Fossil Record 27 (3) 2024, 445–471 | DOI 10.3897/fr.27.133803

Evolution of the tetrapod skull: a systematic review of bone loss

Kim Julia Kean[1], Marylène Danto[2], Celeste Pérez-Ben[2,3], Nadia Belinda Fröbisch[1,2]

1 *Institut für Biologie, Humboldt Universität zu Berlin, Berlin, Germany*
2 *Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany*
3 *Laboratorio de Biología Integral de Sistemas Evolutivos, IEGEBA, FCEN, UBA / CONICET, CABA, Argentina*

https://zoobank.org/65576914-26C6-47D6-8A71-7EAA354B1970

Corresponding author: Kim Julia Kean (kimjulia.kean@mfn.berlin)

Academic editor: Florian Witzmann ♦ **Received** 2 August 2024 ♦ **Accepted** 20 October 2024 ♦ **Published** 30 December 2024

Abstract

The simplification of the tetrapod skull occurred convergently in various tetrapod lineages from the Devonian into the Mesozoic, leading to some groups (e.g. lissamphibians) to retain only 19 of the original 41 dermal roof bones present in stem-tetrapods. Despite the potential to shed light on the functional adaptations and developmental mechanisms behind skull simplification, little work has been done on the distribution of bone loss across tetrapod phylogeny. We conducted maximum likelihood ancestral state reconstructions for the presence/absence of temporal and median dermatocranial bones using two large composite trees that placed Lissamphibia either within Temnospondyli or Lepospondyli, reflecting the ongoing debate on lissamphibian origins. Our results indicate that the temporal series did not form a developmental module, as the loss of these bones was quite variable. With the exception of Sauropsida, the intertemporal bone was lost first, followed by the supratemporal, and then the tabular and/or postparietal. In Sauropsida, the tabular and/or postparietal was the second bone to be lost. The supratemporal was lost and regained repeatedly, and was found to be the most variable element, while the nasal, frontal, and parietal were the least variable. Interestingly, the ontogenetic timing of ossification does not correlate with the propensity for a certain bone to be re-acquired or lost. No obvious relationship was found between skull simplification and lifestyle or body size. In summary, the simplification of the dermatocranium is a more complex process than previously thought, and likely involved a mixture of developmental, ecological, and functional drivers.

Key Words

Ancestral state reconstruction, dermatocranium, lepospondyl, lissamphibians skull simplification, temnospondyl, tetrapod

Introduction

The skull is one of the most complex and versatile components of the vertebrate body plan. In addition to housing the sensory organs that allow vertebrates to navigate and interact with the world, this anatomical unit is also used in feeding (Heiss et al. 2018), locomotion (Wake 1993), combat (Farke et al. 2009), and sexual display (Knell et al. 2013). The main components of the skull include the (1) endocranium (chondrocranium and neurocranium) which protects the brain, the (2) viscerocranium (gill arches and splanchnocranium) which originates from the branchial arches, and (3) the dermatocranium, which acts as a vault for these structures (Walker et al. 2000). The complexity and multifunctional nature of the skull is a direct result of selection pressures applied to these individual components over evolutionary time.

One of the most significant moments in the evolution of the skull was the water-to-land transition in Tetrapodomorpha (the clade made up of extant tetrapods and extinct species more closely related to them than to lungfish) during the Devonian, which was a time of rapid change, morphological innovation, and ecological radiation (Long and Gordon 2004; Clack 2009, 2012). Previous studies have already outlined some of the morphofunctional shifts in the skull during this period, including the evolution of the tetrapod otic region, and adaptations associated with feeding and breathing on land (Coates and Clack 1991; Clack 1992, 1994, 1998; Clack et al. 2003; Brazeau and Ahlberg 2006; Schoch and Witzmann 2011). Another key change that occurred at this transition was the apparent reduction of bone elements in the dermal skull. This can first be seen in *Acanthostega* and *Ichthyostega* which lack the extrascapular and operculogular bones present in finned tetrapodomorphs such as *Eusthenopteron* (Andrews and Westoll 1970; Jarvik 1980). The loss of the extrascapulars was a pivotal moment in tetrapodomorph evolutionary history, marking the origin of the neck as the skull became detached from the dermal pectoral girdle (Clack 2002; Sefton et al. 2016; Maddin et al. 2020) (note, a functional 'neck' has been reported in the tetrapodomorph fish *Mandageria fairfaxi* (Johanson et al. 2003)).

The trend towards a simplified skull continued after the Devonian and can be observed throughout tetrapod evolutionary history, occurring independently (i.e. convergently) in several lineages with a diversity of skull morphologies and functional adaptations (Rawson et al. 2022) (Fig. 1). Skull simplification has been extensively documented in reptiles (Williston 1925; Lee et al. 2020), birds (Smith-Paredes et al. 2018; Plateau and Forth 2020; Asakura and Kawabe 2022), synapsids (Sidor 2001), and lissamphibians (caecilians, salamanders, and frogs), with the latter only retaining 19 of the original 41 bony elements found in many stem-tetrapod skulls (Fig 1; Shoch 2014). Interestingly, the convergent bone loss across tetrapod lineages is not only seen in the overall number of elements lost, but also in the consistent loss of particular bones, the intertemporals being a prime example (at least as separately ossified elements). In contrast, bones such as the parietals have been conserved for over 400 million years from the first osteichthyans to extant tetrapods (Fig. 1). This would suggest that there is a commonality in the evolutionary pathways towards skull simplification, regardless of morphofunctional differences in cranial construction. Surprisingly, the distribution of bone loss across tetrapod phylogeny has received little attention. Research has instead been largely focused on quantifying simplification in terms of changes in complexity through network analyses (Esteve-Altava et al. 2013, 2014; Lee et al. 2020; Plateau and Forth 2020; Asakura and Kawabe 2022; Rawson et al. 2022; Strong et al. 2022), and determining the mode of loss in extant taxa through fate mapping (Maddin et al. 2016), histological (Arnaout et al. 2022), and embryological studies (Koyabu et al. 2012; Smith-Paredes et al. 2018).

At the developmental level, bone loss in the skull is known to occur in one of two ways: either through (1) fusion or (2) lack of ossification. Fusion of adjacent bones can occur when ossification centres merge with neighbouring ones early in development due to the premature closure of suture joints, or when the cartilaginous anlagen fuse before the suture joint develops. This then forms a composite bone which is made up of multiple ossification centres, and thus gives the impression that a bone element has been lost (Koyabu et al. 2012; Esteve-Altava et al. 2013; Schoch et al. 2014). The mammalian interparietal is an example of such a composite bone, consisting of four fused ossification centres thought to be homologous to the postparietals and tabulars (Koyabu et al. 2012). The second developmental mechanism of skull bone loss is the failure of ossification centres to form, often caused by heterochronic truncation. This typically affects those bones that form in the final stages of ancestral skull ossification, as the shortened ontogenetic trajectory prevents them from forming (Schoch 2014). In other words, ossification fails to occur in bones which, primitively, tend to ossify in the later stages of skull development. The missing dermal bones in the skulls of extant lissamphibians, for instance (e.g. the postfrontal, postorbital, and tabular), are those that form late in the ontogeny of temnospondyls (Schoch 2002), the putative stem group of Lissamphibia (Carroll 2007; Ruta and Coates 2007; Anderson 2007, 2008; Schoch et al. 2020). However, dermal bones can also fail to ossify if the minimum population size of stem cells in the mesenchymal tissue layer where these bones form is not reached (Atchley and Hall 1991), as may be the case in instances of miniaturised body size (Pérez-Ben et al. 2018; see below).

Various functional adaptations have been proposed as potential evolutionary drivers of cranial simplification. For example, it has been hypothesised that a reduction in the number of bony elements would increase the degree of connectivity in the individual remaining cranial bones (Strong et al. 2022), which in turn would lead to a more robust skull capable of withstanding the biomechanical stresses associated with certain lifestyles such as crevice dwelling (e.g. in extant lepidosaurians) (Herrel et al. 2007) and head-first burrowing (e.g. in recumbirostran microsaurs, caecilians, amphisbaenids, dibamids, and scolecophidian snakes) (Pardo et al. 2015; Szostakiwskyj et al. 2015; Pardo and Anderson 2016; Strong et al. 2022). In the case of batrachians (frogs and salamanders), Schoch (2014) suggested that the skull morphology and bone reduction may have been driven by the rearrangement of jaw musculature related to skull flattening. The study proposed that a highly fenestrated skull morphology and the emargination of the cheek region in salamanders and frogs (via the loss of the postfrontal, postorbital, jugal, postparietal, supratemporal, and tabular) would allow for an extension of the muscles onto the dorsal surface of their flattened skull. In synapsids, it has been hypothesised that skull simplification occurred as an adaptation to strengthen the skull in response to biomechanical forces applied to the skull roof by jaw abductor muscles (Sidor 2001). An alternative argument was presented by Koyabu (2023) who posited that skull simplification in synapsids may be the by-product of increasing brain size over the evolution of the clade instead of a functional adaptation. Evidence supporting this hypothesis comes from the presence of genes such as Dlx5 and Lmx1b which are known to influence both brain expansion and suture closure in the skulls of mammals (Koyabu 2023).

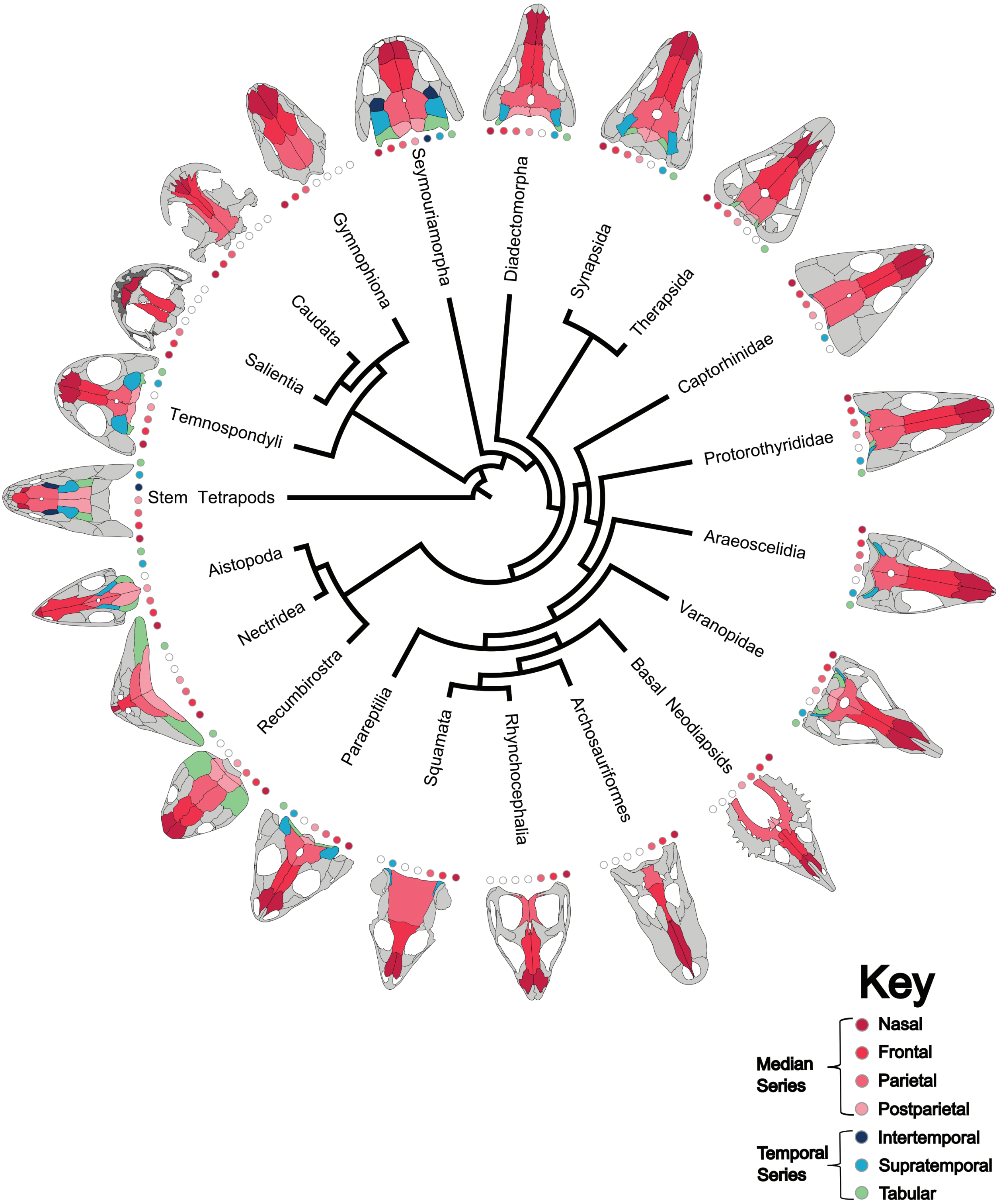


Figure 1. Summary of the changes in composition of the median and temporal series in tetrapods. For a more detailed overview of the presence/absence of median and temporal series elements see Fig. 2. (Stem tetrapod = *Eusthenopteron* (Carroll 1988); Temnospondyli = *Apateon* (Schoch and Milner 2014); Salientia = *Bombina* (Maglia and Púgener 1998); Caudata = *Cryptobranchus* (Elwood and Cundall 1994); Gymnophiona = *Ichthyophis* (Wilkinson et al. 2014); Seymouriamorpha = *Seymouria* (Berman et al. 2000); Diadectomorpha = *Tseajaia* (Berman et al. 1992); Synapsida = *Eothyris* (Reisz et al. 2009); Therapsida = *Suminia* (Rybczynski 2000); Captorhinidae = *Captorhinus* (Fox and Bowman 1966); Protorothyrididae = *Paleothyris* (Carroll 1969); Araeoscelidia = *Petrolacosaurus* (Reisz 1981); Varanopidae = *Mesenosaurus* (Reisz and Berman 2001); Basal Neodiapsida = *Weigeltisaurus* (Pritchard et al. 2021); Archosauriformes = *Alligator* (Jollie 1962); Rhynchocephalia = *Sphenodon* (Jones et al. 2009); Squamata = *Cordylus* (Evans 2008); Parareptilia = *Macroleter* (Tsuji 2006); Recumbirostra = *Eryodus* (Carroll and Gaskill 1978); Nectridea = *Diplocaulus* (Carroll et al. 1998); Aïstopoda = *Pseudophlegethontia* (Anderson 2003).

