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Palaeontology

A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs

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Cretaceous ichthyosaurs have typically been considered a small, homogeneous assemblage sharing a common Late Jurassic ancestor. Their low diversity and disparity have been interpreted as indicative of a decline leading to their Cenomanian extinction. We describe the first post-Triassic ichthyosaur from the Middle East, *Malawania anachronus* gen. et sp. nov. from the Early Cretaceous of Iraq, and re-evaluate the evolutionary history of parvipelvian ichthyosaurs via phylogenetic and cladogenesis rate analyses. *Malawania* represents a basal grade in thunnosaurian evolution that arose during a major Late Triassic radiation event and was previously thought to have gone extinct during the Early Jurassic. Its pectoral morphology appears surprisingly archaic, retaining a forefin architecture similar to that of its Early Jurassic relatives. After the initial latest Triassic radiation of early thunnosaurians, two subsequent large radiations produced lineages with Cretaceous representatives, but the radiation events themselves are pre-Cretaceous. Cretaceous ichthyosaurs therefore include distantly related lineages, with contrasting evolutionary histories, and appear more diverse and disparate than previously supposed.

1. Introduction

Several Mesozoic reptile clades invaded the marine realm [1]. Increasing specialization for pelagic life occurred in many lineages, notably in ichthyosaurs, plesiosaurs, metriorhynchids and mosasaurs, resulting in numerous successive events where archaic taxa became extinct while younger, more pelagically specialized close relatives replaced them in ecological terms; notably, evidence for long-term morphological stasis is conspicuously absent in these groups [1–7]. The youngest major ichthyosaurian clade, Ophthalmosauridae, possesses the most 'derived' versions of several ichthyosaurian adaptations to pelagic life, notably in terms of limb morphology [8]. Ophthalmosauridae appear in the fossil record during the Aalenian (Middle Jurassic; [9]) and persist long after other lineages disappeared; it is the only clade considered to have Cretaceous representatives. Cretaceous taxa are traditionally considered to be low in diversity and disparity [10,11] and to represent the descendants of a Late Jurassic ancestor [12–14]. Both ideas have contributed to the popular hypothesis that Cretaceous ichthyosaurs represent the last remnants of a group that was in decline ever since the Middle or Late Jurassic [10,11], a view challenged only recently [15,16].

We report new data that causes us to further modify this view of ichthyosaur evolution. A new ichthyosaur from the Early Cretaceous of Iraq, the first ever reported from the post-Triassic of the Middle East, is identified as a late-surviving non-ophthalmosaurid thunnosaurian, providing the first evidence of a long-term morphological stasis in Ichthyosauria. In addition, we propose a novel evolutionary hypothesis for parvipelvian ichthyosaurs based on thorough phylogenetic and cladogenesis rate analyses.

2. Systematic palaeontology

Ichthyosauria Blainville, 1835 [17]
Parvipelvia Motani, 1999 [18]
Thunnosauria Motani, 1999 [18]
Malawania anachronus gen. et sp. nov.

(a) Etymology

From Kurdish 'Malawan': swimmer and Latinized Greek noun in apposition 'anachronus' meaning 'out of time'.

(b) Holotype, locality and age

NHMUK PV R6682 (see figure 1 and electronic supplementary material, S2 and S3); articulated partial skeleton comprising a fragmentary skull, cervical and thoracic vertebrae, ribs, partial shoulder girdle and a nearly complete left forefin. The specimen is unequivocally dated to the late Hauterivian–Barremian (Early Cretaceous) by palynomorphs (see the electronic supplementary material, figure S1); it is from Chia Gara, Amadia, Kurdistan region, Iraq.

(c) Diagnosis

Thunnosaurian ichthyosaur characterized by four autapomorphies: posteriorly projecting process of capitulum of humerus; short (axial length/distal width = 0.99; electronic supplementary material, table S1), trapezoidal humerus; intermedium almost equal in size to radius; cervical and anterior thoracic neural spines trapezoidal.

