
Peer reviewed version

Link to published version (if available):
10.1080/14772019.2017.1394922
10.1080/14772019.2017.1394922

Link to publication record in Explore Bristol Research
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Taylor & Francis at http://www.tandfonline.com/doi/full/10.1080/14772019.2017.1394922?scroll=top&needAccess=true. Please refer to any applicable terms of use of the publisher.

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A new phylogeny of ichthyosaurs (Reptilia: Diapsida)

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Abstract

The largest phylogenetic analysis of ichthyosaurs to date is presented, with 114 ingroup taxa coded at species level. Completeness of the taxa included varied from >98% to <2%; ten taxa were removed a priori using Concatabominations, due to incompleteness and taxonomic uncertainty. The data were analysed using three widely used optimisation criteria: maximum parsimony, maximum likelihood, and Bayesian inference; while similar, each criterion produced different topologies, support, and levels of resolution. Maximum parsimony found a well-resolved consensus tree with minor improvement from a posteriori pruning of unstable taxa; however, general support remains low. Tree resolution was reduced more by taxa that lacked codings from phylogenetically important regions of the tree, rather than by those that simply lacked many codings. Resolution present in the most likely tree is poorly supported; sister relationships cannot be confirmed, although similarities are found to the most parsimonious tree. Bayesian inference found poorly resolved consensus trees. While more resolved, an equal-distribution rate prior is significantly worse than the null gamma-distribution rate prior for morphological data, but suggests rate heterogeneity across ichthyosaur phylogeny. Tree comparisons under each analytical criterion failed to select a single best tree, however, the Bayesian inference tree with gamma-distribution rate prior is

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selected as the best tree based on recent analyses showing improved accuracy using this
criterion. Unequivocally resolved clades include Ichthyopterygia, Ichthyosauria, Shastasauria,
Euichthyosauria, Parvipelvia, and Neoichthyosauria, but with variation in their taxonomic
components. Mixosauridae and Ophthalmosauridae are similarly recovered, but their
definitions are modified to stem-based definitions to prevent substantial variation of included
taxa. Several genera are not monophyletic: Brachypterygius, Leptonectes, Mixosaurus,
Ophthalmosaurus, Paraophthalmosaurus, Phalarodon, Platypterygius, Stenopterygius,
Temnodontosaurus, and Undorosaurus. Complex and variable relationships suggest the need
for new characters and a re-evaluation of the state of ichthyosaur phylogenetics.

Keywords: Bayesian inference, Ichthyosauriformes, Ichthyosauria, maximum likelihood,
imimum parsimony, tree selection.

Introduction

Ichthyosaurs are members of a clade of marine reptiles known from the Early Triassic
through to the early Late Cretaceous (McGowan & Motani 2003). Their relative commonness,
compared to other marine reptile groups, longevity, and worldwide distribution means that
they are a diverse and well-known group. There are currently 114 valid species in 70 genera,
with some taxa represented by several hundreds or thousands of specimens – e.g.
Ichthyosaurus and Stenopterygius (Maisch & Matzke 2000) – although most are known from
fewer, and less complete specimens (Cleary et al. 2015). Ichthyosaurs rapidly and profoundly
adapted to the marine realm early in their evolution. Even the earliest known ichthyosaurs
show many derived characters: paddle-like limbs; elongate, streamlined body; partial
development of a tail bend and fluke; and viviparity (Motani 1999a, 2005; Motani et al. 2014;
Chen et al. 2014b). Rapid diversification through the Triassic led to their occupying many
niches, resulting in disparate forms (Camp 1980; Massare 1987; Sander et al. 2011; Motani et
Ichthyosaurs are historically important as one of the earliest recognized extinct vertebrate groups (Howe et al. 1981; Torrens 1995).

Most recent work has concerned the taxonomy of ichthyosaurs: many taxa were originally described over a century ago, and so are in need of revision (McGowan & Motani 2003; Maisch 2010). However, the interrelationships of ichthyosaurs have also been investigated with the description of new species (e.g. Fischer et al. 2013; Roberts et al. 2014).

Increasingly, macroevolutionary trends within the group are being considered, including palaeobiogeography (Bardet et al. 2014), diversification and extinction rates (Fischer et al. 2012; Fischer et al. 2016), response to extinction events (Thorne et al. 2011), and ecology (Sander et al. 2011; Fröbisch et al. 2013; Motani et al. 2013; Dick & Maxwell 2015). Despite this, there has been no recent attempt to include all ichthyosaur taxa in a single phylogenetic analysis; this is the purpose of the present study.

Numerical cladistic analyses have been performed on ichthyosaurs for three decades (Mazin 1981, 1982), and computational analyses for over two decades (Callaway 1989; Caldwell 1996). The largest studies included most taxa only to generic level (Motani 1999c; Sander 2000; Maisch & Matzke 2000; Motani et al. 2015), but have since had taxa and characters added or modified (Thorne et al. 2011; Sander et al. 2011; Fröbisch et al. 2013; Cuthbertson et al. 2013a, b). Many analyses have focused upon ichthyosaur subclades, including Shastasauria (e.g. Nicholls & Manabe 2001), Mixosauridae (e.g. Jiang et al. 2005; Jiang et al. 2006), Parvipelvia (e.g. Maxwell et al. 2012; Fischer et al. 2013), and Thunnosauria and Ophthalmosauridae (e.g. Fernández 2007; Druckenmiller & Maxwell 2010; Fischer et al. 2012; Druckenmiller & Maxwell 2014; Fischer et al. 2014b; Roberts et al. 2014; Arkhangelsky & Zverkov 2014).
This study aims to (1) present an inclusive phylogenetic analysis of ichthyosaurs, for both taxa and characters; (2) reappraise the definitions of the major ichthyosaur clades; and (3) provide a comparison of the different methodologies and results for estimating phylogeny.

Previous work

Joseph and Mary Anning found the first recognized ichthyosaur materials in 1810–1811 in the Lias Group at Lyme Regis, Dorset (Home 1814; Torrens 1995). Numerous ichthyosaur finds were reported throughout the nineteenth century, initially from the Lower Jurassic of the United Kingdom (Young 1821), but soon followed by materials collected worldwide from much of the Mesozoic (Jaeger 1824; Carter 1846; Quenstedt 1852; McGowan & Motani 2003).

The first consideration of the internal classification of ichthyosaurs was by Kiprijanoff (1881, p. 88), who separated them into two groups: Ichthyosauri Longipinnipedes and Ichthyosauri Latipinnipedes, with each split into two subgroups based on tooth morphology. This dichotomy was principally based upon the size and shape of the forelimb: longipinnipeds have long, narrow fore and hind limbs, whereas latipinnipedes had short and wide fore and hind limbs, with the hind limbs much shorter than the forelimbs, forelimb bones without notches, and more phalanges than longipinnipeds. Baur (1887a, b) separated ichthyosaurs into three families: Mixosauridae, Ichthyosauridae, and Ophthalmosauridae, again based on forelimb morphology. Lydekker (1888) combined these two, applying Kiprijanoff’s (1881) classification to the Ichthyosauridae of Baur (1887a, b). Later classifications and phylogenetic hypotheses extended the latipinnate-longipinnate separation to all ichthyosaurs (Merriam 1908; von Huene 1922, 1923a, b).

The first cladogram of Ichthyopterygia was included in Mazin’s (1981) revision of *Grippia longirostris*, featuring five characters that defined outgroups to Ichthyosauria: *Grippia* was found to be the most basal ichthyopterygian, with Mixosauria and *Utatsusaurus* as
successive ingroups. This was then expanded to include more ichthyosaurs the following year (Mazin 1982) in a cladistic analysis with 54 taxa and 14 characters (Fig. 1A). Mazin’s (1982) characters are like those used in many later analyses, although several of his characters have later been combined. The resulting cladogram did not show a latipinnate-longipinnate split, but instead a series of nested subclades, from which several families split – largely like those previously conceived. Callaway (1989) determined the relationships of shastasaurid ichthyosaurs, and used *Grippia* and *Petrolacosaurus* as outgroups, based upon his analysis of the diapsid affinities of ichthyosaurs (Mazin 1981; Callaway 1989; Massare & Callaway 1990). This was the first use of computational parsimony analysis, with 9 taxa and 33 characters. Most characters were multistate, with many being discretized ratios, but these characters have survived in many subsequent analyses and serve to mark not only Shastasauridae, but other ichthyosaur clades too.

A major advance in the understanding of ichthyosaur phylogeny marked the years 1999 and 2000: three large, independent analyses were published that included many ichthyosaur taxa and over 100 characters each (Figs 1B–D; Motani 1999c; Sander 2000; Maisch & Matzke 2000). These phylogenies yielded similar topologies, and agreed with previous cladistic analyses in having a series of nested clades marked by stepwise addition of characters (Figs 1B–D). However, several families – e.g. Shastasauridae and Grippiidae – were found to be paraphyletic, leading to the concept of ichthyosaur grades (Motani 2005). Despite the different conceptions of these analyses, many of the characters were similar, but often used different coding styles: Maisch & Matzke (2000) favoured more strictly binary characters. So too did Motani (1999c), as well as tentatively using discretized ratios like Callaway (1989). Sander (2000) included several multistate characters to capture presence/absence and variation (‘composite coding’ of Strong & Lipscomb (1999)). In all analyses, the historical taxa of Mixosauridae (= Mixosauria *sensu* Motani [1999c]), and post-Triassic ichthyosaurs...
(Neoichthyosauria) were recovered. Motani (1999c) and Sander (2000) also included extensive outgroups – Maisch & Matzke (2000) used only an all-zero outgroup – marking the first indication of ichthyosaurs’ hupehsuchian affinities in a phylogeny, while confirming previous ideas on diapsid affinities. Criticism of all the above analyses was made in McGowan & Motani (2003).

