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A plant-eating crocodyliform reptile from the Cretaceous of China

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WITH few exceptions, tooth shape among crocodyliform reptiles (Crocodylia of traditional use) is rather uniform¹. We report here on the presence of multicuspid molariform teeth in a remarkable new crocodyliform from the Lower Cretaceous of China, which may represent the first known herbivorous member of that group. The overall structure of these teeth is very similar to that of the postcanine teeth of tritylodontid synapsids and represents a particularly striking example of convergent evolution. It indicates back-to-front (proal) motion of the mandible produced by the posterior pterygoid muscle during jaw closing, much as in the extant tuatara, *Sphenodon*^{2,3}. Certain derived features indicate that the new Chinese crocodyliform is closely related to the Notosuchidae from the Cretaceous of Gondwana⁴. Its discovery thus casts further doubts on claims⁵ concerning an endemic Gondwanan tetrapod fauna during the Cretaceous.

Reptilia
Archosauria
Crocodyliformes

Chimaerasuchus paradoxus gen. et sp. nov.

Etymology. Generic name from Greek *chimaira*, mythical monster combining body parts of several animals, and *souchos*, Greek name for the Egyptian crocodile-headed god Sebek. Specific name Latin from Greek *paradoxos*, strange.

Holotype. Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing (IVPP) V8274, partial skeleton including snout and mandible, fifteen vertebrae, girdle and limb bones, and an osteoderm (Figs 1–3).

Type locality and horizon. Hill near the southern bank of Yangtze River, opposite Yichang city, Hubei province, China; Wulong Formation, Lower Cretaceous (Aptian–Albian)⁶. No other vertebrate fossils have been recovered from the site.

Diagnosis. Differing from all other known crocodyliforms in the possession of the following autapomorphies: two caniniform, procumbent premaxillary teeth; four molariform maxillary teeth, each with three longitudinal rows of recurved cusps; anterior end of jugal expanded laterally, overhanging posterior part of tooth row; angular with pronounced lateral projection posterior to suture between angular and dentary; splenial strap-like, apparently restricted to ventromedial surface of lower jaw. Additional possibly diagnostic features of currently equivocal status (because unknown in presumably related taxa) include: ilium without distinct blade and with rod-like preacetabular process; humerus with rounded fossa just distal to proximal head on lateral surface; osteoderm with peg-like ventrolateral process.

The formation of a complete secondary bony palate by the premaxillae and maxillae (Figs 1c, 2b), exclusion of the jugal from the antorbital fenestra (Fig. 1b), and elongation of the proximal carpals (Fig. 3f) support reference of *Chimaerasuchus* to the Crocodylomorpha^{7,8}. Diagnostic crocodyliform features include the broad ventromedial process of the coracoid (Fig. 3a) and the partial or complete exclusion of the pubis from the acetabulum by the anterior process of the ischium.

Chimaerasuchus has four closely appressed molariform teeth in each maxilla (Fig. 1c). Each molariform has three longitudinal rows of cusps that extend parallel to the midline (Fig. 1d). Each row comprises seven recurved cusps that decrease in size posteriorly so that the seventh is a mere cuspule. Each individual cusp bears a single concave, sharp cutting edge posteriorly. A cuspidate cingulum is developed along the anterolateral margin

