A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil

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The skull of a new, and highly unusual crested dinosaur with an elongate rostrum is the first dinosaur to be named from the Santana Formation of NE Brazil. *Irritator challengeri* gen. et sp. nov was most likely a maniraptoran dinosaur, but its affinities to other maniraptorans remain to be established. Unique features for *Irritator* include the pattern of tooth replacement, a highly reduced supratemporal fenestra, extreme lateral compression of the rostrum and a saggital crest comprised of the frontal and parietal bones. *Irritator* was most probably a piscivore. A land link between South America and the dinosaurian faunal province of North America and Asia is indicated, probably via Africa.

Keywords: Brazil, Lower Cretaceous, dinosaurs, biogeography.

The almost complete skull of an unusual tetrapod from the Santana Formation (Lower Cretaceous) of Brazil (Fig. 1) in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS), does not obviously resemble any other tetrapod known from the Santana Formation, or indeed from the Cretaceous (Fig. 2). Dinosaurs are rare in the Santana Formation, and theropods in general are extremely rare in the Southern Hemisphere. The Santana Formation is well known for the abundance and diversity of its vertebrate fauna, but until now, no dinosaur has been well enough preserved to warrant formal description. The new specimen adds yet further to the wealth of palaeontological information from this unique palaeontological site.

The specimen was taken to the UK for computer aided tomography (CAT scan imaging) as well as a more thorough mechanical preparation. CAT scan imaging revealed that the tip of the rostrum had been artificially reconstructed to increase its length by reassembly of portions of the maxilla on to the premaxilla. This fabrication was concealed by blocks of matrix removed from other parts of the specimen and a thick layer of IsoponTM car body filler (see Martill 1904)

Locality and stratigraphy. The specimen (SMNS 58022) occurs within an early diagenetic concretion typical of those from the Romualdo Member of the Santana Formation (Martill 1993). Exact details of the locality are unknown but

the concretion closely resembles those dug commercially in and around Porteiras and the Serra da Maozina, at the eastern most outcrop of the Santana Formation on the slopes of the Chapada do Araripe, in Ceará State, northeast Brazil. Associated fish remains, including scales of *Cladocyclus* sp. confirm the stratigraphic horizon.

The Santana Formation lies toward the top of a sequence of fluvio-lacustrine and quasi-marine/lagoonal sediments in a half graben within the north east Brazilian shield. Although considered to be Lower Cretaceous, the exact age of the Romualdo Member is in debate. Ostracods appear to indicate an Aptian age (Bate pers. com.), while an Albian age has been suggested on the basis of the fish fauna, and Martill (1993) did not rule out a Cenomanian age.

Systematic description

Class Dinosauria Owen, 1842 Order Saurischia Seeley, 1888 Suborder Theropoda Marsh, 1881 Tetanurae Gauthier, 1986 Maniraptora Gauthier, 1986 Bullatosauria Holtz, 1994 Family Irritatoridae n.f.

Diagnosis for family. As for the type genus Irritator (see below).

Genus Irritator n.g.

Etymology: from irritation, the feeling the authors felt (understated here) when discovering that the snout had been artificially elongated.

Species I. challengeri g. et n. sp.

Etymology: from Professor Challenger, the ficticious hero and dinosaur discoverer of Sir Arthur Conan-Doyle's *Lost World*.

Holotype: SMNS 58022, in the collection of the Staatliches Museum für Naturkunde Stuttgart, Germany.

Locus typicus: Southern Ceará, northeast Brazil.

Stratum typicum: Romualdo Member of the Santana Formation.