Most cladistic studies following these three have tended to be extensions of Motani (1999c) or Maisch & Matzke (2000), including new taxa or character modifications. Consequently, the broad topology of ichthyosaur phylogeny has varied little since 1999. With the finding of new taxa, studies focused on subclades of Ichthyopterygia. These include Shastasauridae (Fig. 2A; Nicholls & Manabe 2001; Fröbisch et al. 2006; Sander et al. 2011), Mixosauridae (Fig. 2B; Jiang et al. 2005; Maisch & Matzke 2005; Jiang et al. 2006; Chen & Cheng 2010), and Parvipelvia and Thunnosauria (Figs 2C–E; Fernández 2007; Druckenmiller & Maxwell 2010; Fischer et al. 2012; Fischer et al. 2013). The analysis by Fröbisch et al. (2013) was the first to Bayesian inference rather than parsimony (Fig. 1E). Many of these studies have found genera to be non-monophyletic, and relationships to be unstable and prone to collapse. The recent discovery and description of Chinese Early and Middle Triassic fossils has added several taxa towards the base of Ichthyosauriformes, increased our knowledge of other poorly known taxa, and helped resolve the relations of ichthyosaurs to other reptile groups (Benton et al. 2013; Chen et al. 2014a; Ji et al. 2016). New specimens of hupehsuchians, and a general diapsid phylogenetic analysis, have lent support to an Ichthyopterygia-Hupehsuchia sister relationship, but the position of Ichthyosauromorpha within Diapsida remains uncertain (Chen et al. 2014a).

In summary, the most recent work on ichthyosaur phylogeny has resolved the group as a single clade, with a sister relationship to Hupehsuchia. The internal topology has mostly been constructed using parsimony methods as series of nested ingroups, but several large clades –
particularly Mixosauridae, Parvipelvia, and Neoichthyosauria – are commonly recovered and well supported. Individual taxa are, however, prone to change position depending on taxon and character sampling. These inconsistencies and lack of investigation of alternative methodologies are the impetus behind the present study.

**Materials and methods**

The compilation of the matrix and subsequent analysis follows previous studies in its methodology, but with substantial extensions to improve understanding of the tree. Specifically, a modified ‘supermatrix methodology’ was used to compile the data, and then maximum parsimony, maximum likelihood, and Bayesian inference methods were used for analysis. De Queiroz & Gatesy (2007) describe this method: concatenate separate phylogenetic matrices, which are then analysed as a single dataset. This is modified here to include the critical analysis of the characters from the input phylogenetic datasets; they are not simple concatenated. The aim of this is to exclude repeated, uninformative, and misleading characters, and to modify the characters to bring them into line with the most recent coding styles.

**Taxon selection**

Almost all valid ichthyosaur species were included: 115 operational taxonomic units (OTUs) – 114 Ichthyosauriformes plus an outgroup taxon (see Online Supplemental Material Document S1.1). *Cetarthrosaurus walker*i Seeley, 1873 was excluded as the only known material – two propodials from the Cretaceous of the UK – cannot be assigned to the fore or hind limb so cannot be reliably coded (Fischer et al. 2014c). While most taxa have good coverage in the literature, for some taxa – e.g. *Mixosaurus kuhnschnyderi* – specific details were not present in the publications. Twenty-five taxa (22%) have been personally observed; 13 of which (11%)
include the holotype (see Online Supplemental Material Document S1.2). For the ingroup, taxa considered valid up to September 2017, both in previous studies and from literature review, were included; the most recently named included taxon is *Ichthyosaurus somersetensis* Lomax & Massare, 2017. Taxa that could be removed safely *a priori* were identified using the Concatabominations method of Siu-Ting *et al.* (2015), an extension of Wilkinson’s (1995) Safe Taxon Removal (STR).

*Hupehsuchus nanchangensis* was selected as the outgroup, based upon previous analyses, which have consistently found this taxon to be the immediate sister taxon to Ichthyopterygia/Ichthyosauriformes (Motani 1999c; Chen *et al.* 2014b). This taxon represents the best-known hupehsuchian: *Nanchangosaurus* and *Parahupehsuchus* are known only from specimens where phylogenetically important parts of the body are missing or less well known, particularly the skull (Chen *et al.* 2014a, b). Most of the methods used allow only a single outgroup to be explicitly selected, otherwise relying on the similarities of these outgroup taxa to maintain close relationships.

**Character list & coding**

The character list was assembled by critically comparing the characters used in previous analyses. First, the characters of Motani (1999c) were compared with Maisch & Matzke (2000), which incorporated many similar characters; Maisch & Matzke (2000, p. 8) noted this similarity despite the separate genesis of the two analyses. Characters were selected based upon their informativeness in the analyses from which they were derived, and their relevance to ichthyosauriform ingroup relationships: characters relating specifically to a diapsid outgroup were excluded. Next, additional characters from Sander (2000) were added. These three large analyses incorporated most relevant characters from previous phylogenetic studies on ichthyosaurs, so it was necessary to review previously suggested characters only
Characters from subsequent analyses were incorporated, in the same manner, up to the most recent available (Roberts et al. 2014; Motani et al. 2015). In some cases, characters had been modified for certain subclades. In these cases, the characters were either reverted to the original form, or compared to the other clades and additional states or modifications added as necessary. All characters were treated as unweighted, and most characters were unordered unless they were ordered in the source analyses (see Online Supplemental Material Document S1.3).

In evaluating each character, the following were considered: (1) similarity to other characters; (2) uniqueness of character states; (3) informativeness of the character. While most characters were incorporated unchanged, some were modified to meet these criteria. In particular, characters were modified in accordance to their uniqueness of states using reductive coding, following the suggestions of Strong & Lipscomb (1999) and Brazeau (2011). Spurious groupings created by the algorithms used in maximum parsimony were circumvented by collapsing zero-length branches, the default in TNT (Brazeau 2011). Some characters were originally formulated to incorporate ecological differences, or their morphological correlates, into phylogenetic analyses, particularly several within the study of Sander (2000). These characters have been explicitly excluded in the present study. Where ecologically-informative morphological characters are retained is if these do show putative phylogenetic relationships – e.g. the length of the postorbital skull, abbreviated lower jaw, loss of teeth. Further characters received minor modifications in polarity, as state 0 was preferred for the non-ichthyosauriform outgroup. Besides designating an outgroup, most characters were treated as unordered in the analyses, so this is purely an aesthetic change. The matrix was assembled into NEXUS format with Mesquite version 3.2(801) (Maddison & Maddison 2016).
As many new species and characters were being incorporated into the data matrix, this was largely completed anew from the literature, with reference to previous datasets. Where characters had not been previously coded for taxa, these were added from personal observation and the literature (see Online Supplemental Material Document S1.2). This is the first complete, species-level phylogeny of Ichthyosauriformes; many taxa are being coded, or at least separated, for the first time. Taxa in need of revision were preferentially coded from the type material, but for all taxa, this was not exclusively the case.

**Phylogenetic analyses**

Two analytical criteria were used: parsimony and likelihood, under three inference methods. These criteria, and several analyses, were used to compare the results, tree selection, and support from a palaeontological dataset, a novel approach in palaeontological phylogenetic analyses. For each analysis, the commands used are included in the Online Supplemental Material Document S1.4.

**Maximum parsimony analyses.** Parsimony analysis was performed using TNT version 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) with the new technology tree fusing, ratchet, and sectorial searching algorithms of Nixon (1999) and Goloboff (1999). This was followed by tree bisection-reconnection (TBR) branch swapping to find all most parsimonious trees (MPTs) up to a maximum of 100,000 held. These settings allow for rapid analysis, while still covering many tree topologies, minimising entrapment within local minima, and all within a reasonable timeframe. An *a posteriori* analysis of ‘wildcard taxa’ used the iterative position congruence (reduced) (PCR) method of Pol & Escapa (2009). This method, and the TNT script provided by Pol & Escapa (2009), identifies taxa that cause the collapse of clades into polytomies, lists the characters that cause this instability, and suggests additional data that may solve the relationships. Instability of taxa was illustrated using a 25% cluster network of
all MPTs in Dendroscope version 3.5.7 (Huson & Scornawacca 2012) and a mean 25%
consensus network of all MPTs in SplitsTree version 4.14.2 (Huson & Bryant 2006). Bremer
(single decay) support values were calculated in TNT by TBR swapping on the MPTs, as were
symmetrical resampling frequencies (Goloboff et al. 2003) using 10,000 replicates, holding
one tree each time, with change probability of 33%.

**Maximum likelihood analyses.** Maximum likelihood analysis was carried out using RAxML
AVX version 8.1.21 (Online Supplemental Material Document S1.4; Stamatakis 2014) to find
the most likely tree (MLT). This used the multistate gamma-distribution mode of rate
substitution within the Mkv model (Lewis 2001). RAxML is unable to accept polymorphic
data, so these were replaced with uncertainties, which is how polymorphism is treated in
TNT. All characters were treated as unordered. The analysis was run 2000 times, to produce a
MLT with clade bootstrap values, then log likelihood (SH-tests; Shimodaira & Hasegawa 1999)
were computed between this the MLT and the other trees produced.