(d) Description

The skull is poorly preserved and highly incomplete, including only the sclerotic rings and parts of the jugals and lacrimals. The right sclerotic ring incorporates 13 plates. The jugal process of the lacrimal is elongated, reaching the middle of the orbit. The anterior part of the lacrimal houses a shallow, triangular cavity, possibly for the lacrimal gland.

Approximately 25 centra are visible; at least five are cervicals. The parapophyses and diapophyses are confluent with the anterior margins of some thoracic centra, as is the case in non-parvipelvian ichthyosaurs [18]. The atlas is nearly twice as long as the axis; both are fused together, though with the lateral suture still present. The centra are constant in length along the preserved vertebral column, even in the cervical region. In the cervical and anterior thoracic regions, the unusual trapezoidal shapes of the neural spine apices mean that they are widely separated. The ribs are eight-shaped in cross section, as is typical for thunnosaurians [11].

The anterior edge of the scapula is straight and lacks a prominent acromial process, in marked contrast to the condition in *Stenopterygius* and Ophthalmosauridae [19]. The humerus is proportionally shorter than that of other parvipelvians and lacks the constriction present in most non-ophthalmosaurid neoichthyosaurians [8]. The capitulum is not hemispherical but, uniquely, forms a long posterior process. The humerus lacks a distal expansion and possesses two distal facets. The radius and ulna are hexagonal, longer than wide, and lack anterior notches. There is no spatium interosseum. The intermedium is unusual in being nearly as large as the radius; it is hexagonal and supports two digits (the 'latipinnate' condition). The radiale is rhombic, as it is in one specimen of *Macgowania* (Royal Ontario Museum, Toronto, Canada 41991; [13]). Carpals, metacarpals and most phalanges are hexagonal and form a tight mosaic similar to that of *Macgowania* [20] and some basal neoichthyosaurians [8]. The forefin is tetradactyl and there are no accessory digits. Notching is present on the leading digit, here on the first phalanx. The phalangeal count is nine, but must originally have been higher because the distal-most part of the forefin is missing.

3. Results

Our phylogenetic analyses (see electronic supplementary material) recover *Malawania* as a basal member of Thunnosauria (see figure 2*a*,*b* and electronic supplementary material, S4–S12): it shares bicapitate dorsal ribs (character 30.1) and the absence of a prominent leading edge tuberosity on the anterodistal extremity of the humerus (character 44.1) with other members of this clade, in our main analysis. *Malawania* lacks ophthalmosaurid synapomorphies, including accessory preaxial digits and an unnotched leading edge to the forefin [19]. Good Bremer support (= 3) for Thunnosauria means that we are confident about the inclusion of *Malawania* within this clade. Within Thunnosauria, our main and reduced analyses recover *Malawania* as closely related to *Ichthyosaurus communis*, sharing a 'latipinnate' forefin architecture (character 51.1). Incorporation of *Malawania* in other, smaller and less updated analyses [21,22] also results in its exclusion from Ophthalmosauridae, although its relationships with basal neoichthyosaurians are less well resolved. As in previous analyses [13,19], our analyses indicate that *Stenopterygius quadriscissus* and Ophthalmosauridae form a moderately well-supported clade (Bremer support = 2/3), here named Baracromia nov.

Rather than finding successive parvipelvian lineages to be arranged in a pectinate, 'linear' fashion as was the case in previous analyses [13,18], we find the respective taxa to belong to a lower number of larger radiations (see figure 2 and electronic supplementary material): a major, latest Triassic 'Neoichthyosaurian Radiation', an Aalenian (Middle Jurassic) 'Ophthalmosaurid Radiation' and a Kimmeridgian (Late Jurassic) 'Platypterygiine Radiation'.

