. rollinati* (e.g. Caraven-Cachin 1880; Astre 1931; Weitzel 1938; Berg 1966; de Lapparent de Broin *et al.* 1993; Windolf 1994; Rossmann 1998; Kotsakis *et al.* 2004; Sachse 2005). These might, indeed, represent a single species. Some of them are also of approximately the same age as the type – fossils from Argenton, Messel, and the lower horizons at Geiseltal are all of early Lutetian age (European Mammal Paleogene Zone [MP] 11; Sudre & Lecomte 2000; Franzen 2005). Most of the Geiseltal fossils studied for this analysis are geologically younger, deriving from MP 12, 13a, or 13b, but they are morphologically indistinguishable from older Geiseltal specimens and those from Messel, and they can be referred to the same species (Berg 1966; Rossmann 1998). It would thus be reasonable to suspect that the Lutetian ziphodont eusuchians from Europe represent a single species.

However, as suggested by Langston (1975), there is nothing diagnostic at the species level in the type material. The syntype serrated tooth and procoelous vertebra are enough to establish the presence of a ziphodont eusuchian at the type locality, but nothing more. Even if we include all of the material figured and discussed by Cuvier (1824), we would be unable to refer it, on morphological grounds alone, to the same species as the Messel/Geiseltal form and not to *P. vorax*. It follows that *Pristichampsus rollinati* (Gray 1831) is a nomen dubium.

1.1.1. Status of *Pristichampsus*. Because its type species is a nomen dubium, *Pristichampsus* Gervais, 1853 itself is undiagnosable. The oldest generic name available for the eusuchians formerly called *Pristichampsus* appears to be *Boverisuchus* Kuhn, 1938. *Limnosaurus* Marsh, 1872 is based on material probably conspecific with *P. vorax*, but it can no longer be identified (Langston 1975) and is, thus, a nomen nudum.

I do not say this lightly; *Pristichampsus* is widely used. Its elimination may lead to confusion in the literature and, in all likelihood, my own violent death at the hands of my colleagues. Taxonomic stability should be promoted, and I would rather not be killed. The ideal solution would be the discovery of a more complete and diagnosable specimen from Argenton that can serve as a neotype. In the absence of such material, we are obliged to set the name aside.

1.1.2. Clade name. The ICZN (1999) recommends, but does not mandate, the rejection of suprageneric names based on nomina dubia. The draft PhyloCode (Cantino & de Queiroz 2007; article 11.8) requires that definitions of clade names derived from typified names include the types of these names as specifiers. It also requires that the specifier be included, either in a reference phylogeny or in a statement clarifying how the specifier relates to taxa in the phylogeny, but this does not necessarily mean that clade names become invalid should one of the specifying species be diagnostically problematic; a type species may not be diagnosable at the species level, but we may nonetheless be able to affirm a close relationship with a clade of better-known species.

The name Pristichampsinae is defined in reference to *Pristichampsus rollinati* and all crocodylians more closely related to it than to *Gavialis gangeticus*, *Alligator mississippiensis* and *Crocodylus niloticus* (Brochu 2003). We could maintain *P. rollinati* as a specifier for Pristichampsinae if we could comfortably assume it to be closely related to something like *Boverisuchus magnifrons*. This would have the desirable result of maintaining a widely-used name.

Nevertheless, there are reasons against following this approach. The association of ziphodont teeth with procoelous vertebrae is enough to distinguish the Argenton crocodile from any of the putative sebecids known from the European Palaeogene (Berg 1966; Buffetaut 1982b, 1988; Vasse 1995; Ortega *et al.* 1996; Rossmann *et al.* 2000), but the specimens, by themselves, are just as referable to the mekosuchine crocodyloid *Quinkana* as they are to *Boverisuchus*. A close relationship with coeval material from the same continent is somewhat more likely than with a substantially younger animal from the other side of the world, but taxonomic conclusions should be drawn on the specimens and the specimens alone. Analyses of historical biogeography and stratigraphic diversity patterns become circular if the taxa underpinning the analyses are based, in part, on biogeography or stratigraphy (Bell *et al.* 2010). Independence of taxonomic data from nonbiotic signals (such as time and space) must outweigh taxonomic stability, however important taxonomic stability is.

The oldest suprageneric name available for these forms is Planocranidae Li 1976. The correct Latin spelling should actually be Planocraniidae, and as first reviser I amend the name as such. Planocraniidae is defined in reference to *Planocrania datangensis* 1976 and all eusuchians more closely related to it than to *Alligator mississippiensis* (Daudin 1802), *Crocodylus niloticus* Laurenti, 1768, *Gavialis gangeticus* (Gmelin 1789), *Borealosuchus sternbergii* (Gilmore 1910), *Thoracosaurus macrorhynchus* (Blainville 1835), *Allodaposuchus precedens* Nopcsa, 1928, or *Hylaeochampsa vectiana* Owen, 1874. The number of specifiers is increased because of the lability shown by basal crocodylians and related lineages in recent analyses (Martin & Buffetaut 2008; Pol *et al.* 2009; Turner & Brochu 2010; Puértolas *et al.* 2011; Brochu 2011; Brochu *et al.* 2012).

The name Pristichampsinae, in the phylogenetic sense, has not actually been suppressed. Assuming the phylogenetic relationships presented in this paper are upheld, Planocraniidae would become redundant along with Pristichampsinae, should we someday be able to diagnose *P. rollinati*. This might happen if, for example, more complete material sufficient to create a neotype is found at the type locality. But unless that happens, we cannot provide a robust link between the Argenton sample and any particular ziphodont eusuchian without including nonbiotic information.

1.2. *Boverisuchus vorax* (Troxell 1925) and the North American Planocraniid record

Boverisuchus vorax, new combination, is based on material described by Troxell (1925, as *Crocodilus vorax*), though now-lost material described by Marsh (*Crocodilus ziphodon*; 1871) probably belonged to this species. Langston (1975), following comparison with European material, referred it to *Pristichampsus*.

The specimens used in this analysis are all from Wyoming. Most, including the holotype (Fig. 3d), are from the Bridger Formation (and most of these are from the Grizzly Buttes area), and the exceptionally preserved skull described by Langston (1975; FMNH PR399, Fig. 3a, b, c) is from the correlative Lower Washakie Formation. All are thus from the later part of the Bridgerian North American Land Mammal Age (NALMA), corresponding approximately with the lower part of MP 11 in Europe.

1.2.1. Other North American occurrences. *Boverisuchus* has been reported from North American deposits ranging in age from the Uintan down to the base of the Palaeocene (Bramble & Hutchison 1971; Bartels 1980; Gingerich 1989; Westgate 1989, 2008; Gunnell *et al.* 1992; Hanson 1996; Stucky *et al.* 1996; Gunnell & Bartels 1999; Zonneveld *et al.* 2000; Alexander & Burger 2001). Most are limited to fragmentary material, primarily teeth, and cannot be referred to *Boverisuchus*, or even to Planocraniidae, without making spatiotemporal assumptions.

The oldest reported occurrence is an isolated tooth, PU 17074, from the early Palaeocene (Puercan) Mantua beds of Wyoming (Bartels 1980). The specimen was not figured, and it can no longer be located in the PU collections (now housed at the YPM). We would predict the presence of planocraniids in rocks of this age, but without a specimen, it is difficult to substantiate.

Some have suggested that *Orthogenysuchus olseni* Mook, 1924, an enigmatic crocodylian from the Wasatchian of Wyoming, is a planocraniid (Gunnell *et al.* 1992; Rauhe & Rossmann 1995; Rossmann 1998). *Orthogenysuchus* is known only from a poorly-preserved skull, but the teeth are neither compressed nor serrated (Brochu pers. obs.), and in spite of being dorsoventrally compressed, it does not appear to have been especially deep-snouted. It preserves several character states unique to alligatoroids, and some phylogenetic analyses support a close relationship with the outlandishly bizarre South American caimanine *Mourasuchus* Price, 1964 (Brochu 1999, 2010; Aguilera *et al.* 2006; Hill & Lucas 2006; Bona 2007; Martin 2007). This hypothesis is not universally accepted (Langston 2008), and recent discoveries in Utah (Masters *et al.* 2010) suggest a close relationship with another poorly-known alligatoroid from the Palaeogene of North America, *Listrognathosuchus multidentatus* (Mook 1930). Moreover, the close relationship between *Orthogenysuchus* and *Mourasuchus* has collapsed in recent analyses, largely because of some newly-included incomplete early caimanines (Brochu 2011). Nonetheless, *Orthogenysuchus* appears to be an alligatoroid and not a planocraniid.

The oldest Cenozoic North American ziphodont crocodyliforms presently in museum collections are isolated teeth from the late Palaeocene (Tiffanian) of Moffatt County, Colorado (Fig. 4) and Park County, Montana (Gunnell *et al.* 1992). If these are planocraniid, the coarse serrations indicate a closer relationship to *Boverisuchus* than to *Planocrania datangensis*.

Uintan occurrences include an isolated maxilla from San Diego County, California (Fig. 5a, b), and fragmentary material from elsewhere in California, Oregon, and southern Texas (Bramble & Hutchison 1971; Westgate 1989, 2008; Hanson 1996). The most informative material is from the Devil's Graveyard Formation of Brewster County, western Texas, including an isolated left premaxilla (TMM 41747-52, Fig. 5c, d, e) that Busbey (1986) tentatively referred to *Pristichampsus vorax*. It differs from Bridgerian *Boverisuchus* premaxillae in some respects – it is mediolaterally narrower, and whereas occlusal pits for the dentary teeth are lingual to the alveoli in *B. vorax*, they are between the alveoli in the Devil's Graveyard form. The Devil's Graveyard specimen is comparatively small and possibly immature, and Busbey (1986) suggested that the differences between Bridgerian premaxillae and TMM 41747-52 might be ontogenetic. Although the shape of the premaxilla changes during ontogeny in modern crocodylians, occlusal patterns generally do not (Brochu pers. obs.), and in-line occlusion between the premaxillary and anteriormost dentary teeth is characteristic of *Boverisuchus* from Germany. The Devil's Graveyard form might be a distinct species, but more material is needed before it can be characterised.

Jamaica was also home to a ziphodont crocodyliform during the middle Eocene (Vélez-Juarbe & Brochu in press). Other vertebrates from the locality are of North American origin (Domning *et al.* 1997; Pregill 1999), which would suggest a planocraniid affinity for the tooth, but such a conclusion cannot be drawn from the specimen itself.

1.3. *Boverisuchus magnifrons* Kuhn, 1938 and the European Planocraniid record

The holotype of *B. magnifrons* is from the Lagerstätte at Geiseltal near Halle, Germany (Kuhn 1938). Codings in this analysis are based primarily on this and other well-preserved skeletons

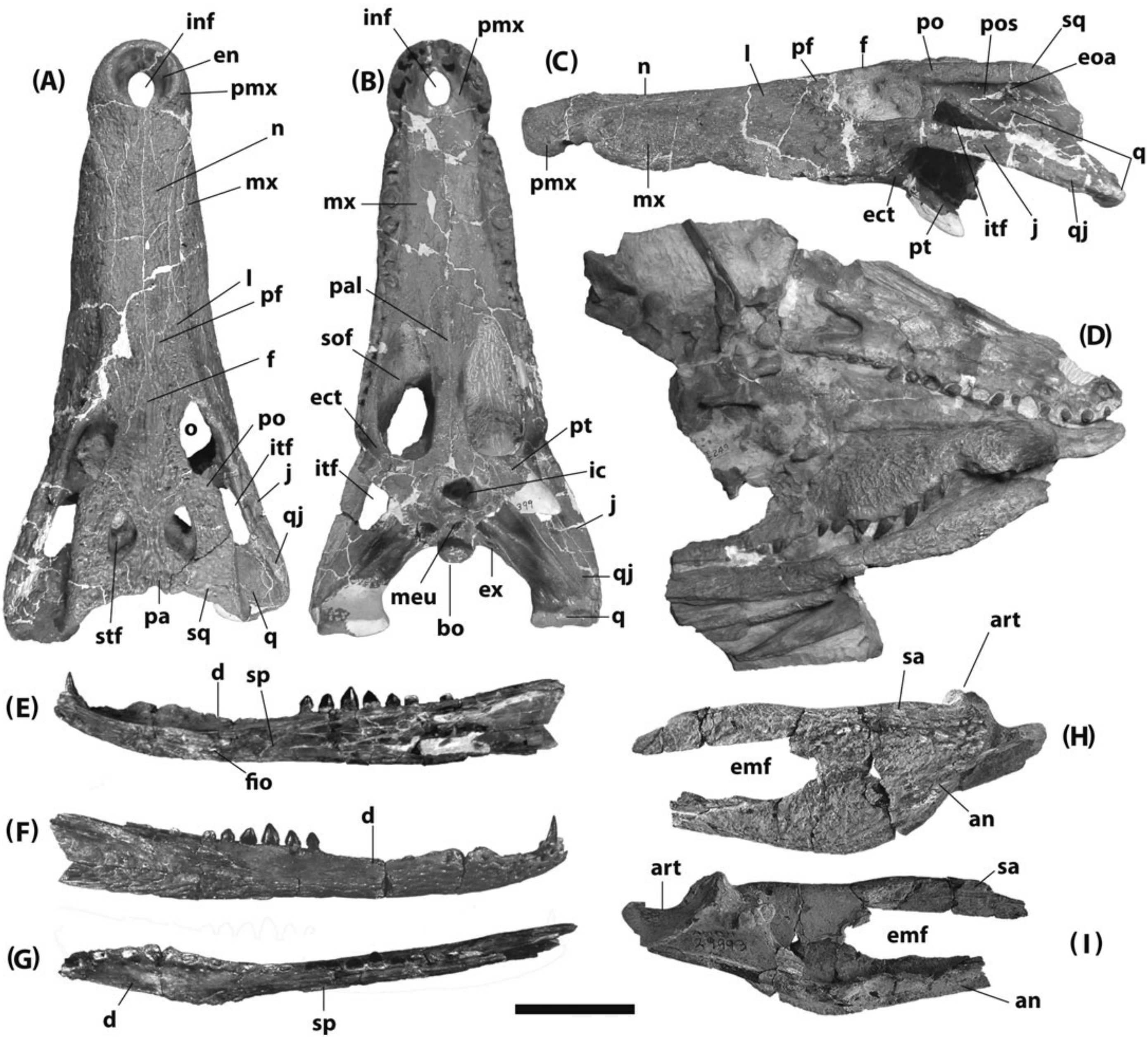

Figure 3 *Boverisuchus vorax,* middle Eocene (Bridgerian), Wyoming: (A–C) FMNH PR399, skull, in dorsal (A), ventral (B) and left lateral (C) views; (D) YPM 249 (holotype), disarticulated skull with associated postcranial material; (E–G) UCMP 170767, right dentary, in medial (E), lateral (F) and dorsal (G) views; (H–I) AMNH 29993, postdentary region of right mandibular ramus, in lateral (H) and medial (I) views. FMNH PR399 is from the lower Washakie Formation; remaining specimens are from the Bridger Formation. Scale bars = 10 cm (A–D); 5 cm (E–I). Abbreviations: an = angular; art = articular; bo = basioccipital; d = dentary; ect = ectopterygoid; emf = external mandibular fenestra; en = external naris; eoa = external otic aperture; ex = exoccipital; f = frontal; fio = foramen intermandibularis oralis; ic = internal choana; inf = incisive foramen; itf = infratemporal fenestra; j = jugal; l = lacrimal; meu = median Eustachian foramen; mx = maxilla; n = nasal; o = orbit; pa = parietal; pal = palatine; pf = prefrontal; pmx = premaxilla; po = postorbital; pos = preotic siphonium; pt = pterygoid; q = quadrate; qj = quadratojugal; sa = surangular; sof = suborbital fenestra; sp = splenial; sq = squamosal; stf = supratemporal fenestra.

and skulls from Geiseltal (Fig. 6; Kuhn 1938; Rossmann 1998, 2000a). Material from Messel (Weitzel 1938; Berg 1966) was also considered. All of these specimens are of Lutetian age.