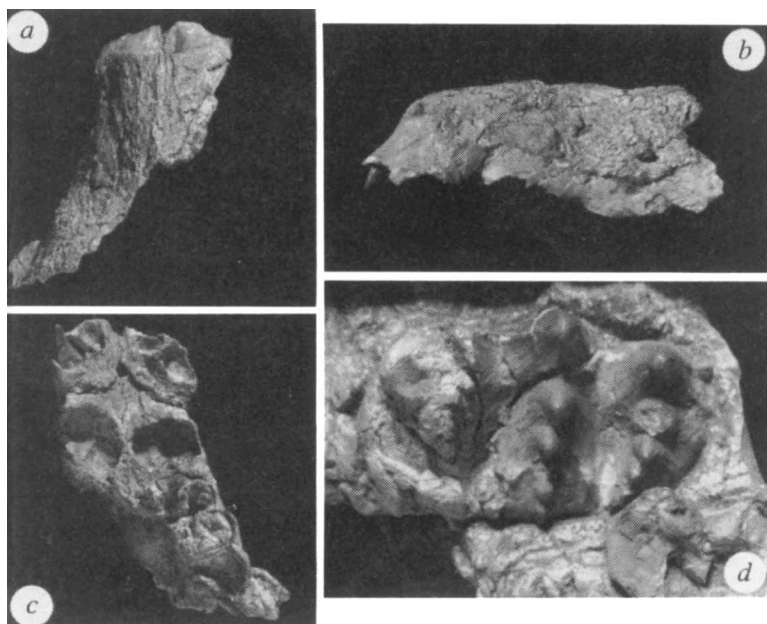


FIG. 1 *Chimaerasuchus paradoxus*, IVPP V8274 (holotype), from the Lower Cretaceous Wulong Formation of Hubei. Snout in dorsal (a), lateral (b) and ventral (c) views; left second maxillary tooth in occlusal view (d). Length of the snout fragment measured dorsally along the midline is ~4.3 cm; maximum width of tooth crown is ~1.6 cm. Most cranial bones bear pronounced external sculpturing comprising short ridges and grooves. The snout is relatively short and deep. The terminal external nares are confluent and face directly forward. A small antorbital fenestra is present. The complete maxillary tooth row on the left side comprises two teeth and two empty alveoli.

of the well preserved tooth crown. The molariform teeth are implanted in broad, shallow alveoli. The lower teeth are unknown, but the presence of more posterior molariform teeth is indicated by a broad and shallow alveolus for the posterior tooth on either side.

The articular facet of the jaw joint is distinctly longer than wide (Fig. 2c), indicating capacity for mandibular fore-and-aft motion⁹. The direction of the jaw movement during jaw closing is reflected by the curvature of the leading edge of the cusps of the molariform teeth¹⁰. Thus mandibular motion in *Chimaerasuchus* was back-to-front (proal), as in *Sphenodon*^{2,3} and inferred for a notosuchid crocodyliform from the Lower Cretaceous of Malawi⁹.

The maxillary teeth of *Chimaerasuchus* strikingly resemble the upper postcanines of the Tritylodontidae, highly derived non-mammalian synapsids of mainly Early and Middle Jurassic age¹¹. The cusps on the lower molariforms of *Chimaerasuchus*

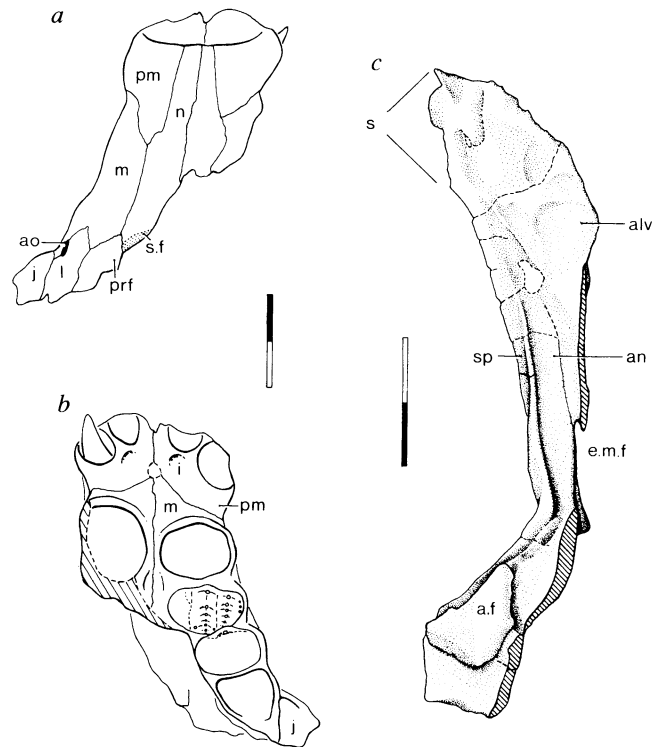


FIG. 2 *Chimaerasuchus paradoxus*, IVPP V8274 (holotype), from the Lower Cretaceous Wulong Formation of Hubei. a, b, Outline drawings of snout in (a) dorsal and (b) ventral views. c, Right mandibular ramus in dorsal view; note distortion due to extensive dorsoventral crushing. Scale bars, 2 cm. The articular facet of the jaw point is distinctly longer than wide and lacks a buttress-like posterior edge. The retroarticular process is broad and short. Abbreviations: a.f, mandibular articular facet of jaw joint; alv, posterior alveolus on dentary; an, angular; ao, antorbital fenestra; e.m.f, external mandibular fenestra; i, pit for incisiform anterior dentary tooth; j, jugal; l, lacrimal; m, maxilla; n, nasal; pm, premaxilla; prf, prefrontal; s, symphysis (incomplete); s.f, sutural facet for frontal; sp, splenial. Broken lines and cross-hatching denote fractures and broken surfaces, respectively.