**Bayesian inference likelihood analysis.** Two Bayesian-inference analyses used the Mkv
model each with equal and gamma distribution priors for site rate variation respectively as
implemented in MrBayes version 3.2.6 (Online Supplemental Material Document S1.4; Lewis
2001; Ronquist et al. 2012). Character states were unweighted and unordered, and state
frequencies were defined using a symmetrical Dirichlet hyperprior fixed at infinity; this latter
setting makes all state transitions equally likely. Site substitution could occur at different
rates, but was time-reversible. The analyses were run for $10^8$ generations with four runs of
four chains that were sampled every 1000 generations, discarding the first 25%. A stop value
of 0.007 was included; this was chosen as a value somewhat less than the typical convergence
level of 0.01 for recovery of most supported clades. Taxon instability was shown using 25%
cluster and mean consensus networks as for maximum parsimony above.
Tree selection. A combination of tests was used to select trees. All resultant trees were compared under maximum parsimony using Templeton tests in PAUP* version 4.0a150 (Swofford 1998). Under maximum likelihood, the tree likelihoods were estimated in RAxML, and then CONSEL was used to compare trees using approximate unbiased tests (Shimodaira & Hasegawa 2001; Stamatakis 2014). In CONSEL, a random sample of up to 2000 trees from each of the maximum parsimony, maximum likelihood, and gamma-distributed Bayesian posterior distribution (selected using marginal likelihoods, see below) was used due to excessive computational requirements. The MLT, MPTs, and both Bayesian trees were compared with marginal likelihoods under Bayesian inference using a stepping-stone analysis in MrBayes (Fan et al. 2011; Xie et al. 2011). This used 30 steps, sampling every 1000 generations for $3.1 \times 10^7$ generations, with $\alpha = 0.4$. Computational requirements meant that not all MPTs or MLTs could be tested individually, so the strict consensus-MPT and single MLT were used to constrain two stepping-stone analyses. With these tests, we attempted to reject the consensus trees under alternative inference criteria. The recent work of Wright & Hillis (2014) and O'Reilly et al. (2016) has shown that Bayesian inference with a gamma distribution prior produces the more accurate trees in analyses of morphological data; we therefore use this criterion as the null hypothesis against which to test. Similarity of the best trees was compared using pairwise Robinson-Foulds metrics calculated in PAUP* (Robinson & Foulds 1981).

Character optimization

Synapomorphies of the MPTs were optimized in TNT for unambiguous character changes across the strict consensus tree (listed under parsimony in Systematic Palaeontology below). Ancestral states for each node of the MLT were optimized under maximum likelihood in RAxML using the Mkv model (listed under likelihood in Systematic Palaeontology below).
Ancestral states each node, were compared to sister nodes to identify synapomorphies for named clades. Where ancestral states are uncertain due to incompleteness, these are identified as ambiguous. See also Online Supplemental Material Document S1.6.

Results

Concatabomination analysis identified five problematic taxa that could be removed:

- *Cymbospondylus piscosus*, *Isfjordosaurus minor*, *Dearcmhara shawcrossi*, and *Pervushovisaurus bannovkensis* (Fig. 3). With the removal of these taxa, no other redundant similarities between taxa were identified. Taxa that were coded but excluded due to poor knowledge, incompleteness, or taxonomic uncertainty include:

  - *Himalayasaurus tibetensis* Young & Dong, 1972: known only from isolated jaw, teeth, and limb material (Motani & Manabe 1999).
  - *Maiaspondylus lindoei* Maxwell & Caldwell, 2006: material is only known for this taxon from juveniles (Maxwell & Caldwell 2003, 2006). Ontogenetic changes in morphology are known to occur in ichthyosaurs, and may affect the coding (McGowan 1973; Motani & You 1998; Dick et al. 2016), although potentially only to a limited degree in the few identifiable in utero remains of Cretaceous ichthyosaurs (Kear & Zammit 2014). Here *M. lindoei* is conservatively excluded due to its juvenile nature and incompleteness.
  - *Malawania anachronus* Fischer et al., 2013: this taxon was considered equally removable to *Temnodontosaurus eurycephalus* after Concatabominations, but is less complete, missing potentially important cranial features, and is preferentially removed.
  - *Pervushovisaurus bannovkensis* Arkhangelsky, 1998: this taxon is considered equally problematic to *Grendelius zhuravlevi* after Concatabominations, but is less complete and
so preferentially removed, despite removing all species within *Pervushovisaurus*; the phylogenetic position of this genus is uncertain in this study.

- *Thaisaurus chonglakmanii* Mazin *et al.*, 1991: is poorly known and only described briefly and the material is not completely prepared. McGowan & Motani (2003, p. 63) suggested that this may represent a specimen of *Chaohusaurus* and that the original description included discrepancies to the material itself.

- *Tholodus schmidi* Meyer, 1849: poorly known and described, and is taxonomically ambiguous, having been allied to Omphalosauridae, which is excluded here following Motani (2000).

The analyses reported below were carried out after removal of these taxa: 104 OTUs – 103 ingroup taxa and one outgroup.

All analyses recover the familiar stepwise backbone relationships found in previous analyses in their resulting best trees (Figs 4, 6, 7; Online Supplemental Material figures S1, S2, S3). Successive ingroup clades are mostly 'ladderized', representing stepwise evolution where each clade is marked by a gradual acquisition of characters from its sister clade. Several genera are found to be monophyletic throughout all or most analyses, such as *Toretocnemus*, *Cymbospondylus* – excluding the problematic *C. piscosus* – and *Shastasaurus*, even when member species were largely incomplete. Monophyletic Mixosauridae and Shastasauria, complete as previously found, or parts thereof, are also recovered. However, several clades repeatedly form unresolved polytomies in consensus – particularly the most basal ichthyosaurs and Ophthalmosauridae. Removing the least stable taxa improves the resolution of the basal ichthyosaurs and Ophthalmosauridae somewhat.

The term 'core' is used below to mean the monophyletic clade including most species within a genus, and specifically the type species of a genus. Unnamed clades are referred to
with a ‘+’ – i.e. *Ophthalmosaurus icenicus + Platypterygius hercynicus*, indicating the minimally inclusive clade including the named taxa.

**Parsimony analysis**

Parsimony analysis found 11,536 MPTs each with length 1666 steps. The strict consensus is poorly resolved, with four large polytomies (Fig. 4): one basally (the clade comprising *Parvinatator wapitiensis + Ichthyosaurus communis*), one at the base of Hueneosauria (*Mixosaurus cornalianus + Ichthyosaurus communis*), one at the base of Neoichthyosauria (*Temnodontosaurus platyodon + Ichthyosaurus communis*), and Ophthalmosauridae (*Ophthalmosaurus icenicus + Platypterygius hercynicus*). However, many basal Euichthyosauria and clades within Neoichthyosauria are resolved. Resolution is substantially increased in the 50% majority rule tree (Online Supplemental Material Figure S1). The consistency (CI) and retention indices (RI) for both strict consensus and 50% majority rule trees are low: CI = 0.150 and 0.175; RI = 0.521 and 0.601 respectively; rescaled consistency indices (RCI) = 0.0782 and 0.105 respectively; homoplasy is rife. All resolved clades have a Bremer support value ≥ 1; many clades have support ≥ 2; Neoichthyosauria, Leptonectidae, Stenopterygiidae (*sensu* Maisch 1998), and Ophthalmosauridae, among others, have support ≥ 3. Resampling values were, however, low: few clades have support ≥ 50%; the highest support was found for core *Toretocnemus* (79%), *Suevoleviathan* (69%), core *Temnodontosaurus* (89%). Regions of instability are shown in cluster and consensus networks largely around the base of Hueneosauria and Ophthalmosauridae (Fig. 5; Holland & Moulton 2003; Huson & Bryant 2006; Huson & Scornawacca 2012).

PCR pruning identified 31 OTUs and two nodes to remove (Table 1). Analysis using the script of Pol & Escapa (2009) did not complete due to the number of taxa pruned; using the version built into TNT removed the taxa listed in Table 1. These represent some of the least
known of the included taxa, but these may still be coded for many characters (i.e. *Ichthyosaurus conybeari*). The resultant pruned tree has slightly greater resolution in basal Neoichthyosauria and Ophthalmosauridae (Online Supplemental Material Figure S2). The CI, RI, and RCI values are also increased by removing OTUs (not nodes) to 0.223, 0.706, and 0.157 in strict consensus and 0.233, 0.721, and 0.168 for the 50% majority rule consensus respectively.

**Maximum likelihood analysis**

The MLT found using RAxML is qualitatively like to the majority rule consensus of MPTs (Fig. 6). The basal taxa are paraphyletic with respect to Ichthyosauria, and the overall topology comprises a series of nested ingroups. Bootstrap supports are generally low, particularly for the backbone of the tree. Several small clades do receive values > 50%: *Toretocnemus* (93%), core *Temnodontosaurus* (75%), *Shastasaurus* (62%), and *Suevoleviathan* (61%). Eight bootstrap recovered trees were found to be significantly worse than the MLT (5%) using SH-tests (also eight trees at 2% and 1%; Online Supplemental Document S1.5). Despite Mixosauridae being recovered, this clade is not strongly supported (57% bootstrap), nor are other major clades such as Hueneosauria (31%) and Merriamosauria (8%).