The Messel form has always been referred to *P. rollinati* (Weitzel 1938; Berg 1966), but at Geiseltal, the specimens were initially thought to represent two forms – a caiman-like alligatorid, *Boverisuchus magnifrons*, and a crocodylid, *Weigeltisuchus geiseltalensis* Kuhn 1938. I follow Kälin (1955) and recognise *W. geiseltalensis* as a junior synonym of *B. magnifrons*. Kuhn (1938) acknowledged similarities between them, and the caiman-like features he indicated in *B. magnifrons* (larger dorsal supraoccipital exposure and constricted supratemporal fenestrae) are concentrated on the skull table, which is very poorly preserved on the holotype (Brochu pers. obs.).

Rauhe & Rossmann (1995) and Rossmann (1998) argued that *B. vorax* and *B. magnifrons*, along with *Planocrania datangensis* from the Early Eocene of China, represent a single pan-Laurasian species. They referred all such material to *P. rollinati*. Skulls from Wyoming (Fig. 3) are consistently mediolaterally broader than those from Germany (Fig. 6a, b), but care must be taken to consider the levels of variation seen in modern species (Kälin 1933). Moreover, most known skulls

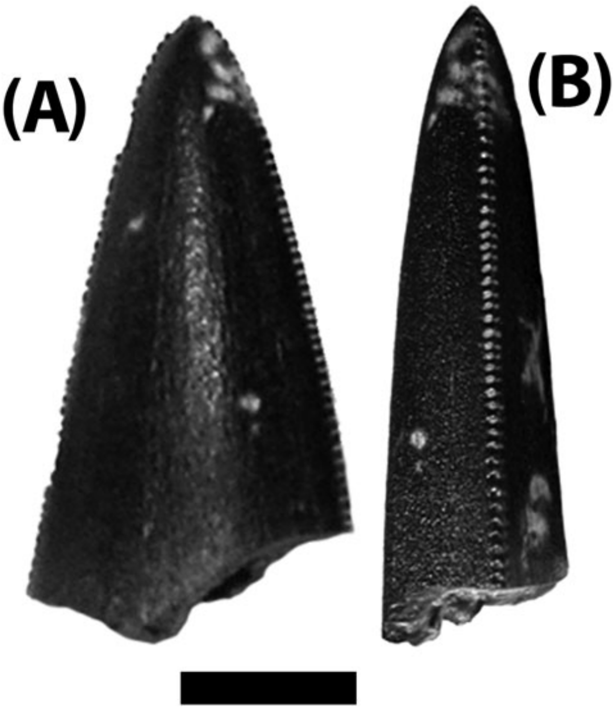

Figure 4 UCM 98628, ?planocraniid tooth, DeBeque Formation (Tiffanian), Moffat Co., Colorado: (A) labial view; (B) mesial view. Scale bar = 1 cm.

are compressed, distorting the original shape and complicating our comparisons. Rossmann (1998, 2000a) argued that the differences between American and European samples were insufficient to justify species-level separation.

Nonetheless, there are consistent differences that lie outside the observed ranges of variation for modern crocodylian species. They also appear to be unrelated to ontogenetic stage or body size. One of these is the relationship between the nasals and the external naris. Rossmann (2000a) stated that the nasals of *P. rollinati* contact the external naris except in one specimen from Geiseltal. One of his figures (Rossmann 2000a, fig. 2) implies a similar situation in at least one specimen from North America (USNM 12957), but the surface of the rostrum is not preserved immediately behind the naris, and the nasals enter the naris in all other appropriately preserved Bridgerian specimens (Fig. 7a). Conversely, there are no known Geiseltal specimens in which the nasals contact the naris, and those specimens in which the relevant part of the skull is preserved invariably show a broad separation between them (Fig. 7b, c). The dorsal surface of the rostrum is imperfectly preserved on the most complete Messel specimen (HLMD Me-5326), but the orientation of the right nasopremaxillary suture relative to the sagittal plane strongly suggests that the premaxillae completely surrounded the naris (Brochu pers. obs.).

Dental occlusion patterns at the tip of the rostrum differ between samples. Based on occlusal pits preserved on the premaxillae, the dentary teeth occluded lingual to their premaxillary counterparts in *B. vorax* (Fig. 7d). The occlusal pits are between, rather than lingual to, premaxillary alveoli in *B. magnifrons* (Fig. 7e). And although the anterior maxillary teeth are ziphodont in both forms, the first six alveoli are circular in *B. vorax* (Fig. 3b) and labiolingually compressed in *B. magnifrons* (Fig. 6a)

The mandibular symphysis of *B. magnifrons* (Fig. 6i) is narrower in dorsal view than that of *B. vorax* (Fig. 3e). This, of course, is consistent with the relatively narrower snout in the German form, and one could argue that such differences are intraspecific in nature. But the anterior end of the dentary between the first and fourth alveoli is also more deeply concave in *B. magnifrons*, even taking postmortem distortion into account (Fig. 6e, h).

Snout shape, by itself, is not a robust difference between known Middle Eocene planocraniids. But taken along with the other consistent differences – whether or not the nasals contribute to the narial rim, whether occlusal pits are lingual to or between premaxillary alveoli, whether the frontoparietal suture contacts the supratemporal fenestrae, and the shape of the dentary – synonymy between *B. vorax* and *B. magnifrons* can be rejected.

1.3.1. *Crocodilus bolcensis*. *Crocodilus bolcensis* Sacco, 1896, based on a skull and articulated skeleton from the Lutetian Monte Purga di Bolca locality of northeastern Italy, is a possible complicating factor. Synonymy with the German material was suggested by Berg (1966) and accepted by later authors (e.g. Rossmann 1998; Kotsakis *et al.* 2004). Skull shape is constent with Messel and Geiseltal material, and fossils from that locality are correlative with Argenton, Messel and lower Geiseltal. One might expect the planocraniids from these regions to be conspecific.

Determining the status of this species bears on nomenclature. *Pristichampsus rollinati* (Gray 1831) has priority over *Crocodilus bolcensis* Sacco, 1896, but *C. bolcensis* has priority over *Boverisuchus magnifrons* Kuhn, 1938. The correct name for the European planocraniid would thus be *Boverisuchus bolcensis* (Sacco 1896).

Nevertheless, there are reasons to be cautious. Surface details are not readily visible on the holotype (Sacco 1896, fig. 5b), and derived character states diagnostic of *B. magnifrons* (e.g. exclusion of the nasals from the naris) are not readily apparent. The teeth of another specimen (Fig. 8) appeared to be unserrated when examined with a 10× hand lens (Brochu pers. obs.), and the mandibular symphysis appears to be craniocaudally short and mediolaterally wide compared with those of *B. magnifrons* or *B. vorax*. This specimen shows no evidence of the ventral armor preserved on articulated *B. magnifrons* skeletons from Geiseltal.

Because so little morphological detail could be obtained from these specimens (in spite of their completeness), the species was not included in this analysis. A closer examination of this material is warranted.

1.3.2. Other European occurrences. In Europe, as in North America, fragmentary specimens might extend the range of planocraniids below the Lutetian. Berg (1969) cited a possible planocraniid from the Paleocene Walbeck locality of Germany, and fossils from the early Eocene might be referable to the group (Berg 1966; Russell 1982; Buffetaut 1985; Antunes 1986; Vasse 1992; Augé *et al.* 1997). They have also been reported from the Bartonian (Russell 1982; Antunes 1986).

But while only Planocraniidae is known with certainty in the Palaeogene of North America, non-eusuchian ziphodont crocodyliforms have been found in the Eocene of Europe (Kuhn 1938; Berg 1966; Antunes 1975; Buffetaut 1982b, 1988; Vasse 1995; Ortega *et al.* 1996; Rossmann *et al.* 2000). Amphicoelous vertebrae consistent with these forms are known from the middle Paleocene of Belgium (Groessens-Van Dyck 1986) and the Bartonian of France (Buffetaut 1986), and they are found in some of the same deposits preserving *Boverisuchus* at Messel and Geiseltal (Berg 1966; Rauhe & Rossmann 1995). Although some have argued that the teeth of a planocraniid can be distinguished from those of a non-eusuchian ziphodont form (Antunes 1986), there is considerable dental variation within these groups (Legasa *et al.* 1993; Prasad & de Lapparent de Broin 2002) and more work is needed before we can distinguish the stratigraphic ranges of planocraniids and similar-looking but unrelated groups.

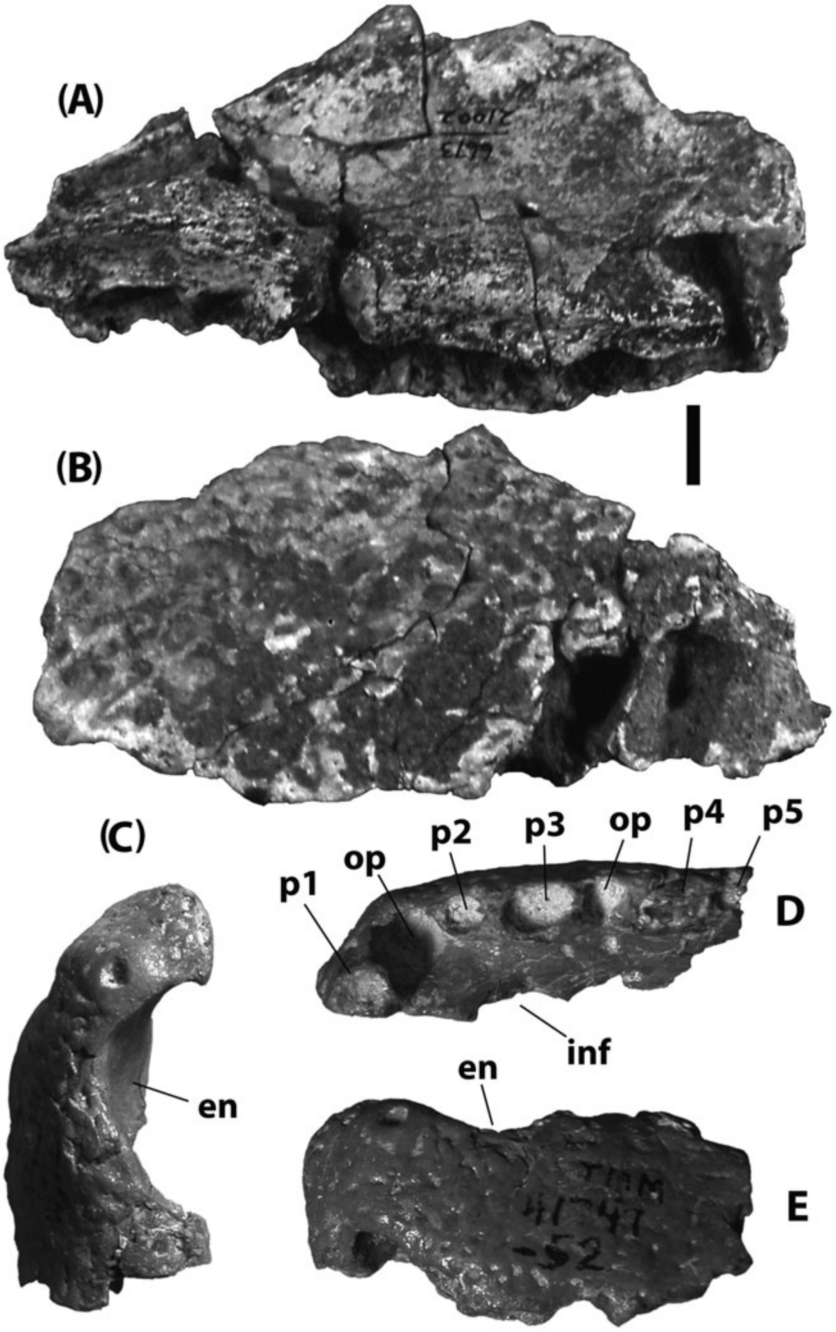

Figure 5 Uintan planocraniids from North America: (A–B) LACM 21002, left maxilla, San Diego Co., California, in lateral (A) and medial (B) views; (C–E) TMM 41717-52, left premaxilla, Devil's Graveyard Formation, Brewster Co., Texas, in dorsal (C), ventral (D) and lateral (E) views. Scale bar = 1 cm. Abbreviations: en = external naris; inf = incisive foramen; op = occlusal pit; p1–p5 = premaxillary alveoli.

Atacisaurus glareae Astre, 1931 from the middle Eocene of Issel, France, has also sometimes been referred to *Boverisuchus* (Rossmann 1998). Vasse (1992) argued that its systematic position was not determinable. The holotype, the symphyseal part of a lower jaw, is now lost (Ortega *et al.* 1996). As figured by Astre (1931), the symphysis appears to have extended back past the tenth dentary alveolus and included a more substantial splenial component than in *Boverisuchus*, and Astre (1931, p. 37) described the carinae of the teeth as "non crénelée."

Astre (1931) also referred a skull (Fig. 9a) to *A. glareae*. It appears to share no derived states with planocraniids. It does, however, share similarities with basal tomistomines such as *Megadontosuchus* Mook, 1955. The lateral squamosal groove flares anteriorly (a feature also found in gavialoids), the supratemporal fenestrae are large and separated by a narrow interfenestral bar, and the skull table is concave at the midline in posterior view. The snout is relatively slender, but the lateral margins are concavoconvex in dorsal view and not linear, as they would be in a planocraniid. The teeth are unknown. A non-eusuchian ziphodont crocodyliform is known from Issel (Ortega *et al.* 1996), but *A. glareae* appears to be a tomistomine and not a planocraniid.

1.4. *Planocrania datangensis* Li, 1976

This is based on an articulated skull and partial mandible from the Nongshan Formation of Guandong Province, China (Li 1976; Fig. 10). It is the only known specimen of the species. The Nongshan Formation is thought to be of Paleocene (Salandian) age (Ting *et al.* 2003, 2011).

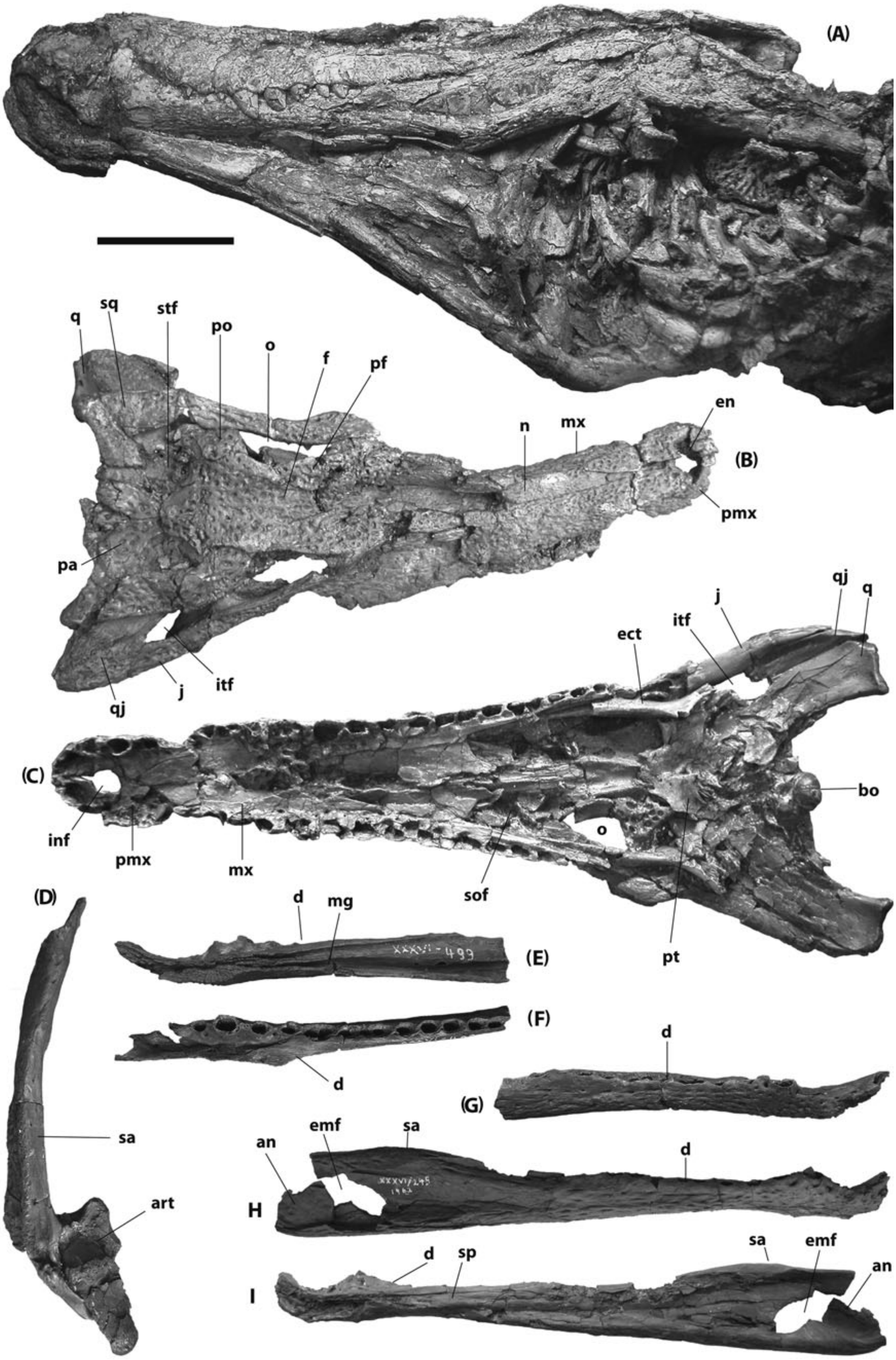

Figure 6 *Boverisuchus magnifrons*, middle Eocene, Geiseltal, Germany: (A) GM LEO X 8001 (holotype, *Weigeltisuchus geiseltalensis*), skull, oblique ventral view ; (B) GM XXXVI 274, skull, dorsal view; (C) GM XVIII 3094, skull, ventral view ; (D) GM XXXV 216, left surangular and articular, dorsal view; (E–G) GM XXXVI 499, anterior end of right dentary, in medial (E), dorsal (F) and lateral (G) views; (H–I) GM XXXVI 245, right mandibular ramus, in lateral (H) and medial (I) views. Scale bar = 5 cm. Abbreviations: an = angular; art = articular; bo = basioccipital; d = dentary; ect = ectopterygoid; emf = external mandibular fenestra; en = external naris; f = frontal; inf = incisive foramen; itf = infratemporal fenestra; j = jugal; mg = Meckelian groove; mx = maxilla; n = nasal; o = orbit; pf = prefrontal; pmx = premaxilla; po = postorbital; pt = pterygoid; q = quadrate; qj = quadratojugal; sa = surangular; sof = suborbital fenestra; sp = splenial; sq = squamosal; stf = supratemporal fenestra.

