

Research



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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 parvipelvic 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-parvipelvic 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 2a,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 parvipelvic 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, clavide; 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.)

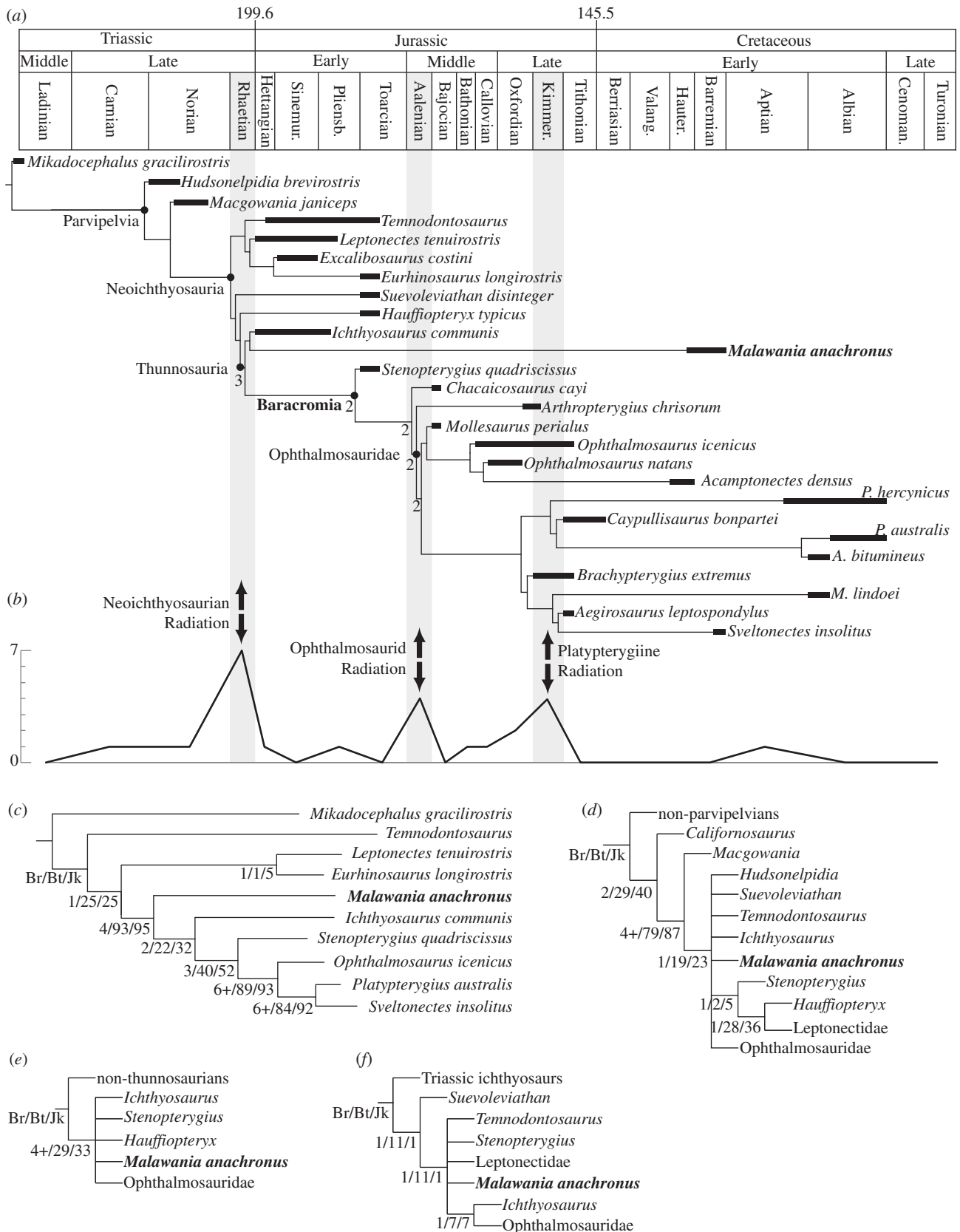


Figure 2. Evolutionary history of parvipelvic ichthyosaurs. (a) Time-calibrated phylogeny of Parvipelvica, using the new dataset (Bremer support > 1 are indicated near each node; see the electronic supplementary material for details). (b) Cladogenesis rate for the Ladinian–Turonian interval based on 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, Jackknife 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 ōmos' (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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Electronic Supplementary Material

Table of Contents

| | |
|---|----|
| Institutional abbreviations..... | 2 |
| Specimens examined..... | 2 |
| Research history..... | 3 |
| Palynomorph analysis and dating | 4 |
| Supplementary anatomical information..... | 6 |
| Phylogeny: methods..... | 9 |
| Phylogenetic characters list..... | 10 |
| Character states for each taxon | 15 |
| Tree description | 18 |
| Comparison with previous analyses..... | 30 |
| Additional analyses..... | 32 |
| Reduced dataset | 32 |
| Incorporation in other datasets | 33 |
| Cladogenesis analysis | 38 |
| Supplementary references..... | 39 |
| Supplementary acknowledgements..... | 44 |

Institutional abbreviations

BGS, British Geological Survey, Keyworth, Nottingham, UK; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; CM, Carnegie Museum, of Natural History, Pittsburgh, PA, USA; GLAHM, The Hunterian Museum, University of Glasgow, Glasgow, UK; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MHNH, Muséum d'Histoire Naturelle du Havre, Le Havre, France; NHMUK, Natural History Museum, London, UK; RGHP, Réserve naturelle géologique de Haute-Provence, Digne-les-Bains, France; SNHM, Staatliches Naturhistorisches Museum, Braunschweig, Braunschweig, Germany.

Specimens examined

Leptonectes tenuirostris (NHMUK PV R498 and NHMUK PV OR3612); *Eurhinosaurus longirostris* (NHMUK PV R3938 and NHMUK PV R5465); *Temnodontosaurus platyodon* (IRSNB R122, IRSNB R123, NHMUK PV OR2003*, and NHMUK PV R1158); *Suevoleviathan disinteger* (RGHP RO 1); *Ichthyosaurus communis* (NHMUK PV R5595); *Stenopterygius quadriscissus* (NHMUK PV R4086); *Ophthalmosaurus natans* (CM material); *Ophthalmosaurus icenicus* (NHMUK and GLAHM material); *Aegirosaurus* sp. (RGHP LA 1); *Platypterygius hercynicus* (MHNH 2010.4 and a cast of the holotype held at the SNHM); *Sveltonectes insolitus* (IRSNB R269); *Acamptonectes densus* (GLAHM 132855, NHMUK PV R11185, and SNHM1284-R); *Malawania anachronus* (NHMUK PV R6682).

Research history

The specimen (NHMUK PV R6682) was discovered by D.M. Morton, F.R.S. Henson, R.J. Wetzel and L.C.F. Damesin in 1952 (the following account was reconstructed by J.L. and D.N. from R.M.A.'s extensive correspondence on this subject). It was not found in situ, but at the side of a wadi and was possibly placed there for use as a paving block for a mule track. Donated to the NHMUK in 1959, the specimen was first investigated by R.M.A. with a view to publication in 1974. Over the course of the following 15 years, R.M.A. attempted to reconcile the stratigraphy of the local section with the opinions of relevant fieldworkers as to where in the succession the specimen could have originated. Ultimately, this led to an impasse caused by conflicting interpretations of the specimen's stratigraphic provenance. The adamant opinion of those working on local stratigraphy was that it must have come from the Sargelu Formation, most likely from the Aalenian rhynchonellid zone within that unit.

However, micropaleontological data showed that the slab containing the specimen was not an exact match for Sargelu Formation strata: as of 1980, the only samples tested from the matrix were those worked on by N.F. Hughes (CAMSM), who felt that the palynology clearly showed a Lower Cretaceous (probably pre-Aptian) assemblage. The disparity between this opinion and that of the field workers seems to have led to doubts over Hughes' conclusion, the suspicion being that perhaps he had inadvertently been sent the wrong palynomorph data. In an attempt to repeat the analysis, Hughes arranged for samples to be taken directly from the matrix of the ichthyosaur slab at the NHMUK. While these further samples were rich in organic content, Hughes could only recover decayed cuticle and wood fragments. Thin sections of the matrix were also sent to H.V. Dunnington for comparison with the Chia Gara Succession held by the University of Reading. Although Dunnington found no perfect match of the lithofacies, there was sufficient similarity for him to be "reasonably certain" that the block came from the *Rhynchonella* beds of the Sargelu Formation (Dunnington, pers. comm. to R.M.A., 1979).

Palynomorph analysis and dating

Since NHMUK PV R6682 was not found *in situ*, it is necessary to discuss its provenance. Members of the original field party stated that the specimen was most likely to have originated from within the *Rhynchonella*-bearing beds of the Sargelu Formation (see Dunnington et al. 1959): according to Dunnington (pers. comm. to RMA., 1979), there is little probability that it could have originated from below the base of this unit. The stream in the wadi at Chia Gara, where the specimen was found, runs north and eastwards down the succession, and the massive dolomite cliff (stratigraphically below the Sargelu Formation in this section) faces the same way: the specimen could not, therefore, have been washed up the succession from within the underlying Sehkaniyan Formation.

In an attempt to resolve this matter, we obtained a fresh sample from the slab in 2008. After processing with hydrofluoric acid, the fresh matrix sample yielded an organic residue overwhelmingly dominated by amorphous organic material (AOM), as initially observed by Norman Hughes in the sample that he obtained directly from the NHMUK. This is consistent with the bituminous nature of this unit observable in the specimen. In order to isolate and concentrate the palynomorphs, the raw organic residue was separately oxidised using Schultze's solution and fuming nitric acid in order to break up and dissolve the AOM. This process yielded dinoflagellate cysts, pollen and spores; finally providing definitive results and allowing the age of the specimen to be determined with confidence.