**Bayesian-inference likelihood analysis**

Analyses in MrBayes converged in both cases, but the resultant 50% majority rule consensus trees are poorly resolved, although the equal-distribution rates prior tree has greater resolution than the gamma-distribution rates prior tree (Fig. 7; Online Supplemental Material Figure S3). The posterior distributions in all cases overlap, but are different to the prior distributions (Online Supplemental Material Figure S4). The gamma-distribution rates prior is strongly supported over the equal-distribution rates prior (Bayes factor differences,
\[ \delta B = 267.52; \text{Online Supplemental Material Document S1.5; Kass \& Raftery 1995}, \]

so discussion below will focus on that analysis. The consensus tree comprises a series of polytomies: the largest found at the base of Hueneosauria, Merriamosauria, Neoichthyosauria, and Ophthalmosauridae – comprising approximately the Middle–Late Triassic, Early Jurassic, and post-Early Jurassic taxa respectively (Fig. 8). Clade credibility values, where resolved, are often high – e.g. Toretocnemus (99% and 96% for equal- and gamma-distribution rate priors respectively), Shastasaurus (90% and 99%), Neoichthyosaurus (73% and 98%), and Ophthalmosauridae (95% and 97%).

**Tree selection**

Templeton tests found the MPTs to be equally the best; all other trees were significantly worse (\( p \leq 0.05; \text{Online Supplemental Material Document S1.5, S5} \)). Approximate unbiased tests found the MLT to be the best; 1859 trees were significantly different from this tree \( (p \leq 0.05; \text{Online Supplemental Material Document S1.5, S5}) \). Of the non-significantly different trees, 327 were MPTs, 341 from the gamma distribution rates prior Bayesian inference posterior distribution, and 1191 from the ML bootstrap search. Under Bayesian inference, the consensus-MPT and MLT were significantly worse than the Bayesian inference tree \( (\delta B > 2000; \text{Online Supplemental Material Document S1.5, S5}) \). The strict consensus-MPT and MLT were the most different (Robinson-Foulds metric, \( RF = 97 \)), whereas the consensus-MPT \( (RF = 37) \) was more like the consensus gamma-distribution rate prior Bayesian inference tree than the MLT \( (RF = 84) \) was. Following O'Reilly et al. (2016), the Bayesian inference tree with gamma-distribution rate prior is selected as the best tree (Fig. 7; Online Supplemental Material Document S5). However, additional unresolved relationships are inferred based on consensus in the other trees found.
**Systematic palaeontology**

The following taxonomy is based upon the preferred phylogeny (Fig. 7). Unambiguous synapomorphies optimised in TNT (parsimony) and in RAxML (likelihood) are shown where the clade is resolved for the MPTs, MLT, and preferred tree (see Online Supplemental Material Document S1.6 and S1.7).

**Clade Ichthyosauromorpha** Motani *et al.*, 2015

**Definition.** The last common ancestor of *Hupehsuchus nanchangensis* and *Ichthyosaurus communis*, and all of its descendants [node-based] (Motani *et al.* 2015).

**Discussion.** Motani (1999c) suggested the name Ichthyosauromorpha for the stem-based equivalent definition of his Ichthyopterygia as the maximally inclusive clade of ichthyosaurs, but refrained from a formal proposition, as the sister group was then uncertain. Recent discovery and re-description of several hupehsuchians has shown that this group is consistently found as the sister to ichthyosaurs (Chen *et al.* 2014a, b). Motani *et al.* (2015) found *Cartorhynchus* and *Chaohusaurus* to be the most basal ichthyosaur taxa. They erected Ichthyosauromorpha and Ichthyosauriformes for the node that includes *Hupehsuchus nanchangensis* + *Ichthyosaurus communis*, and the stem that includes *Ichthyosaurus communis* but not *Hupehsuchus nanchangensis* respectively.

**Clade Ichthyosauriformes** Motani *et al.*, 2015

**Definition.** The most inclusive clade that includes *Ichthyosaurus communis*, but not *Hupehsuchus nanchangensis* [stem-based] (Motani *et al.* 2015).

**Discussion.** Motani *et al.* (2015) found *Cartorhynchus* and *Chaohusaurus* to be the most basal ichthyosauriform taxa, and indicated in their fig. 4 that Ichthyopterygia was at the node that
includes Chaohusaurus and all other ichthyosaurs, but no definitions were formally emended. Here, the most recent definitions of Motani (1999c) are used in assigning names to these clades.

Clade Ichthyoportunity Owen, 1859

**Definition.** The last common ancestor of Ichthyosaurus communis, Utatsusaurus hataii, and Parvinatator wapitiensis, and all its descendants [node-based] (Motani 1999c).

**Discussion.** Ichthyoportunity was erected by Owen (1859, p. 159) as an order within Reptilia to hold the known ichthyosaur taxa – then limited to the genus Ichthyosaurus. Wiman (1929, 1933) later suggested that Grippia longirostris should be positioned alongside Ichthyosauria within Ichthyoportunity. Parvinatator wapitiensis is consistently found to be more basal than U. hataii, which places Ichthyosauria within this Ichthyoportunity as was found previously by Motani (1999c) (see discussion of Ichthyosauria below).

Grippioidea is recovered only in the MLT, and basal Ichthyoportunity are poorly resolved. The lack of the most basal Ichthyosauriformes – e.g. Cartorhynchus and Sclerocormus – in the study of Ji et al. (2016) makes it difficult to compare the character trends to this study.

However, in the preferred tree here, the change from a dorsally to laterally located external naris occurs around the Ichthyoportunity–Hueneosauria transition; the presence of a manual pisiform in this study comes with Ichthyoportunity also. Multiple maxillary rows are found in the most basal Ichthyosauriformes, but lost early in Ichthyosauria, so that it is not present in Hueneosauria (Maisch & Matzke 2000; Ji et al. 2016). Ichthyoportunity possess enlargement of the supratemporal, but is reduced in basal Hueneosauria. The definition of ‘moderate enlargement’ used here reflects the changing cases in basal Ichthyoportunity versus more derived taxa; more extensive enlargement occurs in Neoichthyosauria. A modified definition
for this character could define Eoichthyosauria or Hueneosauria more clearly by including contacts with the supratemporal, although these are incorporated into other characters.

Clade **Eoichthyosauria** Motani, 1999b

**Definition.** The last common ancestor of *Grippia longirostris* and *Ichthyosaurus communis*, and all its descendants [node-based] (Motani 1999c).

**Discussion.** This clade is not resolved typically due to a polytomy at the base of Ichthyopterygia. Under the original definition, *Chaohusaurus* was included as the sister to *Grippia* in Grippidia (Motani 1999c). Eoichthyosauria is recovered in the majority rule consensus-MPT as including Ichthyosauria and Ichthyopterygia within as *Grippia longirostris* is recovered more basal than *Utatsusaurus hataii*. (See also Ichthyopterygia above.)

Clade **Ichthyosauria** de Blainville, 1835

**Definition.** All taxa more closely related to *Ichthyosaurus communis* than to *Grippia longirostris* [stem-based] (Motani 1999c).

**Discussion.** Class Ichthyosauria was erected by de Blainville (1835) to include *Ichthyosaurus*, which was the only named genus at that time. Later, Owen (1859) placed ichthyosaurs in Order Ichthyopterygia, within Class Reptilia. Again, *Ichthyosaurus* was then the only included genus, but this included specimens that would later be split into the genera *Leptonectes*, *Mixosaurus*, *Stenopterygius*, and *Temnodontosaurus*. Wiman (1929) originally included *Grippia* in an order separate from Ichthyosauria, but later suggested that both these should be included as suborders within Order Ichthyopterygia (Wiman 1933). Mazin (1982) followed this, in portraying Ichthyopterygia to include all ichthyosaurs *sensu lato*, with an ingroup clade Ichthyosauria that excluded his Mixosauridae, *Grippia longirostris*, *Phalarodon fraasi*,...
and *Omphalosaurus*. In revising this, Motani (1999c) redefined Ichthyopterygia based on his reversed topology of *Grippia* and *Utatsusaurus*: following Mazin’s (1982) definitions on Motani’s (1999c) topology would place Ichthyopterygia as a clade within Ichthyosauria, respecting the relative position from their Linnaean origins (order- vs. class-level respectively). With *Utatsusaurus* being recovered basally here, the relative positions of Ichthyosauria and Ichthyopterygia are retained from Wiman (1933) and Motani (1999c), except in the majority rule consensus-MPT in which these clade positions are reversed.

Clade **Hueneosauria** Maisch & Matzke, 2000

**Definition.** The last common ancestor of *Mixosaurus cornalianus* and *Ophthalmosaurus icenicus*, and all its descendants [node-based] (Maisch & Matzke 2000).

**Synapomorphies. Parsimony.** prefrontal-postfrontal contact absent [37:1→0]; anterior terrace of the temporal fenestra present [74:0→1].

**Discussion.** Hueneosauria is recovered within Ichthyosauria, but containing some that have been considered more basal (Fig. 7; *Parvinatator wapitiensis* and *Pessopteryx nisseri*). *Cymbospondylus* is found within Hueneosauria in all analyses (Sander 2000; Maisch & Matzke 2000), but was recovered more basal to Hueneosauria by Motani (1999c) and Ji et al. (2016). The support for this clade moderate to high (80% in the preferred tree; Fig. 7), and subclades within Hueneosauria are better defined and supported. Similarly, which taxa are also within the subclade Merriamosauria is variable. An important resolution is the presence of the postparietal in *Cymbospondylus* and *Phantomosaurus*: is it present in both taxa? Is this a single medial ossification or paired lateral ossifications? does the same condition occur in both taxa? The previous interpretations of these taxa disagree with each other (Maisch & Matzke 2004;
Fröbisch et al. 2006; Maisch & Matzke 2006) leading to uncertainty: should *Phantomosaurus* form a clade with *Cymbospondylus* united by this feature? or are separate conditions represented?