4. Baracromia nov.

(a) Diagnosis

Thunnosaurian ichthyosaurs with reduced root striations (character 4.1), absence of a supratemporal–postorbital

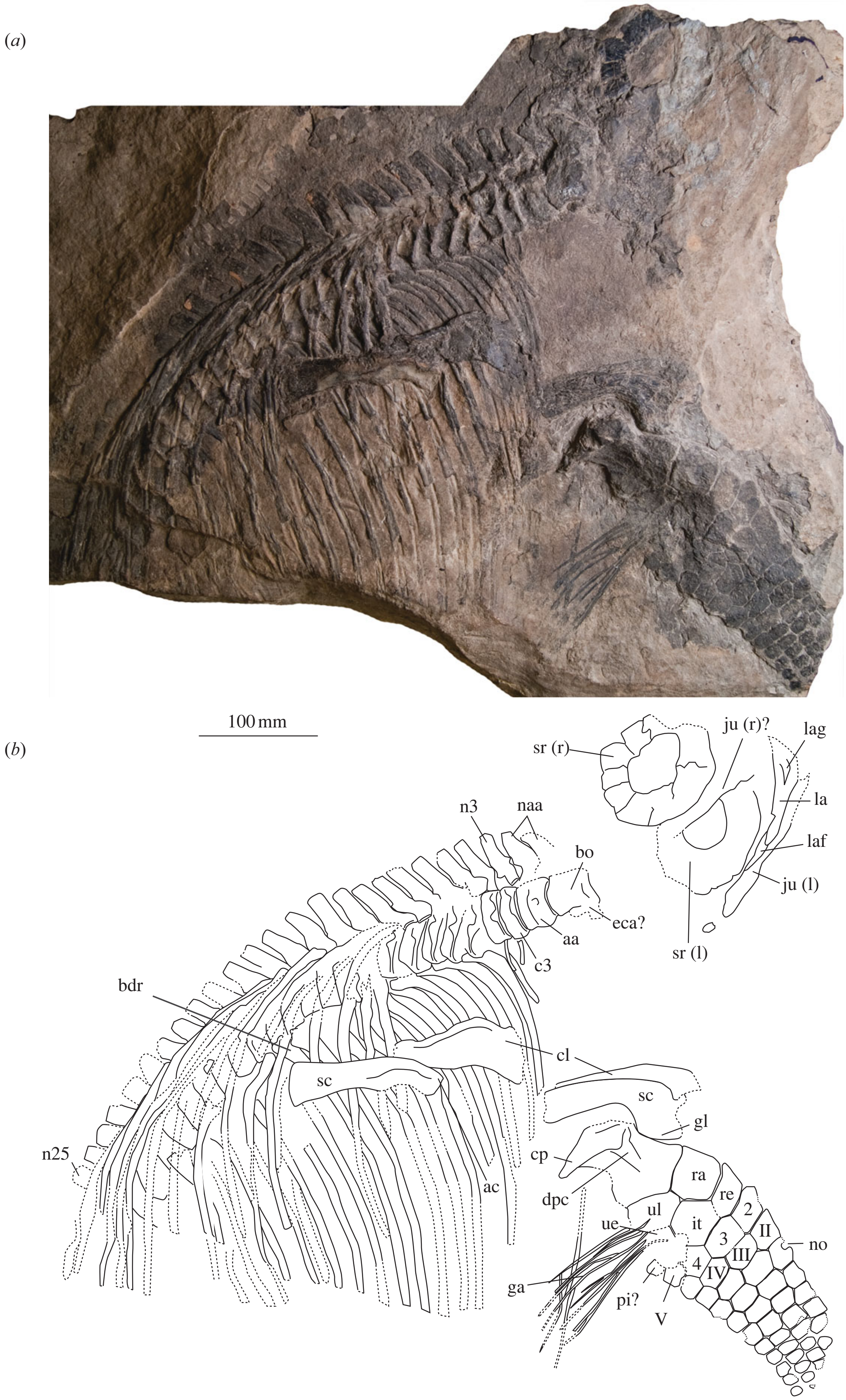

Figure 1. Holotype specimen of *Malawania anachronus* gen. et sp. nov., NHMUK PV R6682. (*a*) Specimen as preserved. (*b*) Morphological identification. 2–4, carpals; II–V, metacarpals; aa, atlas-axis; ac, acromial process of scapula; bdr, bicipital dorsal rib; bo, basioccipital; c3, third cervical centrum; cl, clavicle; cp, capitular process; dpc, deltopectoral crest; eca, extracondylar area; ga, gastralia; gl, glenoid contribution of the scapula; it, intermedium; ju, jugal; la, lacrimal; laf, lacrimal facet of jugal; lag, lacrimal gland impression; n3–25, cervical and thoracic neural arches; naa, atlas-axis neural arches; no, phalangeal notch; pi, pisiform; ra, radius; re, radiale; sc, scapula; sr, sclerotic ring; ue, ulnare; ul, ulna. (Online version in colour.)