Miniaturisation is another developmental change linked to skull bone loss; this is the evolution of an adult body size so small that it surpasses a threshold at which dramatic changes in morphology, physiology, and ecology can occur (Hanken and Wake 1993; Yeh 2002; Pérez-Ben et al. 2018). Different explanations have been given to link extremely small body sizes to skull simplification. On the one hand, bone loss might occur as a by-product of ontogenetic truncation, which seems to be a frequent mechanism for the evolutionary reduction of body size, as miniaturised species typically resemble the juvenile stages of related non-miniaturised taxa (Hanken and Wake 1993). In this regard, miniaturised species lack bones that form late in the ontogeny of these larger species (Hanken and Wake 1993; Yeh 2002; Schoch and Rubidge 2005; Schoch 2013a; Scherz et al. 2019). Whereas skull simplification by ontogenetic truncation is related to the causes of miniaturisation, the small body size itself may impose developmental constraints that lead to bone loss (Yeh 2002; Pérez-Ben et al. 2018). As discussed above, it has been suggested that the minimum number of mesenchymal cells required to induce bone formation cannot be reached at extremely small body sizes, thus preventing bones from ossifying (Atchley and Hall 1991; Pérez-Ben et al. 2018).

Physical and functional constraints may also play a role. For example, certain structures, such as the eye, require a minimum size to be functional and are therefore proportionally much larger in small species. Consequently, the need to retain functionality in a sense organ might lead to major morphological rearrangements of the skull to accommodate the organ within a miniaturised structure. One instance of this is found in geckos, which are thought to have lost their postorbital and supratemporal because of the space taken up by their large eyes (Herrel et al. 2007). Together, all these proposed evolutionary drivers highlight the complexities of skull bone reduction and show that the evolutionary underpinnings of this trend might not be uniform among clades.

In addition to providing insight on the functional and developmental drivers of skull evolution, the simplification of the dermal skull roof has also been used in phylogenetic studies that address the relationships of early tetrapods. Many such studies have utilised the absence of specific cranial roof bones as 'loss characters' which have been central to ongoing discussions surrounding the origin of lissamphibians. Currently there are two main lines of thought: (1) the Temnospondyl Hypothesis (TH) which is favoured by most authors and states that lissamphibians form a monophyletic group within temnospondyls and are nested within Dissorophoidea, likely with Amphibamidae (Anderson 2007, 2008; Carroll 2007; Ruta and Coates 2007; Schoch et al. 2020) but Branchiosauridae have also been suggested as putative lissamphibian relatives (Milner 1993; Anderson 2007; Carroll 2007; Ruta and Coates 2007), and (2) the Lepospondyl Hypothesis (LH) which suggests that a monophyly is formed between lissamphibians and lepospondyls (Laurin 1998; Vallin and Laurin 2004; Marjanović and Laurin 2008, 2009; Laurin et al. 2022). There are some variants of the TH, Pardo et al. (2017a), for instance, hypothesised that caecilians are derived from stereospondyls, while frogs and salamanders are nested within dissorophoids. Previously, a third hypothesis had also been considered to explain lissamphibian origins, namely the Polyphyly Hypothesis, which placed frogs and salamanders with temnospondyls, and caecilians with lepospondyls (Carroll 2001, 2009; Anderson et al. 2008a; Lee and Anderson 2006); this has received very little attention, though, in more recent analyses.

The first step to unravelling the evolutionary factors that underlie the convergent evolution of bone loss is to identify any patterns of loss and regain. This presents a challenge, however, as determining whether or not a bone has been truly lost or has simply fused with others is often impossible, in particular when dealing with fossil forms. Establishing whether or not the loss of a specific bone is comparable across the phylogeny is, therefore, quite complicated. Another limitation is that the presence/absence of these skull bones are often used as characters in phylogenetic analyses based on morphological data. Consequently, mapping the presence/absence of these bones on phylogeny to study their evolution is somewhat circular. Nonetheless, quantifying patterns of loss and regain can still provide helpful insights into the comparable evolvability of certain bones, and whether convergent bone loss (even if by fusion) occurred in a modular manner (i.e. bones are lost together and not independently).

In light of this, we present the first reconstruction of the evolutionary history of bone loss in the tetrapod skull. We aim to set a framework for future discussions and to detect if there are distinct patterns of presence/absence, or loss/regain of bones that have not been recognised in previous studies due to more limited taxonomic samples or focus on specific groups.

Materials and methods

The skull morphology of 313 extinct and extant tetrapod taxa were examined. The material includes finned and limbed stem-tetrapods, as well as extant tetrapods (lissamphibians plus amniotes) and their closest extinct relatives (Figs 2, 3; Suppl. material 1). The species sampling was designed to represent the phylogenetic and morphological diversity within tetrapods. We have focused solely on bones in the median and temporal series in the dermatocranium for two reasons: (1) the dorsal bones of the dermatocranium are typically the best-preserved skull bones in the fossil record, and (2) the median and temporal series represent the most and least stable series of the dermatocranium, respectively. The median series is largely involved with protecting the brain and other sensory organs, it includes the nasal, frontal, parietal and postparietal (sometimes referred to as the interparietal (Koyabu et al. 2012)). The temporal series, on the other hand, is variably made of the intertemporal, supratemporal, and tabular. The supratemporal and tabular are associated with the otic region of the skull (Clack et al. 2003), and the tabular along with the postparietal act as attachment sites for muscles associated with the neck (Carstens 2023).

Two composite trees were constructed by hand in Mesquite (Maddison and Maddison 2021) which showed the relationships of all major stem and crown tetrapod groups with Lissamphibia either nested within Temnospondyli or Lepospondyli (Figs 2, 3; Suppl. materials 2, 3). While the phylogenetic position of several major clades is not well clarified, we chose to only consider the alternative hypotheses on the origin of lissamphibians (i.e. Temnospondyl and Lepospondyl Hypotheses) because: (1) the position of Lissamphibia radically affects the phylogenetic structure of early tetrapod relationships, and (2) as mentioned previously, the use of 'loss characters' to construct the Temnospondyl and Lepospondyl Hypothesis phylogenies impacts the interpretation of the loss of cranial bones.

The backbone of the trees was taken from the comprehensive and highly cited (e.g. Anderson et al. 2008b; Pyron 2011; Pardo et al. 2017b; Marjanović and Laurin 2019) strict consensus tree found by Ruta and Coates (2007), the stem tetrapods, Nectridea, and Aistopoda sections of the tree was left unchanged. Other portions of the tree, however, were altered. The microsaur topology was taken from MacDougall et al. (2021); the temnospondyl branch was replaced with trees recovered by Schoch (2013b) and Schoch (2022). The lissamphibian topology was taken from Jones et al. (2022), while the branch leading to the Reptiliomorpha was replaced by the tree from Ford and Benson (2020). For our purposes, the neodiapsid section of the Ford and Benson (2020) tree was not exhaustive enough as it only includes six taxa, all of which are extinct. To address this, the neodiapsid portion was replaced with that from Simoes et al. (2018). The position of Testudinata shown in the Simoes et al. (2018) tree, however, was altered so that it was a member of Archelosauria, as proposed by Crawford et al. (2015). The placement of Saurosphargidae was also updated from that shown in Simoes et al. (2018) to follow the position in Wang et al. (2022) which places them as sister to Sauropterygia. Within therapsids, the topology recovered by Huttenlocker et al. (2021) was used as a backbone, while the topology from Fraser-King et al. (2019) was used for Biarmosuchia, Anomodontia, Gorgonopsia, and Dinocephalia, and the topologies from Huttenlocker (2009) and Wallace et al. (2019) were used for Therocephalia and Cynodontia, respectively.

The trees were later time calibrated in R using the 'timePaleoPhy' function in the 'paleotree' package (Bapst 2012), with 'randres' set to TRUE to allow polytomies to be randomly resolved and using the 'minMax' date treatment. 'minMax' was chosen over other treatments such as 'firstLast' because it incorporates uncertainty by randomly assigning an age to a species within the provided time data (Bapst and Wagner 2022). This is often necessary when dealing with the vertebrate fossil record as it is rarely possible to provide precise first and last appearance dates, especially given that so many of the clades in the composite tree are poorly sampled. The minimum and maximum ages of the first appearance datum (FADs) for each tip were provided for the time calibration. The FAD ages were taken from the age of the rock formations that the oldest known specimen of each tip or clade was found in. There were four exceptions where it was not possible to ascertain the age of a tip based on geology, in these cases ages were taken from palynological analyses (Clack et al. 2019), estimations from molecular clock methods (van Tuinen and Dyke 2004), time calibrated phylogenetic analyses (Joyce et al. 2013), and biogeographically calibrated phylogenies (Leavitt et al. 2007) (see Suppl. material 4).

Presence/absence data for the bones in the temporal and median series in the skull roof were gathered for each of the 313 tips in the composite tree and scored as a binary trait. Where possible, presence/absence data was gathered from first hand examination of specimens, but this was not feasible in the majority of cases, and so data was largely taken from the literature (see Suppl. material 1). A bone element was defined based on its sutures separating it from its neighbours, therefore, any reported embryonic bones were marked as absent, except for the homology hypothesis for Mammaliaformes mentioned below. In instances where there are mixed reports on the presence/absence of a given bone, such as the intertemporal in *Greererpeton* and the temnospondyl *Micromelerpeton*, the bone was coded as absent as its presence is rare and its identity uncertain. Birds and frogs, which have frontoparietals (although see Arnaout et al. (2022) as there is still some debate on the homology of the frontal in birds), were coded as having both the frontal and parietal.

To ensure that uncertainties on bone homology were taken into account, several alternative hypotheses were collated from the literature, and a separate dataset was constructed for each with alternative coding for the relevant taxa. These different hypotheses of homology are shown in Table 2 and were based on: (1) the temporal series of the Early Jurassic stem-caecilian, *Eocaecilia*, which has a single bone that is presumed to be either the supratemporal or tabular (Jenkins et al. 2007); (2) the single interparietal in mammals, whose embryological data suggests may be composed of paired postparietals fused to the tabulars, instead of just the paired postparietals (Koyabu et al. 2012); (3) the median series in extant birds, which is composed of two bones that are either the frontal and parietal, or the frontoparietal and postparietal (Maddin et al. 2016; Arnaout et al. 2022); (4) the temporal series of the Permian nectridean, *Diplocaulus*, which is composed of a single bone that is either the supratemporal or tabular (Olson et al. 1951; Carroll et al. 1998), and (5) the uncertainty in the presence of a supratemporal in the stem testudines *Odontochelys* and *Proganochelys* (Gaffney and Meeker 1983; Li et al. 2008; Scheyer et al. 2022).

Table 1. Presence/Absence data in Hypothesis A of tips associated with alternative homology hypotheses.

Affected Tips	Presence/Absence Data in Hypothesis A
Eocaecilia micropodia	supratemporal = 0; tabular = 1
Mammaliaformes	tabular = 0
Gallus domesticus	postparietal = 1
Diplocaulus magnicornis	supratemporal = 0; tabular = 1
Proganochelys quenstedtii	supratemporal = 1
Odontochelys semitestacea	supratemporal = 1

Table 2. Alternative analyses based on uncertainties in homology.