Contact between the prefrontal and postfrontal is not present in many of the most basal taxa, but has been reported in *Chaohusaurus chaoxianensis* and *Sclerocormus parviceps* (Jiang et al. 2016; Zhou et al. 2017). It is not present in the most basal Ichthyopterygia, but almost all known Hueneosauria do possess this state. Short caudal centra are a feature of all adequately known Hueneosauria, but is also found in *Sclerocormus parviceps* (Jiang et al. 2016). The definition of ‘short’ is vague, and this interpretation could be open to change, in which case this will be a feature of Hueneosauria alone. Additionally, the chosen definition ‘short’ must take in the variable size of ichthyosaur caudal vertebrae. Many Neoichthyosauria have vertebral centrum height/length ratios (i.e. apparent ‘shortness’) of 2–4 (Buchholtz 2001; Fischer et al. 2011), but this becomes less posteriorly. Similar data for Triassic ichthyosaurs is less frequent, so it’s difficult to be certain whether they reach a similar ratio, or that ratio is noticeably less and centra relatively longer. Hueneosauria are also united by a regularly rounded anterior orbital margin, although in some more derived taxa this is modified into an angled margin – e.g. *Cryopterygius kristiansenae* (Druckenmiller et al. 2012). It also in basal Hueneosauria that the coronoid becomes non-ossified. At the base of Hueneosauria, the number of presacral vertebrae is optimized to be >55. This is due to the non-Mixosauridae that have elongated trunk regions – e.g. *Cymbospondylus* and *Shastasaurus* – and is reduced in Euichthyosauria. An alternative interpretation of this character could be that presacral vertebral count is increased only in the *Cymbospondylus + Shastasaurus* clade, not including the basal Hueneosauria; there would still be a reversal in more derived Merriamosauria, however.
Clade Mixosauridae Baur, 1887a

Emended definition. All taxa more closely related to Mixosaurus cornalianus than to Ichthyosaurus communis [stem-based].

Synapomorphies. Likelihood. Maxilla meets prefrontal [14:0→1]; external naris elongate [26:0→1]; postparietals absent [52:1→0]; parietal foramen well anterior to supratemporal fenestra [54:0→1]; postfrontal-supratemporal contact present [57:0→1]; large anterior terrace of the temporal fenestra [75:0→1]; interpterygoid vacuity absent [86:1→0]; basioccipital without notochordal pit [95:1→0]; posterior tooth crown rounded [149:0→1]; interclavicle triangular [181:2→1]; coracoid with anterior notch [185:1→0]; intermedium with one facet larger than the other(s) [235:0→1].

Discussion. Motani’s (1999c) original definition of Mixosaurus used Mixosaurus cornalianus and M. nordenskioeldii. The latter of these taxa is now considered a nomen dubium (Schmitz 2005). The definition of this clade was emended by Ji et al. (2016) as the M. cornalianus + Phalarodon fraasi node, however, in the present phylogeny that demarcates only those two taxa (Fig. 7); a stem-based definition that includes all similar taxa is preferred. Mixosauridae are known from good specimens, with well-defined apomorphies, but their internal taxonomy needs revision. This redefinition aims to provide stability to the clade.

That Mixosauridae is not resolved under parsimony is surprising considering the number of potential apomorphies present in these taxa. Support for Mixosauridae in the preferred tree is strong (98%), a relatively high support is found under maximum likelihood too (57%), and most trees support the resolution of Mixosauridae in the majority rule consensus-MPT (85%). There is, however, notable uncertainty in the topology of basal Huenchosauria (Fig. 5). Further characters that can be optimized support the monophyly of Mixosauridae; these are mostly
like those previously defined and reflect the modifications of the skull due to their unusual ecology: large anterior terrace of the temporal fenestra, supratemporal sheet over temporal fenestra, short postorbital region, rounded posterior teeth (Motani 1999b, c; Maisch & Matzke 2000). The incompleteness of Phalarodon major and its position within Merriamosauria in the preferred tree suggests that this taxon may be the cause of Mixosauridae non-monophyly in the consensus-MPT.

Clade **Merriamosauria** Motani, 1999b

**Definition.** The last common ancestor of Shastasaurus pacificus and Ichthyosaurus communis, and all its descendants [node-based] (Motani 1999c).

**Discussion.** Basal Merriamosauria form a polytomy (Fig. 7). Many of the unresolved merriamosaurian taxa here have been previously resolved in Euichthyosauria (Motani 1999c; Maisch & Matzke 2000). Where recovered, the support for Merriamosauria is low. The poor resolution of this clade means that taxa otherwise described as ‘shastasaur-grade’ are not certainly with Shastasauria or Euichthyosauria.

Loss of the postparietal occurs in some optimizations of this clade as Phantomosaurus neubigi and Cymbospondylus and near sister taxa to Merriamosauria; however, this character is problematic due to interpretation of the cranium of Cymbospondylus (Maisch & Matzke 2004; Fröbisch et al. 2006), and is a reversal to the same state as more basal non-Hueneosauria. Equally, several characters associated with the skull and dentition may be spread across basal Hueneosauria due to the derived positions of Phalarodon major and Wimanius odontopalatus, which have otherwise been considered more basal (Motani 1999c).

Reduction of the maxilla occurs in Merriamosauria, and is coded to some degree in Neoichthyosauria + Callawayia neoscapularis, Shastasaurus, and Shonisaurus, as was coded by
Sander (2000). However, the degree of reduction in the maxilla is variable, despite the maxilla being reduced compared to more basal Hueneosauria. Differences of interpretation may occur based on the lateral coverage of the maxilla by the premaxilla anteriorly and the lachrymal and jugal posteriorly. Additionally, the loss of teeth in Shastasauria was accounted for by Sander (2000) and Maisch & Matzke (2000). Contribution of the frontal to the supratemporal fenestra is present in basal Hueneosauria, but also found in more derived Ophthalmosauridae – e.g. *Platypterygius australis* (Kear 2005) – it is not present in basal Merriamosauria and Neoichthyosauria (Ji *et al.* 2016). However, the ventral extent of the frontal can be much greater posteriorly than dorsally; should this character incorporate the total dorsal and ventral contribution of the frontal, it would overlap more with character 41 (Fischer *et al.* 2011), but potentially also exclude the reversal of this character.

Clade **Shastasauria** Motani, 1999b

**Definition.** All taxa more closely related to *Shastasaurus pacificus* than to *Ichthyosaurus communis* [stem-based] (Motani 1999b).

**Synapomorphies. Likelihood.** Maxilla hidden laterally by jugal [13:0→1]; nasal-postfrontal with extensive contact [22:0→1]; frontals flat to concave in dorsal view [39:0→1]; postorbital triradiate [58:1→0]; squamosal without posterior descending process [71:1→0]; pterygoid with posteromedial process [90:1→0]; surangular without dorsal process [119:1→0]; teeth absent [128:0→1]; anterior dorsal centra rib facets not confluent with anterior margin [162:0→1]; scapula with blade shaft [196:0→1]; ulna proximally narrower than distally [224:1→0]; ilium plate-like [254:1→0]; femur ventral process same size as dorsal process [268:0→1]; femur with anterodistal facet [270:0→1]; tibia wider than long [272:0→1].

**Discussion.** This clade is defined as stem-based alongside a polytomy with other taxa that are
usually considered part of this group, or closely related – ‘shastasaur-grade’, e.g. *Besanosaurus leptorhynchos* and *Euichthyosauria* as in Ji *et al.*’s (2016) *Shastasauridae*. However, because of this lack of resolution, this clade, as defined, includes only *Shastasaurus*.

Numerous synapomorphies are found under maximum likelihood due to the small size of the clade and the similarity and monogeneric relations of the taxa included within. Additional characters that separate *Shastasaurus* include medium to large foramina on the lachrymal; slender lower jaw; and interosseous foramen between the fore limb epipodials (Maisch & Matzke 2000; Sander *et al.* 2011). Other features that have been attributed the ‘shastasaur-grade’ related to the skull and fore limb become paraphyletic character transitions through the non-Parvipelvia *Euichthyosauria*: similar limb morphologies are present in *Guizhouichthyosaurus* and *Besanosaurus* (Dal Sasso & Pinna 1996; Ji *et al.* 2013).

Clade **Euichthyosauria** Motani, 1999b

**Definition.** All taxa more closely related to *Ichthyosaurus communis* than to *Shastasaurus pacificus* [stem-based] (Motani 1999c).

**Synapomorphies**. Parsimony. Nasal reaches distinctly over orbit [17:0→1]; nasal contacts postfrontal [21:0→1].

**Discussion.** *Euichthyosauria* defines the branch between the two polytomies of *Merriamosauria* and *Parvipelvia* in the preferred phylogeny (Fig. 7), but is better resolved and includes numerous non-parvipelvian taxa in the consensus-MPT and MLT (Figs 4, 6). The possibility of a novel, although poorly supported, *Euichthyosauria* ‘side clade’ – *Toretocnemus californicus* + *Californosaurus perrini* – is presented in the MLT but poorly supported (Fig. 6).
The posterior extent of the nasal bones in Neoichthyosauria is greater than in more basal ichthyosaurs (Motani 1999c; Maisch & Matzke 2000), yet the extent is continuous. The location ‘above the orbit’ can be arbitrarily defined, however, here it is applied generally to traditional Neoichthyosauria. More basal Euichthyosauria do present nasal bones extended dorsal to the anterior orbit margin but these do not extend so far posteriorly; there may be contact with the postfrontal posteriorly as in _C. neoscapularis_ and _G. tangae_ (Nicholls & Manabe 2001; Maisch _et al._ 2006; Shang _et al._ 2012; Ji _et al._ 2016). In these taxa, the nasal is not so visible in lateral view. Including these taxa would position the extensive posterior nasal as a more basal feature of Merriamosauria, or potentially include _C. petrinus_ to include basal Hueneosauria (Fröbisch _et al._ 2006).