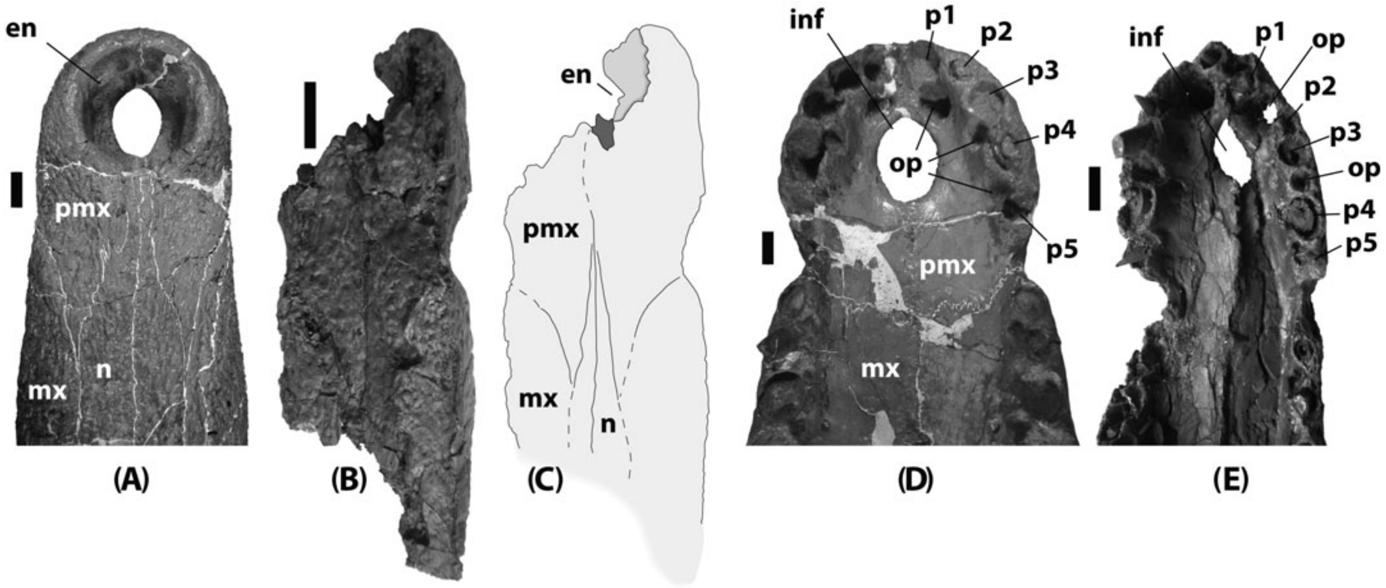

Figure 7 Anterior end of rostrum: (A) FMNH PR399, *Boverisuchus vorax*, dorsal view; (B–C) GM XXXVI 245, *Boverisuchus magnifrons*, dorsal view; (D) FMNH PR399, *Boverisuchus vorax*, ventral view; (E) GM XVIII 526, *Boverisuchus magnifrons*, ventral view. Scale bars = 1 cm. Abbreviations: en = external naris; inf = incisive foramen; mx = maxilla; n = nasal; op = occlusal pit; pmx = premaxilla; p1–p5 = premaxillary alveoli.

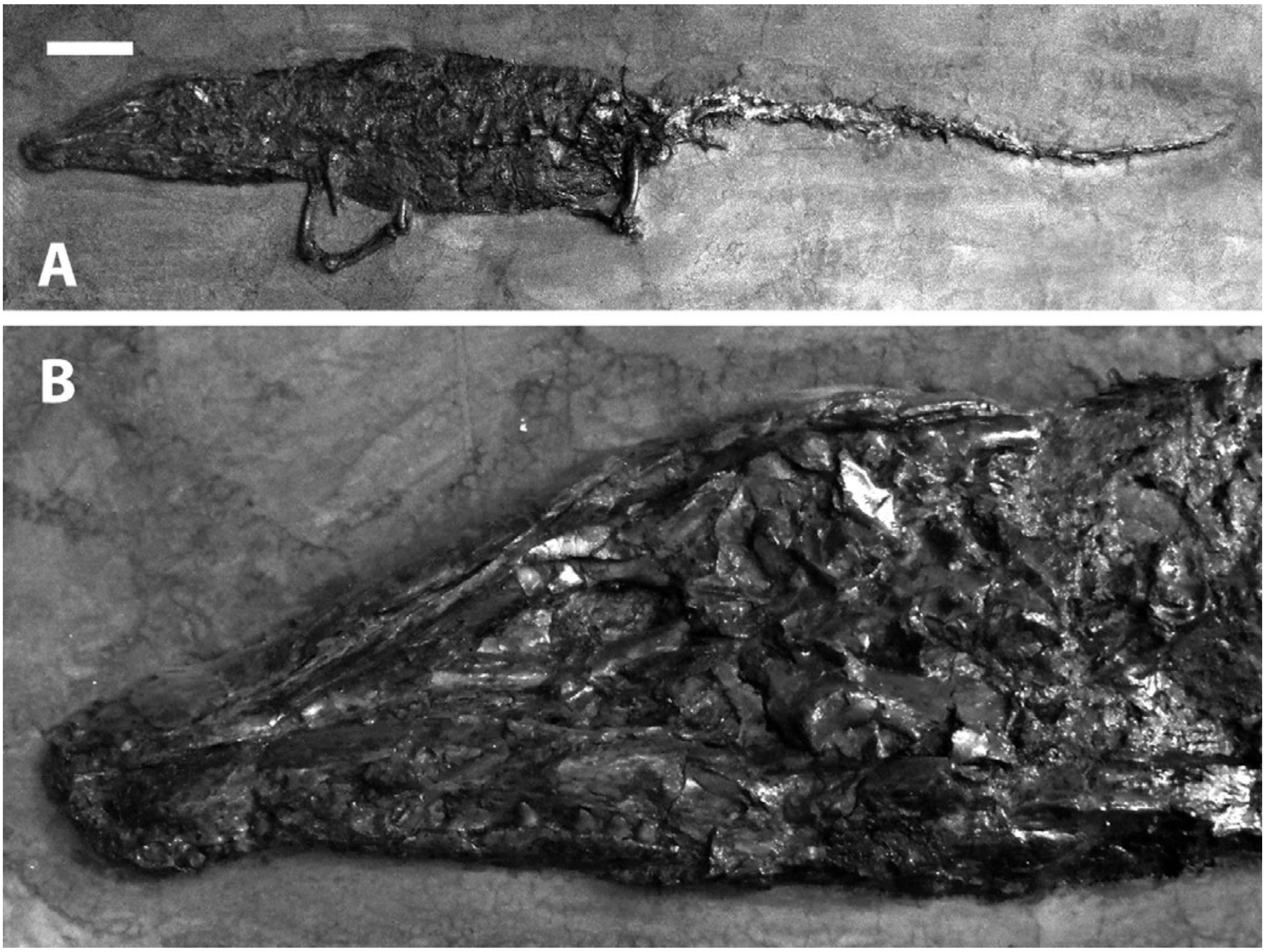

Figure 8 MGPD 27567, *Crocodilus bolcensis*, middle Eocene, Purga di Bolca, Italy: (A) skeleton. Scale bar = 10 cm; (B) closeup of skull and lower jaws.

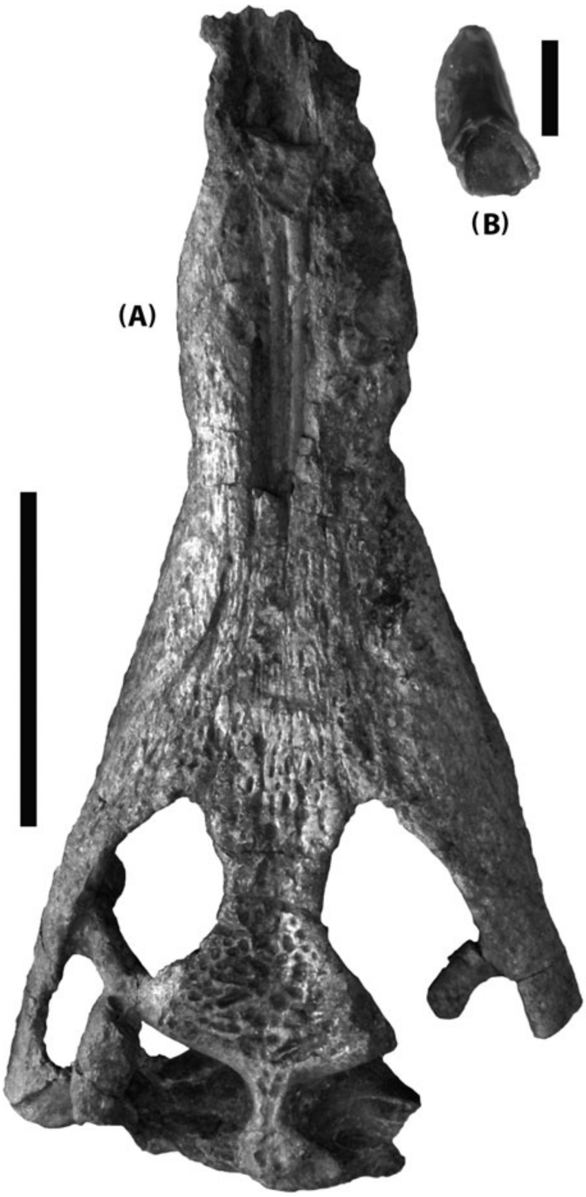

Figure 9 (A) unnumbered specimen at MNHT referred by Astre (1931) to *Atacisaurus glareae*, middle Eocene, France: skull, dorsal view. Scale bar = 10 cm. (B) NHMUK R.4112: Vertebrata indet. tooth, Miocene, Nyanza Province, Kenya. Scale bar = 1 cm.

Planocrania datangensis was referred to *Pristichampsus rollinati* by Rossmann (1998). The overall shape of the snout is similar between the two forms, but there are some clear differences. Most notably, although the teeth of *P. datangensis* are labiolingually compressed, serrations are not apparent (Fig. 11) even with a 10× hand lens. This does not appear to be a preservational artifact. If serrations were present (Li 1976), they were very fine and unlike the more robust serrations found in both species of *Boverisuchus*. The holotype of *P. datangensis* is somewhat smaller than most *Boverisuchus* skulls, but smaller *Boverisuchus* nonetheless have serrated teeth. The nasal bones also reach the external naris and the frontoparietal suture passes through the supratemporal fenestrae in *P. datangensis*.

1.5. *Planocrania hengdongensis* Li, 1984

Like *P. datangensis*, *P. hengdongensis* is known from only a single specimen (Li 1984; Fig. 12). It was collected from what Li (1984) described as red beds of possible Palaeocene age in Hunan Province, China. These are now known to be part of the late Palaeocene Lower Lingcha Formation (Ting *et al.* 2003).

Li (1984) stated that the maxillary teeth of *P. hengdongensis* are serrated. This is difficult to assess, as there are very few preserved tooth crowns available. The premaxilla described by Li (1984) is no longer with the specimen. Only one maxillary tooth crown is preserved, and although compressed, it does not appear to be serrated. The same is true for teeth preserved on the left dentary.

There are several other differences between *P. hengdongensis* and *P. datangensis*. The frontal between the orbits is unusually broad in *P. datangensis*, as it is in *Boverisuchus*, but not in *P. hengdongensis*. The splenial does not contribute to the mandibular symphysis in *P. hengdongensis*, as it does in *P. datangensis* and *Boverisuchus*. *Planocrania hengdongensis* also appears to have a shorter maxillary toothrow than *P. datangensis*. Li (1984) estimated 11 to 12 maxillary teeth in *P. hengdongensis*. The alveolar series on both maxillae are damaged, and the number could have been larger, but would not have exceeded 14 (and was most likely 12 or 13; Brochu pers. obs.). *Planocrania datangensis*, however, had 15 or 16 maxillary alveoli (Li 1976), as did *Boverisuchus* (Rossmann 2000a).

The holotype of *P. hengdongensis* might be from an immature animal. Nevertheless, although some differences between *P. datangensis* and *P. hengdongensis* might be ontogenetic in nature, the number of alveoli in any of the tooth-bearing bones never increases ontogenetically in crocodylians. Indeed, the number sometimes decreases by one or two – faster-growing alveoli might crowd out their more slowly-growing neighbors. Even if *P. hengdongensis* is known from an immature individual, it can be distinguished from all other planocraniids.

1.6. Other Asian occurrences

Ziphodont crocodyliform teeth are known from the Eocene of the Indian Subcontinent (Sahni & Srivastava 1976; Buffetaut 1978; Sahni *et al.* 1978; Sah & Schleich 1990; Srivastava & Kumar 1996). A partial premaxilla with teeth from the early Eocene of Himachal Pradesh, India, was described by Panadés I Blas *et al.* (2004).

Two putative planocraniids – *Pristichampsus birjukovi* Efimov, 1988 and *Pristichampsus kuznetzovi* Efimov, 1988 – have been described from middle Eocene deposits in the Zaysan Depression region of Kazakhstan. They have sometimes been synonymised with *B. magnifrons* (Rossmann 1998). The holotype of *P. kuznetzovi* has not been figured. The skull of the holotype of *P. birjukovi* is limited to a skull table, braincase and left quadrate ramus but, as figured by Efimov (1993), the quadrate condyle appears similar to those of *B. magnifrons* and *B. vorax*. This material should be revisited and reevaluated.

1.7. Australasia

A ziphodont eusuchian, *Quinkana* Molnar, 1981, is also known from the Late Oligocene through Quaternary of Australia and New Guinea (De Vis 1905; Molnar 1981; Megirian 1994; Willis & Mackness 1996; Willis 1997). Phylogenetic analyses suggest that *Quinkana* is a mekosuchine crocodyloid and, thus, part of a diverse endemic Australasian radiation (Willis 1993; Salisbury & Willis 1996; Willis & Mackness 1996; Molnar *et al.* 2002; Brochu 2007), but a relationship to *Boverisuchus* has also been proposed (Rauhe & Rossmann 1995; Rossmann 1998). This would suggest transoceanic dispersal from Laurasia and a substantial missing history for the group.