Hypothesis	Affected Tips	Changes in Presence/ Absence Data
b	*Eocaecilia micropodia*	supratemporal = 1; tabular = 0
c	Mammaliaformes	tabular = 1
d	*Gallus domesticus*	postparietal = 0
e	*Diplocaulus magnicornis*	supratemporal = 1; tabular = 0
f	*Proganochelys quenstedtii*	supratemporal = 0
g	*Odontochelys semitestacea*	supratemporal = 0
h	*Proganochelys quenstedtii* and *Odontochelys semitestacea*	supratemporal = 0

Maximum likelihood ancestral state reconstructions were conducted for each bone, except for the nasals, frontals, and parietals, as these were found to be present in all taxa. Analyses were performed on the different datasets considering the different homology hypotheses, and alternatively under the temnospondyl and lepospondyl phylogenetic hypotheses for the origin of Lissamphibia. The reconstructions were performed in R using the ‘ace’ function from the ‘ape’ package (Paradis and Schliep 2019). The weights and AICs (Akaike Information Criterion) from ancestral state reconstructions using the ER (Equal Rates, i.e., all possible character state transitions occur at the same rate) and ARD (All Rates Different, i.e., all possible character state transitions can occur at a different rate) models were compared for each bone, and it was determined that the ARD model was the most appropriate to use for all the bones (see Suppl. material 5). Plots showing the ancestral state reconstructions with the ARD model for each bone under Homology Hypothesis A in both the Temnospondyl and Lepospondyl Hypothesis can be found in the supplementary, along with the data and R script used (Suppl. materials 6–23). To reconstruct the ancestral states in nodes (i.e. presence or absence of the bones), the ratio of the likelihoods of two estimates is used to gauge the level of support for the maximum likelihood estimate. A likelihood ratio of 7.4:1 is commonly employed as a rough minimum threshold to determine the likely state of a node (Schulter et al. 1997; Rüber et al. 2004; Dalerum 2007). With this threshold, gains and losses of bones were identified by manually tracing character changes in the branches. At each node the presence % likelihood returned from the analysis was multiplied by 7.4, if this value was less than the absence % likelihood at that node, then the bone in question was deemed to be absent. If a transition was thought to have occurred at a node (e.g. from present to absent), then a second calculation was undertaken to determine if the character change was statistically significant or not. A transition threshold was calculated by dividing the absence % likelihood by 7.4, if this value was equal to or greater than the presence % likelihood then the transition from present to absent was statistically significant.

Results

Pattern of bone loss

Our analyses indicate that the intertemporal is the first bone to be lost; in stem-tetrapods it is lost multiple times, for instance in *Acanthostega*, *Ichthyostega*, *Ossinodus*, and at the node leading to Colosteidae, adelospondyls, and *Acherontiscus* (Figs 2, 3A). Within the lissamphibian stem-group (temnospondyls), the intertemporal bone is lost convergently numerous times and is only present in basal temnospondyls such as Edopoidea and most Dvinosauria (Figs 2, 3A). Following the intertemporal, the supratemporal is the next bone that is lost; once within stem-tetrapods at the node leading to the adelospondylids, and once at the lissamphibian node (Figs 2, 3A). After the supratemporal is lost, the tabular and/or postparietal can be lost. These bones are both lost twice within Lissamphibia, once in Gymnophiona (caecilians), and once at the Batrachia node. In Batrachia, the supratemporal is surprisingly regained in the karaurid stem-salamanders *Karaurus*, *Marmorerpeton*, and *Kokartus* (Figs 2, 3A). In Gymnophiona, the exact position of the loss of the tabular and postparietal is uncertain as only a partial jaw of the stem-caecilian *Rubricaecilia* has been described (Evans and Sigogneau-Russell 2001). As the stem-caecilian *Eocaecilia* retains the tabular and postparietal, the loss of these bones either occurs at the node leading to *Rubricaecilia*, *Epicrionops*, and *Ichthyophis* (Figs 2, 3A), or the node leading to *Ichthyophis* and *Epicrionips* (Suppl. material 24). It is also possible that the tabular and postparietal are lost at the lissamphibian node and are regained in *Eocaecillia* (Suppl. material 24). In Homology Hypothesis B, where *Eocaecilia* is coded as having a supratemporal and no tabular, the presence/absence of the supratemporal is ambiguous at the node leading to *Rubricaecilia*, *Epicrionops*, and *Ichthyophis*. At the node leading to *Epicrionops*, and *Ichthyophis* the supratemporal is absent. The state of the tabular, on the other hand, is ambiguous at node Gymnophiona, and is absent at the node leading to *Rubricaecilia*, *Epicrionops*, and *Ichthyophis*.

As in stem-tetrapods and temnospondyls, the intertemporal is the first bone that is lost in the stem-amniotes, followed by the supratemporal (Figs 2, 3B). The intertemporal is lost once, at the base of the tree, the supratemporal is then either lost at the base of

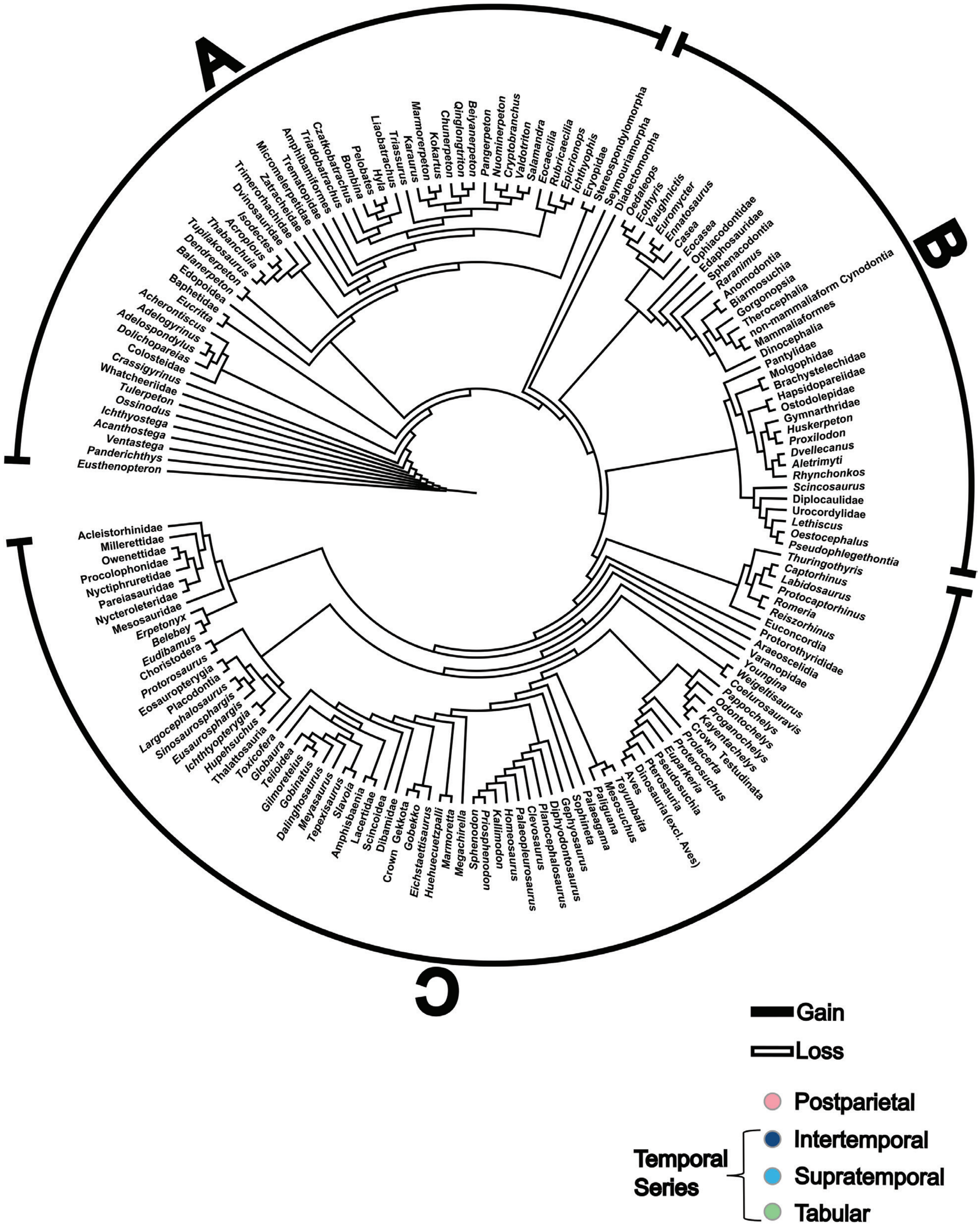
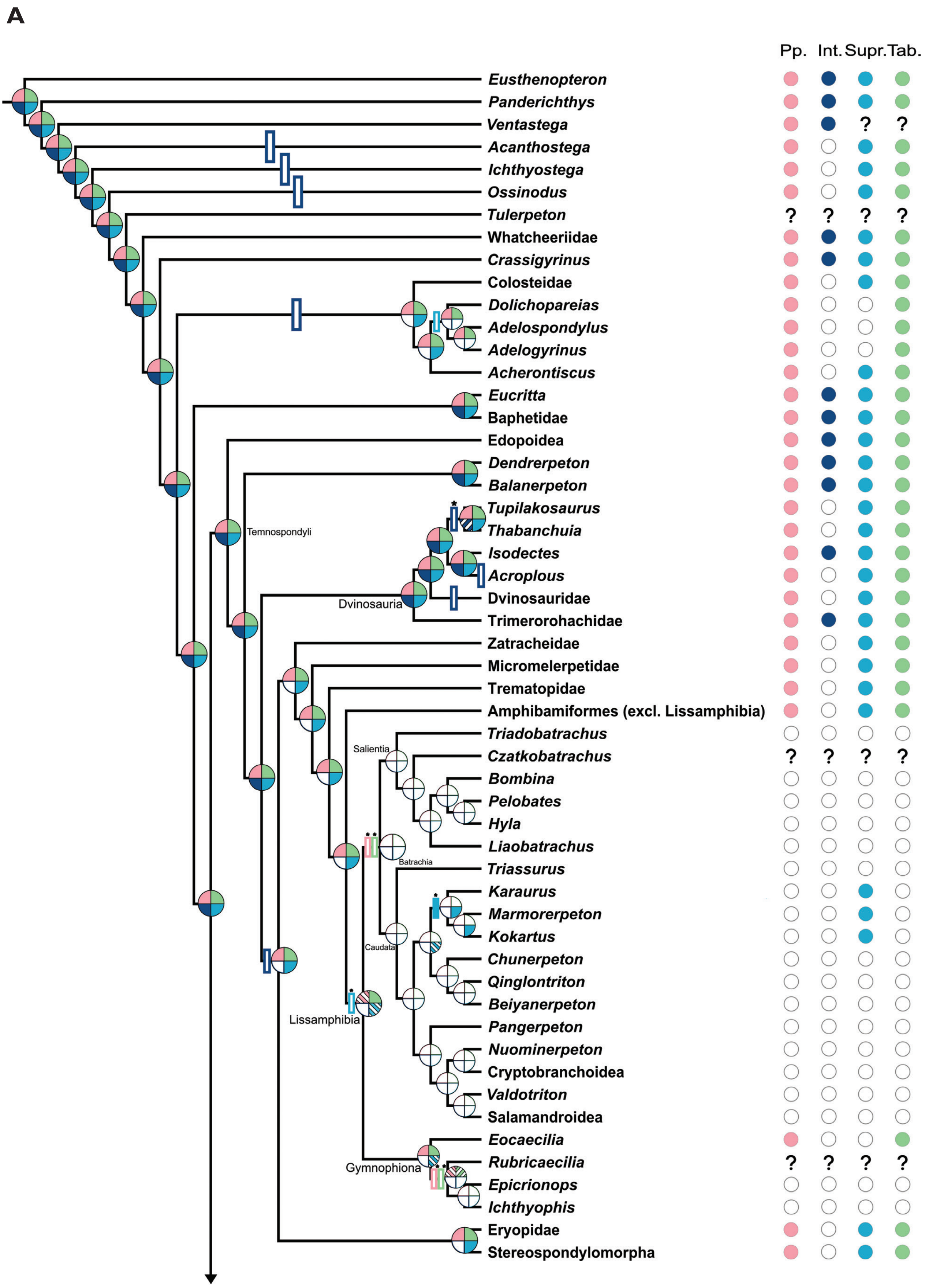


Figure 2. Maximum likelihood ancestral state reconstruction of the presence/absence of the postparietal, intertemporal, supratemporal, and tabular (see key for colour associations) under Temnospondyl Hypothesis a. At the nodes, a filled in quadrant = presence; empty quadrant = absence; striped quadrant = presence/absence is ambiguous. On the branches, empty rectangle = loss of element; filled rectangle = gain of element. At the branch tips, filled in circle = presence of element; empty circle = absence of element; half-filled circle = mixed presence/absence of element. Tree A = Tetrapodomorpha, Temnospondyli, and Lissamphibia. Tree B = Seymouriamorpha, Diadectomorpha, Synapsida, and Lepospondyli. Tree C = Captorhinidae, Protorthyrididae, Araeoscelidia, Varanopidae, Neodiapsida, and Parareptilia.



	Pp.	Int.	Supr.	Tab.
Eusthenopteron	●	●	●	●
Panderichthys	●	●	●	●
Ventastega	●	●	?	?
Acanthostega	●	○	●	●
Ichthyostega	●	○	●	●
Ossinodus	●	○	●	●
Tulerpeton	?	?	?	?
Whatcheeriidae	●	●	●	●
Crassigyrinus	●	●	●	●
Colosteidae	●	○	●	●
Dolichopareias	●	○	○	●
Adelospondylus	●	○	○	●
Adelogyrinus	●	○	○	●
Acherontiscus	●	○	●	●
Eucritta	●	●	●	●
Baphetidae	●	●	●	●
Edopoidea	●	●	●	●
Dendrerpeton	●	●	●	●
Balanerpeton	●	●	●	●
Tupilakosaurus	●	○	●	●
Thabanchuia	●	○	●	●
Isodectes	●	●	●	●
Acroplous	●	○	●	●
Dvinosauridae	●	○	●	●
Trimerorohachidae	●	●	●	●
Zatracheidae	●	○	●	●
Micromelerpetidae	●	○	●	●
Trematopidae	●	○	●	●
Amphibamiformes (excl. Lissamphibia)	●	○	●	●
Triadobatrachus	○	○	○	○
Czatkobatrachus	?	?	?	?
Bombina	○	○	○	○
Pelobates	○	○	○	○
Hyla	○	○	○	○
Liaobatrachus	○	○	○	○
Triassurus	○	○	○	○
Karaurus	○	○	●	○
Marmorerpeton	○	○	●	○
Kokartus	○	○	●	○
Chunerpeton	○	○	○	○
Qinglontriton	○	○	○	○
Beiyanerpeton	○	○	○	○
Pangerpeton	○	○	○	○
Nuominerpeton	○	○	○	○
Cryptobranchoidea	○	○	○	○
Valdotriton	○	○	○	○
Salamandroidea	○	○	○	○
Eocaecilia	●	○	○	●
Rubricaecilia	?	?	?	?
Epicrionops	○	○	○	○
Ichthyophis	○	○	○	○
Eryopidae	●	○	●	●
Stereospondylomorpha	●	○	●	●

Figure 2. Continued.