Clade **Parvipelvia** Motani, 1999b

**Emended definition.** The last common ancestor of _Macgowania janiceps, Hudsonelpidia brevirostris_, and _Ichthyosaurus communis_, and all of its descendants [node-based] (Motani 1999c).

**Synapomorphies. Parsimony.** Intermedium proximally pointed [232:0→1]; ischium and pubis similarly sized [259:0→1]; ischium or ischiopubis rod-like [260:0→1].

**Likelihood.** Humerus with markedly concave anterior margin [199:1→2].

**Discussion.** Parvipelvia is resolved but not well supported (53%) in the preferred phylogeny (Fig. 7), but not separated from Neoichthyosauria or Thunnosauria. The relationships between _M. janiceps_, and more derived taxa are uncertain and there is no consensus between the resultant trees (Figs 4, 6, 7). The original definition referred only to the genus _Ichthyosaurus_, whereas here this is extended and clarified to the type species, _I. communis_.


Parvipelvia includes *H. brevirostris, M. janieps*, and Neoichthyosauria at its greatest extent, and few characters support this clade separate to Neoichthyosauria. These most basal Parvipelvia taxa are poorly known, and most of the discussion of Neoichthyosauria is applicable to Parvipelvia also (see below). Most clearly, Parvipelvia is associated with the strong reduction of the pelvic girdle, but this is a continuation of reduction in Merriamosauria or throughout all Ichthyosauriformes, incorporating the loss of contact between the pelvis and vertebral column in Hueneosauria (Eoichthyosauria?). There is no easy definition of the size of the pelvis beyond, so states have been coded largely based on previous hypotheses of relations (Motani 1999c; Maisch & Matzke 2000; Ji et al. 2016). Specifically in the pelvis, the ilium becomes styloidal in the clade containing *Qianichthyosaurus zhoui* + Parvipelvia; another indicator of pelvic reduction. That ichthyosaurs do not lose the hind limbs completely is interesting considering that they are lost in Cetacea; perhaps they still served some purpose in swimming? Perhaps related to the lateral versus dorsoventral undulatory modes of locomotion?

Clade **Neoichthyosauria** Sander, 2000

**Emended definition.** The last common ancestor of *Temnodontosaurus platyodon* and *Ichthyosaurus communis*, and all of its descendants [node-based] (Sander 2000).

**Synapomorphies. Parsimony.** Ulnare smaller than intermedium [229:0→1].

**Discussion.** Neoichthyosauria was erected to include the monophyletic post-Triassic ichthyosaur taxa (Sander 2000). The base of this clade is a large polytomy with Parvipelvia and *Temnodontosaurus* is polyphyletic within this clade. The original definition used only the genus *Ichthyosaurus*; here it is clarified to the type species *I. communis*. Maisch & Matzke (2000) used a definition involving *T. platyodon* and *Ophthalmosaurus icenicus*, but the
emendation from Sander’s (2000) original is preferred here. The base of this clade is
confluent with Parvipelvia in the preferred phylogeny (Fig. 7) and the positions of taxa within
and immediately sister to Neichthyosauria is highly variable across the recovered trees (Figs
4, 6, 7; Online Supplemental Material Figure S1). Neichthyosauria is better resolved under
equal-distribution rather than gamma-distribution rates prior Bayesian inference suggesting
heterogeneity in state transitions between characters in this part of the tree.

Neoichthyosauria here potentially includes the development of the caudal fluke into a
crescentic tail fin, although this may extent to Parvipelvia. While this is most clearly known
from ichthyosaurs with soft tissue preservation, osteological correlates are present in the
development of a clear tail bend. This has been preserved in many Early Jurassic taxa from the
UK and Germany, including T. trigonodon, L. tenuirostis, I. communis, and E. longirostris
(McGowan & Motani 2003). Diagnoses of Thunnosauria (see below) include the shortening of
the tail relative to the body (Maisch & Matzke 2000), which occurs in only some taxa showing
the well-developed tail bend. This suggests a two-step evolution of improved swimming
efficiency within Parvipelvia: tail fluke, followed by stockier (more powerful?) tail.

Neoichthyosauria share aulacodont dentition (Sander 2000; Maisch & Matzke 2000),
however, poor preservation of more basal Euichthyosauria makes it uncertain whether this is
limited to Neoichthyosauria or more extensive. The dorsoventral extent of the maxilla is
reduced posteriorly in Neoichthyosauria (Druckenmiller & Maxwell 2010), however, this
coincides with a reduction of the postnarial process of the maxilla and the anterior extent of
the jugal and lachrymal to cover the maxilla. A large postnarial process of the maxilla is found
prominently in Mixosauridae, but a similar structure is also present in Platypterygius australis
(Jiang et al. 2005; Kear 2005; Jiang et al. 2006); despite the morphological similarity these do
not represent homology. However, the effects of the extensive postnarial process are
widespread: several other characters related to bones surrounding the external naris and
anterior orbit are affected by this structure, and mutually exclusive states – e.g. the premaxilla-lachrymal contact; prefrontal-external naris contact.

Clade **Leptonectidae** Maisch, 1998

**Definition.** The last common ancestor of *Eurhinosaurus longirostris* and *Leptonectes tenuirostris*, and all of its descendants [node-based] (Maisch 1998).

**Synapomorphies. Parsimony.** Frontal with widest exposure posteriorly [40:1→0]; supratemporal fenestra posteriorly narrower than anterior [73:1→0]; quadratojugal located posteriorly [77:0→1]; quadratojugal mostly exposed posteriorly [78:0→1]; cheek largely oriented posteriorly [85:0→1]; radial and ulnar facets of the humerus equal size [209:0→1]; manual metacarpals II & IV rounded [246:2→1]; proximal manual phalanges mostly rounded [250:2→1]; femur with smaller ventral process than dorsal [268:1→0].

**Likelihood.** Maxilla excluded from external naris [15:0→1]; nasal contacts postfrontal [21:0→1]; prefrontal with little exposure [35:1→2]; dentition strongly reduced [129:0→1]; haemapophyses present [176:1→0]; rounded manual metacarpals II & VI [246:2→1]; metacarpal V absent [247:0→1]; mostly rounded proximal manual phalanges [250:2→1]; ischium and pubis not fused laterally [257:1→0]; tibia and fibula do not contact proximally [277:1→0].

**Discussion.**

*Excalibosaurus costini* is most frequently recovered as the sister taxon to *Leptonectes solei*, despite the well-documented similarities with *E. longirostris*. Leptonectidae is not recovered in the preferred tree (Fig. 7), but is found under both maximum parsimony and likelihood (Figs 4, 6). While the position of this clade within Neoichthyosauria is unresolved in the
consensus-MPT, it is located within Thunnosauria in the MLT; a more derived position than previously found (Ji et al. 2016; Fischer et al. 2016). Leptonectidae also shows possible morphological convergence with the evolution of several longirostrine ichthyosaurs in the Early Jurassic – e.g. *Temnodontosaurus azerguensis* and *Hauffiopteryx typicus* (Martin et al. 2012; Marek et al. 2015). While *H. typicus* is typically resolved in a more derived position close to Thunnosauria, similar to Marek et al. (2015), the position of *T. azerguensis* is less certain and has a relatively long branch.

The allying of *H. typicus* with Leptonectidae (but not in the preferred tree) is mostly a result of morphological convergence associated with the shortening of the posterior skull and slender snout. *Hauffiopteryx* does not have the distinctly posterior orientation of the cheek region seen in more derived Leptonectidae, but the similar morphology of the skull has effected similar changes between this taxon and Leptonectidae. Synapomorphies of Leptonectidae + *H. typicus* include the slender premaxillary segment, which was defined here based on the condition in Leptonectidae, as this was not clearly defined by Motani (1999c); such a condition is also found in the longirostrine *Temnodontosaurus azerguensis*. While these taxa are here recovered together, these ecological convergences may be due to homoplasic characters reducing their utility.

Clade **Thunnosauria** Motani, 1999b

**Definition.** The last common ancestor of *Stenopterygius quadriscissus* and *Ichthyosaurus communis*, and all of its descendants [node-based] (Motani 1999c).

**Discussion.** Thunnosauria is not found separately from Neoichthyosauria in the preferred tree (Fig. 7) or consensus-MPT (Fig. 4) as the latter clades are not resolved basally (Figs 5, 8). Thunnosauria is recovered in the MLT, poorly supported (Fig. 6), but in a similar position
relative to other taxa as found by Motani (1999c) and Ji et al. (2016) – more derived than *Temnodontosaurus*, but more basal than *Stenopterygius*.