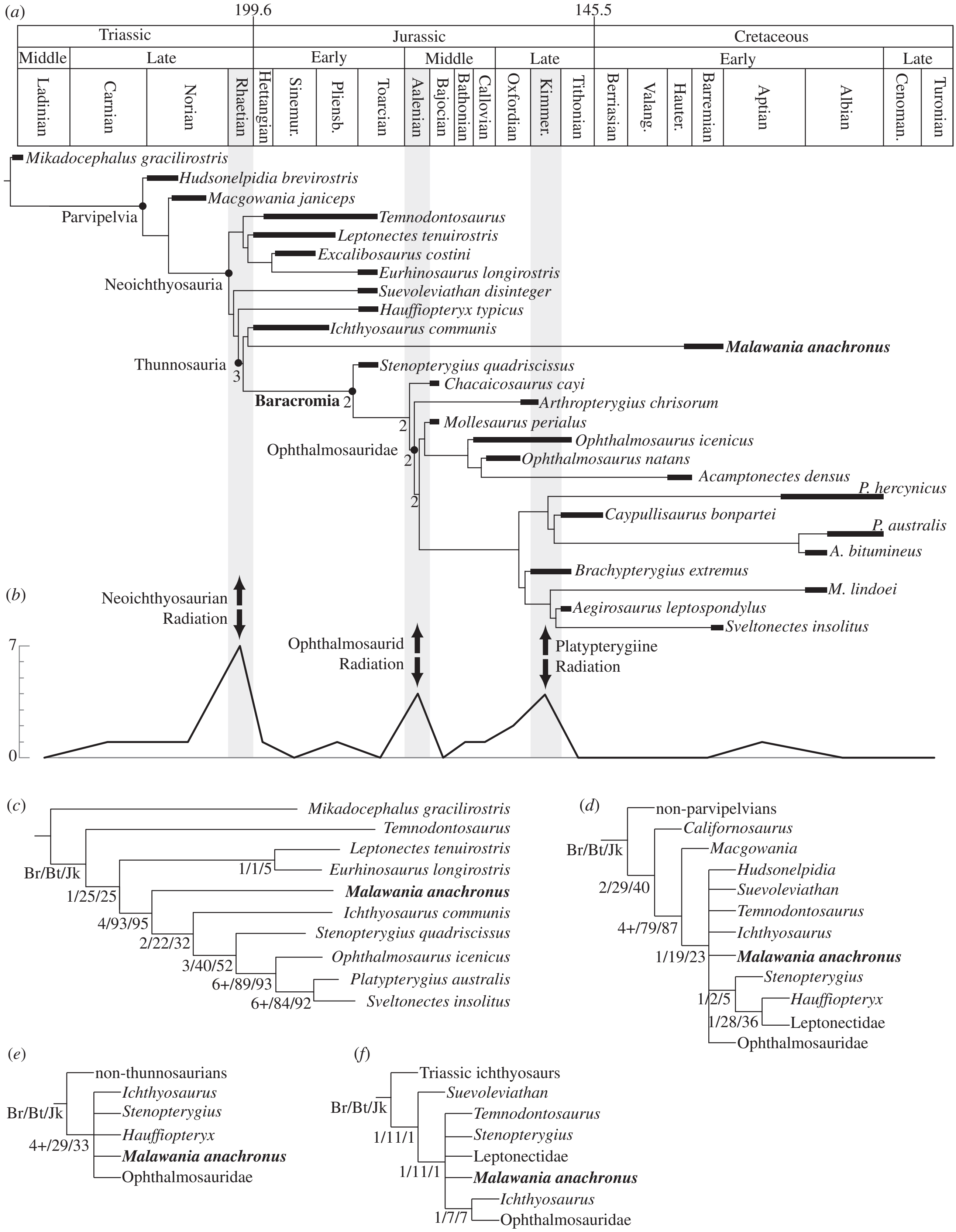

Figure 2. Evolutionary history of parvipelvian ichthyosaurs. (*a*) Time-calibrated phylogeny of Parvipelvia, using the new dataset (Bremer support >1 are indicated near each node; see the electronic supplementary material for details). (*b*) Cladogenesis rate for the Ladinian–Turonian interval based on the results of (*a*). The time interval for *Malawania* is the time range given by the palynomorph dating, not a stratigraphic range. (*c,d,e,f*) Additional tests of the phylogenetic position of *Malawania* (see the electronic supplementary material for details). Br, Bremer Support; Bt, bootstrap; Jk, Jacknife values. (*c*) Single most parsimonious tree arising from the second parsimony analysis of the new data matrix, restricted to nearly completely coded taxa (greater than or equal to 80%) + *Malawania* + outgroup; the support for *Malawania* as a basal thunnosaurian is high. (*d,e*) Simplified version of the cladograms resulting from the analysis of Caine & Benton [21] datasets. (*f*) Simplified version of the cladograms resulting from the analysis of Thorne *et al*. [22] dataset.

contact (character 15.1), loss of apical chevrons (character 29.1), presence of a prominent acromial process (character 36.1) and fused ischiopubis (character 57.1–2).

(b) Etymology

From Latinized Greek 'barys': heavy and 'akros õmos' (acromion); referring to the prominent acromial process of the scapula.

(c) Phylogenetic definition

The node-based clade that includes *Stenopterygius quadriscissus* and *Ophthalmosaurus icenicus*, and all descendants of their most recent common ancestor, but not *Ichthyosaurus communis*.

5. Discussion

The oldest occurrence of *Ichthyosaurus*, in the lowermost Hettangian 'pre-Planorbis' beds of England [13], pushes the origin of the *Malawania* lineage back to the latest Triassic, during the Neoichthyosaurian Radiation. It was previously thought that baracromians were the only ichthyosaurs to survive beyond the Early Jurassic. However, *Malawania* reveals a ghost lineage of about 66 Ma in duration and indicates that two thunnosaurian lineages coexisted until the Early Cretaceous. All three major