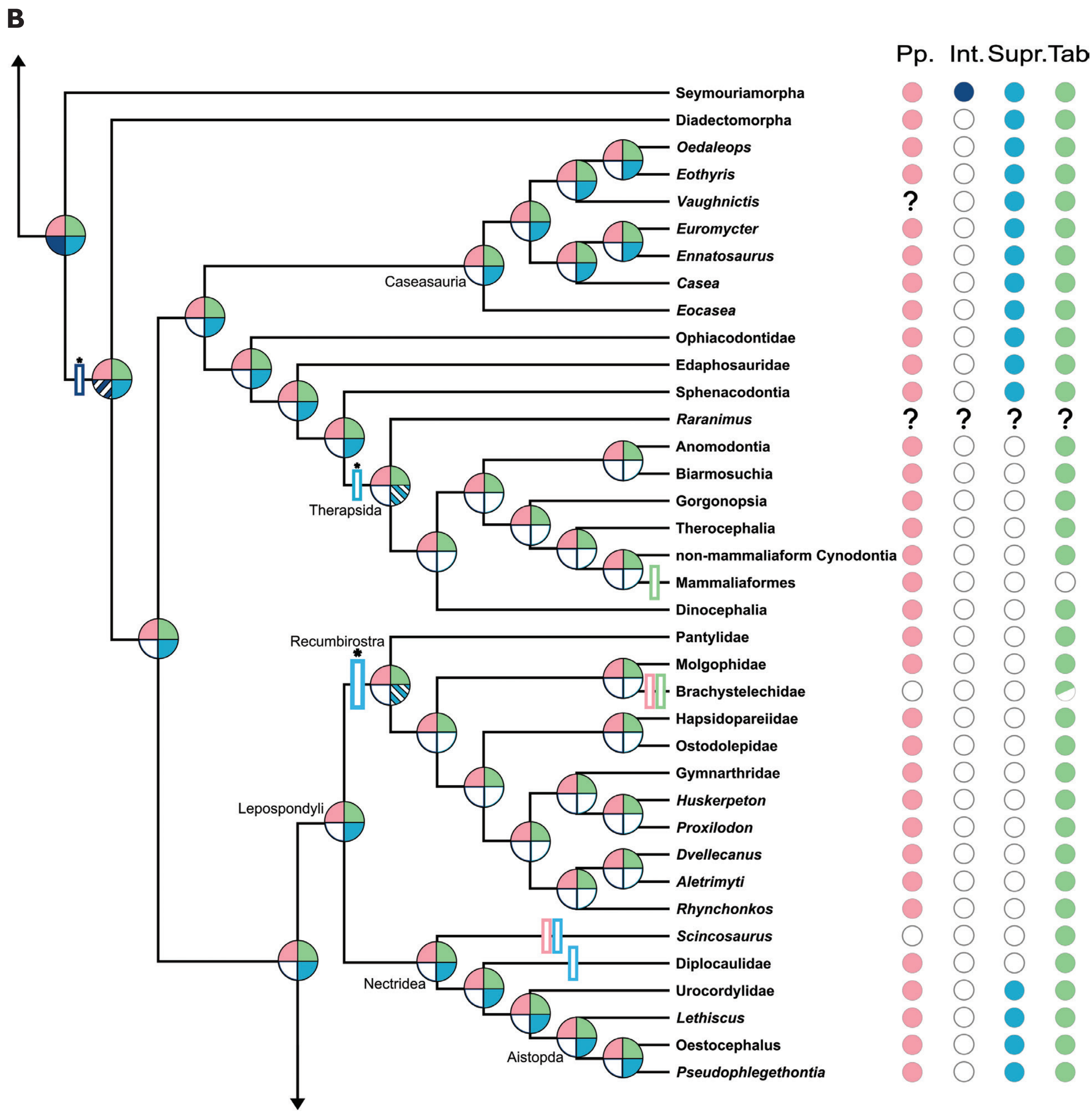


Figure 2. Continued.

Therapsida (Suppl. material 24) or within Therapsida (Figs 2, 3B). The uncertainty again is due to a lack of data, this time in *Raranimus* which is considered to be the basal-most therapsid, and is only known from a partial snout (Liu et al. 2009; Huttenlocker et al. 2021). With the exception of Mammaliaformes which lose their tabular, all other therapsids maintain this temporal series bone (Figs 2, 3B). The tabular is present at all nodes in Therapsida, irrespective of whether or not it is coded as present or absent in Mammaliaformes (Homology Hypothesis C). There is a little more variety in the composition of the temporal series in lepospondyls. Here, the intertemporal is absent, the supratemporal and postparietal are lost multiple times, and the tabular is present in all taxa besides some brachystelechids (namely *Quasicaecilia*, *Diabloroter*, and *Carrolla*; Suppl. material 1). The supratemporal is lost in the nectridean *Scincosaurus*, and at the node Diplocaulidae. It is also potentially lost at the node leading to Recumbirostra. The postparietal is lost with the tabular in Brachystelechidae, and with the supratemporal in *Scincosaurus*, which marks the only point at which the postparietal is not lost on its own, or with the tabular (Figs 2, 3B). The coding of *Diplocaulus* as having a supratemporal and no tabular (Homology Hypothesis E) has no effect on the results, as the supratemporal is still lost at node Diplocaulidae and the tabular remains present.

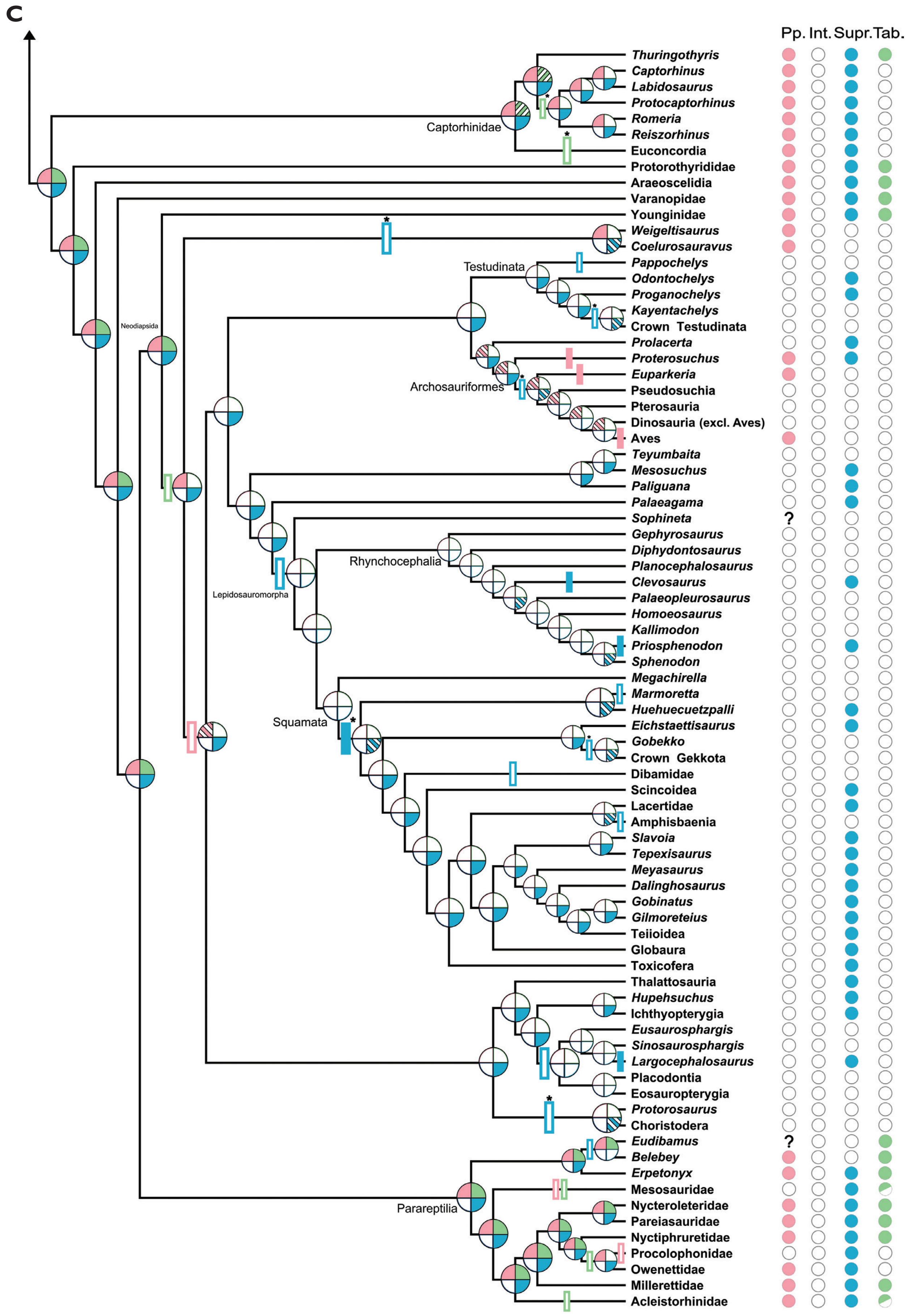


Figure 2. Continued.

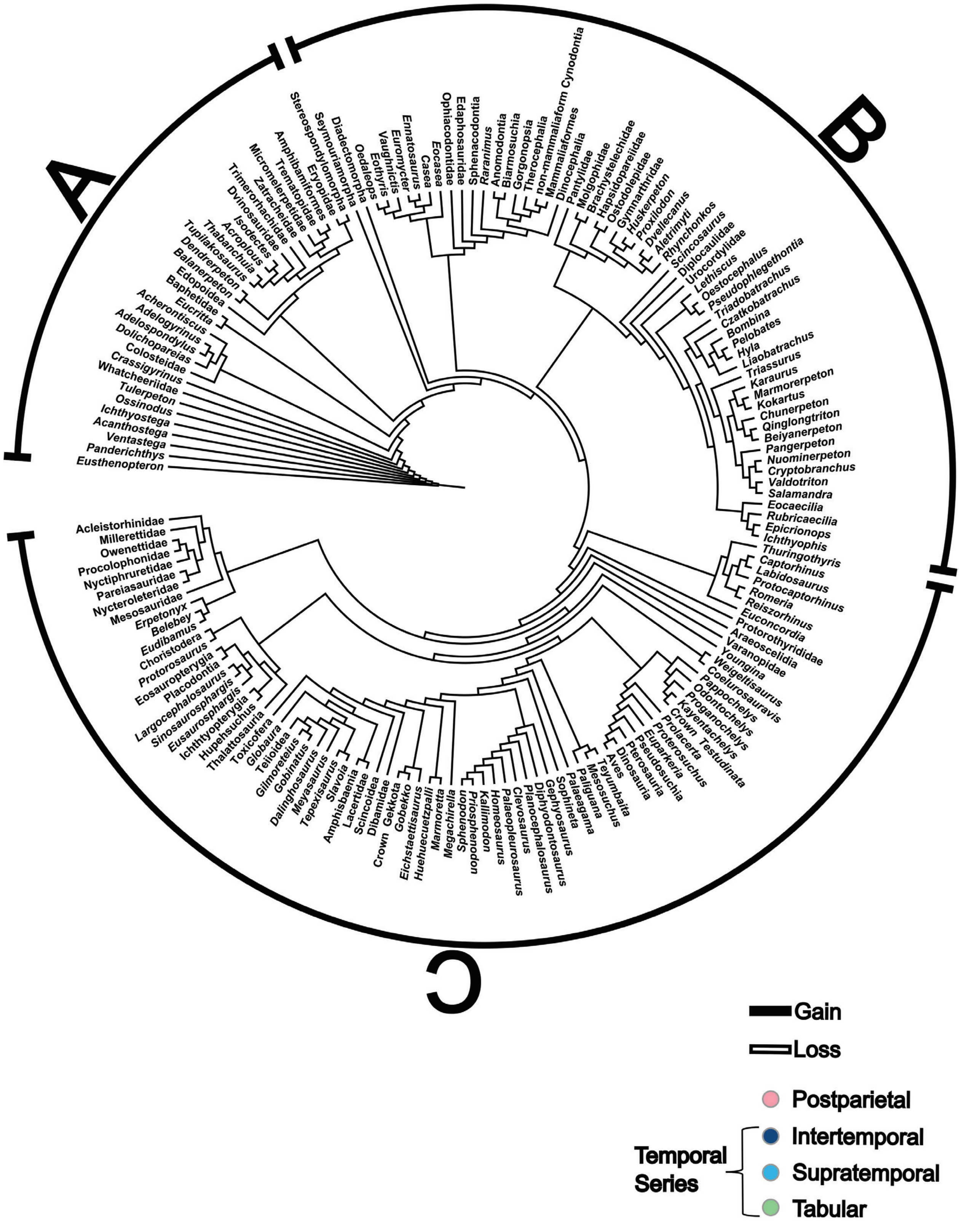


Figure 3. Maximum likelihood ancestral state reconstruction of the presence/absence of the postparietal, intertemporal, supratemporal, and tabular (see key for colour associations) under Lepospondyl Hypothesis a. At the nodes, a filled in quadrant = presence; empty quadrant = absence; striped quadrant = presence/absence is ambiguous. On the branches, empty rectangle = loss of element; filled rectangle = gain of element. At the branch tips, filled in circle = presence of element; empty circle = absence of element; half-filled circle = mixed presence/absence of element. Tree A = Tetrapodomorpha and Temnospondyli. Tree B = Seymouriamorpha, Diadectomorpha, Synapsida, Lepospondyli, and Lissamphibia. Tree C = Captorhinidae, Protorthyrididae, Araeoscelidia, Varanopidae, Neodiapsida, and Parareptilia.