None of the described species is well known, and it was represented by a composite taxon in earlier analyses based on this matrix (e.g. Brochu 2007; Vélez-Juarbe & Brochu in press). Most data came from *Q. fortirostrum* Molnar, 1981, which was observed first-hand, and *Q. timara* Megirian, 1994, which was coded from the literature. The other two species (*Q. babarra* Willis & Mackness, 1996 and *Q. meboldi* Willis, 1997) were

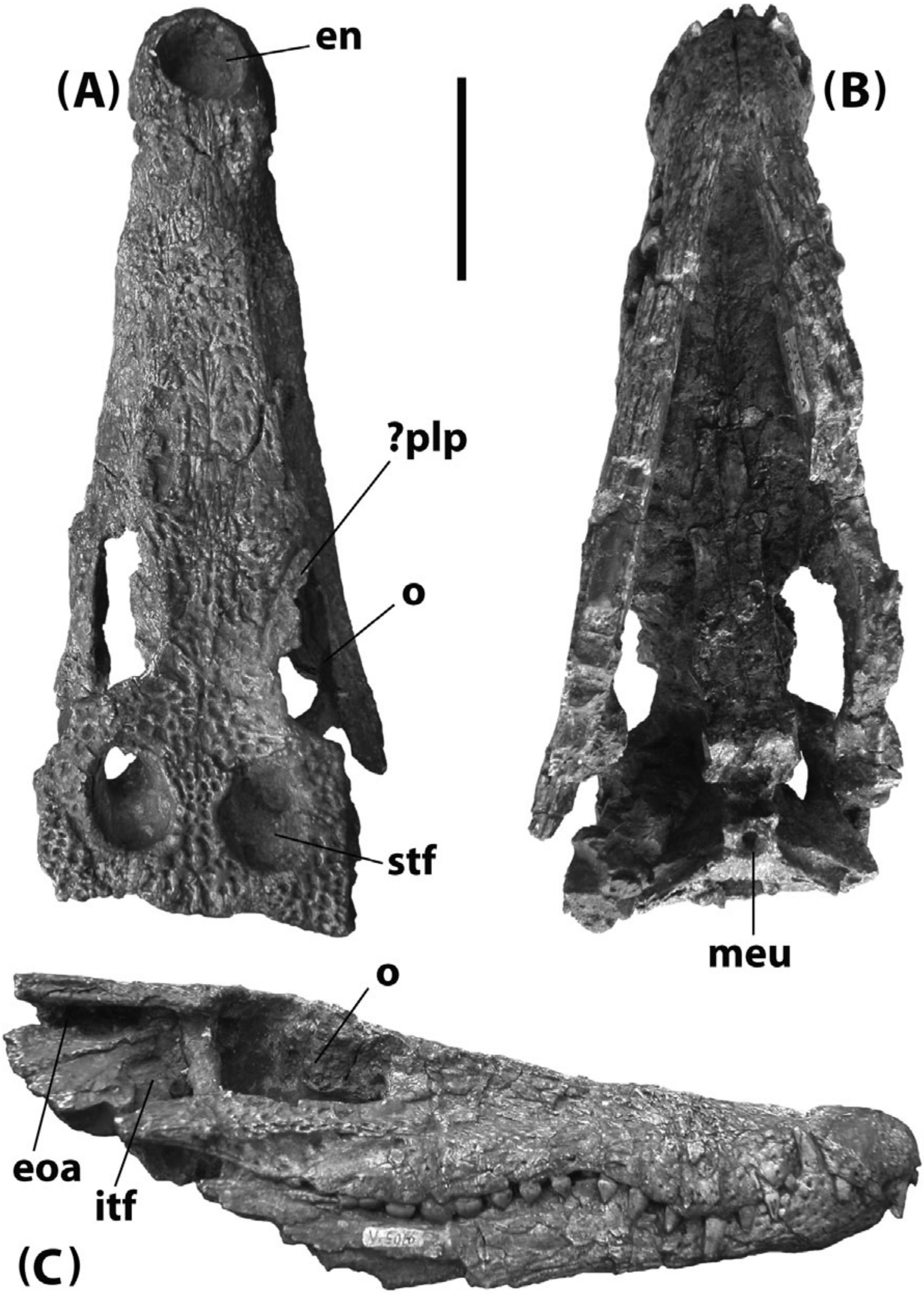

Figure 10 IVPP V5016 (holotype), *Planocrania datangensis*, Palaeocene, China: skull and articulated dentaries in dorsal (A), ventral (B) and right lateral (C) views. Scale bar = 5 cm. Abbreviations: en = external naris; eoa = external otic aperture; itf = infratemporal fenestra; meu = median Eustachian foramen; o = orbit; ?plp = possible palpebral bone; stf = supratemporal fenestra.

largely redundant with *Q. fortirostrum* and *Q. timara* in the matrix. The analyses unambiguously put *Quinkana* among the mekosuchines, and moving the composite to Planocraniidae increases tree length by at least 12 steps.

Depending on how they are applied, composite taxa make *a priori* assumptions about phylogenetic relationships that should be tested. Unfortunately, although the species currently referred to *Quinkana* collectively support a mekosuchine affinity, they are individually incomplete enough to limit their informative value and were not included in this analysis. Additional material relevant to mekosuchine phylogeny is currently under study (Salisbury *et al.* 2010), and its inclusion, along with a more detailed comparison with the known species of *Quinkana*,

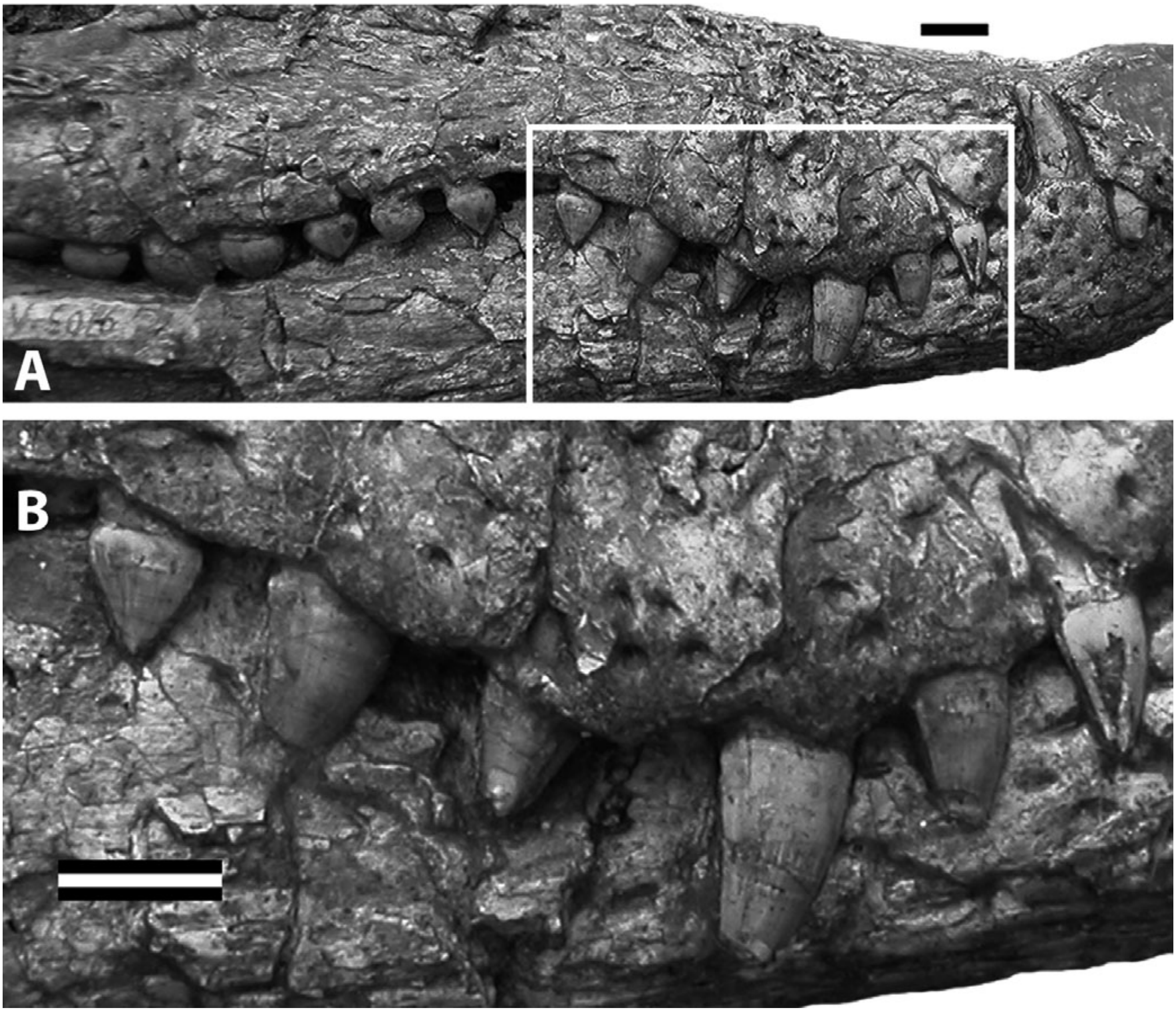

Figure 11 (A) IVPP V5016 (holotype), *Planocrania datangensis*; (B) closeup of teeth of right maxilla. Scale bars = 1 cm.

will enhance our capacity to test the relationships of these species.

1.8. Africa

The Cenozoic fossil record of ziphodont crocodyliforms in Africa is spotty at best. Non-eusuchian forms have been described from the Eocene of Algeria (Buffetaut 1982a, 1989), and an isolated tooth from the Miocene of present-day Kenya was discussed by Andrews (1914), who suggested a possible referral to Planocraniidae. If correct, it would represent a substantial geographic and stratigraphic range extension for the group.

The tooth is compressed, but although the carinae are expansive, they are unserrated (Fig. 9b). The enamel is translucent, and it is not clear it had a root. It is difficult to refer the specimen to Crocodyliformes, much less Planocraniidae.

2. Phylogenetic analysis

2.1. Methods

A maximum parsimony analysis was conducted based on a matrix of 89 ingroup taxa and 189 discrete morphological characters (Appendix 1). All characters had equal weight, and multistate characters were treated as unordered. *Bernissartia fagesii* was the outgroup. One hundred heuristic searches were conducted using PAUP* (Swofford 2002) with the starting order of ingroup taxa randomised for each iteration.

A list of planocraniid specimens used for scoring the matrix is provided in Appendix 2.

2.2. Results

The analysis recovered 5044 equally optimal trees 633 steps in length (CI excluding uninformative characters = 0·367, RI = 0·820). A strict consensus of these trees (Fig. 13) is consistent with the results of previous morphological analyses of Crocodylia (e.g., Salisbury & Willis 1996; Brochu 1997, 2004, 2006, 2011; Delfino *et al.* 2005, 2008a, b; Piras & Buscalioni 2006; Martin 2007; Ösi *et al.* 2007; Shan *et al.* 2009; Puértolas *et al.* 2011; Brochu & Storrs 2012), albeit with diminished resolution at some levels. The closest relatives of Crocodylia in this study are the hylaeochampsids, and the root node of Crocodylia is a polytomy involving gavialoids, *Borealosuchus* and a lineage including Crocodyloidea, Alligatoroidea and Planocraniidae. Planocraniidae is the sister lineage to Brevirostres.

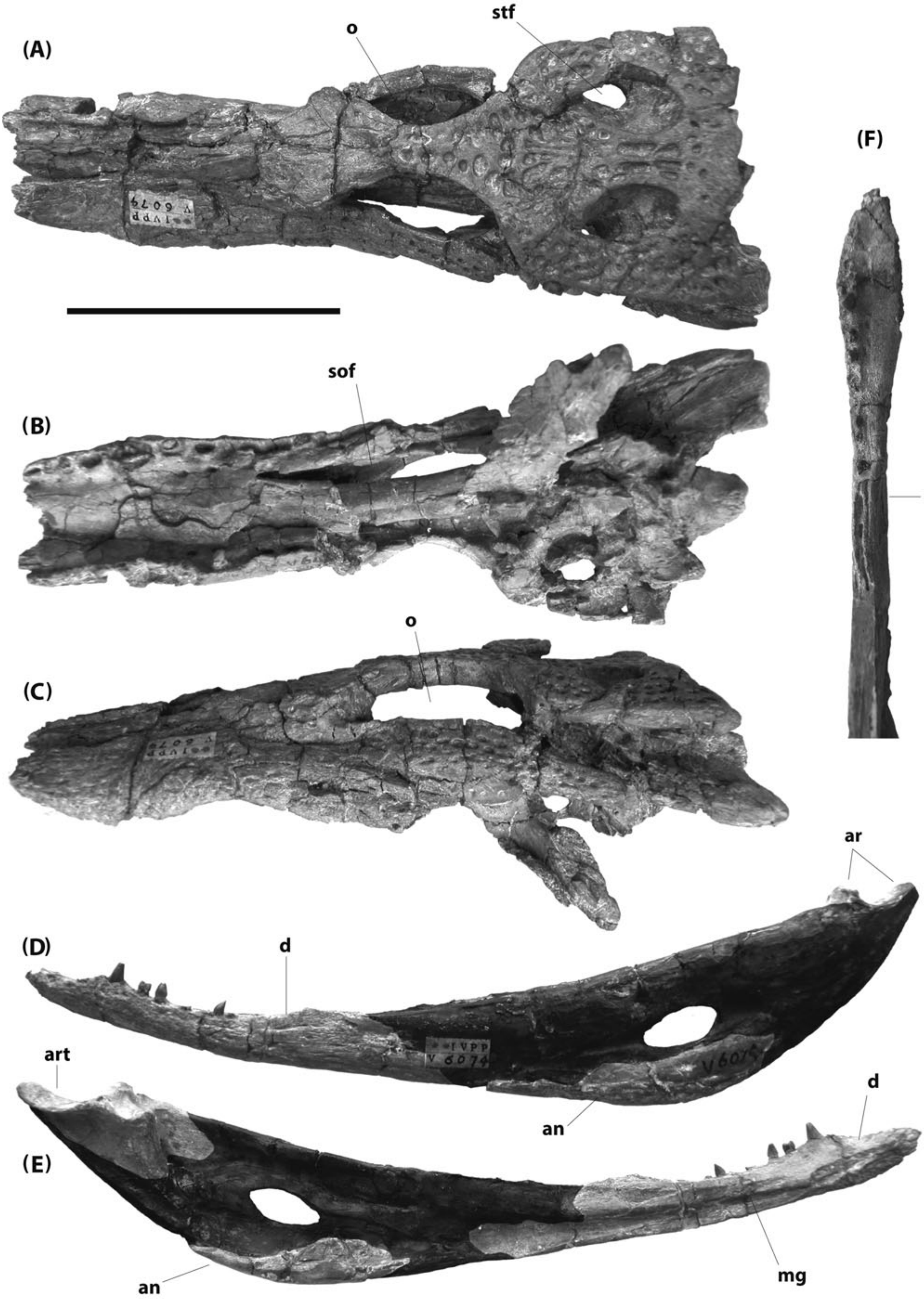

Figure 12 IVPP V6079 (holotype), *Planocrania hengdongensis*, Palaeocene, China: (A–C) skull in dorsal (A), ventral (B) and left lateral (C) views; (D–E) left mandible in lateral (D) and medial (E) views; (F) left dentary in dorsal view. Portions of mandibular ramus restored with epoxy digitally darkened in (D) and (E). Scale bar = 5 cm. Abbreviations: an = angular; art = articular; d = dentary; mg = Meckelian groove; o = orbit; sof = suborbital fenestra; stf = supratemporal fenestra.