Thunnosauria was diagnosed by Ji et al. (2016) including an absence of the anterior flange of the humerus. This was originally coded by Motani (1999c) as ‘present, but reduced proximally’ and is coded as such for some Thunnosauria by Ji et al. (2016). The definition of this character is open to interpretation, and loss of the anterior flange removes an important defining feature of Triassic Ichthyosauriformes. In the interpretation used here, the anterior flange is reduced proximally in Neoichthyosauria as there is clearly no anterior projection present anterior to the main humeral shaft. However, the anterodistal process or tuberosity of the humerus is present in many basal Parvipelvia, which is treated as the distal extent of the anterior flange, as implied by Motani (1999c), and included by Ji et al. (2016). The tail of ichthyosaurs progressively shortens through phylogeny, however, the change from being longer to shorter than the body is uncertain; this was optimized as a synapomorphy of Thunnosauria by Maisch & Matzke (2000). The coding scheme used finds this true for most traditional Thunnosauria, excluding – e.g. *Temnodontosaurus* and *Leptonectes* – yet more basal Merriamosauria are also coded with short tails – e.g. *Qianichthyosaurus zhoui*. This appears to be some level of convergence, but the proportions of *Q. zhoui* suggests that it could be coded with a longer tail.

Clade **Baracromia** Fischer et al., 2013

**Definition.** The last common ancestor of *Stenopterygius quadriscissus* and *Ophthalmosaurus icenicus*, and all of its descendants [node-based] (Fischer et al. 2013).

**Synapomorphies. Parsimony.** Strongly reduced dentition in adults [129:0→1].

**Discussion.** Unexpectedly, *Stenopterygius* is not monophyletic in any analysis (Figs 4, 6, 7).
but instead is paraphyletic to Ophthalmosauridae, with *S. triscissus* typically found more basally than other species of *Stenopterygius*. Where this occurs, this places the occurrence of the prominent acromion process (one of the defining features of Baracromia; Fischer *et al.* 2013) more basal to the location of this taxon. This character change does occur in the preferred phylogeny due to the polytomy that includes all species of *Stenopterygius*.

Optimization of characters does suggest that the angular extent increases and the ischium and pubis fuse completely in Baracromia (Maisch & Matzke 2000), and that the proximal processes on the femur relatively increase in size (Fischer *et al.* 2013). Additionally, the relative sizes of the dorsal and ventral humeral processes are increased, although this has often been associated with Ophthalmosauridae (Fischer *et al.* 2012; Fischer *et al.* 2013). While these are larger in Ophthalmosauridae, the definition for these characters is non-specific and so was applied to these non-Ophthalmosauridae Baracromia. Platypterygiinae have been defined including the large ventral process, with distinct concavities (Fischer *et al.* 2011), and similarly, Ophthalmosauridae are separated by the plate-like dorsal ridge on the humerus (Fischer *et al.* 2012) indicating the increased development of this and the musculature associated with the humerus (Moon & Kirton 2016). In this study, these features of the humerus have been treated as separate characters, however, if interpreted as a continuum of humeral development through phylogeny, they could alternatively be treated as a single multistate character with states, for example: poorly developed humeral processes (non-Merriamosauria Ichthyosauriformes); developed ventral process (Merriamosauria); developed dorsal and ventral processes (Baracromia); plate-like dorsal process (Ophthalmosauridae); well developed, plate-like dorsal and ventral processes (Platypterygiinae).
Clade **Ophthalmosauridae** Baur, 1887a

**Emended definition.** All taxa more closely related to *Ophthalmosaurus icenicus* and *Platypterygius hercynicus* than to *Stenopterygius aalenensis* and *Chacaicosaurus cayi* [stem-based].

**Synapomorphies. Parsimony.** Humerus with plate-like dorsal ridge [207:0→1]; acute angle at anterodistal humerus [212:0→1].

**Discussion.** Following Fischer et al.'s (2011) emended definition, Ophthalmosauridae would refer to a small clade in consensus-MPT and MLT (Figs 4, 6). To maintain stability in the included taxa, the definition is extended to formally include *Platypterygius hercynicus*—following Fischer et al.'s (2012) definitions of Ophthalmosaurinae and Platypterygiinae – and exclude *Stenopterygius aalenensis* – the immediate sister taxon to Ophthalmosauridae – and *Chacaicosaurus cayi*. While *C. cayi* is here located more basally in Neichthysosauria in the preferred phylogeny due to lack of resolution (Fig. 7), it has been recovered as the immediate sister taxon to Ophthalmosauridae previously (Fischer et al. 2011).

Ophthalmosauridae can be diagnosed by features that include reduction of the extracondylar area of the basioccipital; plate-like dorsal process on the humerus; increased fusion of the ischium and pubis; and loss of notching in the fore and hind limbs (Motani 1999c; Sander 2000; Maisch & Matzke 2000; Fischer et al. 2012; Ji et al. 2016). However, variability with Ophthalmosauridae reduces the utility of some of these features: the basioccipital extracondylar area is reduced more in Platypterygiinae than in more basal Ophthalmosauridae; similarly, fore limb bone patterns are substantially different between Platypterygiinae than in basal Ophthalmosauridae. These two clades have been separated as sister taxa (Fischer et al. 2011; Fischer et al. 2012; Fischer et al. 2013).
convergences – e.g. the polygonal fore and hind limb elements in more derived Ophthalmosauridae, the secondary loss of three distal humeral facets in Cryopterygius and Nannopterygius; both convergent with more non-Ophthalmosauridae – complicate the resolution of this clade, hence a large polytomy in the preferred phylogeny (Fig. 7). Otherwise prominent features – e.g. the large, plate-like ventral process of Platypterygiinae; the humerus-intermedium contact in Aegirosaurus, Brachypterygius, and Grendelius – similarly do not unite taxa that might form a clade. This inconsistency is particularly well shown by the removal of most Ophthalmosauridae when pruning the consensus-MPT: many taxa are equally unstable and reduce the resolution present here. Further study of this group may benefit from selectively removing the least complete taxa alongside those that are equivalent, however, this may also reduce phylogenetically useful data so was not carried out here.

Discussion

Ichthyosaur evolution: clades and grades

In reviewing ichthyosaur evolution, Motani (2005) recognized three grades within ichthyosaur evolution: a basal grade: Early Triassic ichthyosaurs; an intermediate grade: Middle–Late Triassic ichthyosaurs; and a fish-shaped grade: Late Triassic–Cretaceous ichthyosaurs. Each of these corresponds to a portion of ichthyosaur phylogeny, represented by several clades within Ichthyosauriformes, monophyletic or paraphyletic. In the phylogeny presented here (Fig. 7), the pattern across ichthyosaur evolution is similar. Both the basal and intermediate grades are paraphyletic with respect to the more derived grades, and identified by the resolve polytomous nodes. The basal ichthyosaur grade, which includes the basal-most ichthyosaurians and non-ichthyosaurian Ichthyosauriformes, is marked by the relatively elongate tail, compared to the trunk, and long propodials and epipodials, compared to the whole limb, remnants of their terrestrial ancestry (Motani 2005). The metapodials retain the
basal hourglass-like form comparable with more basal diapsids (Motani 1999c; McGowan & Motani 2003).

In the intermediate grade, most non-parvipelvian ichthyosaurians, there is the gradual acquisition of more fish-like characters: shrinking the size and increasing the number of limb bones to form paddle-like limbs, shortening of the caudal vertebrae, so that the tail becomes shorter relative to the trunk, and the early development of a strong tail bend (McGowan & Motani 2003). This grade may be divided into two subgrades: the earlier, Middle Triassic *Cymbospondylus-Mixosaurus* group, and the Middle–Late Triassic *Shastasaurus-Shonisaurus* group. The former group includes taxa that represent the early ecological diversification of ichthyosaurs, with a broad range of body forms habits, associated with an increase in disparity (Massare 1987; Thorne *et al.* 2011; Fröbisch *et al.* 2013; Dick & Maxwell 2015). This is marked in the above phylogeny by character changes related to the teeth as a potential synapomorphy of Mixosauridae (e.g. character 149:0→1). The more derived members of the intermediate grade than Mixosauridae, which includes traditional ‘shastasaurids’, modify the forelimb further than earlier taxa, particularly through the loss of digits and shortening and rounding of the phalanges (see Online Supplemental Material Document S1.5; Thorne *et al.* 2011; Sander *et al.* 2011; Motani *et al.* 2013).

The latest, fish-like grade, including all parvipelvians, represent an oft-cited example of convergence with modern pelagic fishes (Motani *et al.* 1996; Motani 2005). While this clade is named for the reduction of the pelvis, this is not an unambiguous synapomorphy (see above and Online Supplemental Material Document S1.6). However, this clade and grade are marked by several changes to the pectoral girdle that affect the form and use of this and the forelimb. Within Parvipelvia, there is a shift between the basal taxa and the clade Baracromia, which has several limb-based character changes towards the node. This marks the later evolution and diversification of this clade and the more derived Ophthalmosauridae that succeeded
from the non-baracromian parvipelvian ichthyosaurs in the Middle Jurassic–Cretaceous (Fischer et al. 2012; Fischer et al. 2013). With the proposal of the above phylogeny, it becomes possible to analyse specific traits, discrete and continuous, across ichthyosaur evolution, and test the reality of the ichthyosaur evolution as a series of grades.

**Specimen completeness**

The effects of incomplete taxa have often been associated with a lack of characters rather than simply the proportion of missing data (Wiens 2003). Recent metrics to quantify skeletal and cladistic completeness provide comparative methods that may allow attribution of completeness (Mannion & Upchurch 2010). Studies have applied these to several fossil groups, but only recently to marine reptiles (Cleary et al. 2015). While specimen completeness is highly variable through the Mesozoic, periods of relatively high completeness – e.g. Hettangian–Toarcian – are coincident with the occurrence of better-resolved regions of the trees presented: approximately Merriamosauria through to Baracromia. Conversely, lower levels of completeness are found in Early–Middle Triassic, Middle Jurassic, and Late Jurassic–Cretaceous taxa, which correspond to the less well resolved portions of the trees: basal ichthyosaurs and Ophthalmosauridae, particularly (Figs 4, 6, 7; Online Supplemental Material Figure S3; Cleary et al. 2015). Whether and how skeletal and cladistic completeness of ichthyosaurs is related to phylogeny has yet to be tested.