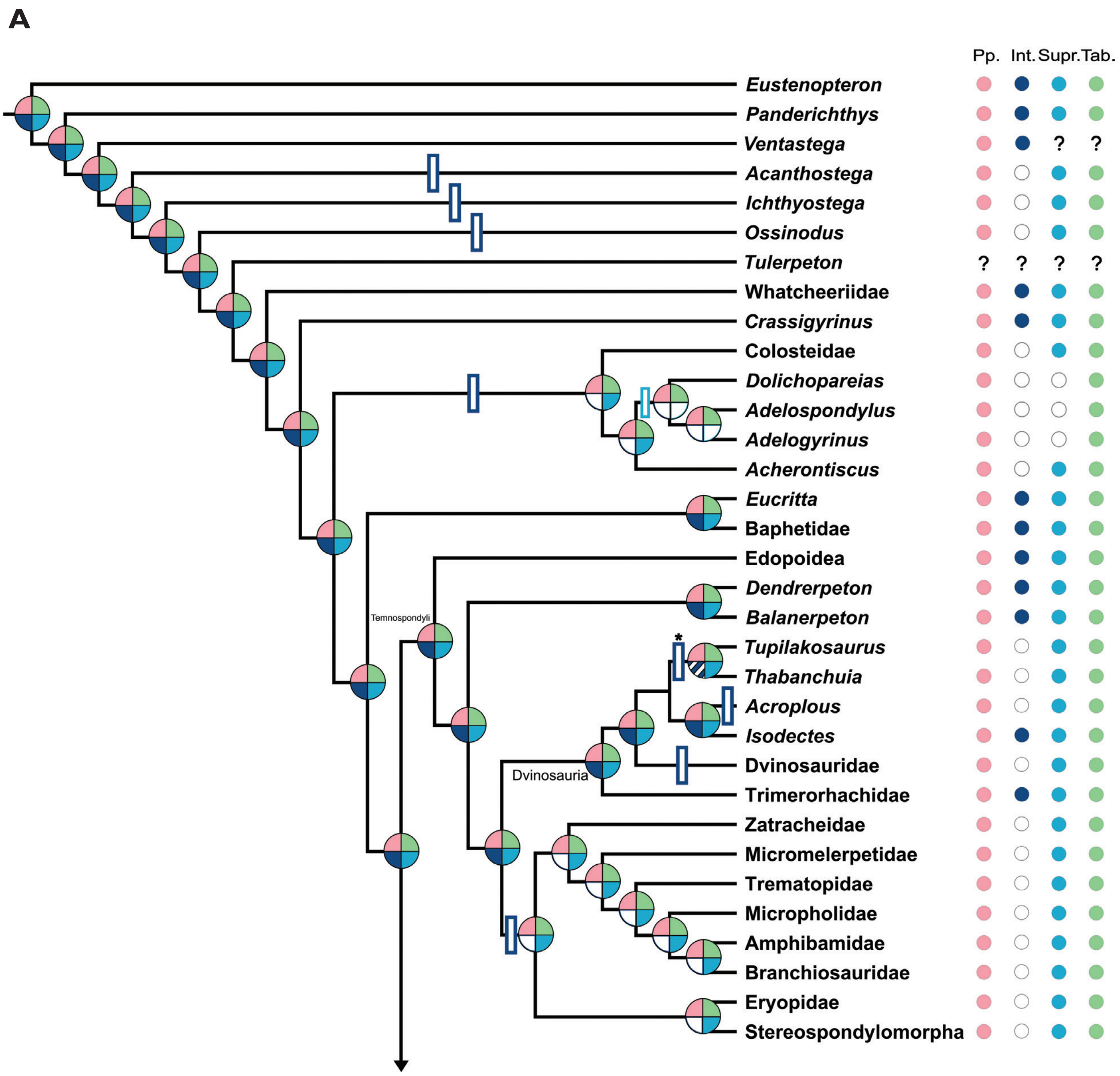


Figure 3. Continued.

In reptiles the pattern of bone loss becomes more heterogenous, especially in Eureptilia (the "true reptiles" and sister group to Parareptilia). Unlike in all the other groups, in Eureptilia the tabular is the second bone to be lost after the intertemporal, followed by the postparietal and then the supratemporal. In Captorhinidae the supratemporal is maintained, while the tabular is either lost twice (Figs 2, 3C), or once at the base of Captorhinidae and is regained in *Thuringothyris* (Suppl. material 24). In neodiapsids the tabular is lost at the base of the tree, shortly followed by the postparietal, although the supratemporal is lost in Weigeltisauridae while the postparietal is retained. The postparietal is regained convergently three times in archosauriformes in *Proterosuchus*, *Euparkeria*, and in Aves. Coding the postparietal as absent in Aves (Homology Hypothesis D) has little effect as the presence/absence of the postparietal remains ambiguous at all nodes in Archosauriformes. The supratemporal is lost a total of 12 times in Neodiapsida, namely at node Weigeltisauridae, node *Kayentachelys*-Crown Testudinata, node Choristodera-*Proterosaurus*, in Archosauriformes, node Lepidosauromorpha, and node Saurosphargidae-Placodontia-Eosauropterygia. Given the uncertainty in the presence of the supratemporal in the stem testudines *Odontochelys* and *Proganochelys* (Gaffney and Meeker 1983; Li et al. 2008; Scheyer et al. 2022), it is possible that the supratemporal is lost up to three times in Testudinata, or is even regained. In Hypothesis A the supratemporal is coded as present for both *Odontochelys* and *Proganochelys*. With this configuration, the supratemporal is present at all testudine nodes besides that leading to *Kayentachelys* and Crown Testudinata, where it is ambiguous. The supratemporal is therefore lost twice, once in *Pappochelys*, and once at the *Kayentachelys*-Crown Testudinata node. In Homology Hypothesis F the supratemporal is coded as present in *Odontochelys* and absent in *Proganochelys*, here the supratemporal is lost convergently three times,

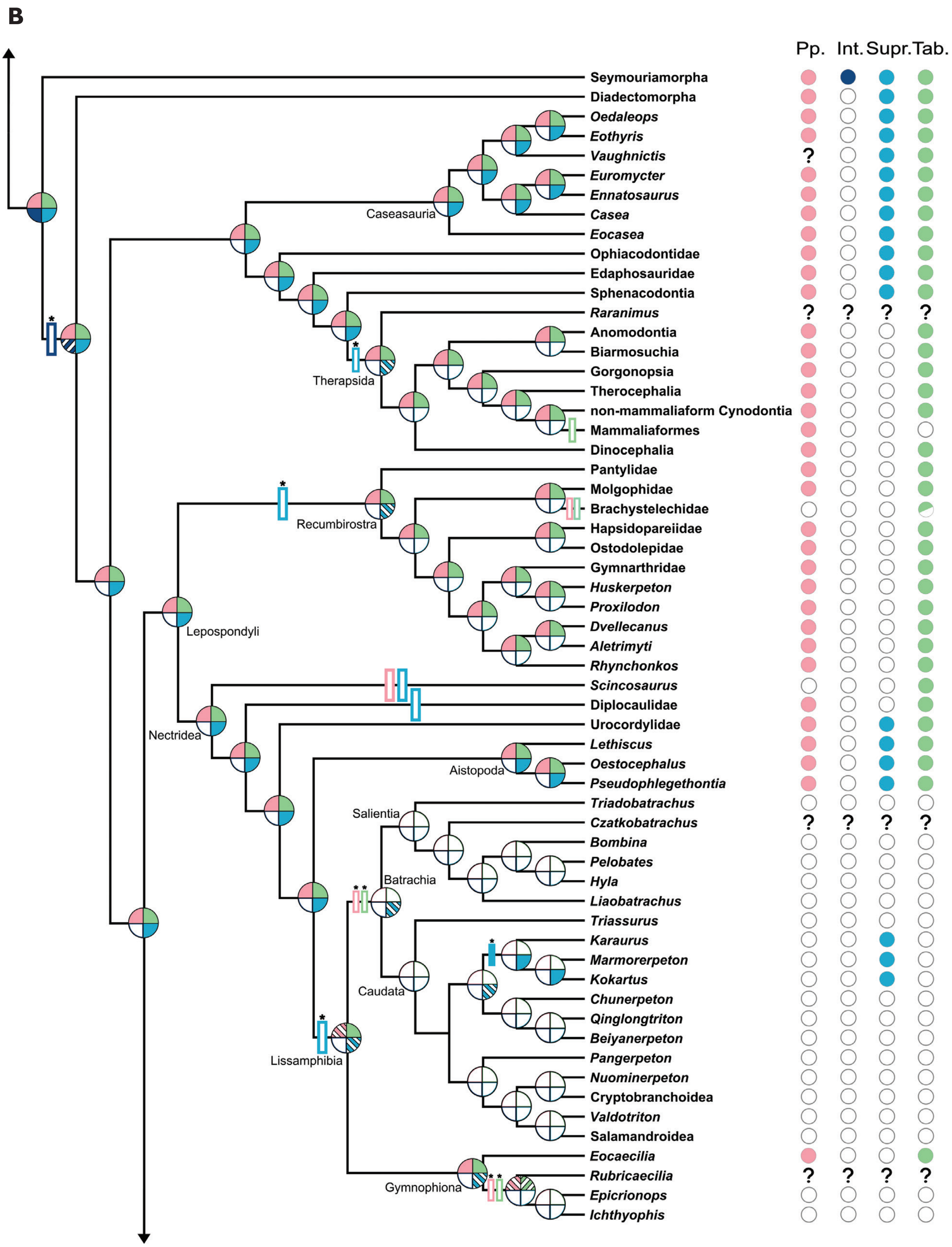


Figure 3. Continued.

once in *Pappochelys*, once in *Proganochelys*, and once at the *Kayentachelys*-Crown Testudinata node. In Homology Hypothesis G the supratemporal is coded as absent in *Odontochelys* and present in *Proganochelys*, similarly to Homology Hypothesis F, the supratemporal is also lost three individual times under this scenario, in *Pappochelys*, at the node leading to *Odontochelys*, *Proganochelys*, *Kayentachelys*, and Crown Testudinata, and at the *Kayentachelys*-Crown Testudinata node. However, the supratemporal is then also regained in

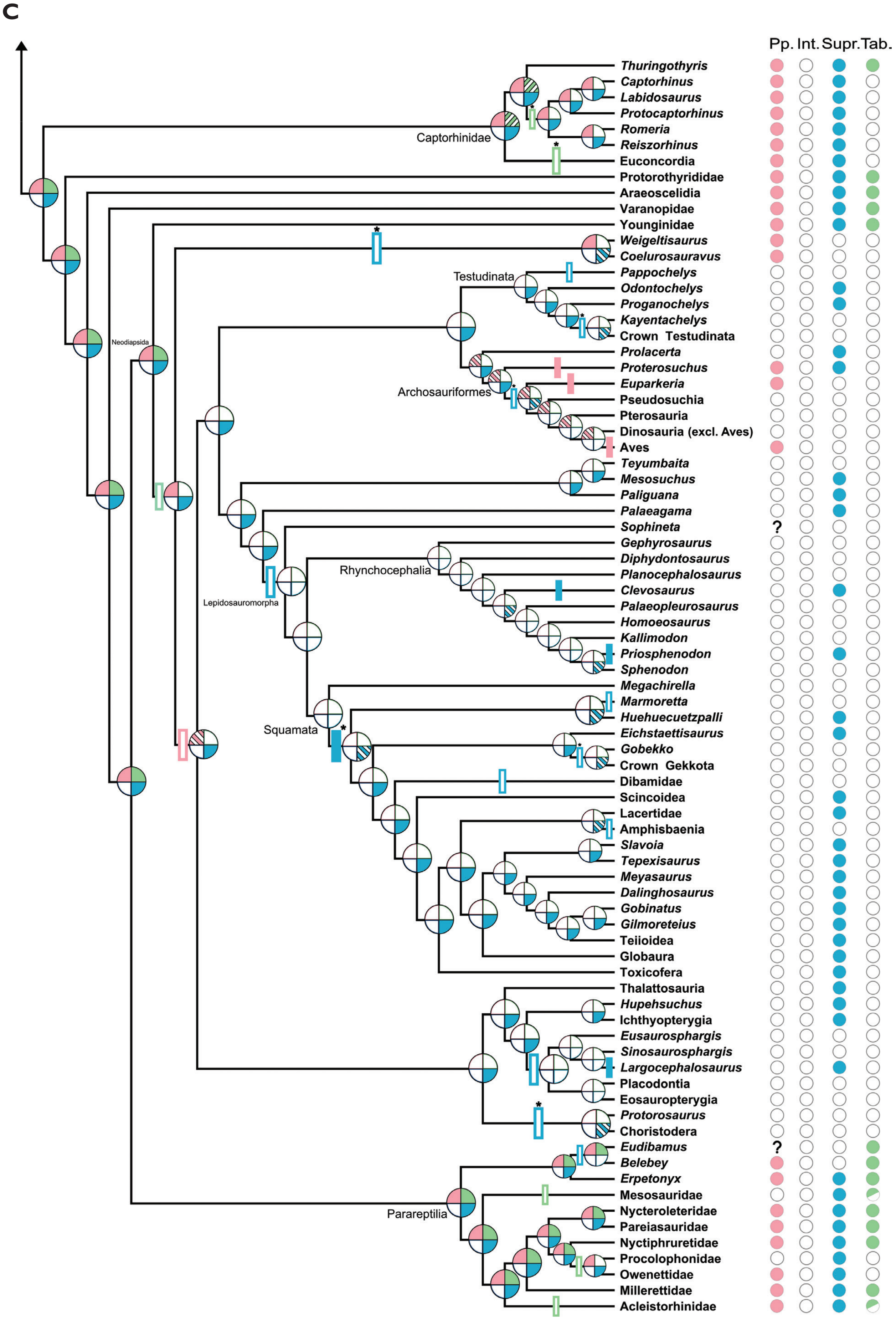


Figure 3. Continued.