Figure 13 Strict consensus of 5044 equally optimal trees recovered from maximum parsimony analysis of 89 ingroup taxa and 189 morphological characters (length = 633, CI excluding uninformative characters = 0·367, RI = 0·820). Trees rooted on *Bernissartia fagesii.*

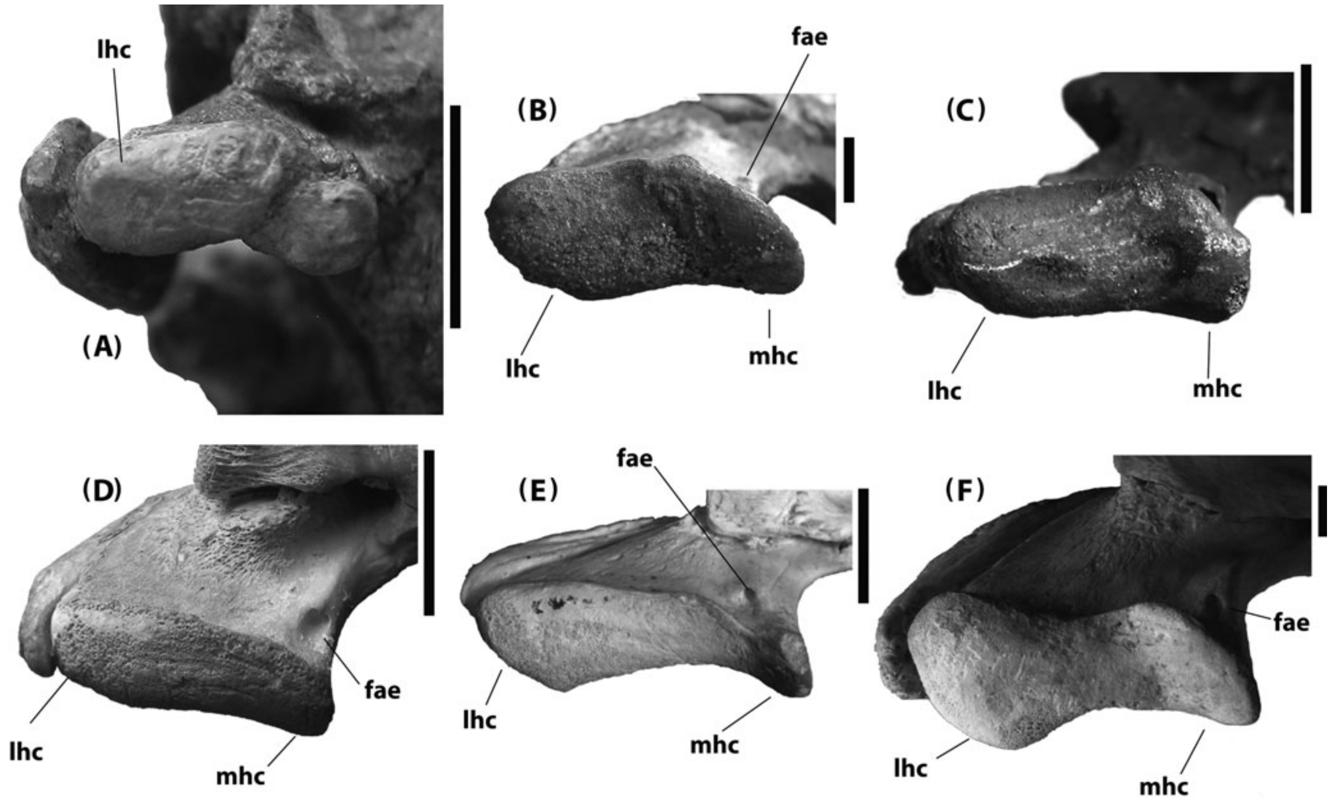

Figure 14 Morphology of the left quadrate condyle in planocraniids (A–C) and other crocodylian groups (D–F): (A) IVPP V6079 (holotype), *Planocrania hengdongensis;* (B) FMNH PR479, *Boverisuchus vorax*; (C) GM XXII 815, *Boverisuchus magnifrons*; (D) FMNH 23505, *Gavialis gangeticus*; (E) FMNH 69871, *Paleosuchus palpebrosus*; (F) FMNH 17157, *Crocodylus niloticus*. D, E, and F are digitally-reversed right quadrates. Scale bars = 1 cm. Abbreviations: fae = foramen aëreum; lhc = lateral hemicondyle; mhc = medial hemicondyle.

2.3. Position of Planocraniidae within Crocodylia

A distinct convex process or lamina is present on the anterolateral corner of the paramedian osteoderms of gavialoids, *Borealosuchus*, and non-crocodylian eusuchians (Brochu 2004; Brochu *et al.* 2012). This is absent in alligatoroids, crocodyloids and planocraniids. Some basal alligatoroids (e.g. *Diplocynodon*) and crocodyloids (e.g. "*Crocodylus*" *affinis*) preserve a modest concavity on the anterior margin of the paramedian osteoderms (Brochu pers. obs.); this may indicate a remnant of the ancestral lamina, but none of these forms has anything like the plesiomorphic condition, and its absence unites Planocraniidae and Brevirostres in this analysis.

The second unambiguous synapomorphy at this node comes as a surprise – a quadrate ramus with a small and prominently depressed medial hemicondyle. This was previously thought to diagnose Alligatoroidea (Fig. 14e) and to be a consequence of the dorsal shift in the position of the quadrate foramen aëreum (Brochu 1999). But in fact, a similar quadrate is preserved on the holotype of *P. hengdongensis* (Fig. 14a). The foramen aëreum is not located as far dorsally in this form, suggesting that depression of the medial hemicondyle is unrelated to changes in quadrate-articular pneumaticity.

There is some distortion to the quadrate ramus of *P. hengdongensis*. I am confident that the general outline of the condylar region is close to what a fresh skull would reveal, but one could argue that modest damage to a plesiomorphic crocodylian quadrate – one in which the medial hemicondyle is small and ventrally reflected, but without the sharp demarcation – might mimic the condition seen in alligatoroids. Caution is also required because the quadrates are poorly known in *P. datangensis*, and neither *Boverisuchus* (Fig. 14b, c) nor crocodyloids (Fig. 14f) share this condition.

In previous analyses (e.g. Brochu 1997), keeled paramedian osteoderms were thought to diagnose this clade. This is no longer true if *Borealosuchus* is a basal gavialoid lineage (as is the case in some optimal trees in this analysis); the osteoderms of *Bernissartia* and at least some hylaeochampsids (e.g. *Acynodon adriaticus*) are keeled. In that case, the lack of keeled osteoderms links *Borealosuchus* and gavialoids.

Likewise, whether exclusion of the nasal bones from the naris diagnoses this group depends on how basal crocodylian relationships are resolved. The nasals form part of the narial border in most basal eusuchians (including hylaeochampsids), basal planocraniids and (at least ancestrally) in alligatoroids and crocodyloids, but not in gavialoids or *Borealosuchus*. A close relationship between *Borealosuchus*, Planocraniidae and Brevirostres would require loss of this contact at the root of Crocodylia and its reacquisition at this level. A closer relationship between *Borealosuchus* and gavialoids would be supported by this feature, making the condition seen in basal planocraniids ancestral for Crocodylia.

Another complication is the *Gavialis–Tomistoma* issue. Moving all putative gavialoids up with *Tomistoma* (and thus rendering Planocraniidae a non-crocodylian lineage) renders keeled osteoderms and nasals contacting the naris plesiomorphic for Crocodylia. If, following divergence time estimates based on molecular analyses (Harshman *et al.* 2003; Roos *et al.* 2007; Oaks 2011), we move only post-Lutetian gavialoids (*Eogavialis*, *Gavialis*, Gryposuchinae) and leave the thoracosaurs where they are, these conditions would be plesiomorphic for Crocodylia only if *Borealosuchus* and thoracosaurs were closely related.

Some planocraniids preserve a mosaic of crocodile-like and alligator-like features. The iliac blade has a modest indentation in *Boverisuchus* and, ancestrally, in Crocodyloidea.

Indentations arise independently in caimans and *Alligator*, but the iliac blade in basal alligatoroids is smooth. Likewise, the lateral carotid foramen on the exoccipital opens dorsal to the posterolateral exposure of the basisphenoid in *B. vorax* and all crocodyloids. Conversely, the squamosal–quadrate suture of *B. vorax* extends no further than the posteroventral corner of the auditory aperture, as in most alligatoroids. These character states cannot be assessed in other planocraniids.

2.4. Relationships within Planocraniidae

Support for planocraniid monophyly in this study is comparatively thin. Only a single unambiguous synapomorphy unites the group – labiolingually compressed teeth throughout the maxillary or post-caniniform dentary toothrows. The posteriormost teeth are somewhat longer mesiodistally than wide labiolingually in most crocodylians, and strong compression can be observed in the living smooth-fronted caimans (*Paleosuchus*) and dwarf crocodiles (*Osteolaemus*), but this is true only for teeth toward the back of the mouth. Only in planocraniids (and *Quinkana*) do we see strong compression throughout the maxillary series and in most of the dentary teeth.

Planocrania datangensis and *Boverisuchus* share upturned orbital margins. This feature arose multiple times within Crocodylia, but is absent from *Borealosuchus* and the earliest gavialoids, crocodyloids and alligatoroids. At the same time, the frontal is very broad between the orbits in *P. datangensis* and *Boverisuchus*. Indeed, the frontal as a whole and the orbital surfaces in ventral view are comparatively broad in these forms compared with most other eusuchians.

The broad frontal may serve a similar function as the expanded compound palpebrals in living deep-snouted crocodylians such as *Paleosuchus* and *Osteolaemus* – it may help reorient the orbits. The eyes face more laterally in deep-snouted forms than they do in other crocodylians. The large palpebrals of *Paleosuchus* were once thought to help protect the eyes from debris in flowing streams (Medem 1958), but neither *Paleosuchus* nor *Osteolaemus* are exclusively (or even preferentially) found in such environments (Magnusson 1985; Magnusson & Lima 1991; Kofron 1992; Ouboter 1996; Luiselli *et al.* 1999; Riley & Huchzermeyer 1999; Shirley *et al.* 2009). That two groups with similar modifications to the skull and osteoderms would share similar palpebral bones suggests a common cause. These structures are more or less fixed and move very little when the eyelid is closed, and they may instead move the medial margin of the orbit laterally, thereby reorienting the orbit itself. Derived planocraniids may have found a different solution – the frontals themselves expand. The holotype of *P. datangensis* appears to preserve articulated palpebrals (Fig. 10a), and these, too, may have helped impart a lateral orientation to the orbits, but palpebrals are unknown in *Boverisuchus* and are universally lacking in articulated skeletons.

In *Planocrania datangensis* and *Boverisuchus*, the splenials meet at the midline. This is not true for *P. hengdongensis*, but whether this is a synapomorphy at this level depends on how basal crocodylian lineages are resolved. Most basal crocodylians have splenial symphyses, and the lack of this feature could instead diagnose *P. hengdongensis*.

Likewise, occlusal patterns may or may not diagnose this node. Ancestrally for Eusuchia, the dentary caniniforms occluded in a notch between the maxilla and premaxilla, but dentary teeth occluded lingual to their maxillary counterparts otherwise. Derived alligatoroids lost the notch, and derived crocodyloids lost the overbite (Brochu 2003). *Planocrania datangensis* has an intermediate condition with occlusal pits between (and not lingual to) the seventh and eighth maxillary alveoli, but an overbite behind the premaxillary–maxillary notch otherwise. This is the condition found in basal species of *Borealosuchus* (*B. sternbergii*), a few alligatoroids, and in all but the basalmost crocodyloids. Other planocraniids, by contrast, retain the plesiomorphic maxillary overbite. All known gavialoids (including thoracosaurs) have completely interdigitating dentition. As a result, it is difficult to resolve the ancestral condition for this character in early crocodylians.

Boverisuchus is diagnosed by the presence of serrated teeth. The teeth of *P. hengdongensis* and *P. datangensis* are flattened, but the carinae are either smooth or bear serrations that cannot be seen with the unaided eye. In contrast, the teeth of *B. vorax* and *B. magnifrons* bear prominent serrations.

A highly modified quadrate condyle might also diagnose this node, though the absence of information about the quadrates of *P. datangensis* renders it ambiguous. In *Boverisuchus*, there is a prominent dorsal projection on the surface of the quadrate between the hemicondyles (Fig. 14b, c; Langston 1975; Rossmann 2000a). Similar quadrates are seen in some noneusuchian altirostral taxa, such as *Sebecus* (Langston 1975), and there might be a correlation between this quadrate type and lateral snout flattening. Whether *Quinkana* had a similar quadrate is unclear.

3. Discussion

I sought to accomplish two goals with this manuscript: first, clarifiy the nomenclatural status and species-level diversity of Paleogene ziphodont eusuchians; and second, provide a preliminary estimate of their phylogenetic relationships.

The material available to Cuvier in the 1820s was visibly very different from any other crocodyliform known at the time, but subsequent discoveries in Europe, North America and Australia have diminished its diagnostic value. The purposes of precision are best served by constructing our nomenclatural framework on more diagnosable specimens. From the material studied for this analysis, at least four valid species can be recognised – *Boverisuchus magnifrons*, *Boverisuchus vorax*, *Planocrania datangensis*, and *Planocrania hengdongensis*. *Crocodilus bolcensis* and planocraniids of Uintan age from North America may also be distinguishable, but more information is needed.

Although it appears distinctive, phylogenetic support for planocraniid monophyly is weaker than we might like. There are two reasons for this. First, although two derived planocraniids (*B. vorax* and *B. magnifrons*) are well-known, their more basal relatives are not. Neither is the basalmost known crocodyloid (*Prodiplocynodon*). Secondly, relationships at the root of Crocodylia are less stable than in previous analyses. Whether *Borealosuchus* is closer to Brevirostres or to Gavialoidea is an open question, and we are beginning to understand just how alligator-like the closest relatives of Crocodylia were (Turner & Brochu 2010). Characters formerly diagnosing Alligatoroidea and subordinate clades may instead by plesiomorphic at a more inclusive level. For the moment, planocraniids seem to be linked together as animals sharing similar rostral and dental geometry and exclusion from the Alligatoroidea + Crocodyloidea group.

With only four species in the analysis, we can say little about planocraniid historical biogeography, except that the group appears to be of Laurasian origin. All known planocraniids are from North America and Eurasia, as are the earliest known members of proximate clades. This is consistent with broad phylogenetic and biogeographic patterns throughout the Palaeogene; while endemic radiations dominated crocodyliform diversity during the Neogene, lineages from earlier in the Cenozoic tended to be morphologically uniform and geographically widespread (Brochu 2003).

The evolutionary history suggested by our limited sample bears on previous speculation about planocraniid paleoecology. Ziphodont crocodyliforms have generally been interpreted as terrestrial predators (Molnar 1981; Rossmann 1999, 2000b, c), but as noted by Wroe (2002), many of the features thought to indicate a more terrestrial habit for *Boverisuchus* – deep snout, laterally-directed orbits, compressed teeth, improved capacity to hold the head in an elevated position – are found in modern *Paleosuchus*, which is still a semiaquatic animal, even if it sometimes spends less time in the water than other sympatric crocodylians (Medem 1958; Magnusson 1985; Magnusson & Lima 1991; Ouboter 1996). The same is true for *Osteolaemus* – it has a deep snout with compressed teeth, but would not be described as a terrestrial predator (Kofron 1992; Luiselli *et al.* 1999; Riley & Huchzermeyer 1999; Shirley *et al.* 2009). One might instead argue that smooth-fronted caimans and dwarf crocodiles are reasonable modern analogs for planocraniid ecology.

The analogy might be imperfect. Similarities to *Paleosuchus* and *Osteolaemus* are greatest with the oldest planocraniids known from more than teeth – *Planocrania hengdongensis* and *P. datangensis*. Whether the serrated teeth and specialised quadrate seen in *Boverisuchus* indicate an ecological difference is unclear, but their larger body size might. The two known specimens of *Planocrania* might be juveniles, but *Boverisuchus* – though not really a large crocodyliform – regularly exceeded the maximum sizes attained by *Paleosuchus* and *Osteolaemus* (Medem 1958; Luiselli *et al.* 1999; Campos *et al.* 2010). There are also some postcranial differences between *Boverisuchus* and the living dwarf forms, such as the hooflike unguals (which are not a preservational artifact) and substantially more robust muscle attachment surfaces on the limb bones.

In any case, *Boverisuchus* appears to have been derived not directly from a more conventional semiaquatic ambush predator in the immediate aftermath of the Cretaceous–Palaeogene mass extinction, but from something more like a smooth-fronted caiman. This may have been an ecological shift away from the water, or it may merely have been enhancement of the adaptations found in smaller deep-snouted crocodylians.

This question, and the others left unanswered in this paper, can only be addressed with improved sampling. Planocraniids must have been present at least as far back as the Campanian, and some of the Asian species not included in this study – especially those from the Zaysan Depression – should be included. But we must also fortify our sample of characters relevant to this part of the tree; the earliest planocraniids were probably not altirostral, and whether current data sets are capable of recognising planocraniids with a more conventional cranial morphology is doubtful. But the effort may yield benefits beyond the planocraniids – it may shed much-needed light on the origins of Crocodylia itself.