Diagnosis: Theropod dinosaur with skull up to 840 mm in overall length (Figs 2, 3 & 4). Teeth highly elongate with posterior reduction in crown height; anterior maxillary teeth are straight, elongate, with sub-oval cross section and unserrated anterior and posterior carinae. Posterior maxillary teeth orthoconical. Tooth replacement mesolingual, and replacement teeth alternate between functional teeth. The tooth roots occupy almost the complete depth of the maxilla (Fig. 4). Maxilla straight with more than 11 teeth. Snout laterally compressed with triangular crosssection. Nasal opening oval, sited some way back from tip of snout. Frontals and parietals extended posterodorsally to form crest. Supra temporal fenestra very small. Infratemporal fenestra almost as large as orbit. Orbit ovoid. Quadrate massive and almost vertical. Stapes very thin, stick-like with expanded and flattened ends. Lower jaw twice as deep posteriorly than anterior ramus, angular extending only short distance anterior to mandibular fenestra. Mandibular fenestra inverted triangle, twice as long as high. Surangular with prominent, thin lateral shelf. At least posterior half of dentary probably edentulous.

Description. The skull is damaged in several places due to septarian cracking of the concretion and poor preparation,

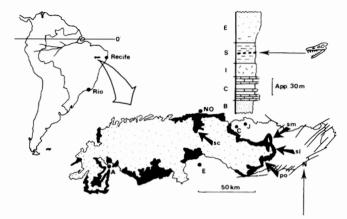


Fig. 1. Simplified geological map of the Araripe Basin, north east Brazil with generalised stratigraphic section for the fossiliferous part of the sequence. Map of South America shows position of Araripe Basin. Map of Araripe Basin; Black shading represent combined Santana, Ipubi and Crato Formations; light stipple represent overlying Exu Formation; white represents various older beds (Lower Cretacous, ?Upper Jurassic and possible Lower Palaeozoic). Towns: A, Araripina; C, Crato; E, Exu; NO, Nova Olinda; Large arrows indicate main commercial fossil collecting areas: po, Porteiras; sc, Santana do Cariri; sl, Sao Phillipe; sm, Serra da Maozina. Simplified stratigraphic section based on logs from around Santana do Cariri: B, Batatieras Fm. C, Crato Fm; I, Ipubi Fm; S, Santana Fm; E, Exu Fm.

mostly by the commercial fossil diggers prior to purchase. However, by taking information from both sides it has been possible to construct most of the skull morphology (Fig. 3). In addition, CAT scan sections have revealed details of tooth replacement (Fig. 4). There are some broken bones, notably in the lower jaws, in which matrix lies adjacent to

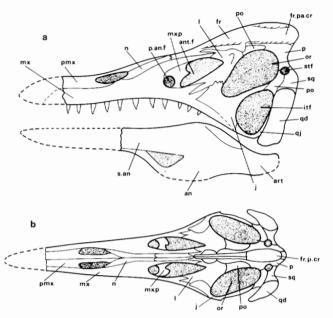


Fig. 3. Reconstruction of skull osteology of *Irritator challengeri* gen. et sp. nov. a, lateral view, b, dorsal view. Abbreviations: *an*, angular; *ant.f*, antorbital fenestra; *art*, articular; *fr*, frontal; *fr.p.cr*, frontal parietal crest; *itf*, inferior temporal fenestra; *j*, jugal; *l*, lachrymal; *mx*, maxilla; *mxp*, maxillary process; *n*, nares; *or*, orbit; *p*, parietal; *p.an.f*, preantorbital fenestra; *pmx*, premaxilla; *po*, postorbital; *prf*, prefrontal; *qd*, quadrate; *qj*, quadratojugal; *s.an*, surangular; *sq*, squamosal; *stf*, supratemporal fenestra.

the unworn fracture, indicating fracturing prior to burial. The snout is laterally compressed, and bears at least 16 large teeth, the crowns of the anterior teeth all about 40 mm



Fig. 2. Holotype of *Irritator challengeri* gen. et sp. nov. (SMNS 58022), from the Romualdo Member, Santana Formation, Ceará, north east Brazil. Specimen in lateral view app. ×0.25. Estimated total length of skull 800 mm.