Our palynological results, although significantly at odds with those inferred earlier by Dunnington et al. (1959), are entirely consistent with Hughes's original 1979 determination from the first microphotographs of an Early Cretaceous, pre-Aptian age. The oxidised residue yielded an extremely sparse palynoflora, which included the dinoflagellate cyst *Muderongia staurota* Sarjeant 1966 (Fig. S1). This distinctive species is indicative of the Late Hauterivian to Barremian interval (Duxbury 1977; Heilmann-Clausen 1987; Costa and Davey 1992), and the holotype is from the Early Barremian of northern England (Sarjeant 1966). Several specimens of the gymnospermous pollen *Classopollis* were encountered, as were bisaccate pollen taxa. The spores *Cicatricosisporites* spp., *Concavissimisporites verrucosus* Delcourt and Sprumont 1955 and *Gleicheniidites* spp. are also present in the assemblage. This association, particularly the dominance of the distinctive spore genus *Cicatricosisporites* is typical of the Early Cretaceous (Dörhöfer 1979). This constrains the age of the specimen to the Late Hauterivian to Barremian

interval. Two Early Cretaceous formations, the Lower Sarmord Formation and the Lower Balambo Formation crop out nearby and represent likely source strata for the specimen.



Fig. S1. The dinoflagellate cyst *Muderongia staurota* Sarjeant 1966. Specimen lacking an operculum extracted from matrix of the slab containing the holotype of the Iraqi ichthyosaur *Malawania anachronus* described herein (NHMUK PV R6682). Figured specimen number MPK 14374, curated in the palynology collection of the British Geological Survey (BGS).

Supplementary anatomical information



Figure S2. Holotype specimen of *Malawania anachronus* gen. et sp. nov., NHMUK PV R6682, close-up of the thoracic region with partial right shoulder girdle. Note the constant length of the centra (partly obscured by ribs), the marked longitudinal grooves on the anterior and posterior surfaces of the ribs, giving them an ‘8-shaped’ cross-section, and the absence of a large acromial process on the scapula (the anterior margin of the scapula is traced in white).

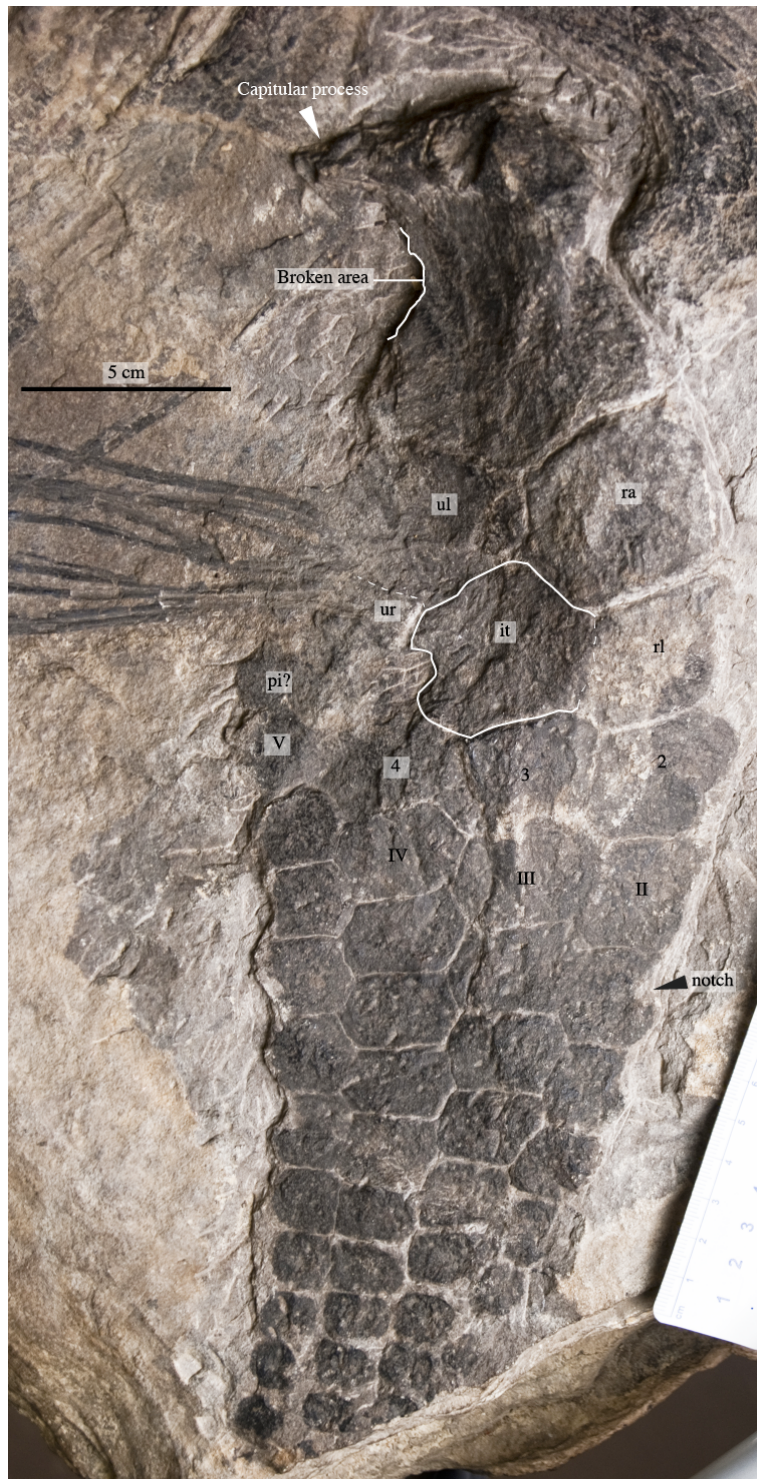


Figure S3. Holotype specimen of *Malawania anachronus* gen. et sp. nov., NHMUK PV R6682, close-up of the left forefin in ventral view. Note the posterior process on the capitulum, the marked trapezoidal shape of the humerus, the large size of the intermedium, the closely fitting elements, the lack of supernumerary digits and the notch on one element of the leading edge. See main text for anatomical abbreviations.

Table S1. Humeral distal width ratio of selected parvipelvian ichthyosaurs.

| Taxon | Distal width ratio | Reference |
|-------------------------------------|---------------------------|-------------------------|
| <i>Hudsonelpidia brevirostris</i> | ≈1.74 | McGowan 1995 |
| <i>Macgowania janiceps</i> | 1.60 | McGowan 1991 |
| <i>Leptonectes tenuirostris</i> | ≈1.25 | McGowan 1993 |
| <i>Leptonectes solei</i> | ≈*1.07 | McGowan 1993 |
| <i>Leptonectes moorei</i> | 1.25 | McGowan and Milner 1999 |
| <i>Excalibosaurus costini</i> | ≈*1.06 | McGowan 1989, 2003 |
| <i>Eurhinosaurus longirostris</i> | 1.04 | McGowan 2003 |
| <i>Suevoleviathan disinteger</i> | 1.16 | Maisch 1998 |
| <i>Temnodontosaurus platyodon</i> | 1.20 | Godefroit 1993a |
| <i>Ichthyosaurus communis</i> | 1.48 | McGowan and Motani 2003 |
| <i>Stenopterygius quadriscissus</i> | 1.25 | Godefroit 1994 |
| <i>Hauffiopteryx typicus</i> | 1.17 | Maisch 2008 |
| <i>Ophthalmosaurus icenicus</i> | ≈1.21 | Kirton 1983 |
| <i>Sveltonectes insolitus</i> | 1.60 | Fischer et al. 2011b |
| <i>Platypterygius hercynicus</i> | 1.23 | Kolb and Sander 2009 |
| <i>Platypterygius australis</i> | 1.29 | Zammit et al. 2010 |
| <i>Malawania anachronus</i> | 0.99 | This work |

The ratio equals the axial length (measured along greatest proximodistal axis) divided by the distal width (greatest anterior–posterior distance). Abbreviations: ≈, mean of left-right ratios; *, some specimens have a ratio <1, but this is due to a prominent leading edge tuberosity on the anterodistal part of the humerus (character state 44.0).

Phylogeny: methods

We compiled a new phylogenetic character set for Parvipelvina (the last common ancestor of *Macgowania janiceps*, *Hudsonelpidia brevirostris* and *Ichthyosaurus communis*, and all its descendants [Motani 1999]) by expanding the Thunnosauria dataset of Fischer et al. (2012). Numerous specimens were examined first-hand (listed above). This is the largest dataset devoted to parvipelvian ichthyosaurs.

Sixty-six discrete characters and 25 in-group taxa are used. All currently valid parvipelvian genera are represented within the data matrix except *Nannopterygius enthekiodon* and *Undorosaurus gorodischensis*: these are, respectively, incompletely described or of questionable validity (Maisch and Matzke 2000; McGowan and Motani 2003). *Mikadocephalus gracilirostris*, the best known euichthyosaurian close to Parvipelvina (Maisch and Matzke 2000), is used as the outgroup for this analysis. Our coding for *Temnodontosaurus* is based on the two best-known species included in that genus: *T. platyodon* and *T. trigonodon*. Sixty-three characters are taken and/or modified from the literature and three characters are new (indicated by an ‘*’ in the list below). Characters were not weighted and, except for characters 20, 39, 49, and 57, were not ordered. Characters were coded from the literature and from personal observations of specimens as listed above. Heuristic algorithms (1000 replications, 10 trees saved per replication) of TNT v1.1 (Goloboff et al. 2010) were used to analyse the character–taxon matrix and calculate the Bremer support and bootstrap (standard bootstrap, 1000 replicates) and Jackknife (removal probability of 36, 1000 replicates) values. We optimized the characters on the consensus tree with unambiguous, slow (DELTRAN), and fast (ACCTRAN) optimizations using Winclada v.0.9 (Nixon 1999). Geological timescale is taken from Ogg et al. (2008).

Phylogenetic characters list

1. Crown striations: presence of deep longitudinal ridges (0); crown enamel subtly ridged or smooth (1) (Druckenmiller and Maxwell 2010: character 25).
2. Base of enamel layer: poorly defined, invisible (0); well defined, precise (1) (Fischer et al. 2011b: character 2).
3. Root cross-section in adults: rounded (0); quadrangular (1) (Fischer et al. 2011b: character 3, modified).
4. *Root striations: present (0); absent or subtle (1).
5. Overbite: absent or slight (0); clearly present (1) (Motani 1999: character 33).
6. Processus postpalatinis pterygoidei: absent (0); present (1) (Maisch and Matzke 2000: character 38).
7. Maxilla anterior process: extending anteriorly as far as nasal or further anteriorly (0); reduced (1) (Fischer et al. 2011b: character 7).
8. Descending process of the nasal on the dorsal border of the nares: absent (0); present (1). (Fernández 2007: character 2).
9. Processus narialis of the maxilla in lateral view: present (0); absent (1) (Fischer et al. 2011b: character 9, inverted coding).
10. Processus supranarialis of the premaxilla: present (0); absent (1) (Maisch and Matzke 2000: character 10).
11. Processus narialis of prefrontal: absent (0); present (1) (Fischer et al. 2011b: character 11).
12. Anterior margin of the jugal: tapering, running between lacrimal and maxilla (0); broad and fan-like, covering large area of maxilla ventrolaterally (1) (Druckenmiller and Maxwell 2010: character 6).
13. Sagittal eminence: present (0); absent (1) (Fernández 2007: character 5, inverted coding Fischer et al. 2011b).
14. Processus temporalis of the frontal: absent (0); present (1) (Fischer et al. 2011b: character 14).
15. Supratemporal-postorbital contact: absent (0); present (1) (Sander 2000: character 27, inverted coding Fischer et al. 2011b).
16. Squamosal shape: square (0); triangular (1); squamosal absent (2) (Fischer et al. 2011b: character 16, inverted coding Fischer et al. 2011b).