Proganochelys. In Homology Hypothesis H, the supratemporal is coded as absent in both *Odontochelys* and *Proganochelys*, in this case the supratemporal is lost once at the Testudinata node. In Squamata the supratemporal is lost four times after being regained at the node leading to Squamata excluding *Megachirella*. The supratemporal is also regained twice within Rhynchocephalia (Figs 2, 3C).

In Parareptilia the pattern of loss observed in stem-tetrapods, temnospondyls, therapsids, and lepospondyls, is only seen in the bolosaurids *Eudibamus* and *Belebey* which lose the supratemporal while retaining the postparietal and tabular (the intertemporal having been lost further down the tree in the stem-amniotes). However, in other parareptiles the postparietal is the second bone to be lost, and not the supratemporal, as is the case in Mesosauridae where the supratemporal is retained, but the postparietal is lost in both *Stereosternum* and *Mesosaurus*, while the tabular is only lost in *Stereosternum* (Suppl. material 1). In Procolophonidae, Owenettidae, and some acleistorhinids (e.g. *Colobomycter*), however, the tabular is the second bone to be lost. In Procolophonidae the postparietal is also lost (Figs 2, 3C).

Placing Lissamphibia with lepospondyls instead of temnospondyls has only a minor effect on where the losses occur along the tree. Both hypotheses have the same number of losses and regains: the intertemporal is lost 9 times, the supratemporal is lost 18 times and regained 5 times, the tabular is lost 9–10 times and possibly regained once, and the postparietal is lost 7 times and regained 3 times. The main difference between the two hypotheses is that temnospondyls only lose the intertemporal and retain the rest of their temporal series and all of their median series elements as these are all lost in lissamphibians. A minor difference is that the presence/absence of the supratemporal at node Batrachia is ambiguous in the Lepospondyl Hypothesis, while it is absent in the Temnospondyl Hypothesis.

Discussion

Pattern of bone loss

Four general principles of loss of the temporal and median series can be gleaned from the results detailed above: (1) the intertemporal is always the first bone to be lost; (2) in general, the supratemporal is the second element to be lost (except in Sauropsida), when this is not the case (i.e. when the tabular is lost before the supratemporal), the supratemporal is largely retained and if lost may be regained; (3) when the supratemporal is the second bone to be lost, the postparietal and tabular are often, but not always, lost together; and (4) the presence/absence of

Table 3. Composition of median and temporal series in groups with reported miniaturisation.

Clade	Frontal	Parietal	Postparietal	Intertemporal	Supratemporal	Tabular
Amphibamidae	1	1	1	0	1	1
Lissamphibia	1	1	1	0	0	0
Mammaliaformes	1	1	1	0	0	0
Squamata	1	1	0	0	1	0
Aves	1	1	0	0	0	0
Recumbirostra	1	1	1	0	0	1
Phlegethontia	1	1	1	0	1	1

Table 4. Composition of median and temporal series in groups associated with terrestrial, aquatic, and semi-aquatic ecologies.

Clade	Frontal	Parietal	Postparietal	Intertemporal	Supratemporal	Tabular
Terrestrial						
Mammaliaformes	1	1	1	0	0	1
Parareptilia	1	1	1	0	1	1
Aistopoda	1	1	1	0	1	1
Lepidosauria	1	1	0	0	0	0
Gorgonopsia	1	1	1	0	0	1
Aquatic						
Clade	**Frontal**	**Parietal**	**Postparietal**	**Intertemporal**	**Supratemporal**	**Tabular**
Diplocaulidae	1	1	1	0	0	1
Dvinosauria	1	1	1	1	1	1
Discosauriscus	1	1	1	1	1	1
Branchiosauridae	1	1	1	0	1	1
Acanthostegidae	1	1	1	0	1	1
Semi-Aquatic						
Clade	**Frontal**	**Parietal**	**Postparietal**	**Intertemporal**	**Supratemporal**	**Tabular**
Crocodylia	1	1	0	0	1	0
Testudinata	1	1	0	0	1*	0
Batrachia	1	1	0	0	0	0

* note the ambiguity in the presence of the supratemporal in stem testudines (Scheyer et al. 2022).

the tabular is not dictated by the presence/absence of the postparietal and vice versa.

The variability we observed in the sequential bone loss in the temporal series across tetrapod phylogeny would indicate that these bones did not form an evolutionary module, and therefore the developmental pathways that control the presence/absence of the individual temporal series bones were not strongly integrated. However, this cannot be confirmed until further work is done to understand the mechanisms of loss undergone by individual bones across the skull, and until we have a clearer consensus on what constitutes bone loss with regards to skull simplification (see below for further discussion). It is also worth noting that the variability in the sequential loss of the supratemporal is restricted to Sauropsida (Eureptilia and Parareptilia, Figs 2, 3C), the group where the diapsid skull morphology appears.

Interestingly, the order in which the temporal series bones are lost does not correspond with the order in which they ossify during development as would be expected. In both the skulls and limbs of lissamphibians, it has been shown that bones are typically lost in reverse order of development, i.e. the last bones to ossify in the sequence are usually the first to be lost (Alberch and Gale 1985; Yeh 2002; Schoch 2014). In fossil tetrapods, the pattern of ossification has mainly been studied in temnospondyl species, in particular in the branchiosaurid *Apateon*, and the stereospondylomorph *Sclerocephalus* (Schoch 1992, 2004; Werneburg et al. 2023; Schoch and Witzmann 2024). These studies show that the ossification of the median series starts with the frontal, followed by the parietal, postparietal, and then the nasal. The ossification sequence of the temporal series has only been described for the branchiosaurid *Apateon*. In this taxon, the supratemporal is the first bone to ossify, followed by the tabular. The tabular ossifies after all other median and temporal series elements. However, contrary to what one would expect given the sequence of ossification during ontogeny, our results show the tabular as often being the last element to be lost, and never the first. This suggests that the pattern of simplification is not driven by a simple heterochronic truncation of the ontogenetic trajectory, but that more complex underlying factors and constraints affect the evolution of skull simplification.

Among the bones analysed here, the supratemporal was shown to be the most evolvable as it was lost and regained the most often (lost 18 times and regained 5 times). In terms of independent losses, the tabular follows suit with a total of 9–10 losses, then the intertemporal with 9 losses, and the postparietal with 7 losses. The postparietal, however, was regained 2–3 times depending on if Aves are coded with a present postparietal or not. The tabular may have been regained once, depending on how the loss of the tabular in Captorhinidae is interpreted (i.e. is it lost twice (in *Euconcordia* and the node leading to Captorhinidae excluding *Euconcordia* and *Thuringothyris*), or is it lost once at the base of Captorhinidae and regained in *Thuringothyris*). In contrast to these elements, the nasal, frontal and parietal of the median series occur at every tip in the tree, suggesting that these were the most stable bones investigated. Neither the relative stability of the median and temporal series bones, nor the order in which these elements are ossified during ontogeny shows a simple correlation with the observed pattern of loss in tetrapodomorphs, again highlighting that more complex evolutionary drivers are at play in the simplification of the skull.

Phylogenetic insights and future directions of study

While the composition of the temporal series can be used to some extent to predict the relative position of groups (e.g. the intertemporal is only present in more basal clades, while the tabular is typically absent in the most derived clades), the loss or regain of the bones reported here are too variable to be useful as phylogenetic characters. This is in large part due to our current understanding of homology in the dermatocranium, and a lack of consensus on what ‘true’ bone loss involves. To date, skull simplification has only been quantified based on the number of individual bone elements defined by clear sutures in adult specimens, and not on embryological data. However, given the difficulties in assessing loss homology in the fossil record, in addition to the prevalence of skull simplification and the variability in the pattern of loss in different tetrapod groups, it is critical that future embryological studies investigate the methods of loss affecting individual bones across the tetrapod phylogeny.

This work has already begun in mammals, as demonstrated by Koyabu et al. (2012) who showed that the mammalian tabular fuses to the postparietal to form the composite interparietal early in development. A possible embryonic tabular was also identified in the archosauriform *Euparkeria capensis* which would have likely later become part of the interparietal (Sookias et al. 2020). A discrete supratemporal was identified in a hatchling of *Sphenodon punctatus* by Rieppel (1992) who concluded that the bone would have later fused with either the parietal or squamosal. In anurans it was proposed that the tabular fuses with the squamosal, and the supratemporal fuses with the frontoparietal (Alcalde and Basso 2013), whereas in Caudata it has been suggested that the supratemporal fuses with the squamosal (Schoch 2014). In avians, a fate-mapping study conducted by Maddin et al. (2016) showed that the frontal and parietal may have fused together to form a frontoparietal, and that the element traditionally referred to as the parietal, is most likely the postparietal. However, a histological study on *Gallus domesticus* did not find evidence of a suture being present between the two ossification centres of Maddin et al.’s (2016) frontoparietal element, which may imply that this bone is in fact just a frontal and not a composite bone (Arnaout et al. 2022), or that two elements are mapped as individual units only early in cellular development, but in later phases of tissue development are not detectable as such anymore.

We would argue that loss by fusion is not 'true' bone loss as the ossification centres are still present. Instead, we agree with the definition of 'true' bone loss as used by Schoch (2014), which requires the ossification centres of the lost bone to have failed to form, often due to heterochronic processes truncating the developmental trajectory. With this in mind, it is necessary to reassess not only how we measure skull simplification, but also how composite bones are named, and how we define bone elements in the context of skull simplification. By not doing so, we run the risk of missing important complexities of skull simplification and potentially having an overly restricted view of the degree to which the skull has been simplified in tetrapod evolutionary history. To avoid this, it may be worthwhile for future studies to focus on re-evaluating tetrapod skull homology across the phylogeny, including fossil clades where possible, and providing revised definitions and new names for composite bones that are formed from fusions, as was done with the mammalian interparietal (Koyabu et al. 2012). This is particularly relevant for phylogenetic analyses, especially those that utilise 'loss characters' as is the case with the Temnospondyl and Lepospondyl Hypotheses for lissamphibian origins. In doing so it would be easier to capture the complexity of skull simplification and perform more detailed versions of the analyses presented here that can attempt to trace evolutionary mechanisms of simplification across tetrapod phylogeny more effectively. It would also make comparisons between the evolutionary lability of individual bones clearer. Although our results indicate that the supratemporal is the most evolutionarily labile bone out of those analysed, while the nasal, frontal and parietal are the least labile, future analyses that are able to incorporate embryological information, and therefore define bone elements based on the presence of their ossification centres may tell a different story.

Phylogenetic inference

Despite the growing number of lissamphibians found in the fossil record, there is still much discourse surrounding the interrelationships of this group, as well as their origin (or origins) (Laurin and Reisz 1997; Meyer and Zardoya 2003; Ruta et al. 2003; Schoch and Milner 2004; Ruta and Coates 2007; Sigurdsen and Green 2011; Marjanovic and Laurin 2013; Schoch 2014; Pardo et al. 2017a, b). The earliest known fossil salamanders (Middle Jurassic *Marmorerpeton* (Jones et al. 2022)), frogs (Early Triassic *Triadobatrachus* (Ascarrunz et al. 2016)), and caecilians (Late Triassic *Funcusvermis* (Kligman et al. 2023)) already display a highly derived morphology, which implies that they radiated from a common ancestor sometime before the Triassic (San Mauro et al. 2005; Zhang et al. 2005; Pardo et al. 2017a; Jones et al. 2022; Kligman et al. 2023). The strong differences in morphology, in addition to the temporal gap between members of the Mesozoic lissamphibian stem-group and Palaeozoic early tetrapods make it harder to determine the origins of lissamphibians. This complication is further augmented by the diversity of developmental mechanisms and life history patterns in early tetrapods, which results in a large number of homoplastic characters and uncertain character polarisations, all of which are similar to the challenges faced when assessing modern amphibian systematics (Wake 1991; Wiens et al. 2005; Schoch 2009; Schoch 2013a).