parvipelvian radiations produced lineages with Cretaceous representatives; Cretaceous ichthyosaurs are thus more diverse, more disparate and less closely related to one another than long thought; they are not a homogeneous group as previously hypothesized [11,12,22]. Moreover, these radiations are all pre-Cretaceous, strongly supporting the hypothesis that no extinction event affected ichthyosaurs near the Jurassic–Cretaceous boundary [16].

The evolutionary history of Baracromia contrasts greatly with that of *Malawania*'s lineage. Baracromians rapidly colonized the entire globe [9,23] and became the dominant ichthyosaur clade after the Toarcian. Cretaceous baracromians differ markedly from their Early Jurassic relatives, notably in forefin architecture [9]. By contrast, *Malawania* represents the only evidence of a non-ophthalmosaurid ichthyosaur in post-Bajocian strata and its forefin closely resembles that of the Late Triassic *Macgowania* or Early Jurassic *Ichthyosaurus*, despite its apomorphic capitular process on the humerus. *Malawania*'s lineage therefore persisted for 66 Ma while conserving an 'Early Jurassic' grade of pectoral anatomy; meanwhile, baracromians underwent extensive morphological evolution involving specialization for improved swimming capabilities. In this sense, they were more comparable with other marine reptile clades, in which consistent morphological specialization for improved swimming efficiency and a pelagic lifestyle are general trends often commented on in the literature [1–7]. *Malawania*'s lineage does not fit into this general pattern and the rarity of this lineage may suggest that unusual and as yet unappreciated events affected its evolution. However, our limited knowledge of this newly recognized, long-lived lineage prevents further discussion of its evolutionary history. Ichthyosaur evolution and diversification is proving more complex than long imagined; *Malawania* joins other recent discoveries [16,19] in showing that the shape of ichthyosaur diversity and the modalities of their decline in the Cretaceous were substantially different from the traditional view.

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