17. Quadratojugal exposure: extensive (0); small, largely covered by squamosal and postorbital (1) (Maisch and Matzke 2000: character 30, modified Fischer et al. 2011b).
18. Lower temporal arch between jugal and quadratojugal: present (0); lost (1) (Sander 2000: character 25, modified).
19. Basispterygoid processes: short, giving basisphenoid a square outline in dorsal view (0); markedly expanded laterally, being wing-like, giving basisphenoid a marked pentagonal shape in dorsal view (1) (Fischer et al. 2011b: character 18).
20. Extracondylar area of basioccipital: wide (0); reduced but still present ventrally and laterally (1); extremely reduced, being nonexistent at least ventrally (2) (Fernández 2007: character 10, modified Fischer et al. 2011b).
21. Basioccipital peg: present (0); absent (1) (Motani 1999: character 29, modified Fischer et al. 2011b).
22. Ventral notch in the extracondylar area of the basioccipital: present (0); absent (1) (Fischer et al. 2012: character 19).
23. Shape of the paroccipital process of the opisthotic: short and robust (0); elongated and slender (1) (Fischer et al. 2012: character 20).
24. Stapes proximal head: slender, much smaller than opisthotic proximal head (0); massive, as large or larger than opisthotic (1) (Sander 2000: character 34, modified Fischer et al. 2011b)).
25. Angular lateral exposure: much smaller than surangular exposure (0); extensive (1) (Motani 1999: character 32, inverted coding Fischer et al. 2011b).
26. Posterior dorsal/anterior caudal centra: 3.5 times or less as high as long (0); four times or more as high as long (1) (Maxwell 2010: character 15, inverted coding Fischer et al. 2011b).
27. Tail fin centra: strongly laterally compressed (0); as wide as high (1) (Maxwell 2010: character 16).
28. Neural spines of atlas-axis: completely overlapping, may be fused (0); functionally separate, never fused (1) (Druckenmiller and Maxwell 2010: character 26).
29. Chevrons in apical region: present (0); lost (1) (Sander 2000: character 72).
30. Rib articulation in thoracic region: predominantly unicapitate (0); exclusively bicapitate (1) (Maisch and Matzke 2000: character 53).
31. Rib cross-section at mid-shaft: rounded (0); '8'-shaped (1) (Sander 2000: character 73, modified).

32. Ossified haemapophyses: present (0); absent (1) (Maisch and Matzke 2000: character 63).
33. Tail as long or longer than the rest of the body (0) distinctly shorter (1) (Maisch and Matzke 2000: character 65).
34. No lunate tailfin (0) well developed lunate tailfin (1) (Maisch and Matzke 2000: character 66).
35. Glenoid contribution of the scapula: extensive, being at least as large as the coracoid facet (0); reduced, being markedly smaller than the coracoid facet (1) (Fischer et al. 2012: character 27)
36. Prominent acromion process of scapula: absent (0); present (1) (Fischer et al. 2011b: character 28).
37. Anteromedial process of coracoid and anterior notch: present (0); absent (1) (Fischer et al. 2011b: character 29, modified).
38. Plate-like dorsal ridge on humerus: absent (0); present (1) (Motani 1999: character 56).
39. Protruding triangular deltopectoral crest on humerus: absent (0); present (1); present and very large, matching in height the trochanter dorsalis, and bordered by concave areas (2) (Fischer et al. 2011b: character 31, modified).
40. Humerus distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0); nearly equal or proximal end slightly wider than distal end (1) (Motani 1999: character 55, modified Fischer et al. 2011b).
41. Humerus anterodistal facet for accessory zeugopodial element anterior to radius: absent (0); present (1) (Godefroit 1993b: character 10, modified Fischer et al. 2011b).
42. Humerus with posterodistally deflected ulnar facet and distally facing radial facet: absent (0); present (1) (Fischer et al. 2011b: character 34, modified).
43. Humerus/intermedium contact: absent (0); present (1) (Fernández 2007: character 15).
44. *Anterodistal extremity of the humerus: prominent leading edge tuberosity (0); acute angle (1).
45. Shape of the posterior surface of the ulna: rounded or straight and nearly as thick as the rest of the element (0); concave with a thin, blade-like margin (1) (Fischer et al. 2012: character 36).
46. Radio-ulnar foramen: present (0); absent (0) (Maisch and Matzke 2000: character 84, modified).

47. Manual pisiform: absent (0); present (1) (Motani 1999: character 67, inverted coding Fischer et al. 2011b).
48. Notching of anterior facet of leading edge elements of forefin in adults: present (0); absent (1) (Motani 1999: characters 59 and 65, modified Fischer et al. 2011b)
49. Posterior enlargement of forefin: number of postaxial accessory ‘complete’ digits: none (0); one (1), two or more (2) (Maisch and Matzke 2000: character 89, modified Fischer et al. 2011b).
50. Preaxial accessory digits on forefin: absent (0); present (1) (Maisch and Matzke 2000: character 91).
51. Longipinnate or latipinnate forefin architecture: one (0); two (1) digit (s) directly supported by the intermedium (Fischer et al. 2011b: character 40).
52. Zeugo- to autopodial elements flattened and plate-like (0); strongly thickened (1) (Maisch and Matzke 2000: character 94).
53. Tightly packed rectangular phalanges: absent, phalanges are mostly rounded (0); present (1) (Maisch and Matzke 2000: character 102, modified Fischer et al. 2011b).
54. Digital bifurcation: absent (0); frequently occurs in digit IV (1) (Fischer et al. 2011b: character 43).
55. Manual digit V: lost or reduced to small floating elements (0); present (1) (Motani 1999: character 73, modified).
56. Forelimb–hind limb ratio: nearly equal (0); forelimb twice as long as hind limb (Godefroit 1993b: character 5, modified).
57. Ischium-pubis fusion in adults: absent or present only proximally (0); present with an obturator foramen (1); present with no obturator foramen (Mazin 1982: character 13, modified Fischer et al. 2011b).
58. Ischium or ischiopubis shape: plate-like, flattened (0); rod-like (1) (Motani 1999: character 87, modified Fischer et al. 2011b).
59. Iliac antero-medial prominence: present (0); absent (1) (Motani 1999: character 81).
60. Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft: absent (0); present (1) (Fischer et al. 2011b: character 46).
61. *Wide distal femur blade: present (0); absent, the proximal and distal extremity of the femur being sub-equal in dorsal view (1).
62. Astragalus/femoral contact: absent (0); present (1) (Maxwell 2010: character 33).

63. Femur anterodistal facet for accessory zeugopodial element anterior to tibia: absent (0); present (1) (Fischer et al. 2011b: character 48).
64. Spatium interosseum between tibia and fibula: present (0); absent (1) (Maisch and Matzke 2000: character 114, modified).
65. Hind fin leading edge element in adults: notched (0); straight (1) (Motani 1999: character 92, modified).
66. Postaxial accessory digit: absent (0); present (1) (Fischer et al. 2011b: character 50).

Character states for each taxon

Mikadocephalus gracilirostris

????0?0000 00??0000?? ?????0????? ?????000000 0000?0?0?? ??????00000 00000?

Hudsonelpidia brevirostris

????0????? ?????????? ?????????? ?0?????000 000000??00 0?0?100010 000000

Macgowania janiceps

?0?00?100? ??????100?? ?????0????? ??????????0 000?00?000 1?001????? ??????

Leptonectes tenuirostris

10010??00? 00000111?0 ??????0????? 0100000000 0000000000 0?00010000 000000

Excalibosaurus costini

100?1??0?? ??????????0 0?????????0 0?00010000 0000010000 0?000?0000 000000

Eurhinosaurus longirostris

1000111000 00000111?0 ??0000?100 01000000?0 0000011000 0?00A00000 000000

Temnodontosaurus spp.

0000000000 0000110100 0000000000 1100000000 000A010000 0000000000 000000

Suevoleviathan disinteger

0??0001000 00?00101?? ?????0????? ?101?000?0 000001?100 0001100010 000100

Ichthyosaurus communis

000000101A 00000B1100 0000000001 1111A00011 000101A110 1011110000 100100

Hauffiopteryx typicus

1???0?100? ??000111?0 0??100???1 1?110?00?0 000?010000 0?001100?0 000100

Stenopterygius quadriscissus

1001011010 0000111100 0001011111 1111110010 00010110A0 00A111100? 100100

Chacaicosaurus cayi

????0?0?? ? ??????????0 01????????? ????????0?? 0?0?0?1000 0100??????? ??????

Ophthalmosaurus icenicus

0101011111 01101111A1 A011110111 1111010121 1101111111 1100111001 100110

Ophthalmosaurus natans

10?1011111 0??01111?1 ?01110?0?? ?????110?11 110111?1?1 1?001????? ??????

Mollesaurus perialus

?????????1? 0????01111 1001?0???? ?????????? ?????????? ?????????? ??????

Acamptonectes densus

11?1???1?? ?1?1?????11 1111100?1? A???010111 1101111??1 ??0???????? ??????

Brachypterygius extremus

01110?0110 ?1?????112 11??1????? ??????101?1 0011011111 11001????? ??????

Arthropterygius chrisorum

?????????? ?????????02 01?1?11?1? ??????0111 110101?1?? 0?????????0 ?0????