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5. Appendices

5.1. Appendix 1. Character list and matrix used in phylogenetic analysis

The number in square brackets following the character number indicates the original character number in the analyses of Brochu (1997, 1999).

(1) [1]: Ventral tubercle of proatlas more than one-half (0) or no more than one half (1) the width of the dorsal crest.

(2) [2]: Fused proatlas boomerang-shaped (0) strap-shaped (1) or massive and block-shaped (2).

(3) [10]: Proatlas with prominent anterior process (0) or lacks anterior process (1).

(4) [17]: Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1).

(5) [5]: Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0) or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1). (Modified from Clark 1994, character 89.)

(6) [14]: Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1).

(7) [16]: Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end.

(8) [15]: Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other.

(9) [20]: Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1).

(10) [21]: Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1).

(11) [11]: Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1).

(12) [12]: Axis neural spine crested (0) or not crested (1).

(13) [3]: Posterior half of axis neural spine wide (0) or narrow (1).

(14) [4]: Axis neural arch lacks (0) or possesses (1) a lateral process (diapophysis). (Adapted from Norell 1989, character 7.)

(15) [6]: Axial hypapophysis located toward the center of centrum (0) or toward the anterior end of centrum (1).

(16) [19]: Axial hypapophysis without (0) or with (1) deep fork.

(17) [7]: Hypapophyseal keels present on eleventh vertebra behind atlas (0) twelfth vertebra behind atlas (1) or tenth vertebra behind atlas (2).

(18) [8]: Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1). (Adapted from Norell 1989, character 12; Norell & Clark 1990, character 11; Clark 1994, character 91.)

(19) [9]: Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1).

(20): Cervical and anterior dorsal centra lack (0) or bear (1) deep pits on the ventral surface of the centrum.

(21) [18]: Presacral centra amphicoelous (0) or procoelous (1). (Adapted from several previous analyses, e.g. Benton & Clark 1988; Norell & Clark 1990, characters 8 and 10; Clark 1994, characters 92 and 93.)

(22) [13]: Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0) or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1).

(23) [22]: Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1). (Adapted from Benton & Clark 1988.)

(24) [23]: Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1).

(25) [24]: Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1).

(26) [25]: Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1).

(27) [26]: Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

(28) [29]: *M. teres* major and *M. dorsalis* scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1).

(29) [27]: Olecranon process of ulna narrow and subangular (0) or wide and rounded (1).

(30): Distal extremity of ulna expanded transversely with respect to long axis of bone; maximum width equivalent to that of proximal extremity (0) or proximal extremity considerably wider than distal extremity (1). (Salisbury *et al.* 2006, character 173.)

(31) [30]: Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2).

(32) [31]: Anterior end of interclavicle flat (0) or rodlike (1).

(33) [34]: Iliac anterior process prominent (0) or virtually absent (1). (Adapted from Benton & Clark 1988; Clark 1994, character 84; although transformation here is different.)

(34) [28]: Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (wasp-waisted; 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4).

(35) [32]: Supraacetabular crest narrow (0) or broad (1).

(36) [33]: Limb bones relatively robust, and hindlimb much longer than forelimb at maturity (0) or limb bones very long and slender (1).

(37) [160]: M. caudofemoralis with single head (0) or with double head (1).

(38) [35]: Dorsal osteoderms not keeled (0) or keeled (1). (Adapted from Buscalioni *et al.* 1992, character 22.)

(39) [36]: Dorsal midline osteoderms rectangular (0) or nearly square (1). (Adapted from Norell & Clark 1990, character 16; Clark 1994, character 95.)

(40) [37]: Four (0) six (1) eight (2) or ten (3) contiguous dorsal osteoderms per row at maturity (adapted from Norell & Clark 1990, character 12; Clark 1994, character 97.)

(41) [38]: Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3).

(42) [39]: Ventral armor absent (0) or single ventral osteoderms (1) or paired ventral ossifications that suture together (2). (Adapted from Buscalioni *et al.* 1992, character 21.)

(43) [40]: Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1). (Adapted from Norell & Clark 1990, character 13; Clark 1994, character 96.)

(44) [155]: Ventral scales have (0) or lack (1) follicle gland pores (Poe 1997.)

(45) [156]: Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2). (Poe 1997.)

(46) [157]: Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales (2). (Poe 1997.)

(47) [52]: Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0) or fourth alveolus larger than third and alveoli are separated (1).

(48) [53]: Anterior dentary teeth strongly procumbent (0) or project anterodorsally (1).

(49): Dentary symphysis extends to fourth or fifth alveolus (0) or sixth through eighth alveolus (1) or behind eighth alveolus (2). (Modified from Brochu 2004, character 166.)

(50) [68]: Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli.

(51): Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14. (Modified from Brochu 2004, character 167.)

(52) [41]: Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1). (Adapted in part from Norell 1988, character 15; Norell 1989, character 8.)

(53) [42]: Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2). (Adapted in part from Norell 1988, character 15; Norell 1989, character 8.)

(54) [43]: Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer

than five dentary alveoli; splenial forms wide V within symphysis (3) or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow V (4). (Adapted from Clark 1994, character 77.)

(55) [46]: Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2). (Adapted from Norell 1988, character 12.)

(56) [54]: Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1).

(57) [55]: Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

(58) [56]: Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1).

(59) [59]: Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1).

(60) [47]: Angular–surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1). (Adapted from Norell 1988, character 40.)

(61) [48]: Anterior processes of surangular unequal (0) or subequal to equal (1).

(62) [61]: Surangular with spur bordering the dentary toothrow lingually for at least one alveolus length (0) or lacking such spur (1).

(63) [62]: External mandibular fenestra absent (0) or present as narrow slit, no discrete fenestral concavity on angular dorsal margin (1) or present with discrete concavity on angular dorsal argin (2) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (3). (Clark 1994, character 75; incorporates information from Norell 1988, character 14.)

(64) [65]: Surangular–dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1).

(65) [66]: Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1).

(66) [67]: Surangular–angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1).

(67) [106]: Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1).

(68) [44]: Articular-surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3).

(69) [45]: Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1).

(70) [49]: Foramen aerum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1). (Adapted from Norell 1988, character 16.)

(71) [50]: Retroarticular process projects posteriorly (0) or projects posterodorsally (1). (Adapted from Benton & Clark 1988; Clark 1994, character 71; Norell & Clark 1990, character 7.)

(72) [51]: Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1). (Adapted from Norell 1988, character 42.)

(73) [162]: Surangular–articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

(74) [60]: Sulcus between articular and surangular (0) or articular flush against surangular (1).

(75) [57]: Dorsal projection of hyoid cornu flat (0) or rodlike (1).

(76) [58]: Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1).

(77) [158]: Lingual osmoregulatory pores small (0) or large (1).

(78) [159]: Tongue with (0) or without (1) keratinised surface.

(79) [166]: Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2). (Modified from Brochu 2004, character 165.)

(80): Maxillary and dentary teeth with smooth carinae (0) or serrated (1).

(81) [79]: Naris projects anterodorsally (0) or dorsally (1).

(82) [95]: External naris bisected by nasals (0) or nasals contact external naris, but do not bisect it (1) or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3). (Adapted from Norell 1988, character 3; Clark 1994, characters 13 and 14.)

(83) [161]: Naris circular or keyhole-shaped (0) or wider than long (1) or anteroposteriorly long and prominently teardrop-shaped (2).

(84): External naris of reproductively mature males (0) remains similar to that of females or (1) develops bony excrescence (ghara).

(85): External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest.

(86) [142]: Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1).

(87) [97]: Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny (Norell 1988, character 17.)

(88) [124]: Incisive foramen small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects premaxillary–maxillary suture (2).

(89) [153]: Incisive foramen completely situated far from premaxillary toothrow, at the level of the second or third alveolus (0) or abuts premaxillary toothrow (1) or projects between first premaxillary teeth (2).

(90) [145]: Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1).

(91) [77]: Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). (Norell 1988, character 29.)

(92) [78]: All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between 7th and 8th maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with maxillary toothrow (2). (Adapted from

Norell 1988, character 5; Willis 1993, character 1; states modified from original.)

(93) [89]: Largest maxillary alveolus is #3 (0) #5 (1) #4 (2) #4 and #5 are same size (3) #6 (4) or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6). (Adapted from Norell 1988, character 1.)

(94) [135]: Maxillary toothrow curved medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli. (Adapted from Clark 1994, character 79.)

(95) [101]: Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1).

(96) [143]: Canthi rostralii absent or very modest (0) or very prominent (1) at maturity (Norell 1988, character 34.)

(97) [144]: Preorbital ridges absent or very modest (0) or very prominent (1) at maturity.

(98): Antorbital fenestra present (0) or absent (1). (Norell & Clark 1990, character 2; Salisbury *et al.* 2006, character 176.)

(99) [125]: Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary–maxillary suture (1). (Adapted from Norell 1988, character 22.)

(100) [126]: Vomer entirely obscured by maxillae and palatines (0) or exposed on palate between palatines (1).

(101) [148]: Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1).

(102) [120]: Medial jugal foramen small (0) or very large (1).

(103) [111]: Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1).

(104) [91]: Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1). (Norell 1988, character 19.)

(105): Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of the lower temporal bar (1).

(106): Penultimate maxillary alveolus less than (0) or more than (1) twice the diameter of the last maxillary alveolus.

(107): Prefrontal dorsal surface smooth adjacent to orbital rim (0) or bearing discrete knoblike processes (1).

(108) [137]: Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1). (Adapted from Norell 1988, character 41.)

(109) [136]: Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1).

(110) [99]: Prefrontal pillar solid (0) or with large pneumatic recess (1). (State 1 describes prefrontal recess of Witmer 1997.)

(111) [138]: Medial process of prefrontal pillar wide (0) or constricted (1) at base.

(112) [105]: Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making lateral margin concave (1).

(113) [108]: Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1).

(114) [109]: Anterior ectopterygoid process tapers to a point (0) or forked (1).

(115) [110]: Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra. (Adapted from Willis 1993, character 2.)

(116) [118]: Palatine process generally broad anteriorly (0) or in form of thin wedge (1).

(117) [94]: Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1).

(118) [85]: Palatine–pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra.

(119) [88]: Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1).

(120) [90]: Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1). (Adapted from Norell 1988, character 2.)

(121) [71]: Anterior border of the choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1). (Benton & Clark 1988; Clark 1994, character 43; Norell & Clark 1990, character 1.)

(122) [72]: Choana projects posteroventrally (0) or anteroventrally (1) at maturity.

(123) [73]: Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form neck surrounding aperture (2) or everted from flat surface to form neck surrounding aperture (3).

(124) [107]: Posterior rim of internal choana not deeply notched (0) or deeply notched (1).

(125) [152]: Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2).

(126) [116]: Ectopterygoid–pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1).

(127) [149]: Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity (adapted from Norell 1988, character 32.)

(128) [93]: Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2).

(129) [100]: Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1). (Norell 1988, character 27.)

(130) [117]: Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2). (Modified from Norell 1988, character 7.)

(131): Anterior tip of frontal (0) forms simple acute point or (1) forms broad, complex sutural contact with the nasals.

(132) [133]: Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).

(133) [70]: Postorbital bar massive (0) or slender (1). (Norell 1989, character 3.)

(134) [134]: Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0) or bears process that is short and generally not prominent (1). (Adapted from Norell 1989, character 2.)

(135) [146]: Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1). (Adapted from Benton & Clark 1988; Norell & Clark 1990, character 3.)

(136): Postorbital bar continuous with anterolateral edge of skull table (0) or inset (1). (Norell & Clark 1990, character 3; Salisbury *et al.* 2006, character 175.)

(137) [103]: Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or orbital margin telescoped (2).

(138) [139]: Ventral margin of orbit circular (0) or with prominent notch (1).

(139) [96]: Palpebral forms from single ossification (0) or from multiple ossifications (1). (Adapted from Norell 1988, character 8; Clark 1994, character 65.)

(140) [69]: Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1). (Adapted from Norell 1989, character 1.)

(141) [114]: Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1).

(142) [75]: Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (2). (Adapted from Norell 1989, character 10.)

(143) [76]: Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3).

(144) [83]: Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1).

(145) [80]: Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1). (Adapted from Buscalioni *et al.* 1992, character 6.)

(146) [163]: Postorbital–squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

(147) [84]: Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1).

(148) [132]: Squamosal–quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1).

(149) [102]: Posterior margin of otic aperture smooth (0) or bowed (1).

(150) [81]: Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2).

(151) [86]: Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae.

(152) [87]: Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1) or supratemporal fenestra closes during ontogeny (2). (Adapted from Norell 1988, character 9.)

(153) [92]: Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1).

(154) [104]: Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1). (Norell 1988, character 51.)

(155) [131]: Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2).

(156) [123]: Skull table surface slopes ventrally from sagittal axis (0) or planar (1) at maturity.

(157): Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete horn (1).

(158) [140]: Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1).

(159) [150]: Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process.

(160) [82]: Supraoccipital exposure on dorsal skull table small (0) absent (1) large (2) or large such that parietal is excluded from posterior edge of table (3). (Norell 1988, character 11.)

(161) [164]: Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum.

(162) [122]: Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1).

(163) [129]: Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen. (Adapted from Norell 1989, character 5.)

(164) [74]: Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). (Adapted from Norell 1989, character 5.)

(165) [115]: Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process or palatine (1).

(166) [130]: Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

(167) [154]: Parietal with recess communicating with pneumatic system (0) or solid, without recess (1).

(168) [127]: Significant ventral quadrate process on lateral braincase wall (0) or quadrate–pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1).

(169) [128]: Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity.

(170): External surface of basioccipital ventral to occipital condyle oriented posteroventrally (0) or posteriorly (1) at maturity. (Modified from Hua & Jouve 2004, character 167; Salisbury *et al.* 2006, character 174.)

(171) [98]: Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2).

(172) [113]: Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital.

(173) [119]: Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1).

(174) [141]: Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital process; process lateral to cranioquadrate opening long (1).

(175) [147]: Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. (Adapted from Norell 1988, character 46.)

(176) [151]: Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process ventrally to basioccipital tubera (2). (Adapted from Norell 1988, character 20; Clark 1994, characters 57 and 60.)

(177) [121]: Quadrate foramen aerum on mediodorsal angle (0) or on dorsal surface (1) of quadrate.

(178) [165]: Quadrate foramen aereum is small (0), comparatively large (1), or absent (2) at maturity.

(179): Quadrate lacks (0) or bears (1) prominent, mediolaterally thin crest on dorsal surface of ramus.

(180): Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0) or prominent knob (1). (Ösi *et al.* 2007, character 165.)

(181) [112]: Quadrate with small, ventrally-reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aerum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3).

(182): Iris (0) greenish/yellowish or (1) brown.

(183): Two or more (0) or one (1) row of postoccipital osteoderms.

(184): Fewer than eight (0) or eight to 14 (1) or more than 14 (2) paired midline scale rows. (There is considerable variation in this character within species, and further work is needed to clarify the situation; data from Fuchs 2006.)

(185): Ectopterygoid maxillary ramus forms less than (0) or more than (1) two-thirds of lateral margin of suborbital fenestra.

(186): Ectopterygoid maxillary ramus terminates at lateral margin of suborbital fenestra (0) or lateral to it, with maxilla separating the ectopterygoid from fenestra for short distance.

(187): Palatine–maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1).

(188): Frontal lacks (0) or bears (1) prominent midsagittal crest between orbits.

(189): All cervical neural spines anteroposteriorly broad (0) or posterior neural spines thin and rod-like (1). (Modified from Clark 1994, character 90; Pol *et al.* 2009, character 90.)