As previously discussed, there are currently two main hypotheses that explain the origins of lissamphibians, namely the Temnospondyl Hypothesis (TH) and the Lepospondyl Hypothesis (LH). The Temnospondyl Hypothesis argues that lissamphibians form a monophyletic clade and are derived from dissorophoid temnospondyls (Ruta et al. 2003; Schoch and Milner 2004; Caroll 2007; Ruta and Coates 2007; Sigurdsen and Bolt 2010; Sigurdsen and Green 2011; Maddin et al. 2012; Kligman et al. 2023). The Lepospondyl Hypothesis, on the other hand, places lissamphibians within lepospondyls (Laurin and Reisz 1997; Laurin 1998; Vallin and Laurin 2004; Marjanovic and Laurin 2008, 2009, 2013; Laurin et al. 2022).

For all of these cladistic analyses, the reduction in the number of skull bones is used as a character trait to assess the relationships between lissamphibians and stem-tetrapods. However, as we have already noted, the losses of these bones may not be homologous as we cannot determine which developmental processes were responsible for bone loss in fossils. This possible lack of homology highlights not only the complexity of evolutionary processes, but also the potential pitfalls this may create in phylogenetic analyses.

Drivers of loss

A number of ecological and functional selection pressures, developmental mechanisms, and various physical constraints have been proposed in the literature as potential drivers of skull simplification (Atchley and Hall 1991; Hanken and Wake 1993; Sidor 2001; Yeh 2002; Herrel et al. 2007; Esteve-Altava et al. 2013; Schoch 2013a; Schoch 2014; Pardo et al. 2015; Szostakiwskyj et al. 2015; Pardo and Anderson 2016; Pérez-Ben et al. 2018; Strong et al. 2022; Koyabu 2023). One of the most widely cited functional selection pressures concerns the biomechanical stresses on the skull roof associated with biting (Sidor 2001), and specialised ecologies such as headfirst burrowing (Herrel et al. 2007; Pardo et al. 2015; Szostakiwskyj et al. 2015; Pardo and Anderson 2016; Strong et al. 2022). Bone loss linked to the evolution of small body size (and sometimes even true miniaturisation) within a lineage has also been heavily reported (Hanken and Wake 1993; Yeh 2002; Schoch 2013b; Pérez-Ben et al. 2018). Miniaturisation has been documented in dissorophoid temnospondyls (Fröbisch and Schoch 2009), Lissamphibia (Hanken and Wake 1993; Yeh 2002), Mammaliaformes, Squamata (Rieppel

1996; Glaw et al. 2021), Aves (Ocampo et al. 2018), Recumbirostra (Maddin et al. 2011), and Aistopoda (Anderson 2002). Miniaturised body size can also impose physical constraints that may contribute to the loss of skull bones (e.g. large gecko eyes resulting in the loss of the postorbital and supratemporal (Herrel et al. 2007)). Another physical constraint linked to skull simplification is the relative degree of connectivity of individual bones in the skull. A network analysis conducted by Esteve-Altava et al. (2014) on a range of different tetrapod groups showed that poorly connected bones (i.e. bones in direct contact with comparatively few neighbouring bones) were more likely to be lost randomly compared to well-connected bones, which were more likely to be lost by selective fusion. These composite bones made of several ossification centres were themselves less likely to be lost than less complex bones made of a single ossification centre. This is because the more complex bones have a larger role in shaping skull architecture, and the space that they would leave behind if they were lost would be more difficult to fill than that of a less complex and poorly connected bone (Esteve-Altava et al. 2013).

Both functional and developmental selection pressures impose constraints that often result in characteristic, homoplastic anatomical skull morphologies. Therefore, one may expect to see a correlation between skull simplification and lifestyle or miniaturised body size. Tables 3, 4, however, illustrate that the loss of bones in the median and temporal series has no obvious relationship with ecology or an evolutionary decrease in body size in a clade. Nonetheless, more detailed investigations focused on body size and lifestyle are necessary to definitively identify or refute a correlation between these drivers and skull simplification in different tetrapod clades. It is also worth noting the difficulties in detangling the effects of ecological selection pressures versus phylogeny on simplification. For example, from the comparisons of median and temporal series composition in terrestrial and aquatic clades shown in Table 4, it is possible to conclude that aquatic clades are more likely to have a supratemporal than terrestrial clades. However, this could just be a relic of the relative phylogenetic positions of these clades as aquatic groups are often more basal in the phylogeny than their terrestrial relatives.

In the absence of an obvious relationship between skull simplification and lifestyle, it would be pertinent to assume that the evolutionary simplification of the median and temporal series in both anamniotes and amniotes is largely the result of developmental processes and intrinsic evolutionary drivers. In reality though, skull simplification is likely caused by complex combinations of developmental, ecological, and functional factors unique to specific tetrapod lineages, which may also act differently in various tetrapod lineages and at different times in their evolutionary history. What these developmental, ecological, and functional factors may be, we do not yet know, but it is important to consider that the loss of bones (no matter the process), is much more likely than the (re)appearance of additional elements in the dermal skull roof. With this in mind, it may not be surprising that skull simplification is so prevalent in tetrapods.

Conclusions

In summary, the simplification of the dermatocranium is a well-documented yet poorly understood phenomenon which began in the Devonian and evolved parallelly in various tetrapod lineages into the Mesozoic. By conducting ancestral state reconstructions on the presence/absence of the median and temporal series, we have shown that the evolutionary loss of bones in the dermatocranium was much more complex than initially thought, and likely involved a mixture of developmental, ecological, and functional drivers. As no obvious correlation was found between skull simplification and lifestyle or body size, further work will be required to determine what these factors may be and how they interact with one another both in individual lineages, and across the evolutionary history of different tetrapod lineages. Our analyses also showed that the temporal series did not form an evolutionary module, and consequently that the developmental pathways influencing the presence/absence of these individual bones were unlikely to be strongly integrated as the loss of these bones is quite variable. In general though, the intertemporal is lost first, then followed by the supratemporal, then the tabular and/or postparietal. However, although most groups seem to follow this pattern of loss, this was not the case in Sauropsida (i.e. Eureptilia and Parareptilia) where the tabular or postparietal was the second bone to be lost and not the supratemporal. Of the bones studied, the supratemporal was the most evolvable given that it was lost and regained the most often, while the nasal, frontal, and parietal were the least evolvable as they were always present. Interestingly, the sequence in which the temporal and median series bones were lost did not reflect the order in which they ossify in ontogeny.

The analyses presented here demonstrate that the evolution of skull simplification is much more complex than previously realised. Further work is needed to fully capture the intricacies involved, and we would encourage future studies to focus on reassessing skull homology across tetrapodomorphs, and to apply embryological methods to determine the mode of bone loss in the skulls of extant groups.

Acknowledgements

The authors would like to thank Marcello Ruta and Torsten Scheyer for their kind and constructive reviews which helped improve the manuscript. KJK would like to thank Johannes Müller and Mark MacDougal for helpful discussions on amniotes, and parareptile and recumbirostran phylogeny respectively; Davide Foffa for providing help with R; Antoine Verrière for giving advice both on R and on the figures presented here; and Yara Haridy for proof reading. This work is part of KJK's PhD project and was funded by the Deutsche Forschungsgemeinschaft (grant number 442217617) awarded to MD.

References

Alberch P, Gale EA (1985) A developmental analysis of an evolutionary trend: digital reduction in amphibians. Evolution 39: 8–23. https://doi.org/10.2307/2408513

Alcalde L, Basso NG (2013) Old and new hypotheses about the homology of the compound bones from the cheek and otico-occipital regions of the anuran skull. Zoology 116: 232–245. https://doi.org/10.1016/j.zool.2013.03.002

Anderson JS (2002) Revision of the aïstopod genus *Phlegethontia* (Tetrapoda: Lepospondyli). Journal of Paleontology 76: 1029–1046. https://doi.org/10.1666/0022-3360(2002)076%3C1029:ROTAGP%3E2.0.CO;2

Anderson JS (2003) A new aïstopod (Tetrapoda: Lepospondyli) from Mazon Creek, Illinois. Journal of Vertebrate Paleontology 23: 79–88. https://doi.org/10.1671/0272-4634(2003)23[79:ANATLF]2.0.CO;2

Anderson JS (2007) Incorporating ontogeny into the matrix: a phylogenetic evaluation of developmental evidence for the origin of modern amphibians. In: Anderson JS, Sues HD (Eds) Major transitions in vertebrate evolution. Bloomington: Indiana University Press, Indiana.

Anderson JS (2008) Focal review: the origin (s) of modern amphibians. Evolutionary Biology 35: 231–247. https://doi.org/10.1007/s11692-008-9044-5

Anderson JS, Reisz RR, Scott D, Fröbisch NB, Sumida SS (2008a) A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. Nature 453: 515–518. https://doi.org/10.1038/nature06865

Anderson JS, Henrici AC, Sumida SS, Martens T, Berman DS (2008b) *Georgenthalia clavinasica*, a new genus and species of dissorophoid temnospondyl from the Early Permian of Germany, and the relationships of the family Amphibamidae. Journal of Vertebrate Paleontology 28: 61–75. https://doi.org/10.1671/0272-4634(2008)28[61:GCANGA]2.0.CO;2

Andrews SM, Westoll TS (1970) IX.—The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 68(9): 207–329. https://doi.org/10.1017/S008045680001471X

Arnaout B, MacKenzie EM, Lantigua KE, Brzezinski K, McKinnell IW, Maddin HC (2022) The histology of sutures in chicken skulls: Types, conservation, and ontogeny. Journal of Anatomy 240: 503–515. https://doi.org/10.1111/joa.13574

Asakura Y, Kawabe S (2022) Anatomical network analyses reveal evolutionary integration and modularity in the lizards skull. Scientific Reports 12: 14429. https://doi.org/10.1038/s41598-022-18222-8

Ascarrunz E, Rage JC, Legreneur P, Laurin M (2016) *Triadobatrachus massinoti*, the earliest known lissamphibian (Vertebrata: Tetrapoda) re-examined by µCT scan, and the evolution of trunk length in batrachians. Contributions to Zoology 85: 201–234. https://doi.org/10.1163/18759866-08502004

Atchley WR, Hall BK (1991) A model for development and evolution of complex morphological structures. Biological Reviews 66: 101–157. https://doi.org/10.1111/j.1469-185X.1991.tb01138.x

Bapst DW (2012) Paleotree: An R package for paleontological and phylogenetic analyses of evolution. Methods in Ecology and Evolution 3: 803–807. https://doi.org/10.1111/j.2041-210X.2012.00223.x

Babst DW, Wagner PJ (2022) Package 'paleotree'. [pdf] CRAN. http://cran.fhcrc.org/web/packages/paleotree/paleotree.pdf

Berman DS, Sumida SS, Lombard RE (1992) Reinterpretation of the temporal and occipital regions in *Diadectes* and the relationships of diadectomorphs. Journal of Paleontology 66: 481–499. https://doi.org/10.1017/S0022336000034028

Berman DS, Henrici AC, Sumida SS, Martens T (2000) Redescription of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker locality assemblage. Journal of Vertebrate Paleontology 20: 253–268. https://doi.org/10.1671/0272-4634(2000)020[0253:ROSSSF]2.0.CO;2

Brazeau MD, Ahlberg PE (2006) Tetrapod-like middle ear architecture in a Devonian fish. Nature 439(7074): 318–321. https://doi.org/10.1038/nature04196

Carroll RL (1969) A Middle Pennsylvanian Captorhinomorph, and the Interrelationships of Primitive Reptiles. Journal of Paleontology 43: 151–170.

Carroll R, Gaskill P (1978) The Order Microsauria. Memoirs of the American Philosophical Society 126: 1–211.

Carroll RL (1988) Vertebrate Paleontology and Evolution. WH Freeman, New York.

Carroll RL, Bossy KA, Milner AC, Andrews SM, Wellstead CF (1998) Handbook of paleoherpetology part 1. Lepospondyli. München, Germany: Verlag Dr. Friedrich Pfeil.

Carroll RL (2001) The origin and early radiation of terrestrial vertebrates. Journal of Paleontology 75: 1202–1213. https://doi.org/10.1666/0022-3360(2001)075%3C1202:TOAERO%3E2.0.CO;2

Carroll RL (2007) The Palaeozoic ancestry of salamanders, frogs, and caecilians. Zoological Journal of the Linnean Society 150: 1–140. https://doi.org/10.1111/j.1096-3642.2007.00246.x

Carroll RL (2009) The Rise of Amphibians: 365 Million Years of Evolution. Johns Hopkins University Press, Baltimore.