Caypullisaurus bonapartei

????0?0010 0???0001?? ????10???? ????111121 1001011121 01101121?1 10?111

Aegirosaurus leptospondylus

00010?1111 11?11111?? ????1????? ?11????1?1 0011011111 1?101121?? 100111

Platypterygius australis

0111000000 0101120112 110110111? ?11?011121 1001011121 01101120?1 101111

Platypterygius hercynicus

01100?101? 01111A11?2 ?1?1??1?11 1???011121 1001011121 01101????1 11011?

Maiaspondylus lindoei

?110??1?11 ?1???????0? ??????0???? ????????1?1 0011011?1? 0?101????? ?10???

Athabascasaurus bitumineus

10?1??0001 ?1101001?2 ???110?1?? ?????????? ?????????? ??????2001 ??????

Sveltonectes insolitus

10110?1111 1111???102 11?1100?1? 11??110121 0001?1?111 11101121?1 101111

Malawania anachronus

?????????? ?????????? ?????????? 1????00??11 000101?000 1?001????? ??????

Tree description

Bremer support values that are >1 are indicated next to the respective clade name, followed by Bootstrap values when >50 (but all the Bremer, Bootstrap and Jackknife values are given in fig. S8). Changes are keyed to internodes indicated in Fig. S4 by alphabetic codes; unequivocal (non-homoplasious) synapomorphies [consistency index=1] are marked with an asterisk. Because we recover *Malawania anachronus* as the sister-taxon to *Ichthyosaurus communis*, it is probably appropriate to co-opt the name Ichthyosauridae Bonaparte 1841 for the *Malawania anachronus* + *Ichthyosaurus communis* clade. However, the second analysis (see below) recovers *Malawania* as being outside the clade that includes *Ichthyosaurus*, *Stenopterygius* and Ophthalmosauridae.

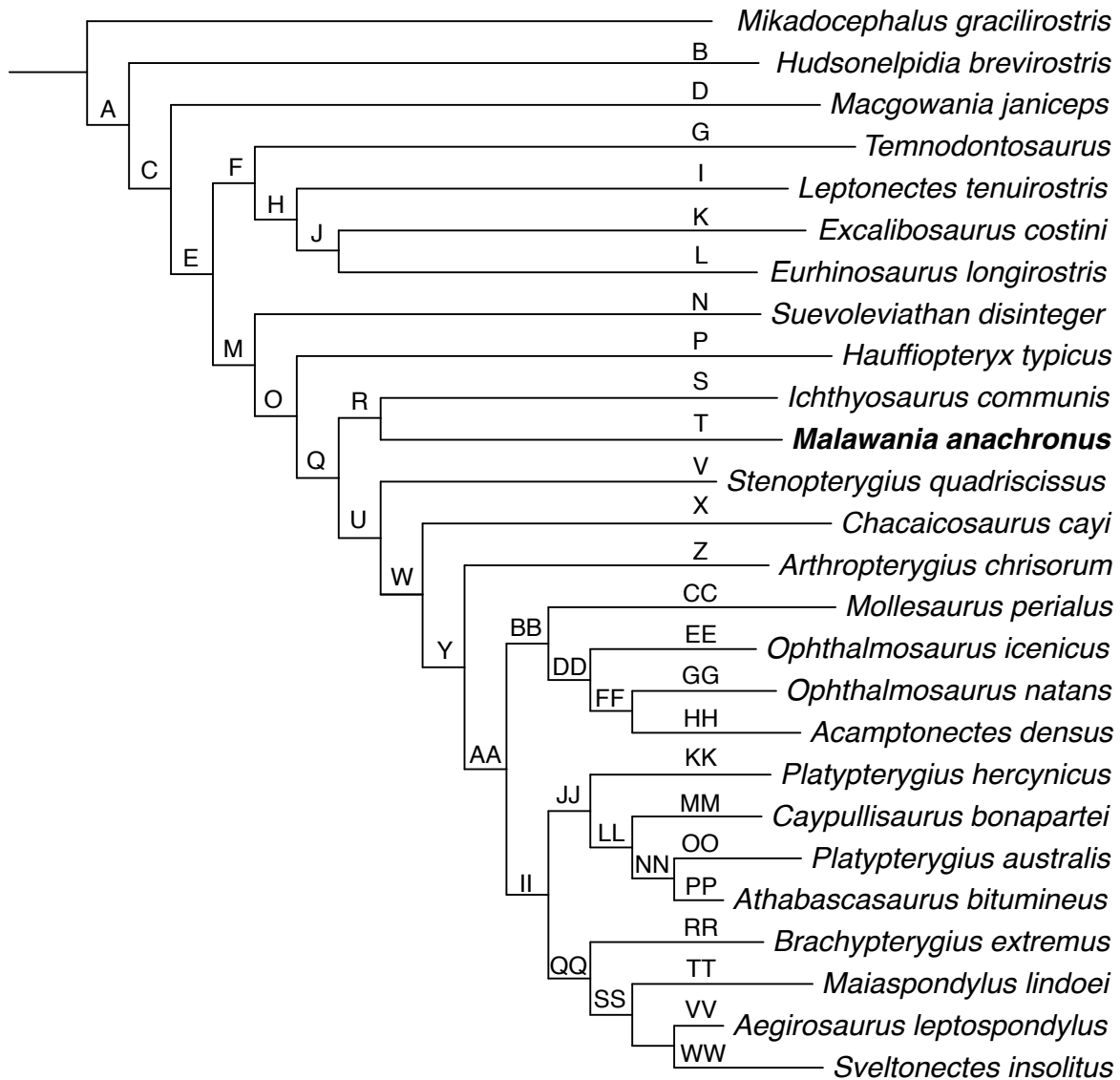


Fig. S4. Single most parsimonious tree arising from parsimony analysis of the character matrix. The tree is 137 steps long, the consistency index is 0.51, the retention index is 0.75 and the rescaled consistency index is 0.38. Clades and changes are keyed to internodes indicated in Fig. S4 by alphabetic codes.

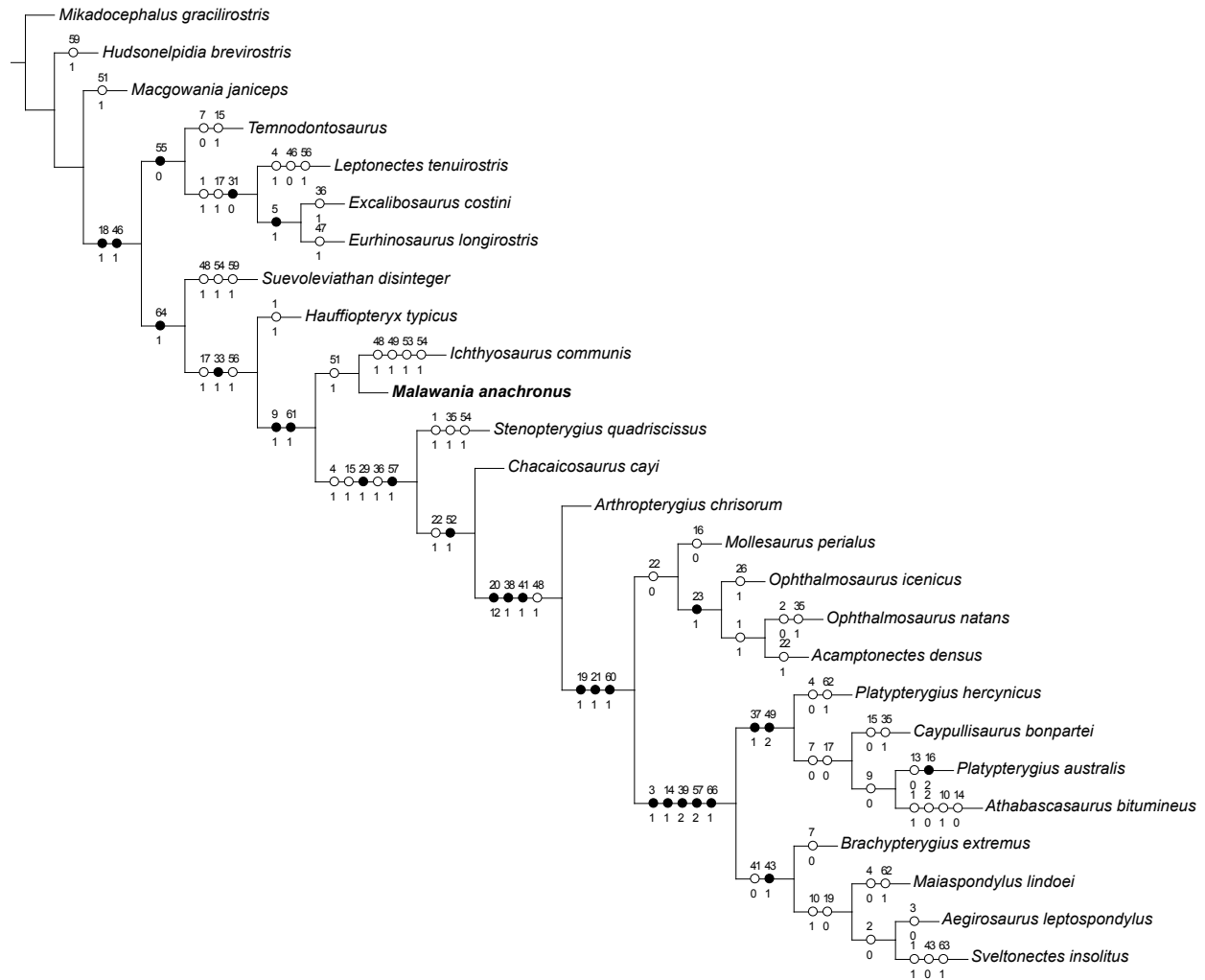


Fig. S5. Single most parsimonious tree arising from parsimony analysis of the character matrix, using unambiguous optimization.