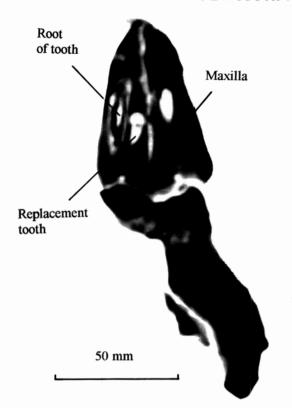


Fig. 4. CAT scan section through the rostrum of *Irritator challengeri* gen. et sp. nov. showing deeply emplaced and dorsally converging teeth and detail of dental replacement modus.

high. Some smaller teeth (estimated crown height 6 mm) are seen posteriorly in the upper jaw. Tooth replacement is mesolingual, and replacement teeth alternate between functional teeth, at least in the premaxilla (Fig. 4). CAT scan images through the jaws show that the roots are deeply implanted and occupy almost the full height of the upper jaw, converging medially, almost meeting in the midline. The nostrils are placed high and far back on the snout, but well forward of the antorbital fenestra. The medial margin of the antorbital fenestra is defined by a dorsal extension of the maxilla. There is a deep ovoid orbit, a large infratemporal fenestra and a small, dorsally placed supratemporal fenestra. The frontals are drawn out vertically into a relatively thin dorsomedian crest which also incorporates the upper half of the parietals. The posterior portion of the saggital crest has been fabricated by fossil dealers. The parietals appear to be short, but reflected ventrally. The braincase has prominent basioccipital tubera, and the occipital condyle and foramen magnum are both placed very high under the median crest. The foramen magnum faces posteriorly. The lower jaws are missing their distal half, due to fracturing before burial. The preserved parts of the lower jaw are edentulous. There is a large, subtriangular Meckelian fossa, and the jaw is very deep posterior to the fossa. A slightly undulate lateral shelf runs for approximately 80 mm just below the dorsal margin of the surangular.

Comparisons. That *Irritator* can be assigned to the Theropoda is suggested by a number of characters. Holtz (1994) lists 126 characters unique to Theropoda, of which 44

are cranial features. Of these 44, 11 agree with features seen in the skull of *Irritator*. These are (numbers in brackets refer to character states listed by Holtz 1994 appendix 1): dorsally projected parietal (14); large infra temporal fenestra (15); lacrimal fenestra (27); extreme reduction of the prefrontals (37); elongate, triangular frontals (65); occipital region deflected ventrally (74); narrow nasals (83); deep anterior portion of surangular (104); pronounced, round accessory antorbital fenestra (108); antorbital tooth row (110); loss of interdental plates (114).

Of the 19 taxa Holtz (1994) employs in his comparisons, four or more of the above characters are held in common within six taxa. *Irritator* shares four characters with *Allosaurus* (27,105,108,110); five with the Tyrannosauridae (27, 83, 105, 108, 110); six with *Archaeopteryx* (37, 83, 105, 108, 110, 114). Six characters are shared with the Dromaeosauridae (37, 83, 105, 108, 110, 114), and seven with the Bullatosauria (65, 74, 83, 105, 108, 110, 114).

Clearly the closest resemblance, in terms of character morphology, lies with members of the Tetanurae of Gauthier (1986). Within this group, which includes most of the familiar meat eating dinosaurs and birds, Irritator appears to show similarities with both the Dromaeosauridae (united with Archaeoptervx as an unamed clade (Holz 1994)) and the Bullatosauria (Ornithomimidae + Troodontidae) of Holz (1994). It is difficult, on the basis of skull characters alone, to distinguish these dinosaurs, and we note that Irritator is morphologically highly distinct from those theropods that are known from skull material. All of the characters that Irritator shares with Troodontidae it also shares with Ornithomimosauridae, suggesting that Irritator may well belong within this group. However, we note that no troodontids, ornithomimids, or indeed members of the Arctometatasalia have previously been reported from South America. Frey & Martill (1995) have reported on a dinosaurian synsacrum from the Santana Formation with pleurocoels, and suggested it may have affinities with the Oviraptosauridae. Holtz (1994) notes that pleurocoels are present in the dorsal vertebrae of the Bullatosauria.

