red zone in Fig. 1) in accord with geochemical observations[23,24]. The conduit is at least 250–300 °C hotter than the surrounding mantle and less than about 400 km in diameter in the transition zone, in line with the absence of the plume signature in a recent global tomographic model[25]. Due to the large diameter of the Fresnel zone (300 km at 660 km depth) of the converted waves with 10 s period, the actual size of the anomalous zone at 660 km depth may be much smaller than 400 km. The relatively small size of the plume at 660 km depth suggests that the plume originates below this boundary, similar to the finding for the Iceland plume[7] and consistent with another seismological study indicating lower-mantle origin for another (Bowie) hotspot[26]. Our estimations suggest, however, that the Hawaii plume temperature is at least 100 °C higher than the temperature of the Iceland plume, which is in accord with petrological observations[19] and recent dynamic models of both plumes[27,28].

It is possible that the localized, very-low-velocity zone at asthenospheric depths that we observe is usable as an indicator of a plume conduit. The depth of the top of this zone contains information on the temperature within the plume conduit. □

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A pug-nosed crocodyliform from the Late Cretaceous of Madagascar

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Although the image of crocodyliforms as 'unchanged living fossils' is naive, several morphological features of the group are thought to have varied only within narrow limits during the course of evolution[1]. These include an elongate snout with an array of conical teeth, a dorsoventrally flattened skull and a posteriorly positioned jaw articulation, which provides a powerful bite force. Here we report an exquisitely preserved specimen of a new taxon from the Late Cretaceous of Madagascar that deviates profoundly from this Bauplan, possessing an extremely blunt snout, a tall, rounded skull, an anteriorly shifted jaw joint and clove-shaped, multicusped teeth reminiscent of those of some ornithischian dinosaurs. This last feature implies that the diet of the new taxon may have been predominantly if not exclusively herbivorous. A close relationship with notosuchid crocodyliforms, particularly *Uruguaysuchus* (Late Cretaceous, Uruguay)[2] is suggested by several shared derived features; this supports a biogeographical hypothesis that Madagascar and South America were linked during the Late Cretaceous[3] .

Archosauria Cope 1869
Crocodyliformes Hay 1930
?Notosuchidae Dollo 1924
Simosuchus clarki gen. et sp. nov.

Etymology. Generic name from Greek *simos*, pug-nosed, and Greek *souchos,* the Egyptian crocodile-headed god. Specific name for James M. Clark in recognition of his contributions to crocodyliform systematics.

Holotype. University of Antananarivo UA 8679, complete skull and anterior portion of postcranial skeleton including cervical and anterior dorsal vertebrae, cervical and anterior dorsal osteoderms, and complete pectoral girdle and forelimbs (Fig. 1); discovered by L. L. Randriamiaramanana.

Type locality and horizon. Field locality MAD98-17, southeast of the village of Berivotra, Mahajanga Basin, northwestern Madagascar; Maevarano Formation, Upper Cretaceous (Maastrichtian, perhaps late Maastrichtian[3]).

Diagnosis. Differs from all other crocodyliforms in possessing the following: entire dentition consisting of clove-shaped, multicusped teeth with cusps arranged in single longitudinal row; maxillae do not meet on palatal midline; internarial bar comprising broad ascending premaxillary process; internal nares larger than, and adjacent to, suborbital fenestrae; two ossifications overlying each supratemporal fenestra; quadrate rami project anteroventrally; foramen ovale projects anterolaterally; 14 contiguous quadrilateral osteoderms per mediolateral row in dorsal shield.

Discussion. As indicated by the fusion of neural arches to the vertebral centra, the holotype represents an adult individual[4], with a skull measuring 12.6 cm anteroposteriorly and 8.2 cm transversely (Fig. 1a–f). The dorsal surface of the skull is lightly sculpted, although the lateral margins of the maxillae are smooth and unsculpted. There are two large palpebral bones over each orbit. The supratemporal fenestrae are distinctly shorter than the orbits, with an extensive posterior floor formed by the parietal and squamosal. Each is capped by two small, circular ossifications resembling the palpebrals. The squamosal is broad, forming a large shelf overhanging the otic region, with a pronounced posterior projection. The jugal is robust, with an expanded, heavily sculpted ridge below the laterally directed orbit. An antorbital fenestra, found in nearly all notosuchid crocodyliforms[5], is present and of moderate size. The snout is similar to that of *Comahuesuchus* (Late Cretaceous, Argentina) in being distinctively broad, shortened anteroposteriorly and deep dorsoventrally[6]. Anteriorly, the paired nasals are separated by dorsal extensions of the premaxillae and the paired external nares face forward and laterally.