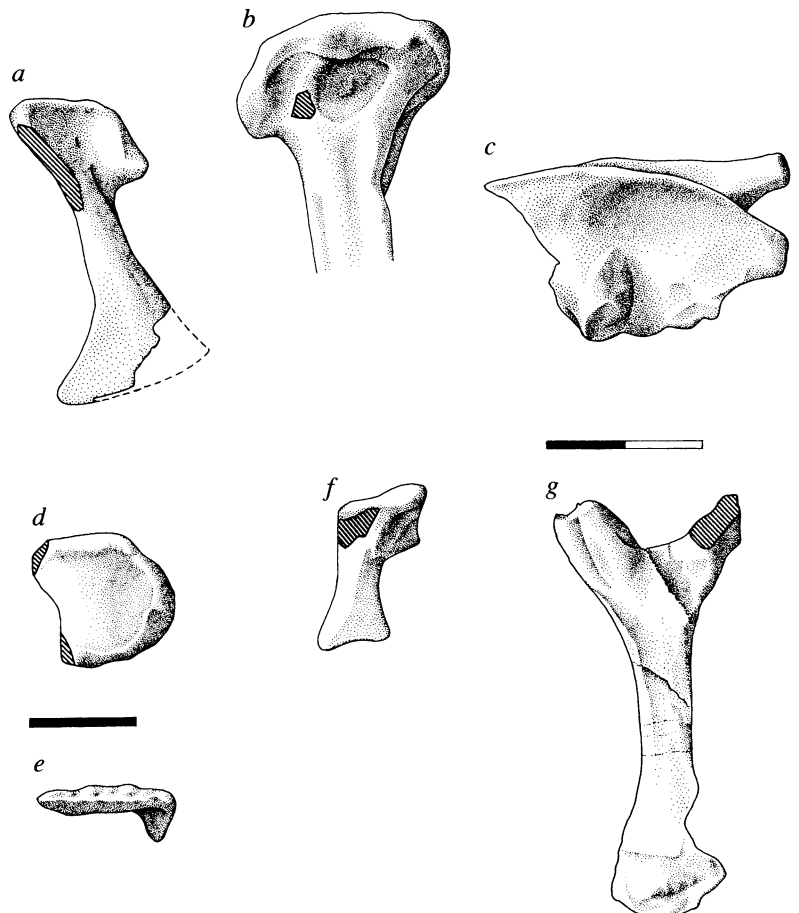


FIG. 3 *Chimaerasuchus paradoxus*, IVPP V8274 (holotype), from the Lower Cretaceous Wulong Formation of Hubei. a, Left coracoid in lateral view; b, proximal portion of right humerus in lateral view; c, right ilium in lateral view; d, e, osteoderm in (d) ventral and (e) end views; f, left radiale in dorsal view; g, right ischium in lateral view. Scale bars, 2 cm (a–c, f, g) and 1 cm (d, e). The coracoid (a) and ischium (g) are typically crocodyliform. The lateral surface of the humerus (b) bears a rounded fossa just distal to the articular head. The combined length of the humerus and ulna exceeds the estimated length of skull. The ilium (c) lacks a dorsal blade but has a rod-like pre-acetabular process; its prominent supra-acetabular rim indicates a more erect posture than in extant crocodylians. The ischium (g) is relatively narrow distally and elongate. The osteoderm (d, e) has a peg-like ventrolateral process.

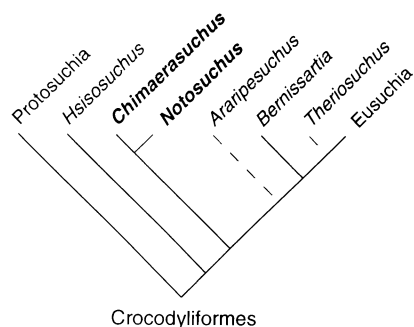


FIG. 4 Cladogram illustrating a hypothesis of the phylogenetic position of *Chimaerasuchus paradoxus*, derived from a numerical cladistic analysis (using PAUP) of 42 characters for 16 taxa of crocodyliforms (results in full to be presented elsewhere). Unequivocal synapomorphies for *Chimaerasuchus* and *Notosuchus*⁴ include: snout relatively broad and shorter than the remainder of the skull (determined in *Chimaerasuchus* from the length of the mandible); external nares vertical and facing directly forward; mandibular articular facet distinctly longer than wide; jaw joint in ventral position.