There are a number of features which render *Irritator* distinct from other maniraptorans, which we consider warrant the creation of a new family, the Irritatoridae. Notably the saggital crest comprising the frontals and the parietals, the unique dental pattern, and the extreme elongation of the laterally compressed rostrum. Irritatoridae appears to be more similar to the Bullatosauria than to the group represented by Dromaeosauridae + *Archaeopteryx*; similarities with this group perhaps being due to convergence reported for a number of groups of Theropoda (Sereno *et al.* 1994)

Biogeographical implications. Theropod dinosaurs are rare from South America and *Irritator* represents the first identifiable specimen from the Lower Cretaceous of Brazil. *Irritator* is also the first non-avian maniraptoran to be described from the Cretaceous of South America, and confirms the existence of a land link between South America and the Cretaceous dinosaur faunas of North America and Asia, presumably via Africa. A route via Africa, while perhaps being the most obvious on tectonic and faunal grounds (Buffetaut 1989; Sereno *et al.* 1994) does pose some problems, in that Cretaceous dinosaurian faunas from North Africa are not well known. Sereno *et al.* (1994) have reported on large theropods from the Aptian of the Sahara

with affinities to the Abelisauridae, while Stromer (1915) described *Spinosaurus* as an enigmatic sailback theropod of gigantic proportions from the Cenomanian of Egypt.

The teeth of Irritator do show some similarities with those of Spinosaurus, but unfortunately the type material of Spinosaurus was destroyed during World War II and little identifiable spinosaur material has been collected subsequently (Buffetaut 1989). Nevertheless, the teeth figured by Stromer (1915) compare well with those of *Irritator*, but the mandible of Spinosaurus would certainly not fit with the dental margin of the maxilla and premaxilla of Irritator. Additionally, some other non-avian Theropoda lack serrations on some or all of their teeth, including the small coelurosaur Compsognathus (Ostrom 1978), the maniraptoran Ornitholestes and all the teeth of dentigerous birds (L. Chiappe pers. com. 1995). Thus, a number of questions are raised. Could Spinosaurus be assigned to the Maniraptora? Are Gondwanan theropods distinct from, but highly convergent upon Laurasian theropods in the same way that marsupial mammals are convergent with placental mammals, a point raised by Bonaparte & Powell (1980)?

The head crest and palaeobiology. Many dinosaurs are known with elaborate headcrests, including members of the hadrosaurian ornithopods, the ceratopsians, some sauropods and some theropods. Within the Theropoda head crests are usually rather small, with conservative morphology compared with those of hadrosaurs. The Late Triassic Dilophosaurus has two crests comprising the nasal and lacrymal bones (Welles 1984). In Ceratosaurus a single crest is comprised of the premaxilla and nasals, and in Cryolophosaurus an anteriorly flexed bony crest is constructed from the lacrymals (Hammer & Hickerson 1994). In the South American abelisaurid Carnotaurus the frontals are extended laterally to produce triangular horns (Bonaparte 1991), but these structures are altogether different from the frontal/parietal crest in Irritator. The head crest of Irritator challengeri appears to be unique for the Theropoda.

The massive construction of the crest and its posterior position indicates an enlarged attachment area for the dorsal neck musculature. Such a musculature would have provided strong dorsally directed forces. This indicates an ability to pull the head upward with reasonable force, or alternatively, to resist drag if the lower jaw was inserted into water.

Such movement would have been consistent with piscivory, a habit also suggested for *Irritator* by the dental pattern and the great elongation of the maxilla and premaxilla (Fig. 4).

Thanks to Dr R. Wild (Stuttgart) for the loan of the specimen; Ms. W. Wright for operating the CAT scanner; Mr J.G. Martin (Leicestershire Museums) and the University of Nottingham for use of facilities. Many people have commented on this unusual animal and we particularly thank Drs D. M. Unwin, M. Barker, L. Witmer, A.C. Milner, A.R. Milner, and L. Chiappe who commented on various versions of the manuscript. Correspondence to D.M. Martill (e-mail: martilld@geol.port.ac.uk).

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