Bernissartia fagesii

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Allodaposuchus precedens

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Acynodon adriaticus

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Acynodon iberoccitanus

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Iharkutosuchus makadii

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Hylaeochampsa vectiana

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Borealosuchus threeensis

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Borealosuchus formidabilis

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Borealosuchus wilsoni

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Borealosuchus acutidentatus

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Borealosuchus sternbergii

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Eothoracosaurus mississippiensis

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Thoracosaurus neocesariensis

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Thoracosaurus macrorhynchus

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Eosuchus minor

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Eosuchus lerichei

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Eogavialis africanus

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Gryposuchus colombianus

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Ikanogavialis gameroi

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Siwalik *Gavialis*

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Gavialis bengawanicus

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Gavialis gangeticus

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Boverisuchus vorax

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Boverisuchus geiseltalensis

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Planocrania hengdongensis

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Planocrania datangensis

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Leidyosuchus canadensis

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Diplocynodon ratelii

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Diplocynodon hantoniensis

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Diplocynodon darwini

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Baryphracta deponiae

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Stangerochampsa mccabei

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Albertochampsa langstoni

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Brachychampsa montana

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Brachychampsa sealeyi

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Alligator sinensis

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Alligator mississippiensis

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Alligator mefferdi

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Alligator thomsoni

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Alligator olseni

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Alligator mcgrewi

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Alligator prenasalis

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Ceratosuchus burdoshi

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Hassiacosuchus haupti

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Allognathosuchus polyodon

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Allognathosuchus wartheni

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Navajosuchus mooki

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Wannaganosuchus brachymanus

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Procaimanoidea kayi

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Procaimanoidea utahensis

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Arambourgia gaudryi

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Necrosuchus ionensis

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Tsoabichi greenriverensis

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Purussaurus mirandae

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Purussaurus neivensis

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Orthogenysuchus olseni

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Mourasuchus atopus

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Eocaiman cavernensis

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Caiman yacare

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Caiman crocodilus

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Caiman latirostris

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Caiman lutescens

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Melanosuchus fisheri

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Melanosuchus niger

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Paleosuchus trigonatus

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Paleosuchus palpebrosus

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Mecistops cataphractus

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Crocodylus niloticus

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Crocodylus porosus

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Crocodylus rhombifer

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Euthecodon arambourgii

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Osteolaemus tetraspis

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Osteolaemus osborni

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Crocodylus megarhinus

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Australosuchus clarkae

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Trilophosuchus rackhami

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Tomistoma schlegelii

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Tomistoma lusitanica

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Tomistoma petrolica

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Penghusuchus pani

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Gavialosuchus eggenbergensis

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Paratomistoma courtii

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Megadontosuchus arduini

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Thecachampsa carolinense

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Dollosuchoides densmorei

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Kentisuchus spenceri

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Brachyuranochampsa eversolei

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Crocodylus acer

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Asiatosuchus grangeri

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Crocodylus depressifrons

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Crocodylus affinis

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Asiatosuchus germanicus

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Prodiplocynodon langi

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References for Appendix 1

Benton, M. J. & Clark, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. *In* Benton, M. J. (ed.) *The Phylogeny and Classification of the Tetrapods*, 295–338. Oxford: Clarendon Press.

Brochu, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Systematic Biology* **46**, 479–522.

Brochu, C. A. 1999. Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoir* **6**, 9–100.

Brochu, C. A. 2004. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *Journal of Vertebrate Paleontology* **24**, 856–72.

Buscalioni, A. D., Sanz, J. L. & Casanovas, M. L. 1992. A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abandlungen* **187**, 1–29.

Clark, J. M. 1994. Patterns of evolution in Mesozoic Crocodyliformes. *In* Fraser, N. C. & Sues, H.-D. (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 84–97. New York: Cambridge University Press.

Fuchs, K. 2006. *The Crocodile Skin: Important Characteristics In Identifying Crocodilian Species*. Frankfurt: Editions Chimaira. 175 pp.

Hua, S. & Jouve, S. 2004. A primitive gavialoid from the Paleocene of Morocco. *Journal of Vertebrate Paleontology* **24,** 341–50.

Norell, M. A. 1988. *Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids*. Ph.D. Thesis/Dissertation, Yale University, New Haven, CT.

Norell, M. A. 1989. The higher level relationships of the extant Crocodylia. *Journal of Herpetology* **23**, 325–35.

Norell, M. A. & Clark, J. M. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **60**, 115–28.

Ösi, A., Clark, J. M. & Weishampel, D. B.. 2007. First report on a new basal eusuchian crocodyliform with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **243**, 169–77.

Poe, S. 1997. Data set incongruence and the phylogeny of crocodilians. *Systematic Biology* **45**, 393–414.

Pol, D., Turner, A. H. & Norell, M. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. *Bulletin of the American Museum of Natural History* **324**, 1–103.

Salisbury, S. W., Molnar, R. E., Frey, E. & Willis, P. M. A. 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society of London B* **273**, 2439–48.

Willis, P. M. A. 1993. *Trilophosuchus rackhami* gen et sp. nov., a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology* **13**, 90–98.

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

5.2. Appendix 2. Planocraniid material used for coding characters in this study

Boverisuchus magnifrons – GM Ce IV 6044 (holotype), GM 10 128, GM VI 180, GM XVIII 3094, GM XVIII 3268, GM XVIII 486, GM XVIII 526, GM XVII 415, GM XXII 543, GM XXII 815, GM ce-II 5894, GM Leo X 8001 (holotype, *Weigeltisuchus geiseltalensis*), GM XXXV 127, GM XXXV 216, GM XXXV 94, GM XXXVI 245, GM XXXVI 274, GM XXXVI 499, GM XXXVII 111, GM XIV 616, HLMD Me 5346, HLMD Me 5609.

Boverisuchus vorax – YPM 249 (holotype), YPM 5890, UCMP 170767, USNM 12957, FMNH PR399, FMNH PR479, AMNH 2090, AMNH 29993.

Planocrania datangensis – IVPP V5016 (holotype).

Planocrania hengdongensis – IVPP V6079 (holotype).

6. Note added in proof

I recently had an opportunity to examine the holotype of *Crocodilus bolcensis* at the Musei Regionale di Scienze Naturali in Turin. Its preservation precludes identifying most cranial sutures, and so whether *C. bolcensis* is a distinct species or conspecific with *Boverisuchus geiseltalensis* remains unclear. However, the holotype does preserve serrated teeth, and several structures in the trunk region could be ventral osteoderms. I thank Massimo Delfino and Daniele Ormezzano for their hospitality and assistance during my visit.

7. References

Aguilera, O. A., Riff, D. & Bocquetin-Villanueva, J. C. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the Upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology* **4**, 221–32.

Alexander, J. P. & Burger, B. J. 2001. Stratigraphy and taphonomy of Grizzly Buttes, Bridger Formation, and the Middle Eocene of Wyoming. *In* Gunnell, G. F. (ed.) *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*, 165–96. New York: Kluwer Academic/Plenum Publishers.

Andrews, C. W. 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quarterly Journal of the Geological Society of London*, **70**, 163–86.

Antunes, M. T. 1975. *Iberosuchus*, crocodile sebecosuchien nouveau, l'Eocene ibérique au Nord de la chaine centrale, et l'origine du canyon de Nazaré. *Comunicações dos Serviços Geológicos de Portugal* **59**, 285–330.

Antunes, M. T. 1986. *Iberosuchus* et *Pristichampsus*, crocodiliens de l'Éocène données complémentaires, discussion, distribution, stratigraphique. *Ciências da Terra* **8**, 111–22.

Astre, G. 1931. Les crocodiliens fossiles des terrains Tertiaires sous-pyrénéens. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **61**, 25–71.

Augé, M., Duffaud, S., de Lapparent de Broin, F., Rage, J. C. & Vasse, D. 1997. Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur. *Géologie de la France* **1**, 23–33.

Bartels, W. S. 1980. Early Cenozoic reptiles and birds from the Bighorn Basin, Wyoming. *University of Michigan Papers in Paleontology* **24**, 73–80.

Bell, C. J., Gauthier, J. A. & Bever, G. S. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary Herpetofaunal Stability Hypothesis. *Quaternary International* **217**, 30–36.

Berg, D. E. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **52**, 1–105.

Berg, D. E. 1969. Characteristic crocodiles of the Paleogene in Europe. *Mémoires du Bureau de Recherches Géologiques et Minières* **69**, 73–75.

Blainville, H. M. 1835. *Système d'Herpetologie.* Paris: Museum National d'Histoire Naturelle.

Bona, P. 2007. Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana* **44**, 435–45.

Bramble, D. M. & Hutchison, J. H. 1971. Biogeography of continental Tertiary Chelonia and Crocodilia of far-western United States. *Geological Society of America Abstracts with Programs* **3**, 86–87.

Brochu, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Systematic Biology* **46**, 479–522.

Brochu, C. A. 1999. Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoir* **6**, 9–100.

Brochu, C. A. 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* **31**, 357–97.

Brochu, C. A. 2004. A new gavialoid crocodylian from the Late Cretaceous of eastern North America and the phylogenetic relationships of thoracosaurs. *Journal of Vertebrate Paleontology* **24**, 610–33.

Brochu, C. A. 2006. Osteology and phylogenetic significance of *Eosuchus minor* (Marsh 1870), new combination, a longirostrine crocodylian from the Late Paleocene of North America. *Journal of Paleontology* **80**, 162–86.

Brochu, C. A. 2007. Morphology, relationships and biogeographic significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological Journal of the Linnean Society* **150**, 835–63.

Brochu, C. A. 2010. A new alligatoroid from the Lower Eocene Green River Formation of Wyoming and the origin of caimans. *Journal of Vertebrate Paleontology* **30**, 1109–26.

Brochu, C. A. 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society* **163**, S228–56

Brochu, C. A., Njau, J. K., Blumenschine, R. J. & Densmore, L. D. 2010. A new horned crocodile from the Plio–Pleistocene hominid sites at Olduvai Gorge, Tanzania. *PLoS One* **5**, e9333.

Brochu, C. A., Parris, D. C., Grandstaff, B. S., Denton, R. & Gallagher, W. B. 2012. A new species of *Borealosuchus* (Crocodyliformes: Eusuchia) from the Late Cretaceous–Early Paleocene of New Jersey. *Journal of Vertebrate Paleontology* **32**, 105–16.

Brochu, C. A. & Storrs, G. W. 2012. A giant crocodile from the Plio–Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa. *Journal of Vertebrate Paleontology* **32**, 587–602.

Buffetaut, E. 1978. Crocodilian remains from the Eocene of Pakistan. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **156**, 262–83.

Buffetaut, E. 1982a. A ziphodont mesosuchian crocodile from the Eocene of Algeria and its implications for vertebrate dispersal. *Nature* **300**, 176–78.

Buffetaut, E. 1982b. Un problème de paléobiogéographie continentale: crocodilens mésosuchiens ziphodontes de l'Éocène européen. *Bulletin de la Société Géologique de France* **24**, 1101–07.

Buffetaut, E. 1985. Les crocodiliens de l'Eocene Inferieur de Dormaal (Brabant, Belgique). *Bulletin de la Société Belge de Géologie* **94**, 51–59.

Buffetaut, E. 1986. Un mésosuchien ziphodonte dans l'Eocene superieur de la Liviniére (Hérault, France). *Geobios* **19**, 101–08.

Buffetaut, E. 1988. The ziphodont mesosuchian crocodile from Messel: a reassessment. *Courier Forschungsinstitut Senckenberg* **107**, 211–21.

Buffetaut, E. 1989. A new ziphodont mesosuchian crocodile from the Eocene of Algeria. *Palaeontographica Abteilung A* **208**, 1–10.

Busbey, A. B. 1986. *Pristichampsus* cf. *P. vorax* (Eusuchia, Pristichampsinae) from the Uintan of West Texas. *Journal of Vertebrate Paleontology* **6**, 101–03.

Campos, Z., Sanaiotti, T. & Magnusson, W. E. 2010. Maximum size of dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807), in the Amazon and habitats surrounding the Pantanal, Brazil. *Amphibia-Reptilia* **31**, 439–42.

Cantino, P. D. & de Queiroz, K. 2007. *PhyloCode, version 4b*.

Caraven-Cachin, A. 1880. Description d'un fragment de crane de *Crocodilus rollinati* des grès éocènes du Tarn. *Bulletin de la Société Géologique de France* **8**, 368–69.

Cuvier, G. 1824. *Recherches Sur les Ossemens Fossiles, où l'On Rétablit les Caractères de Plusieurs Animaux Dont les Révolutions du Globe Ont Détruit les Espèces*. Paris: G. Doufour et Ed. D'Ocagne.

D'Amore, D. C. & Blumenschine, R. J. 2009. Komodo monitor *(Varanus komodoensis)* feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology. *Paleobiology* **35**, 525–52.

Daudin, F. M. 1802. *Histoire Naturelle, Générale et Particulière des Reptiles, Volume II*. Paris: Imprimerie de F. Dufart.

de Lapparent de Broin, F., Merle, D., Fontana, M., Ginsburg, L., Hervat, P., Le Calvez, Y. & Riveline, J. 1993. Une faune continentale a vertébrés dans le Lutétien supérieur de Guitrancourt (Yvelines) et son environnement. *Bulletin d'Information des Géologues du Bassin de Paris* **30**, 3–16.

De Vis, C. W. 1905. Fossil vertebrates from New Guinea. *Annals of the Queensland Museum* **6**, 26–31.

Delfino, M., Piras, P. & Smith, T. 2005. Anatomy and phylogeny of the gavialoid *Eosuchus lerichei* from the Paleocene of Europe. *Acta Palaeontologica Polonica* **50**, 565–80.

Delfino, M., Codrea, V., Folie, A., Dica, P., Godefroit, P. & Smith, T. 2008a. A complete skull of *Allodaposuchus precedens* Nopcsa, 1928 (Eusuchia) and a reassessment of the morphology of the taxon based on the Romanian remains. *Journal of Vertebrate Paleontology* **28**, 111–22.

Delfino, M., Martin, J. E. & Buffetaut, E. 2008b. A new species of *Acynodon* (Crocodylia) from the Upper Cretaceous (Santonian–Campanian) of Villaggio del Pescatore, Italy. *Palaeontology* **51**, 1091–06.

Densmore, L. D. 1983. Biochemical and immunological systematics of the order Crocodilia. *In* Hecht, M. K., Wallace, B. & Prance, G. H. (eds) *Evolutionary Biology* **16**, 397–465. New York: Plenum Press.

Domning, D. P., Emry, R. J., Portell, R. W., Donovan, S. K. & Schindler, K. S. 1997. Oldest West Indian land mammal: rhinocerotoid ungulate from the Eocene of Jamaica. *Journal of Vertebrate Paleontology* **17**, 638–41.

Efimov, M. B. 1988. [The fossil crocodiles and champsosaurides of Mongolia and the USSR]. *Trudy Somestnaya Sovetsko-Mongolskya Paleontologicheskaya Expeditsiya* **36**, 1–108. [In Russian.]

Efimov, M. B. 1993. The Eocene crocodiles of the GUS – a history of development. *Kaupia* **3**, 23–25.

Franzen, J. L. 2005. The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. *Annales de Paléontologie* **91**(4), 329–35.

Gatesy, J., Amato, G., Norell, M., DeSalle, R. & Hayashi, C. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. *Systematic Biology* **52**, 403–22.

Gervais, P. 1853. Observations relatives aux reptiles fossiles de France (première partie). *Comptes Rendus de l'Académie des Sciences de Paris* **36**, 374–77.

Gilmore, C. W. 1910. *Leidyosuchus sternbergii*, a new species of crocodile from the Cretaceous Beds of Wyoming. *Proceedings of the United States National Museum* **38**, 485–502.

Gingerich, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Museum of Paleontology, Papers in Paleontology* **28**, 1–97.

Gmelin, J. 1789. *Linnei Systema Naturae*. Leipzig: G. E. Beer.

Gray, J. E. 1831. *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I: Cataphracta. Tortoises Crocodiles, and Enaliosaurians*. London: Treuttel, Wurtz & Co.

Groessens-Van Dyck, M. C. 1986. Les crocodiliens du gisement "Montien" continental de Hainin (Hainaut, Belgique) et leur environnement faunique. *Annales de la Société Royal Zoologique de Belgique* **116**, 55–60.

Gunnell, G. F., Bartels, W. S., Gingerich, P. D. & Torres, V. 1992. Wapiti Valley faunas: Early and Middle Eocene fossil vertebrates from the North Fork of the Shoshone River, Park County, Wyoming. *Contributions from the University of Michigan Museum of Paleontology* **28**, 247–87.

Gunnell, G. F. & Bartels, W. S. 1999. Middle Eocene vertebrates from the Uinta Basin, Utah, and their relationship with faunas from the southern Green River Basin, Wyoming. *Utah Geological Survey Miscellaneous Publication* **99**(1), 429–42.