The quadrate extends anteroventrally, resulting in a jaw articulation that is much further forward than in all other crocodyliforms, with the exception of *Comahuesuchus*. Except for opening and closing, there appears to have been little mobility in jaw movement.
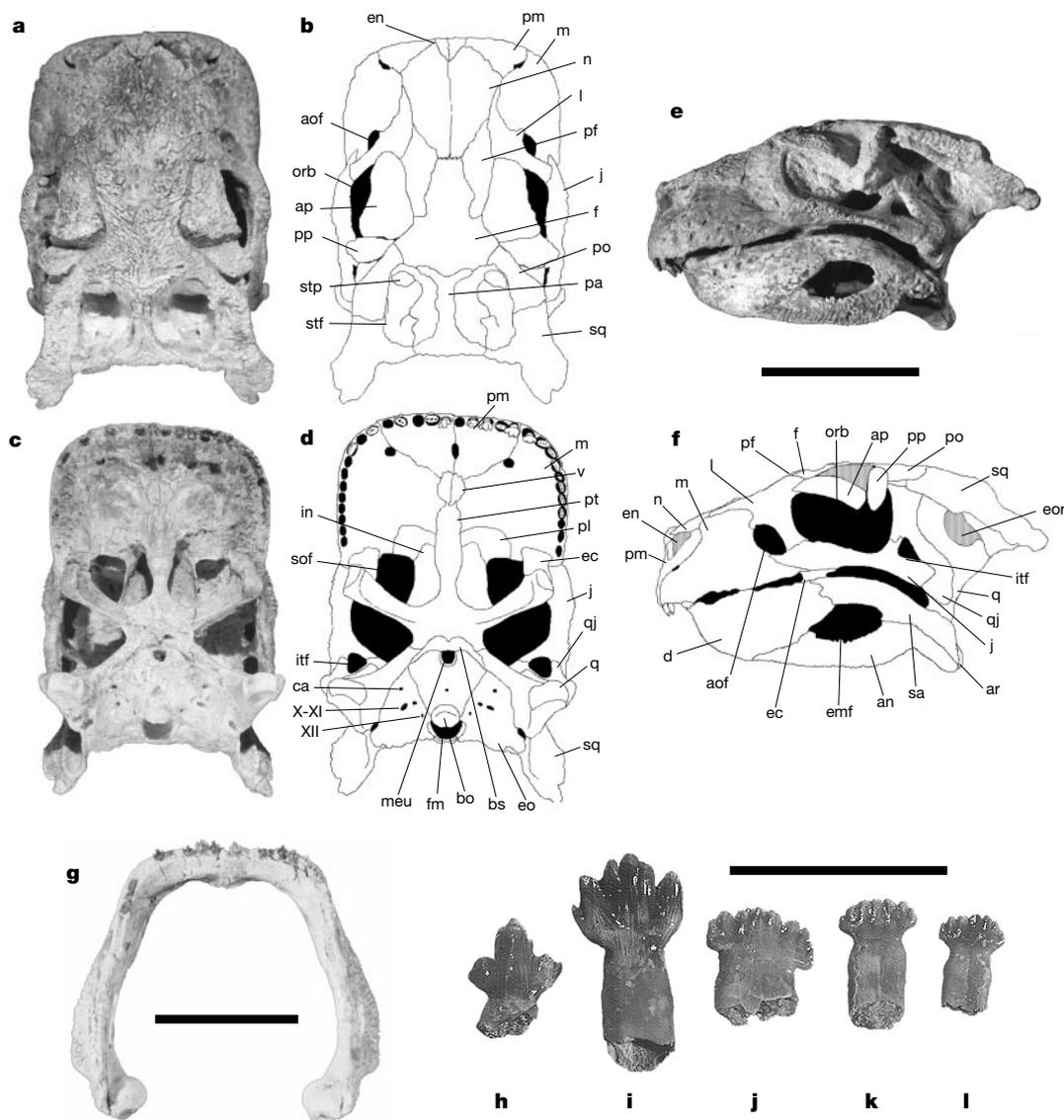