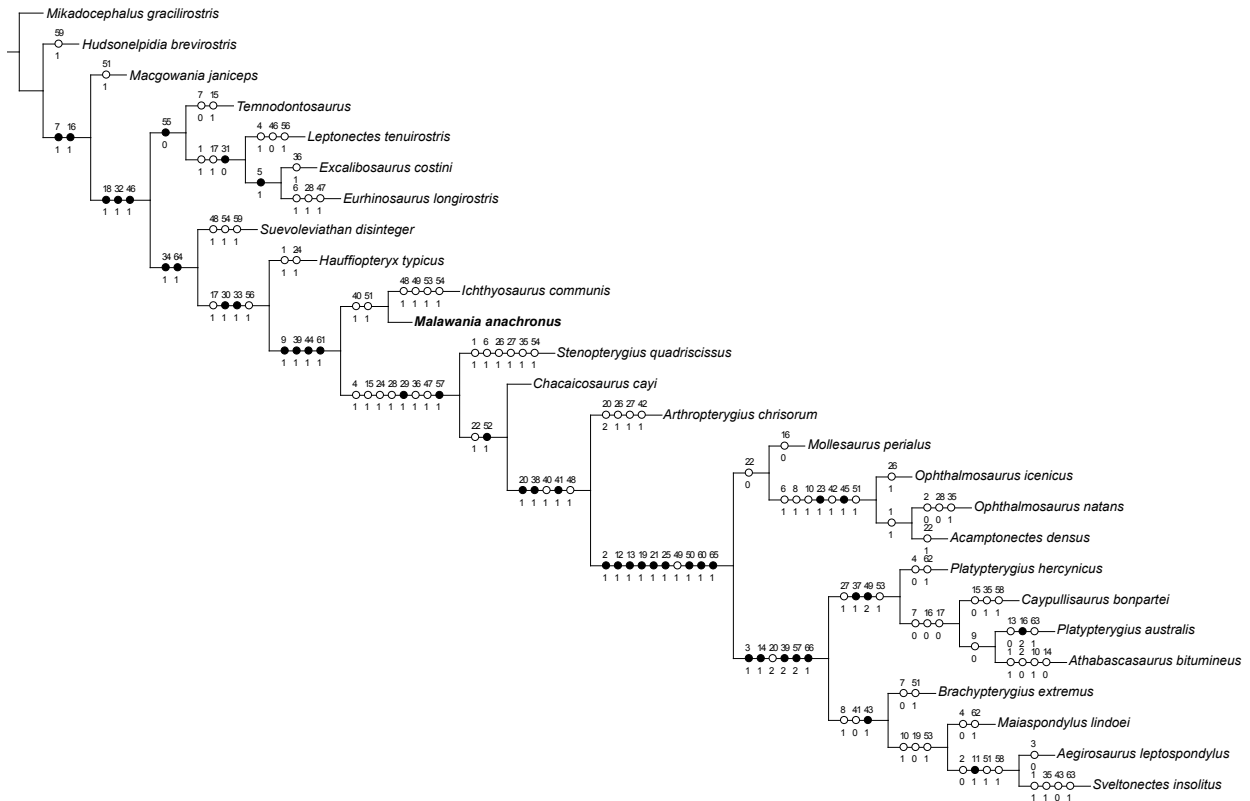


Fig. S6. Single most parsimonious tree arising from parsimony analysis of the character matrix, using slow optimization.

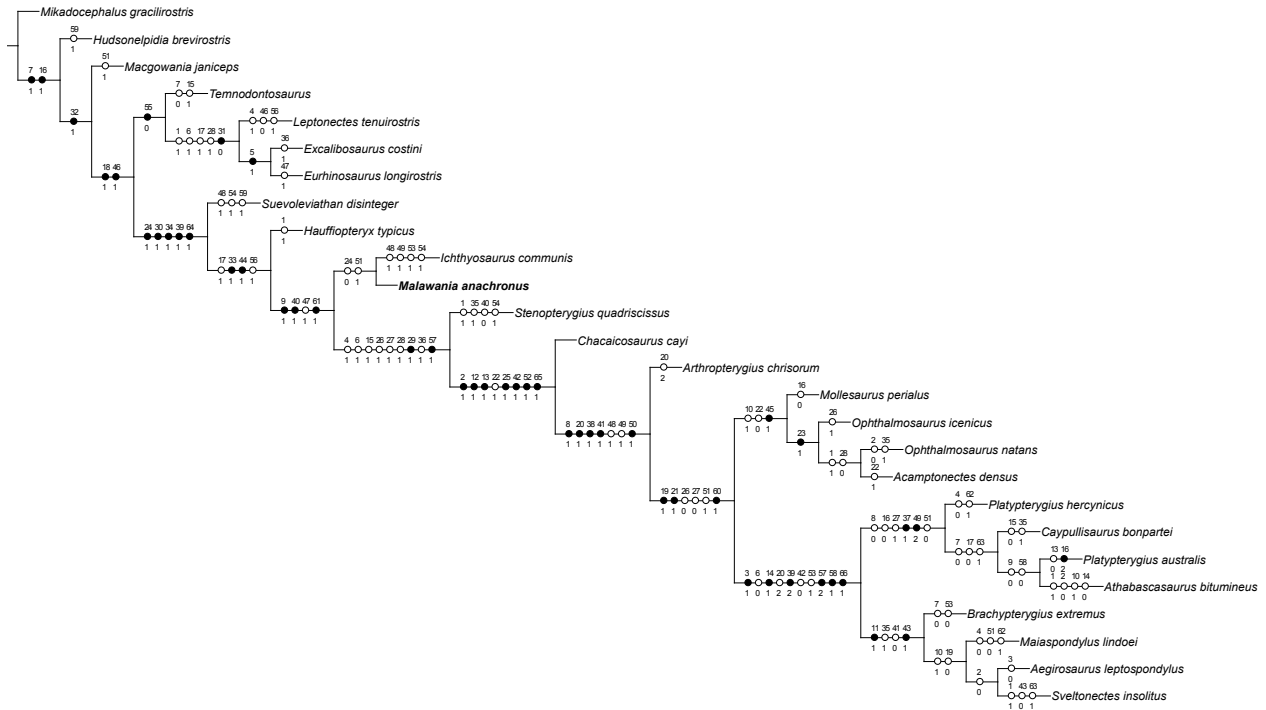


Fig. S7. Single most parsimonious tree arising from parsimony analysis of the character matrix, using fast optimization.

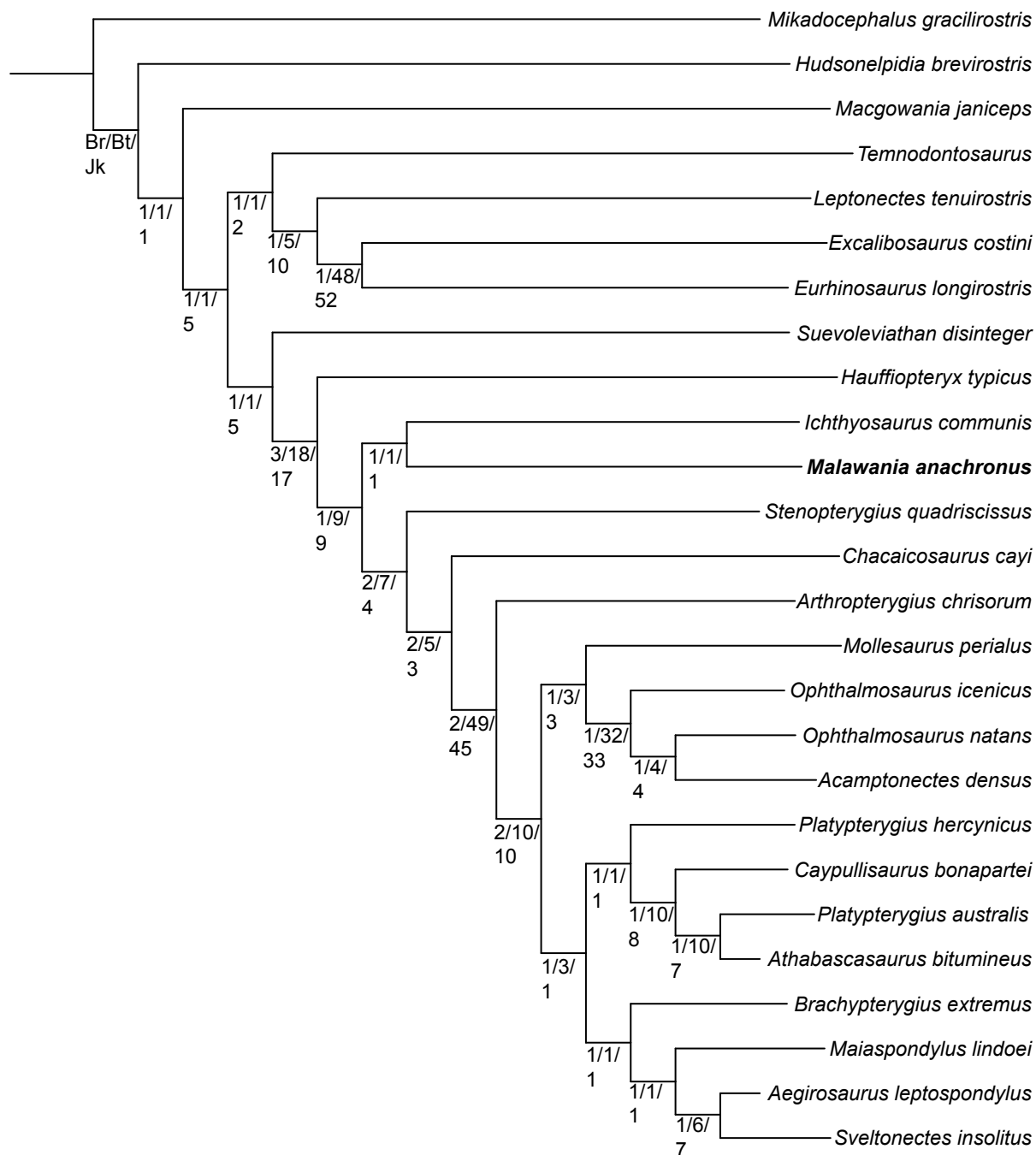


Fig. S8. Single most parsimonious tree arising from parsimony analysis of the character matrix, with Bremer, Bootstrap and Jackknife values.