probably occluded in the grooves between the upper three rows. As in tritylodontids, the reversed concave cutting edges would have met during jaw closing and enclosed an ovoid space, which decreased in size during dynamic occlusion. This reversal of curvature in occluding teeth limited the area of tooth-to-tooth contact and thus served to maximize occlusal pressure between the teeth and food items at any given time. However, mandibular motion was proal (back-to-front) rather than propalinal (front-to-back), and the presence of only a single posterior cutting edge, rather than paired crests, on each cusp indicates less extensive shearing in *Chimaerasuchus* than in tritylodontid synapsids. There are also no wear facets indicative of tooth-to-tooth occlusion. The structure of the maxillary molariforms is consistent with a specialized diet including fibrous material and may indicate at least facultative herbivory in *Chimaerasuchus*. The procumbent premaxillary (and probably anterior dentary) teeth were presumably involved in seizing food items.

The proal mandibular motion in *Sphenodon* is produced by the posterior pterygoid muscle^{2,3}. In extant crocodylians, the homologous muscle pulls the mandible forward and upward^{12,13}. However, as in *Sphenodon*, the jaw joint is ventral in position in *Chimaerasuchus* and the Malawi notosuchid. Consequently, the posterior pterygoid muscle in the latter two was probably similar in its orientation to that in *Sphenodon*. As in *Sphenodon*, mandibular motion in the two crocodyliform reptiles must have been proal during jaw closing because the anterior pterygoid muscle, along with the pterygoid flange, would have restricted mandibular movements to front-to-back motion during jaw opening.

Although the skeleton of *Chimaerasuchus* is not yet fully known, characters indicating close affinities to the Notosuchidae (Fig. 4) include the articular facet of the jaw joint that is much longer than wide⁹, the ventral placement of the jaw joint, and the terminal, directly forward-facing external nares.

Notosuchid crocodyliforms have been considered endemic to the Cretaceous of Gondwana^{4,5,9}. Along with other new fossils¹⁴, the discovery of *Chimaerasuchus paradoxus* casts doubts on claims⁵ that Gondwana had a distinctly endemic tetrapod fauna during the Cretaceous. □

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Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds

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MANY Procellariiform seabirds make their living flying over vast expanses of seemingly featureless ocean waters in search of food. The secret of their success is a mystery, but an ability to hunt by smell has long been suspected^{1–7}. Here we present experimental evidence that Procellariiform seabirds can use a naturally occurring scented compound, dimethyl sulphide, as an orientation cue. Dimethyl sulphide has been studied intensely for its role in regulating global climate^{8–11} and is produced by phytoplankton in response to zooplankton grazing¹². Zooplankton, including Antarctic krill (*Euphausia superba*)¹³, are in turn eaten by seabirds and other animals¹⁴. Results from controlled behavioural experiments performed at sea show that many Procellariiforms can detect dimethyl sulphide, and that some species (for example, storm petrels) are highly attracted to it. To our knowledge, this constitutes the first evidence that dimethyl sulphide is part of the natural olfactory landscape overlying the southern oceans.

Experiments were conducted in sub-Antarctic waters near South Georgia during the Austral summer (January–March 1994). We chose this study area because Procellariiform species are numerous here, and the feeding habits of local species have been monitored for over two decades^{14,15}.

Our first set of experiments was designed to identify whether any Procellariiform species might be attracted to dimethyl sulphide (DMS). Our aim was to produce a down-wind DMS concentration that would be approximately the same as that which might naturally be encountered by a foraging petrel (nmol m⁻³ range)^{10,16,17}. We did this by deploying DMS-scented oil slicks on the ocean surface at ten different locations. Because surface slicks also presented visual cues to seabirds, DMS slicks were always paired with unscented ‘control’ slicks. We reasoned that if birds used DMS as a foraging cue, more birds should be attracted to DMS than to control slicks. At some locations, we also compared the response of birds to DMS with their response to cod liver oil, a well known olfactory attractant^{1,3,4,6,7}.

Results from our paired-slick experiments indicate that DMS is a potent olfactory attractant to many Procellariiform species, including white-chinned petrels, prions and two species of storm petrels (Fig. 1)¹⁸. Wilson’s storm petrels, for example, were sighted more than twice as often flying into DMS slicks than into control slicks. Indeed, when we plot the temporal response profiles of Wilson’s storm petrels to both DMS and cod-liver oil slicks (Fig. 2), we find that the outcomes are remarkably similar suggesting that DMS is as potent an olfactory attractant