Hanson, C. B. 1996. Stratigraphy and vertebrate faunas of the Bridgerian–Duchesnean Clarno Formation, north-central Oregon. *In* Prothero, D. R. & Emry, R. J. (eds) *The Terrestrial Eocene–Oligocene Transition in North America*, 206–39. New York: Cambridge University Press.

Harshman, J., Huddleston, C. J., Bollback, J. P., Parsons, T. J. & Braun, M. J. 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. *Systematic Biology* **52**, 386–402.

Hill, R. V. & Lucas, S. G. 2006. New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*. *Acta Palaeontologica Polonica* **51**, 455–64.

International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature (4th Ed.)*. London: International Trust for Zoological Nomenclature.

Kälin, J. A. 1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. *Zoologische Jahrbücher* **57**, 535–714.

Kälin, J. A. 1955. Crocodilia. *In* Piveteau. J. (ed) *Traité de Paléontologie* **5**, 695–784. Paris: Masson.

Kofron, C. P. 1992. Status and habitats of the three African crocodiles in Liberia. *Journal of Tropical Ecology* **8**, 265–73.

Kotsakis, A., Delfino, M. & Piras, P. 2004. Italian Cenozoic crocodilians: taxa, timing and palaeobiogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **210**, 67–87.

Kuhn, O. 1938. Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. *Nova Acta Leopoldina* **39**, 313–28.

Kuhn, O. 1968. *Die Vorzeitlichen Krokodile*. Munich: Verlag Oeben.

Langston, W. 1975. Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Fieldiana: Geology* **33**, 291–314.

Langston, W. 2008. Notes on a partial skeleton of *Mourasuchus* (Crocodylia, Nettosuchidae) from the Upper Miocene of Venezuela. *Arquivos do Museu Nacional, Rio de Janeiro* **66**, 125–44.

Laurenti, J. N. 1768. *Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentatis Circa Venena et Antiodota Reptilium Austriacorum*. Vienna: J. T. de Trattnern.

Legasa, O., Buscalioni, A. D. & Gasparini, Z. 1993. The serrated teeth of *Sebecus* and the iberoccitanian crocodile, a morphological and ultrastructural comparison. *Studia Geologica Salmanticensia* **29**, 127–44.

Li, J. 1976. Fossil of Sebecosuchia discovered from Nanxiong, Guangdong. *Vertebrata PalAsiatica* **14**, 169–74.

Li, J. 1984. A new species of *Planocrania* from Hengdong, Hunan. *Vertebrata PalAsiatica* **22**, 123–33.

Luiselli, L., Akani, G. C. & Capizzi, D. 1999. Is there any interspecific competition between dwarf crocodiles (*Osteolaemus tetraspis*) and Nile monitors (*Varanus niloticus ornatus*) in the swamps of central Africa? A study from southeastern Nigeria. *Journal of Zoology* **247**, 127–31.

Magnusson, W. E. 1985. Habitat selection, parasites and injuries in Amazonian crocodilians. *Amazoniana* **9**, 193–204.

Magnusson, W. E. & Lima, A. P. 1991. The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. *Journal of Herpetology* **25**, 41–48.

Marsh, O. C. 1871. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *American Journal of Science, Series 3* **1**, 447–59.

Marsh, O. C. 1872. Preliminary description of new Tertiary reptiles. *American Journal of Science* **4**, 298–309.

Martin, J. E. 2007. New material of the Late Cretaceous globidontan *Acynodon iberoccitanus* (Crocodylia) from southern France. *Journal of Vertebrate Paleontology* **27**, 362–72.

Martin, J. E. 2010. *Allodaposuchus* Nopsca, 1928 (Crocodylia, Eusuchia), from the Late Cretaceous of southern France and its relationships to Alligatoroidea. *Journal of Vertebrate Paleontology* **30**, 756–67.

Martin, J. E. & Buffetaut, E. 2008. *Crocodilus affuvelensis* Matheron, 1869 from the Late Cretaceous of southern France: a reassessment. *Zoological Journal of the Linnean Society* **152**, 567–80.

Masters, S., Sandau, S., Burk, D. & Krumenacker, L. J. 2010. A unique Eocene crocodylian from the Uinta Basin, Utah. *Journal of Vertebrate Paleontology* **28**, 131A.

Medem, F. 1958. The crocodilian genus *Paleosuchus*. *Fieldiana: Zoology* **39**, 227–47.

Megirian, D. 1994. A new species of *Quinkana* (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of northern Australia. *The Beagle* **11**, 145–66.

Molnar, R. E. 1981. Pleistocene ziphodont crocodilians of Queensland. *Records of the Australian Museum* **33**, 803–35.

Molnar, R. E., Worthy, T. H. & Willis, P. M. A. 2002. An extinct Pleistocene endemic mekosuchine crocodylian from Fiji. *Journal of Vertebrate Paleontology* **22**, 612–28.

Mook, C. C. 1924. A new crocodilian from the Wasatch beds of Wyoming. *American Museum Novitates* **137**, 1–4.

Mook, C. C. 1930. A new species of crocodilian from the Torrejon beds. *American Museum Novitates* **447**, 1–11.

Mook, C. C. 1955. Two new genera of Eocene crocodilians. *American Museum Novitates* **1727**, 1–4.

Nopcsa, F. 1928. The genera of reptiles. *Palaeobiologica* **1**, 163–88.

Norell, M. A. 1989. The higher level relationships of the extant Crocodylia. *Journal of Herpetology* **23**, 325–35.

Oaks, J. R. 2011. A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution* **65**, 3285–97.

Ortega, F., Buscalioni, A. D. & Gasparini, Z. 1996. Reinterpretation and new denomination of *Atacisaurus crassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha, Metasuchia). *Geobios* **29**, 353–64.

Ősi, A., Clark, J. M. & Weishampel, D. B. 2007. First report on a new basal eusuchian crocodyliform with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen* **243**, 169–77.

Ouboter, P. E. 1996. *Ecological Studies on Crocodilians in Suriname: Niche Segregation and Competition in Three Predators*. Amsterdam and New York: SPB Academic Publishing.

Owen, R. 1874. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. VI. *Hylaeochampsa*. *Palaeontographical Society Monographs* **27**, 1–7.

Panadés I Blas, X., Loyal, R. S., Schleich, H. H. & Agrasar, E. L. 2004. Pristichampsine cranial remains from the basal redbed facies of the Subathu Formation (Himachal Pradesh, India) and some palaeobiogeographical remarks. *PalArch* **3**, 1–8.

Piras, P., Colangelo, P., Adams, D. C., Buscalioni, A. D., Cubo, J., Kotsakis, A., Meloro, C. & Raia, P. 2010. The *Gaviais-Tomistoma* debate: the contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evolution and Development* **12**, 568–79.

Piras, P. & Buscalioni, A. D. 2006. *Diplocynodon muelleri* comb. nov., an Oligocene diplocynodontine alligatoroid from Catalonia (Ebro Basin, Lleida Province, Spain). *Journal of Vertebrate Paleontology* **26**, 608–20.

Pol, D., Turner, A. H. & Norell, M. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. *Bulletin of the American Museum of Natural History* **324**, 1–103.

Prasad, G. V. R. & de Lapparent de Broin, F. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paléontologie* **88**, 19–71.

Pregill, G. K. 1999. Eocene lizard from Jamaica. *Herpetologica* **55**, 157–61.

Price, L. I. 1964. Sobre o cranio de um grande crocodilideo extinto do Alto Rio Jurua, Estado do Acre. *Anais da Academia Brasiliera de Ciencias* **36**, 59–66.

Puértolas, E., Canudo, J. I. & Caruzado-Caballero, P. 2011. A new crocodylian from the Late Maastrichtian of Spain: implications for the intitial radiation of crocodyloids. *PLoS One* **6**, e20011.

Rauhe, M. & Rossmann, T. 1995. News about fossil crocodiles from the middle Eocene of Messel and Geiseltal, Germany. *Hallesches Jahrbuch für Geowissenschaften* **17**, 81–92.

Riley, J. & Huchzermeyer, F. W. 1999. African dwarf crocodiles in the Likouala swamp forests of the Congo Basin: habitat, density, and nesting. *Copeia* **1999**, 313–20.

Roos, J., Aggarwal, R. K. & Janke, A. 2007. Extended mitogenomic phylogenetic analyses yield new insight into crocodylian evolution and their survival of the Cretaceous–Tertiary boundary. *Molecular Phylogenetics and Evolution* **45**, 663–73.

Rossmann, T. 1998. Studien an känozoischen Krokodilen: 2. Taxonomische Revision der Familie Pristichampsidae Efimov (Crocodilia: Eusuchia). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **210**, 85–128.

Rossmann, T. 1999. Studien an känozoischen Krokodilen: 1. Die paläoökologische Bedeutung des eusuchen Krokodils *Pristichampsus rollinatii* (Gray) für die Fossillagerstätte Grube Messel. *Courier Forschungsinstitut Senckenberg* **216**, 85–96.

Rossmann, T. 2000a. Skelettanatomische Beschreibung von *Pristichampsus rollinatii* (Gray) (Crocodilia, Eusuchia) aus dem Paläogen von Europa, Nordamerika und Ostasien. *Courier Forschungsinstitut Senckenberg* **221**, 1–107.

Rossmann, T. 2000b. Studien an känozoischen Krokodilen: 4. Biomechanische Untersuchung am Schädel und der Halswirbelsäule des paläogenen Krokodils *Pristichampsus rollinatii* (Eusuchia: Pristichampsidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **215**, 397–432.

Rossmann, T. 2000c. Studien an känozoischen Krokodilen: 5. Biomechanische Untersuchung am postkranialen Skelett des paläogenen Krokodils *Pristichampsus rollintii* (Eusuchia: Pristichampsidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **217**, 289–330.

Rossmann, T., Rauhe, M. & Ortega, F. 2000. Studies on Cenozoic crocodiles: 8. *Bergisuchus dietrichbergi* Kuhn (Sebecosuchia: Bergisuchidae n. fam) from the Middle Eocene of Germany, some new systematic and biological conclusions. *Paläontologische Zeitschrift* **74**, 379–92.

Russell, D. E. 1982. Tetrapods of the Northwest European Tertiary Basin. *Geologisches Jahrbuch* **60**, 5–74.

Sacco, F. 1896. Il coccodrilli del Monte Bolca. *Memorie della Reale Accademia delle Scienze de Torino, Ser. 2* **45**, 75–87.

Sachse, M. 2005. A remarkable fossiliferous mass flow deposit in the Eocene Eckfeld Maar (Germany) – sedimentological, taphonomical, and palaeoecological considerations. *Facies* **51**, 173–84.

Sah, R. B. & Schleich, H. H. 1990. An Eocene crocodile record from Bhanskati Khola (Dumri area), South Nepal. *Mitteilungen der Bayerischen Staatsammlung für Paläontologie und historische Geologie* **30**, 51–56.

Sahni, A., Srivastava, S. & D'Souza, R. 1978. Eocene ziphodont Crocodilia from northwestern India. *Géobios* **11**, 779–85.

Sahni, A. & Srivastava, V. C. 1976. Eocene rodents and associated reptiles from the Subathu Formation of northwestern India. *Journal of Paleontology* **50**, 922–28.

Salisbury, S. W., Holt, T. R., Worthy, T. H., Sand, C. & Anderson, A. 2010. New material of *Mekosuchus inexpectatus* (Crocodylia: Mekosuchinae) from the Late Quaternary of New Caledonia, and the phylogenetic relationships of Australasian Cenozoic crocodylians. *Journal of Vertebrate Paleontology* **28**, 155A.

Salisbury, S. W. & Willis, P. M. A. 1996. A new crocodylian from the Early Eocene of southeastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa* **20**, 179–227.

Shan, H.-Y., Wu, X.-C., Cheng, Y.-N. & Sato, T. 2009. A new tomistomine (Crocodylia) from the Miocene of Taiwan. *Canadian Journal of Earth Sciences* **46**, 529–55.

Shirley, M. H., Oduro, W. & Beibro, H. Y. 2009. Conservation status of crocodiles in Ghana and Côte-d'Ivoire, West Africa. *Oryx* **43**, 136–45.

Srivastava, S. & Kumar, K. 1996. Taphonomy and palaeoenvironment of the Middle Eocene rodent localities of northwestern Himalaya, India. *Palaeogeography, Palaeoclimatology, Palaeoecology* **122**, 185–211.

Stucky, R. K., Prothero, D. R., Lohr, W. G. & Snyder, J. R. 1996. Magnetic stratigraphy, sedimentology, and mammalian faunas of the early Uintan Washakie Formation, Sand Wash Basin, northwestern Colorado. *In* Prothero, D. R. & Emry, R. J. (eds) *The Terrestrial Eocene–Oligocene Transition in North America*, 40–51. New York: Cambridge University Press.

Sudre, J. & Lecomte, G. 2000. Relations et position systématique du genre *Cuisitherium* Sudre *et al.*, 1983, le plus dérivé des artiodactyles de l'Éocène inférieur d'Europe. *Geodiversitas* **22**, 415–32.

Swofford, D. L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4.0b10*. Sunderland, MA: Sinauer Associates.

Ting, S., Bowen, G. J., Koch, P. L., Clyde, W. C., Wang, Y., Wang, Y. & McKenna, M. C. 2003. Biostratigraphic, chemostratigraphic and magnetostratigraphic study across the Paleocene–Eocene boundary in the Hengyang Basin, Hunan, China. *Geological Society of America Special Paper* **369**, 521–35.

Ting, S.-Y., Tong, Y.-S., Clyde, W. C., Koch, P. L., Wang, Y.-Q., Bowen, G. J., Li, Q. & Snell, K. E. 2011. Asian early Paleogene chronology and mammalian faunal turnover events. *Vertebrata PalAsiatica* **49**, 1–28.

Troxell, E. L. 1925. The Bridger crocodiles. *American Journal of Science, 5th Ser.* **9**, 29–72.

Turner, A. H. & Brochu, C. A. 2010. A reevaluation of the crocodyliform *Acynodon* from the Late Cretaceous of Europe. *Journal of Vertebrate Paleontology* **30**, 178A.

Vasse, D. 1992. Les crocodiles de l'Aude: Aperçu du matériel connu et présentation de quelques nouvelles pièces. *Bulletin de la Societé d'Études Scientifiques de l'Aude* **92**, 37–41.

Vasse, D. 1995. *Ischyrochampsa meridionalis* n. g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **8**, 501–12.

Veléz-Juarbe, J. & Brochu, C. A. in press. Eocene crocodyliforms from Seven Rivers, Jamaica: implications for Neotropical crocodyliform biogeography and the status of *Charactosuchus* Langston, 1965. *In* Portell, R. W. & Domning, D. P. (eds) *The Eocene Fossil Site of Seven Rivers, Jamaica: Geology, Paleontology, and Evolutionary and Biogeographic Implications*. Dordrecht: Springer Verlag.

Weitzel, K. 1938. *Pristichampsus rollinati* (Gray) aus dem Mitteleozän von Messel. *Notizblatt der Hessischen Landes-Amte Bodenforschung* **19**, 47–48.

Westgate, J. W. 1989. Lower vertebrates from an estuarine facies of the Middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas. *Journal of Vertebrate Paleontology* **9**, 282–94.

Westgate, J. W. 2008. Vertebrates from a Middle Eocene estuarine mangrove community in the Rio Grande Embayment. *Geological Society of America Abstracts with Programs* **40**, 3.

Willis, P. M. A. 1993. *Trilophosuchus rackhami* gen et sp. nov., a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology* **13**, 90–98.

Willis, P. M. A. 1997. New crocodilians from the Late Oligocene White Hunter Site, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* **41**, 423–38.

Willis, P. M. A. & Mackness, B. S. 1996. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the Early Pliocene Bluff Downs Local Fauna, northern Australia with a revision of the genus. *Proceedings of the Linnean Society of New South Wales* **116**, 143–51.

Windolf, R. 1994. Krokodilreste aus dem Mittleren Eozän des Eckfelder Maares bei Manderscheid, Deutschland. *Mainzer Naturwissenschaftlische Archiv* **16**, 177–87.

Wroe, S. 2002. A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader implications. *Australian Journal of Zoology* **50**, 1–24.

Zonneveld, J.-P., Gunnell, G. F. & Bartels, W. S. 2000. Early Eocene fossil vertebrates from the southwestern Green River Basin, Lincoln and Uinta Counties, Wyoming. *Journal of Vertebrate Paleontology* **20**, 369–86.

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