Clade A (Parvipelvia; 4+)

Unambiguous: No character changes

Fast: 7 (0 → 1)*; 16 (0 → 1)*

Slow: No additional character changes

Terminal B (*Hudsonelpidia brevirostris*):

Unambiguous: 59 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade C (unnamed clade):

Unambiguous: No character changes

Fast: 32 (0 → 1)*

Slow: 7 (0 → 1)*; 16 (0 → 1)*

Terminal D (*Macgowania janiceps*):

Unambiguous: 51 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade E (Neoichthyosauria):

Unambiguous: 18 (0 → 1)*; 46 (0 → 1)*

Fast: No additional character changes

Slow: 32 (0 → 1)*

Clade F (unnamed clade):

Unambiguous: 55 (1 → 0)*

Fast: No additional character changes

Slow: No additional character changes

Terminal G (*Temnodontosaurus*):

Unambiguous: 7 (1 → 0); 15 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade H (Leptonectidae):

Unambiguous: 1 (0 → 1); 17 (0 → 1); 31 (1 → 0)*

Fast: 6 (0 → 1); 28 (0 → 1)

Slow: No additional character changes

Terminal I (*Leptonectes tenuirostris*):

Unambiguous: 4 (0 → 1); 46 (1 → 0); 56 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade J (unnamed clade):

Unambiguous: 5 (0 → 1)*

Fast: No additional character changes

Slow: No additional character changes

Terminal K (*Excalibosaurus costini*):

Unambiguous: 36 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Terminal L (*Eurhinosaurus longirostris*):

Unambiguous: 47 (0 → 1)

Fast: No additional character changes

Slow: 6 (0 → 1); 28 (0 → 1)

Clade M (unnamed clade):

Unambiguous: 34 (0 → 1)*; 64 (0 → 1)*

Fast: 24 (0 → 1)*; 30 (0 → 1)*; 39 (0 → 1)*

Slow: No additional character changes

Terminal N (*Suevoleviathan disinteger*):

Unambiguous: 48 (0 → 1); 54 (0 → 1); 59 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade O (Thunnosauria; 3):

Unambiguous: 17 (0 → 1); 33 (0 → 1)*; 56 (0 → 1)

Fast: 44 (0 → 1)*

Slow: 30 (0 → 1)*

Terminal P (*Hauffiopteryx typicus*):

Unambiguous: 1 (0 → 1)

Fast: No additional character changes

Slow: 24 (0 → 1)

Clade Q (unnamed clade):

Unambiguous: 9 (0 → 1)*; 61 (0 → 1)*

Fast: 40 (0 → 1)*; 47 (0 → 1)*

Slow: 39 (0 → 1)*; 44 (0 → 1)*

Clade R (*Ichthyosauridae*):

Unambiguous: 51 (0 → 1)

Fast: 24 (1 → 0)

Slow:

Terminal S (*Ichthyosaurus communis*):

Unambiguous: 48 (0 → 1); 49 (0 → 1); 53 (0 → 1); 54 (0 → 1)

Fast: No additional character changes

Slow: 40 (0 → 1)

Terminal T (*Malawania anachronus* gen. et sp. nov.):

Unambiguous: No autapomorphies

Fast: No additional character changes

Slow: No additional character changes

Clade U (*Baracromia* nov.; 2):

Unambiguous: 4 (0 → 1); 15 (0 → 1); 29 (0 → 1)*; 36 (0 → 1); 57 (0 → 1)*

Fast: 6 (0 → 1); 26 (0 → 1); 27 (0 → 1); 28 (0 → 1)

Slow: 24 (0 → 1); 28 (0 → 1); 47 (0 → 1)

Terminal U (*Stenopterygius quadriscissus*):

Unambiguous: 1 (0 → 1); 35 (0 → 1); 54 (0 → 1)

Fast: 40 (1 → 0)

Slow: 6 (0 → 1); 26 (0 → 1); 27 (0 → 1)

Clade W (unnamed clade; 2):

Unambiguous: 22 (0 → 1); 52 (0 → 1)*

Fast: 2 (0 → 1)*; 12 (0 → 1)*; 13 (0 → 1)*; 25 (0 → 1)*; 42 (0 → 1)*; 65 (0 → 1)*

Slow: No additional synapomorphies

Terminal X (*Chacaicosaurus cayi*):

Unambiguous: No autapomorphies

Fast: No additional character changes

Slow: No additional character changes

Clade Y (Ophthalmosauridae; 2):

Unambiguous: 20 (0 → 2)*; 38 (0 → 1)*; 41 (0 → 1)*; 48 (0 → 1)

Fast: 8 (0 → 1)*; 49 (0 → 1); 50 (0 → 1)

Slow: 40 (0 → 1)

Terminal Z (*Arthropterygius chrisorum*):

Unambiguous: 20 (1 → 2)

Fast: No additional character changes

Slow: 26 (0 → 1); 27 (0 → 1); 42 (0 → 1)

Clade AA (unnamed clade; 2):

Unambiguous: 19 (0 → 1)*; 21 (0 → 1)*; 60 (0 → 1)*

Fast: 26 (1 → 0); 27 (1 → 0); 51 (0 → 1)

Slow: 2 (0 → 1)*; 12 (0 → 1)*; 13 (0 → 1)*; 25 (0 → 1)*; 49 (0 → 1); 50 (0 → 1)*; 65 (0 → 1)*

Clade BB (Ophthalmosaurinae):

Unambiguous: 22 (1 → 0)

Fast: 10 (0 → 1); 45 (0 → 1)*

Slow: No additional character changes

Terminal CC (*Mollesaurus perialus*):

Unambiguous: 16 (1 → 0)

Fast: No additional character changes

Slow: No additional character changes

Clade DD (unnamed clade):

Unambiguous: 23 (0 → 1)*

Fast: No additional character changes

Slow: 6 (0 → 1); 8 (0 → 1); 10 (0 → 1); 42 (0 → 1); 45 (0 → 1)*; 51 (0 → 1)

Terminal EE (*Ophthalmosaurus icenicus*):

Unambiguous: 26 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade FF (unnamed clade):

Unambiguous: 1 (0 → 1)

Fast: 28 (1 → 0)

Slow: No additional character changes

Terminal GG (*Ophthalmosaurus natans*):

Unambiguous: 2 (1 → 0); 35 (0 → 1)

Fast: No additional character changes

Slow: 28 (1 → 0)

Terminal HH (*Acamptonectes densus*):

Unambiguous: 22 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade II (Platypterygiinae):

Unambiguous: 3 (0 → 1)*; 14 (0 → 1)*; 20 (1 → 2); 39 (1 → 2)*; 57 (1 → 2)*; 66 (0 → 1)*

Fast: 6 (1 → 0); 42 (1 → 0); 53 (0 → 1); 58 (0 → 1)*

Slow: No additional character changes

Clade JJ (unnamed clade):

Unambiguous: 27 (0 → 1); 37 (0 → 1)*; 49 (1 → 2)*

Fast: 8 (1 → 0); 16 (1 → 0); 51 (1 → 0)

Slow: 53 (0 → 1)

Terminal KK (*Platypterygius hercynicus*):

Unambiguous: 4 (1 → 0); 62 (0 → 1)

Fast: No additional character changes

Slow: No additional character changes

Clade LL (unnamed clade):

Unambiguous: 7 (1 → 0); 17 (1 → 0)

Fast: 63 (0 → 1)

Slow: 16 (1 → 0)

Terminal MM (*Caypullisaurus bonapartei*):

Unambiguous: 15 (1 → 0); 35 (0 → 1)

Fast: No additional character changes

Slow: 58 (0 → 1)

Clade NN (unnamed clade):

Unambiguous: 9 (1 → 0)

Fast: 58 (1 → 0)

Slow: No additional character changes

Terminal OO (*Platypterygius australis*):

Unambiguous: 13 (1 → 0); 16 (0 → 2)*

Fast: No additional character changes

Slow: 63 (0 → 1)

Terminal PP (*Athabascasaurus bitumineus*):

Unambiguous: 1 (0 → 1); 2 (1 → 0); 10 (0 → 1); 14 (1 → 0)

Fast: No additional character changes

Slow: No additional character changes

Clade QQ (unnamed clade):

Unambiguous: 41 (1 → 0); 43 (0 → 1)*

Fast: 11 (0 → 1)*; 35 (0 → 1)

Slow: 8 (0 → 1)

Terminal RR (*Brachypterygius extremus*):

Unambiguous: 7 (1 → 0)

Fast: 53 (1 → 0)

Slow: 51 (0 → 1)

Clade SS (unnamed clade):

Unambiguous: 10 (0 → 1); 19 (1 → 0)

Fast: No additional character changes

Slow: 53 (0 → 1)

Terminal TT (*Maiaspondylus lindoei*):

Unambiguous: 4 (1 → 0); 62 (0 → 1)

Fast: 51 (1 → 0)

Slow: No additional character changes

Clade UU (unnamed clade):

Unambiguous: 2 (1 → 0)

Fast: No additional character changes

Slow: 11 (0 → 1)*; 51 (0 → 1); 58 (0 → 1)

Terminal VV (*Aegirosaurus leptospondylus*):

Unambiguous: 3 (1 → 0)

Fast: No additional character changes

Slow: No additional character changes

Terminal WW (*Sveltonectes insolitus*):

Unambiguous: 1 (0 → 1); 43 (1 → 0); 63 (0 → 1)

Fast: No additional character changes

Slow: 35 (0 → 1)

Comparison with previous analyses

A significant part of the data of all the previous cladistic analyses of Ichthyosauria (Motani 1999; Maisch and Matzke 2000; Sander 2000; Fernández 2007; Maxwell 2010; Druckenmiller and Maxwell 2010; Fischer et al. 2011b; Fischer et al. 2012) is incorporated in our new analysis; therefore, the differences with previous analyses are probably more to do with better coverage of parvipelvian taxa, and do not result from the creation of a distinct and totally novel dataset.

Our data on ophthalmosaurids is directly taken from and similar to that of Fischer et al. (2012), where the topology is discussed at length; accordingly, we will focus on the non-ophthalmosaurid parvipelvians here.

The topology recovered by Sander (2000) is the one most radically different from other cladistic analyses of Ichthyosauria, including ours. Sander (2000) recovered *Temnodontosaurus*, Leptonectidae, Thunnosauria, Baracromia, and Ophthalmosauridae as non-monophyletic, whereas they are in other analyses. While *Stenopterygius* was recovered as close to *Ophthalmosaurus*, *Platypterygius* was recovered as the sister-taxon to a clade that included *Eurhinosaurus* and *Leptonectes* as well as *Ichthyosaurus*, *Stenopterygius* and *Ophthalmosaurus* (Sander 2000). As analysed elsewhere (Fischer et al. 2011b), many of Sander's (2000) characters are problematic and have needed redefinition.