Figure 1 *Simosuchus clarki*, UA 8679 (holotype), from the Upper Cretaceous Maevarano Formation of Madagascar. Skull in dorsal (**a**, **b**), ventral (**c**, **d**) and lateral (**e**, **f**) views; mandible in dorsal view (**g**); teeth, progressing posteriorly in the tooth row from left to right (**h**–**l**). Scale bars, 5 cm (**a**–**g**); 1 cm (**h**–**l**); an, angular; aof, antorbital fenestra; ap, anterior palpebral; ar, articular; bo, basioccipital; bs, basisphenoid; ca, internal carotid foramen; d, dentary; ec, ectopterygoid; emf, external mandibular fenestra; en, external nares; eo, exoccipital; eor, external otic recess; f, frontal; fm, foramen magnum; in, internal nares; itf, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; meu, medial eustachian foramen; n, nasal; orb, orbit; pa, parietal; pf, prefrontal; pl, palatine; pm, premaxilla; po, postorbital; pp, posterior palpebral; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sof, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra; stp, supratemporal ossification; v, vomer; X-XI, opening for posterior cranial nerve; XII, hypoglossal foramen.

The glenoid fossa is narrow anteroposteriorly, suggesting limited propalinal motion. This is in stark contrast to the long jaw articulation in *Notosuchus* (Late Cretaceous, Argentina)[6] and *Malawisuchus* (Early Cretaceous, Malawi)[7,8].

The palatal aspect of the skull is well preserved. The maxillae do not meet along the midline of the palate as in other crocodyliforms, but instead are separated anteriorly by the premaxillae and posteriorly by paired vomers and an extensive anterior projection of the pterygoid. This pterygoid projection also separates the palatines. The shape and position of the vomers in *Simosuchus* are superficially like those of the extant *Melanosuchus*—a diamond-shaped exposure toward the front of the palate[9]. The internal nares open beneath the palatines and the anterior projections of the pterygoid. The occipital condyle is positioned posteroventrally, as in *Notosuchus* and *Malawisuchus*[8], unlike the posterior orientation typical of nearly all other crocodyliforms.

The mandible is broad and horseshoe-shaped with an extremely short fused symphysis and a laterally expanded flange on the lateroventral margins of the angular (Fig. 1e–g). Although the latter feature is atypical, it is not unique within crocodyliforms, with a similar structure developed in the eusuchian *Mekosuchus* (Cenozoic, Australia and New Caledonia)[10,11].

There are 16 tooth positions in each upper jaw quadrant (5 premaxillary and 11 maxillary) and 15 positions in each ramus of the lower jaw. The teeth are unique within crocodyliforms. The dentition of *Simosuchus* is heterodont, although all of the teeth are clove-shaped and multicusped with all of the cusps in a single, longitudinal row. The anteriormost teeth have a large central cusp, with lower accessory cusps (Fig. 1h). Moving back in the tooth row, the cusp number increases and there is greater uniformity in cusp size (Fig. 1i). Still further posteriorly, the crowns are shorter and the teeth become progressively smaller with fewer cusps (Fig. 1j–l). All of the teeth have heavy roots and are strongly compressed buccolingually, with a pronounced constriction at the base of the crown.

Although multicusped teeth are rare in crocodyliforms, they have been reported in *Candidodon* (Early Cretaceous, Brazil)[12,13], *Chimaerasuchus* (Early Cretaceous, China)[14], *Malawisuchus* and *Uruguaysuchus*. The teeth of *Uruguaysuchus* are most similar to those of *Simosuchus*, with the former possessing strongly compressed spatulate teeth with a sharp constriction at the base of the crown. Although the cheek teeth of *Uruguaysuchus* have not been described as multicusped[2], there are distinct cuspules arranged in a single longitudinal row as in *Simosuchus*.