**Phylogeny reconstructions**

Throughout the above analyses, the ichthyosaur matrix has been used as an exemplar of a palaeontological dataset: purely morphological data, many taxa are from a few discrete horizons, and completeness varies greatly between taxa. In previous work on ichthyosaur phylogeny, methods of phylogeny inference other than maximum parsimony were limited to
the Bayesian-inference maximum likelihood analyses of Fröbisch et al. (2013) and Fischer et al. (2016). Simulation data has suggested that Bayesian inference can provide increased accuracy of results over parsimony in palaeontological datasets (Wright & Hillis 2014; O’Reilly et al. 2016). However, the importance of missing data and its effect on phylogeny reconstruction is complex (Prevosti & Chemisquy 2010; Wiens & Morrill 2011; Simmons 2012; Sansom 2014). Simulations of data loss have generally focused on formulaic removal, often of a minority of codings – e.g. Wright & Hillis (2014) removed characters with similar rate changes. The present dataset of ichthyosaurs, however, contains over 50% non-coded characters. While these missing data are not purely random, there is a bias towards absence of certain character sets – e.g. small limb bones, limbs, tail vertebrae, and neural spines.

A posteriori analysis and modification of trees – e.g. by pruning – will often provide an increase in resolution and potentially accuracy (Pol & Escapa 2009; Aberer et al. 2013). This method has proved useful here as a faster addition to a priori STR (Wilkinson 1995; Siu-Ting et al. 2015). Previous studies of ichthyosaurs have used an arbitrary proportion of incomplete characters to remove taxa, presenting this alongside the complete analysis (Fischer et al. 2013; Fischer et al. 2014a). Although this is the simplest method, it does not always prove the best in resolving relationships (Wiens 2003). A posteriori identification of unstable taxa allows a determination of the causes of this instability – in the case of PCR pruning by pinpointing conflicting characters (Pol & Escapa 2009) – which provides a useful indication of where the uncertainty lies. This method is preferred as a means of identifying problematic taxa in phylogenetic analyses.

The lack of resolution here between relatively complete taxa – e.g. *Ichthyosaurus*, *Stenopterygius*, and *Temnodontosaurus* within Parvipelvia/Neoichthyosauria – suggests, however, that the characters used to inform the topology are proving inadequate. This may require a reformulation of characters to reflect newer understanding and methodology –
likelihood vs parsimony – but most immediately suggests that a thorough revision within a
modern phylogenetic framework is necessary. Posterior samples of trees, however, does not
preclude further study based on phylogenetic inference.

The two different topologies found under Bayesian inference imply that different models
support, or resolve, different parts of the tree (Fig. 7; Online Supplemental Material Figure
S3) – i.e. there is rate heterogeneity across the tree, and that different models/priors are
necessary: the posterior distributions found are different to the prior distributions (Online
Supplemental Material Figure S2). This is not surprising, considering that previous studies
have shown that certain parts of ichthyosaur evolution are punctuated by high cladogenesis
rates (Fischer et al. 2012; Fischer et al. 2013). Stratigraphic correlation of trees also shows the
unevenness present (Motani 1999c; Fröbisch et al. 2013). As Bayesian inference has been
shown to be able to recover weak, short branches (Alfaro et al. 2003), those clades recovered
around the base of Parvipelvia in this analysis may be confidently recognized, although that
has not been done here. A full investigation of the effects of Bayesian prior selection is beyond
the scope of this study.

Conclusions

1. Previous hypotheses of ichthyosaur phylogeny are corroborated, but individual taxon
positions can vary greatly producing topological instability and weak support for
relationships. Ichthyosaurs present a stepwise phylogeny with nested clades separated
by acquisition of characters. Monophyletic groups are present, which can be well
supported, and mark diversification within a particular bauplan – e.g. Mixosauridae
and Shastasauria.

2. Non-monophyletic genera reaffirm the need for revision of several ichthyosaur taxa,
particularly those based on poor diagnoses and specimens, or phenetic definitions –
e.g. Temnodontosaurus, Mixosaurus and Phalarodon, Ophthalmosaurus, Stenopterygius, and Platypterygius. These issues may be compounded by the variation of form exhibited by several taxa – e.g. Ichthyosaurus and Stenopterygius – and the wide range of species and specimens available.

3. Unstable ichthyosaur taxa may be the result of inadequate characters as well as inadequate coding (incompleteness). An in-depth, critical re-evaluation of characters may be necessary, particularly for those in the most poorly resolved clades – e.g. basal Ichthyosauriformes, basal Merriamosauria, and Ophthalmosauridae. *A posteriori* identification of unstable taxa and taxon pruning can provide indication of which are inadequately known, and where characters may need revision.

4. Analyses under different phylogeny criteria recover a similar overall topology, but the placement of individual taxa varies greatly, as does consensus resolution. Differences in the resolution of Bayesian inference show that different prior distributions can affect the results, and that a simply distributed prior may not be the most useful.

Supplemental material

Supplemental material for this article can be accessed here:

Acknowledgements

I would like to thank Mike Benton and Emily Rayfield for their supervision and comments; David Button, Phil Donoghue, Joseph Keating, Jessica Lawrence, Erin Maxwell, Luke Parry, Mark Puttick, Aubrey Roberts, Tom Stubbs, and the Radsphere for discussion; the Willi Hennig Society for their support of TNT; and my parents for their support in my PhD. My thanks also to Valentin Fischer and Ben Kear for their helpful reviews of this manuscript. This work has been funded by Leverhulme Trust Research Project Grant RPG-2015-126.
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Captions

analysis.
Figure 3. Resultant networks from Concatabomination analysis showing the more problematic taxa (larger, redder circles) and their similarity to other, less problematic taxa (smaller, yellow circles). *Cymbospondylus piscosus, Dearcmhara shawcrossi, Isfjordosaurus minor,* and *Pervushovisaurus bannovkensis* are identified as the taxa with most redundancy. Other, unconnected taxa and self-referential similarity are not shown.

Figure 4. Strict consensus of 11,536 recovered MPTs recovered from equal weights parsimony analysis in TNT with 104 OTUs: 1666 steps, CI = 0.150, RI = 0.521, RCI = 0.0782. Support values given are: decay index above the branch in roman type, symmetrical resampling per cent below the branch in italic. Named and discussed clades are labelled; node numbers are indicated in square brackets: **A**, Ichthyosauria; **B**, Baracromia; **H**, Hueneosauria; **I**, Ichthyosauriformes; **L**, Leptonectidae; **N**, Neoichthyosauria; **O**, Ophthalmosauridae; **P**, Parvipelvia; **S**, Shastasauria; **U**, Euichthyosauria. Node-based clades are indicated at the node; branch-based clades are indicated with an arrow towards the base of the clade. Outgroup taxon is indicated in orange. See also Online Supplemental Material Figures S1 &
Figure 5. Visualisations of uncertainty in the 11,536 recovered MPTs from equal weights parsimony analysis in TNT with 104 OTUs (see also Fig. 4). A, cluster network showing relationships supported by at least 25% of MPTs; teal edges indicate uncertain relationships. B, consensus network of branches supported by at least 25% of MPTs; distances (branch weights) represent mean support for relationships; for clarity, not all taxa are labelled. Outgroup taxon is indicated in orange. See also Online Supplemental Material Figures S1 & S2.
Figure 6. Most likely tree recovered from analysis in RAxML with 104 OTUs. Bootstrap supports from 2000 replicates are indicated below each branch. Branch lengths are scaled to the substitutions along each branch; scale represents 0.2 substitutions. Named nodes are
indicated as in Fig. 4 with the addition of M, Merriamosauria; T, Thunnosauria; X, Mixosauridae. Outgroup taxon is indicated in orange.

Figure 7. Resultant 50% majority rule consensus tree of 24,710 sampled trees from Bayesian inference analysis in MrBayes using a gamma-distributed site rate variation with 104 OTUs. This is the preferred tree. Clade credibility values are shown to the right of each node. Branch lengths are scaled to the substitutions along each branch; scale represents 0.2 substitutions. Named clades are indicated as in Fig. 4. Outgroup taxon is indicated in orange. Grades are shown by coloured bars. See also Online Supplemental Material figures S3, S4.
**Figure 8.** Visualisations of uncertainty in 24,710 sampled trees from Bayesian inference analysis with a gamma-distributed site variation prior in MrBayes with 104 OTUs (Fig. 7). **A,** cluster network showing relationships supported by at least 25% of sampled trees; teal edges indicate uncertain relationships. **B,** consensus network of branches supported by at least 25% of sampled trees; distances (branch weights) represent mean support for relationships; for clarity, not all taxa are labelled. Outgroup taxon is indicated in orange.
Figure 9. Summarised clade definitions for resolved (solid lines, filled circles) and possible (dashed lines, unfilled circles) clades taken from the preferred phylogeny (Fig. 7). Only
defining taxa are shown. Uncertain clade positions are shown in brackets. Node-based names are in upright font; stem-based names are in italic font. The outgroup is indicated in orange.

Table 1. Taxa pruned by PCR analysis from the strict consensus of 11,536 MPTs recovered under equal weights TNT analysis with 104 OTUs. The polytomous node in strict consensus (Fig. 4) from which each taxon is pruned is indicated, alongside the coded character completeness (%). See also Online Supplemental Material Document S4 and Figure S2.
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