The only other large-scale analyses of Parvipelvian are those incorporated into studies of the whole of Ichthyosauria undertaken by Motani (1999), Maisch and Matzke (2000) and Caine and Benton (2011). These analyses differ in detail, but these are still regarded as the best analyses of Ichthyosauria produced to date. In these analyses, *Macgowania* and *Hudsonelpidia* are recovered as outside the clade that includes all other parvipelvians. Our analysis obtains a similar result, but *Hudsonelpidia* is considered more basal than *Macgowania*. While our results are in better agreement with stratigraphy, there is no unequivocal feature uniting *Macgowania* and Neoichthyosauria in unambiguous optimization, but there is one in fast optimization, and two in slow optimization (see Tree description: Clade C, above). One novelty of our analysis is the link between *Temnodontosaurus* and Leptonectidae, which form a distinct neoichthyosaurian clade. These taxa were, however, close in position in other phylogenies: in Maisch and Matzke's (2000) analysis, *Temnodontosaurus* and Leptonectidae form successively closer sister-groups to their *Suevoleviathan* + Thunnosauria clade, while the two form an unresolved polytomy with Thunnosauria in Motani (1999). As in Maisch and Matzke (2000), *Suevoleviathan* is here

considered closely related to Thunnosauria, given its mosaic of characters (Maisch 1998, 2001; Fischer et al. 2011a). It was considered the basal-most neoichthyosaurian in Motani (1999). In one of the topologies recovered by Caine and Benton (2011), *Hauffiopteryx* is included within Leptonectidae (wrongly named Eurhinosauria), while the other analysis, based on Maisch and Matzke's (2000) dataset, agrees with our topology: *Hauffiopteryx* is recovered as the sister-taxon to Thunnosauria.

All other parsimony-based phylogenetic studies of Ichthyosauria have focussed on Thunnosauria. The main area of controversy has been the relationship between Ophthalmosauridae and the remainder of Thunnosauria (Motani 1999). Three analyses (Motani 1999; Fernández 2007; Maxwell 2010) recover *Ichthyosaurus* as especially close to Ophthalmosauridae, but a larger number of analyses, including the largest and most recent ones, better support a close relationship between *Stenopterygius* and Ophthalmosauridae (Godefroit 1993b; Maisch and Matzke 2000; Druckenmiller and Maxwell 2010; Caine and Benton 2011; Fischer et al. 2011b; Fischer et al. 2012). Fernández (1999) recovered a monophyletic Baracromia, but with a novel *Stenopterygius* + *Chacaicosaurus* sister-group relationship.

Additional analyses

Reduced dataset

In order to test the influence of missing data on the topology and robustness of the resulting cladogram, we ran a second analysis where we eliminated those in-group taxa represented by fragmentary specimens (i.e. with $\leq 20\%$ of missing data) from the dataset presented above, as in Godefroit et al. (2012). However, we retained *Malawania* in the analysis since the ultimate aim of this analysis is to clarify its phylogenetic affinities within Parvipelvina. The dataset remains the same, however, and the same characters are used, unaltered. We used an exact algorithm to analyse the matrix in order to avoid artificial increase of the Bremer Support (see Ketchum and Benson 2010 for an explanation). The analysis protocol remains otherwise similar to that of the large-scale analysis (standard bootstrap: 1000 replicates; Jackknife: removal probability 36, 1000 replicates).

This resulted in a roughly similar topology (Fig. 2): *Malawania* is recovered as a basal Parvipelvina, but this time as the sister-taxon of *Ichthyosaurus* + Baracromia (= Thunnosauria). However, the support for each node is markedly increased, which suggests that the general topology of the cladogram is robust and that the low supports values are mainly due to the presence of fragmentary specimens. Note that these slight variations of topology between the ‘full’ and ‘second’ analyses have no bearing on the cladogenesis rates; indeed the earliest Jurassic taxa *Temnodontosaurus* and *Ichthyosaurus* still drag the origin of both Neoichthyosauria and Thunnosauria during the Rhaetian Neoichthyosauria radiation.

Incorporation in other datasets

To further test the position of *Malawania* within Ichthyosauria, we coded NHMUK PV R6682 into three additional matrices: two were taken from Caine & Benton (2011; which are slightly updated version of the analyses of Maisch & Matzke [2000] and Motani [1999]) and one from Thorne et al. (2011, which is an updated version of the analysis of Motani [1999]). These analyses should be considered, however, as outdated, as these do not incorporate recent advances in the relationships and taxonomy of ophthalosaurids, nor the new observations on Early Jurassic ichthyosaurs incorporated in the analyses presented above. The analysis protocol remains similar to that of the large-scale analysis (Heuristic algorithms: 1000 replications, 10 trees saved per replication; standard bootstrap: 1000 replicates; Jackknife: removal probability 36, 1000 replicates). Bremer, bootstrap and Jackknife values are provided in Figure 2 of the main text.

Coding of Malawania in the dataset of Caine & Benton (2011); based on that of Maisch & Matzke [2000]

????????????????????1????????????????????11??1?0??????0??
????111???121?111101?1?11001?00111111????????????????11??

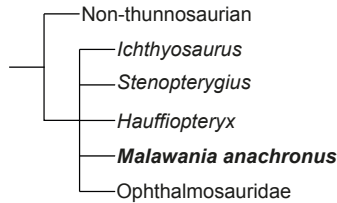
Coding of Malawania in the dataset of Caine & Benton (2011); based on that of Motani [1999]

????????????????????????????????????21????2200001221?20
01?311{1 2}0??0011????????????1??1?1?00???

Coding of Malawania in the dataset of Thorne et al. (2011); based on the dataset of Motani [1999]

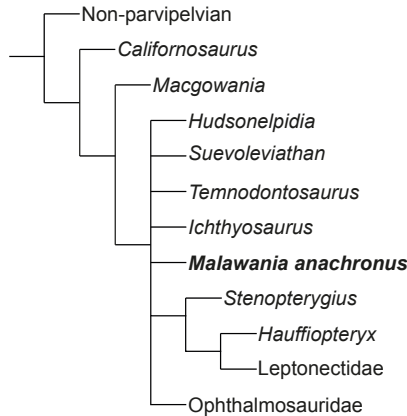
??21????2200001221?20
01?311{1 2}0??0011????????????????????1??1?1?00???

Caine & Benton 2011
(matrix from Maisch & Matzke 2000)



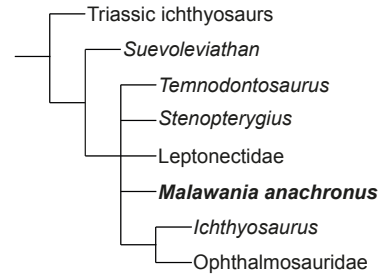
L=203; Ci=0.65; Ri=0.89

Caine & Benton 2011
(matrix from Motani 1999)



L=246; Ci=0.56; Ri=0.81

Thorne et al. 2011
(matrix from Motani 1999)



L=248; Ci=0.54; Ri=0.74

Fig. S9. Summarized version of the strict consensus trees arising from the additional cladistic analyses. A. Strict consensus of the 10 most parsimonious trees arising from the analysis of the dataset from Caine & Benton (2011; based on that of Maisch & Matzke [2000]). B. Strict consensus of the 6 most parsimonious trees arising from the analysis of the dataset from Caine & Benton (2011 based on the dataset of Motani [1999]). C. Strict consensus of the 16 most parsimonious trees arising from the analysis of the dataset from Thorne et al. (2011, based on the dataset of Motani [1999]). See Figure 2 (in main text) for Bremer, bootstrap and Jackknife values.

These analyses also consider *Malawania* as a basal, non-ophthalmosaurid parvipelvian, although its inclusion creates polytomies in these analyses: using the dataset from Caine & Benton (2011; based on that of Maisch & Matzke [2000]), *Malawania* is included a polytomy at the base of Thunnosauria; using the dataset from Caine & Benton (2011; based on that of Motani [1999]), *Malawania* is included in a polytomy near the base of Parvipelvian; using the dataset

from Thorne et al. (2011, based on the dataset of Motani [1999]), *Malawania* is included in a polytomy near the base of Neoichthyosauria (Fig S9; S10; S11; S12). Despite their poor resolution, these analyses are consistent with the results of the analyses presented above: they never recover *Malawania* as an ophthalmosaurid; nor is it recovered as the sister-taxon of Ophthalmosauridae, except in two most parsimonious trees out of six arising from the analysis of from the dataset of Caine & Benton (2011) based on that of Motani [1999]). In all possible cases, this indicates an origin for *Malawania*'s lineages comprised between the Late Triassic and the Early Jurassic, therefore confirming the disparate origins of Cretaceous ichthyosaurs.