Although unusual, *Simosuchus*, with cranial characters that include an antorbital fenestra smaller than the orbits, a sutured maxillary–premaxillary butt joint, a parietal lacking broad occipital exposure, fenestrated dorsal surface of the quadrate, the presence of two large palpebrals and a flat dorsal surface of the skull table, is indubitably a crocodyliform[15]. A phylogenetic analysis, using 22 ingroup taxa and 117 discrete characters, reveals that *Simosuchus* nests firmly within a clade (Fig. 2, node A) consisting of several other small-bodied, short-snouted Gondwanan crocodyliforms, including *Notosuchus* and other putative notosuchids such as *Uruguaysuchus* and *Malawisuchus*. Like all members of this clade, *Simosuchus* possesses a broad and high rostrum, nasals that contact the medial and anterior edges of the lacrimal and a posteroventrally positioned occipital condyle. Within this clade, unambiguous synapomorphies uniting *Simosuchus* with *Uruguaysuchus* and *Malawisuchus* include a long process extending from the posterolateral edge of the squamosal, a cranioquadrate passage enclosed near the lateral edge of the skull by the quadrate, squamosal and otoccipital, and a retroarticular process that is attenuated and projects posteriorly from the ventral part of the mandible. *Simosuchus* and *Uruguaysuchus* are linked by two unambiguous synapomorphies: internal nares divided by a septum and strongly spatulate posterior teeth. The sister-group relationship of *Simosuchus* and *Uruguaysuchus* corroborates the biogeographic

hypothesis, which is based previously on gondwanatherian mammals[16], abelisaurid theropod dinosaurs[17] and peirosaurid crocodyliforms[18], that Madagascar and South America were physically and biotically linked, perhaps through Antarctica, well into the Late Cretaceous.

Simosuchus and *Uruguaysuchus* both possess posterior teeth with multiple cusps in a single row. This is an ambiguous synapomorphy in this analysis. *Simosuchus*, *Uruguaysuchus* and *Malawisuchus* all share multicusped teeth, but in *Malawisuchus* (as in *Chimaerasuchus*) the cusps are arranged in multiple anteroposterior rows, which was treated as a separate character state. As we treated this character as unordered, neither condition (single-rowed or multiple-rowed multicusped teeth) could be regarded as ancestral for the clade including *Malawisuchus*, *Uruguaysuchus* and *Simosuchus*.

The array of unusual morphological features found in *Simosuchus* leads to several preliminary functional and ecological interpretations. The anterolaterally positioned external nares, together with laterally positioned orbits, suggest that *Simosuchus* was not as well adapted for floating at the surface of an aquatic habitat as are modern crocodylians, in which the external nares and orbits are dorsally positioned[19]. Several features suggest that *Simosuchus*, like *Malawisuchus*[7,8], may have been an adept head-burrower. These traits, seen in extant head-burrowing vertebrates, include a short, flat, shovel-like snout and deep cranium, a posteroventrally positioned occipital condyle that would orientate the cranium in a more vertical position, a short, underslung lower jaw that would prevent friction from inadvertently opening the jaws during burrowing, and extensive insertion areas for neck musculature (enlarged hypapophyses and elongated neural spines on the cervical vertebrae, expanded squamosal region and occiput)[20,21].

The relatively anterior position of the jaw joint and the relative brevity of the mandible suggest that *Simosuchus* emphasized neither force nor speed of the bite typical of modern crocodylians. The geometry of jaw adduction forces may in fact more closely resemble that of turtles, suggesting different modes of food processing[22]. This, together with marginal, clove-shaped, multicusped teeth adapted for puncturing and shredding, indicates a specialized dietary preference for *Simosuchus* that is not normally displayed by crocodyliforms. Teeth of this form are typically regarded as indicative of
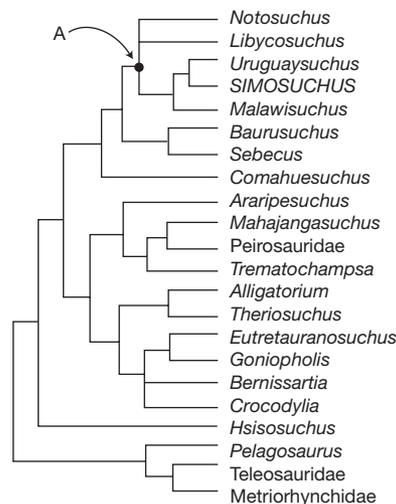

Figure 2 Cladogram showing phylogenetic position of *Simosuchus clarki* based on strict consensus of the six most parsimonious trees (length, 262; Consistency Index (excluding autapomorphies) 0.460; Retention Index, 0.642) generated using PAUP* (version 4.0b2a)[27]. For character list and taxa/character matrix see Supplementary Information. Trees were rooted with *Protosuchus*, *Orthosuchus* and *Hemiprotosuchus* as outgroups.

an exclusively to predominantly herbivorous diet[23,24]. In overall morphology the dentition most closely resembles that of some ornithischian dinosaurs, particularly stegosaurs and ankylosaurs, which are also generally regarded as herbivores[25,26]. Still, there are no modern crocodylian analogues with which to compare the potential function of *Simosuchus*' unique skull and dentition, and the suggestion of an herbivorous diet is speculatively based on dental comparisons with non-crocodylian reptiles. Given the cranial and dental specializations as well as the small size of the adult *Simosuchus*, it can be assumed that *Simosuchus* did not bring down large prey. It is still plausible, however, that the diet may have consisted of arthropods, other invertebrates and potentially small vertebrates such as frogs.

Similarities with ankylosaurid dinosaurs are not limited to dentition. Other features of *Simosuchus* appear to be convergent with those of ankylosaurs, such as the broad compact body, extensive dorsal and ventral shielding, bony protection of the skull above the supratemporal fenestrae and orbits, and a deep cranium with a broad, short snout. A crocodyliform convergent upon an ornithischian dinosaur is intriguing in light of the apparent absence of the latter from the Late Cretaceous of Madagascar. ☐

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Diversity and endemism of the benthic seamount fauna in the southwest Pacific

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Seamounts comprise a unique deep-sea environment, characterized by substantially enhanced currents and a fauna that is dominated by suspension feeders, such as corals[1-4]. The potential importance of these steep-sided undersea mountains, which are generally of volcanic origin, to ocean biogeography and diversity was recognized over 40 years ago[5], but this environment has remained very poorly explored. A review[3] of seamount biota and biogeography reported a total of 597 invertebrate species recorded from seamounts worldwide since the *Challenger* expedition of 1872. Most reports, based on a single taxonomic group, were extremely limited: 5 seamounts of the estimated more than 30,000 seamounts in the world's oceans[4,6] accounted for 72% of the species recorded. Only 15% of the species occurring on seamounts were considered potential seamount endemics. Here we report the discovery of more than 850 macro- and megafaunal species from seamounts in the Tasman Sea and southeast Coral Sea, of which 29–34% are new to science and potential seamount endemics. Low species overlap between seamounts in different portions of the region indicates that the seamounts in clusters or along ridge systems function as 'island groups' or 'chains,' leading to highly localized species distributions and apparent speciation between groups or ridge systems that is exceptional for the deep sea. These results have substantial implications for the conservation of this fauna, which is threatened by fishing activity[7].

Whereas previous studies of the seamount fauna have often focused on particular taxa, the present study sought to describe the benthic community as a whole and enlisted broad taxonomic support (see Acknowledgements). In all, 516 species of fish and macro-invertebrates were obtained from 6 seamounts along the Norfolk Ridge, 108 from 4 seamounts on the Lord Howe Rise, and 297 from 14 seamounts south of Tasmania (Table 1, Fig. 1). Thirty-six per cent of species from the Norfolk Ridge seamounts were new to science and not known from sampling of the open seafloor and are therefore potential endemic species, along with 31% of species from the Lord Howe seamounts and between 16 and 33% from the Tasmanian seamounts.

Over the range of sampling carried out on Norfolk and Lord Howe Ridges, we found a linear relationship between number of species recorded from each seamount and the number of samples obtained there (Fig. 2). This relationship implies that the greater number of species obtained from seamounts on Norfolk Ridge is

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