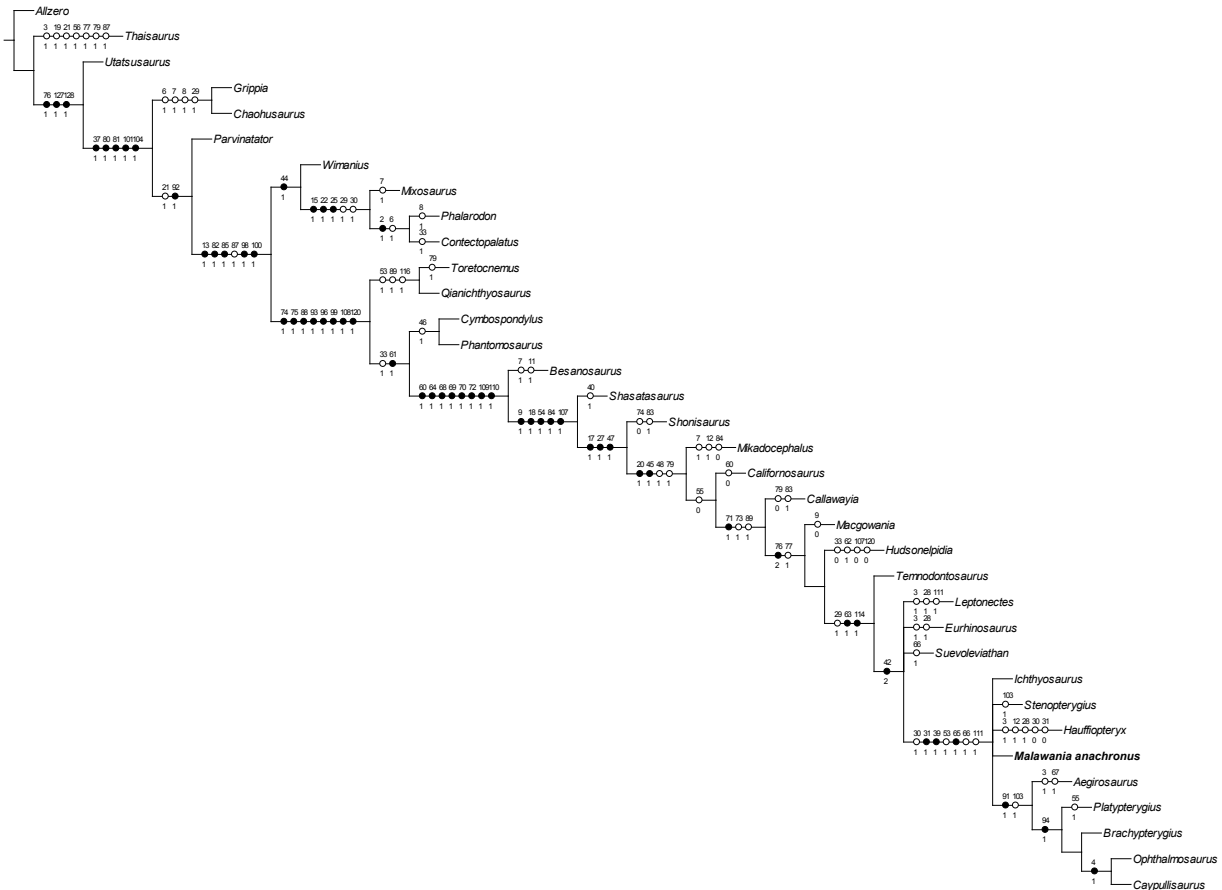


Fig. S10. Strict consensus of the 10 most parsimonious trees arising from the analysis of the dataset from Caine & Benton (2011; based on that of Maisch & Matzke [2000]), in unambiguous optimization. See Fig. S10 for length and indexes values.

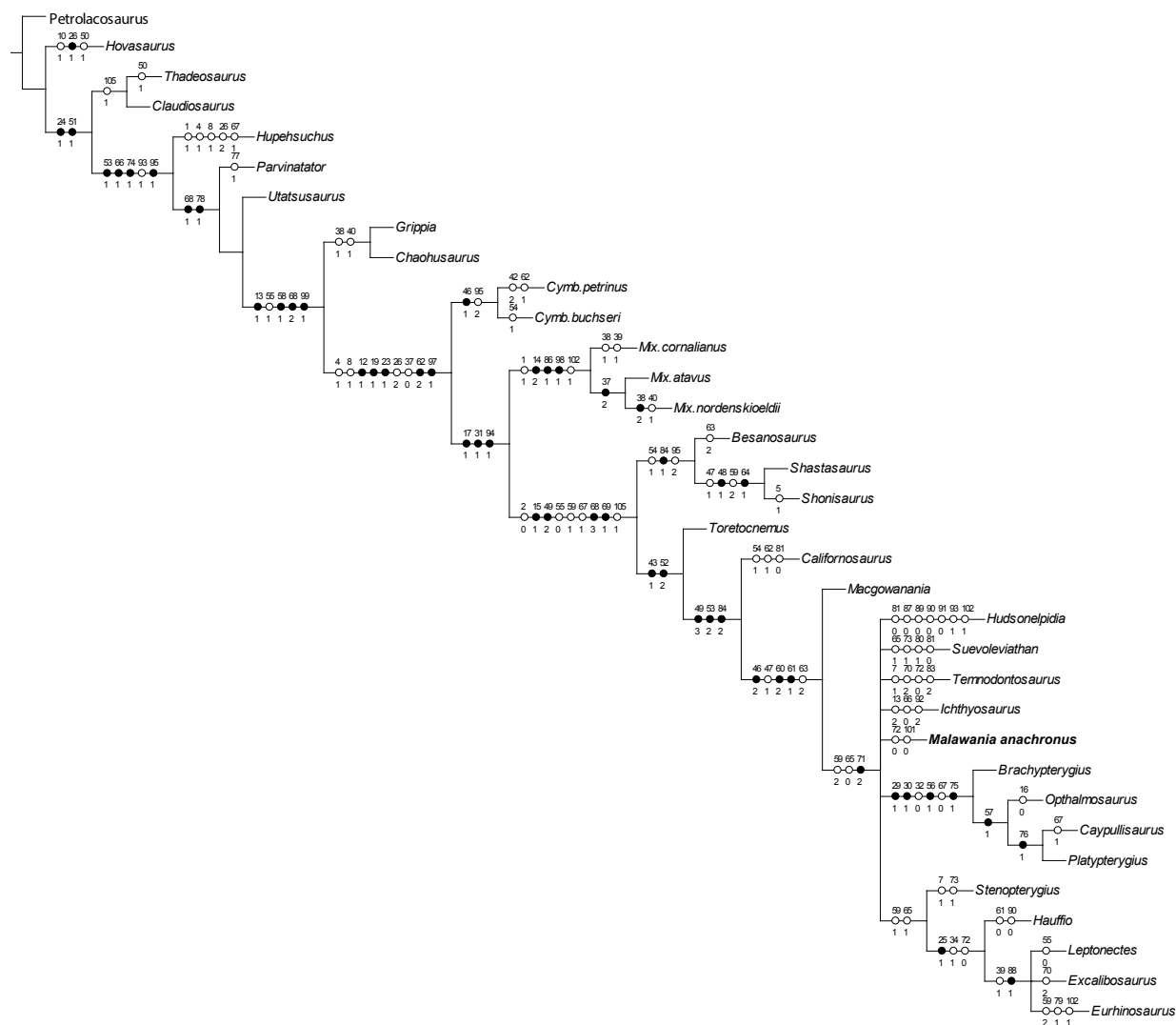


Fig. S11. Strict consensus of the 6 most parsimonious trees arising from the analysis of the dataset from Caine & Benton (2011 based on the dataset of Motani [1999]), in unambiguous optimization. See Fig. S10 for length and indexes values.

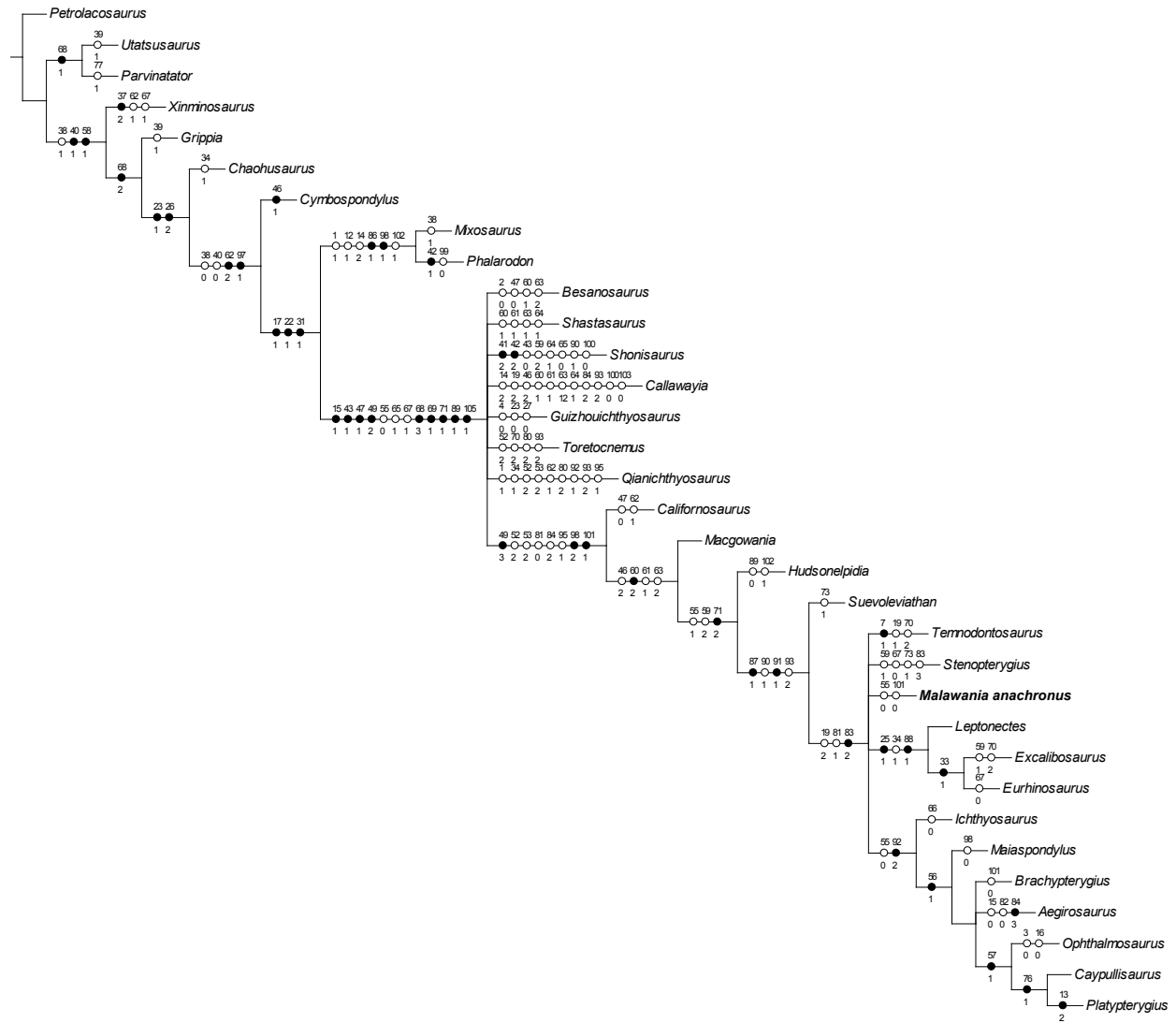


Fig. S12. Strict consensus of the 16 most parsimonious trees arising from the analysis of the dataset from Thorne et al. (2011, based on the dataset of Motani [1999]), in unambiguous optimization. See Fig. S10 for length and indexes values.

Cladogenesis analysis

Each stage of the timescale was, where possible, subdivided into three substages of equal length (lower, middle, upper). This was done such that it was possible to refine the approximate time of appearance for each lineage as much as possible (by not subdividing each stage, we might create the impression that each lineage started its history at the beginning of each respective stage). The cladogenesis rate is determined by counting the number of lineages that appear during each stage of the interval considered. Each node was considered to appear instantaneously, rather than requiring a certain time lapse after the preceding one. Only the first unambiguous occurrence of each lineage was considered.

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