Carstens MH (2023) The Neck: Development and Evolution. In: Carstens MH (Ed.) The Embryologic Basis of Craniofacial Structure: Developmental Anatomy, Evolutionary Design, and Clinical Applications. Springer, Cham, 781–940. https://doi.org/10.1007/978-3-031-15636-6_10

Clack JA (1992) The stapes of *Acanthostega gunnari* and the Role of the Stapes in Early Tetrapods. In: Webster DB, Popper AN, Fay RR (Eds) The Evolutionary Biology of Hearing. Springer, New York, 405–420. https://doi.org/10.1007/978-1-4612-2784-7_24

Clack JA (1994) Earliest known tetrapod braincase and the evolution of the stapes and fenestra ovalis. Nature 369(6479): 392–394. https://doi.org/10.1038/369392a0

Clack JA (1998) A new Early Carboniferous tetrapod with a mélange of crown-group characters. Nature 394(6688): 66–69. https://doi.org/10.1038/27895

Clack JA (2002) The dermal skull roof of *Acanthostega gunnari*, an early tetrapod from the Late Devonian. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 93(1): 17–33. https://doi.org/10.1017/S0263593300000304

Clack JA, Ahlberg PE, Finney SM, Dominguez Alonso P, Robinson J, Ketcham RA (2003) A uniquely specialized ear in a very early tetrapod. Nature 425(6953): 65–69. https://doi.org/10.1038/nature01904

Clack JA (2009) The fish–tetrapod transition: new fossils and interpretations. Evolution: Education and Outreach 2: 213–223. https://doi.org/10.1007/s12052-009-0119-2

Clack JA (2012) Gaining Ground: The Origin and Evolution of Tetrapods. Second Edition. Indiana University Press, Indiana.

Clack JA, Ruta M, Milner AR, Marshall JE, Smithson TR, Smithson KZ (2019) *Acherontiscus caledoniae*: the earliest heterodont and durophagous tetrapod. Royal Society Open Science 6: 182087. https://doi.org/10.1098/rsos.182087

Coates MI, Clack JA (1991) Fish-like gills and breathing in the earliest known tetrapod. Nature 352(6332): 234–236. https://doi.org/10.1038/352234a0

Crawford NG, Parham JF, Sellas AB, Faircloth BC, Glenn TC, Papenfuss TJ, Henderson JB, Hansen MH, Simison WB (2015) A phylogenomic analysis of turtles. Molecular Phylogenetics and Evolution 83: 250–257. https://doi.org/10.1016/j.ympev.2014.10.021

Dalerum F (2007) Phylogenetic reconstruction of carnivore social organizations. Journal of Zoology 273: 90–97. https://doi.org/10.1111/j.1469-7998.2007.00303.x

Elwood JRL, Cundall D (1994) Morphology and behavior of the feeding apparatus in *Cryptobranchus alleganiensis* (Amphibia: Caudata). Journal of Morphology 220: 47–70. https://doi.org/10.1002/jmor.1052200106

Esteve-Altava B, Marugán-Lobón J, Botella H, Rasskin-Gutman D (2013) Structural constraints in the evolution of the tetrapod skull complexity: Williston's law revisited using network models. Evolutionary Biology 40: 209–219. https://doi.org/10.1007/s11692-012-9200-9

Esteve-Altava B, Marugán-Lobón J, Botella H, Rasskin-Gutman D (2014) Random loss and selective fusion of bones originate morphological complexity trends in tetrapod skull networks. Evolutionary Biology 41: 52–61. https://doi.org/10.1007/s11692-013-9245-4

Evans SE, Sigogneau-Russell D (2001) A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. Palaeontology 44: 259–273. https://doi.org/10.1111/1475-4983.00179

Evans SE (2008) The Skull of Lizards and Tuatara. Biology of the Reptilia 20: 1–347.

Farke AA, Wolff EDS, Tanke DH (2009) Evidence of Combat in *Triceratops*. PLOS ONE 4: e4252. https://doi.org/10.1371/journal.pone.0004252

Ford DP, Benson RB (2020) The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. Nature Ecology & Evolution 4: 57–65. https://doi.org/10.1038/s41559-019-1047-3

Fox RC, Bowman MC (1966) Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). University of Kansas Paleontological Contributions 15: 1–80.

Fraser-King, SW, Benoit J, Day MO, Rubidge BS (2019) Cranial morphology and phylogenetic relationship of the enigmatic dinocephalian *Styracocephalus platyrhynchus* from the Karoo Supergroup, South Africa. Palaeontologia Africana 54: 14–29.

Gaffney ES, Meeker LJ (1983) Skull morphology of the oldest turtles: a preliminary description of *Proganochelys quenstedtii*. Journal of Vertebrate Paleontology 3: 25–28. https://doi.org/10.1080/02724634.1983.10011953

Glaw F, Köhler J, Hawlitschek O, Ratsoavina FM, Rakotoarison A, Scherz MD, Vences M (2021) Extreme miniaturization of a new amniote vertebrate and insights into the evolution of genital size in chameleons. Scientific Reports 11: 1–14. https://doi.org/10.1038/s41598-020-80955-1

Hanken J, Wake DB (1993) Miniaturization of Body Size; Organismal Consequences and Evolutionary Significance. Annual Review of Ecology and Systematics 24: 501–519. https://doi.org/10.1146/annurev.es.24.110193.002441

Heiss E, Aerts P, Van Wassenbergh S (2018) Aquatic-terrestrial transitions of feeding systems in vertebrates: a mechanical perspective. Journal of Experimental Biology 221: jeb154427. https://doi.org/10.1242/jeb.154427

Herrel A, Schaerlaeken V, Meyers JJ, Metzger KA, Ross CF (2007) The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. Integrative and Comparative Biology 47: 107–117. https://doi.org/10.1093/icb/icm014

Huttenlocker A (2009) An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). Zoological Journal of the Linnean Society 157: 865–891. https://doi.org/10.1111/j.1096-3642.2009.00538.x

Huttenlocker AK, Singh SA, Henrici AC, Sumida SS (2021) A Carboniferous synapsid with caniniform teeth and a reappraisal of mandibular size-shape heterodonty in the origin of mammals. Royal Society Open Science 8: 211237. https://doi.org/10.1098/rsos.211237

Jarvik E (1980) Basic Structure and Evolution of Vertebrates. Academic Press, London.

Jenkins F.A, Walsh DM, Carroll RL (2007) Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. Bulletin of the Museum of Comparative Zoology 158: 285–365. https://doi.org/10.3099/0027-4100(2007)158[285:AOEMAL]2.0.CO;2

Johanson Z, Ahlberg P, Ritchie A (2003) The Braincase and Palate of the Tetrapodomorph Sarcopterygian *Mandageria fairfaxi*: Morphological Variability near the Fish-Tetrapod Transition. Palaeontology 46: 271–293. https://doi.org/10.1111/1475-4983.00298

Jollie M (1962) Chordate Morphology. Reinhold, New York. https://doi.org/10.5962/bhl.title.6408

Jones ME, Curtis N, O'Higgins P, Fagan M, Evans SE (2009) The head and neck muscles associated with feeding in *Sphenodon* (Reptilia: Lepidosauria: Rhynchocephalia). Palaeontologia Electronica 12.

Jones ME, Benson RB, Skutschas P, Hill L, Panciroli E, Schmitt AD, Walsh SA, Evans SE (2022) Middle Jurassic fossils document an early stage in salamander evolution. Proceedings of the National Academy of Sciences 119: e2114100119. https://doi.org/10.1073/pnas.2114100119

Joyce WG, Schoch RR, Lyson TR (2013) The girdles of the oldest fossil turtle, *Proterochersis robusta*, and the age of the turtle crown. BMC Evolutionary Biology 13: 1–9. https://doi.org/10.1186/1471-2148-13-266

Kligman BT, Gee BM, Marsh AD, Nesbitt SJ, Smith ME, Parker WG, Stocker MR (2023) Triassic stem caecilian supports dissorophoid origin of living amphibians. Nature 614: 102–107. https://doi.org/10.1038/s41586-022-05646-5

Knell RJ, Naish D, Tomkins JL, Hone DWE (2013) Sexual selection in prehistoric animals: detection and implications. Cell Press 28: 38–47. https://doi.org/10.1016/j.tree.2012.07.015

Koyabu D, Maier W, Sánchez-Villagra MR (2012) Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal. Proceedings of the National Academy of Sciences 109: 14075–14080. https://doi.org/10.1073/pnas.1208693109

Koyabu D (2023) Evolution, conservatism and overlooked homologies of the mammalian skull. Philosophical Transactions of the Royal Society B 378: 20220081. https://doi.org/10.1098/rstb.2022.0081

Laurin M, Reisz RR (1997) A new perspective on tetrapod phylogeny. In: Sumida SS, Martin KLM (Eds) Amniote Origins: Completing the Transition to Land. Academic Press, Inc, San Diego, 9–59. https://doi.org/10.1016/B978-012676460-4/50003-2

Laurin M (1998) The importance of global parsimony and historical bias in understanding tetrapod evolution. Part II. Vertebral centrum, costal ventilation, and paedomorphosis. Annales des Sciences Naturelles - Zoologie et Biologie Animale 19: 99–114. https://doi.org/10.1016/S0003-4339(98)80004-X

Laurin M, Lapauze O, Marjanović D (2022) What do ossification sequences tell us about the origin of extant amphibians? Peer Community Journal 2: e12. https://doi.org/10.24072/pcjournal.89

Leavitt DH, Bezy RL, Crandall KA, Sites Jr JW (2007) Multi-locus DNA sequence data reveal a history of deep cryptic vicariance and habitat-driven convergence in the desert night lizard *Xantusia vigilis* species complex (Squamata: Xantusiidae). Molecular Ecology 16: 4455–4481. https://doi.org/10.1111/j.1365-294X.2007.03496.x

Lee MS, Anderson JS (2006) Molecular clocks and the origin (s) of modern amphibians. Molecular Phylogenetics and Evolution 40: 635–639. https://doi.org/10.1016/j.ympev.2006.03.013

Lee HW, Esteve-Altava B, Abzhanov A (2020) Evolutionary and ontogenetic changes of the anatomical organization and modularity in the skull of archosaurs. Scientific Reports 10: 16138. https://doi.org/10.1038/s41598-020-73083-3

Li C, Wu XC, Rieppel O, Wang LT, Zhao LJ (2008) An ancestral turtle from the Late Triassic of southwestern China. Nature 456: 497–501. https://doi.org/10.1038/nature07533

Liu J, Rubidge B, Li J (2009) New basal synapsid supports Laurasian origin for therapsids. Acta Palaeontologica Polonica 54: 393–400. https://doi.org/10.4202/app.2008.0071

Long JA, Gordon MS (2004) The greatest step in vertebrate history: a paleobiological review of the fish-tetrapod transition. Physiological and Biochemical Zoology 77: 700–719. https://doi.org/10.1086/425183

MacDougall MJ, Seeger R, Gee B, Ponstein J, Jansen M, Scott D, Bevitt JJ, Reisz RR, Fröbisch J (2021) Revised description of the early Permian recumbirostran "microsaur" *Nannaroter mckinziei* based on new fossil material and computed tomographic data. Frontiers in Ecology and Evolution 9: 739316. https://doi.org/10.3389/fevo.2021.739316

Maddin HC, Olori JC, Anderson JS (2011) A redescription of *Carrolla craddocki* (Lepospondyli: Brachystelechidae) based on high-resolution CT, and the impacts of miniaturization and fossoriality on morphology. Journal of Morphology 272: 722–743. https://doi.org/10.1002/jmor.10946

Maddin HC, Jenkins Jr FA, Anderson JS (2012) The braincase of *Eocaecilia micropodia* (Lissamphibia, Gymnophiona) and the origin of caecilians. PLOS ONE 7: e50743. https://doi.org/10.1371/journal.pone.0050743

Maddin HC, Piekarski N, Sefton EM, Hanken J (2016) Homology of the cranial vault in birds: new insights based on embryonic fate-mapping and character analysis. Royal Society Open Science 3: 160356. https://doi.org/10.1098/rsos.160356

Maddin HC, Piekarski N, Reisz RR, Hanken J (2020) Development and evolution of the tetrapod skull-neck boundary. Biological Reviews 95: 573–591. https://doi.org/10.1111/brv.12578

Maddison WP, Maddison DR (2021) Mesquite: a modular system for evolutionary analysis. Version 3.7. http://www.mesquiteproject.org

Maglia AM, Púgener LA (1998) Skeletal development and adult osteology of *Bombina orientalis* (Anura: Bombinatoridae). Herpetologica 54: 344–363.

Marjanović DM, Laurin M (2008) A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians. Contributions to Zoology 77: 149–199. https://doi.org/10.1163/18759866-07703002

Marjanović D, Laurin M (2009) The origin(s) of modern amphibians: a commentary. Evolutionary Biology 36: 336–338. https://doi.org/10.1007/s11692-009-9065-8

Marjanović D, Laurin M (2013) The origin (s) of extant amphibians: a review with emphasis on the "lepospondyl hypothesis". Geodiversitas 35: 207–272. https://doi.org/10.5252/g2013n1a8

Marjanović D, Laurin M (2019) Phylogeny of Paleozoic limbed vertebrates reassessed through revision and expansion of the largest published relevant data matrix. PeerJ 6: e5565. https://doi.org/10.7717/peerj.5565

Meyer A, Zardoya R (2003) Recent advances in the (molecular) phylogeny of vertebrates. Annual Review of Ecology, Evolution, and Systematics 34: 311–338. https://doi.org/10.1146/annurev.ecolsys.34.011802.132351

Milner AR (1993) The Paleozoic relatives of lissamphibians. Herpetological Monographs 7: 8–27. https://doi.org/10.2307/1466948

Ocampo D, Barrantes G, Uy JAC (2018) Morphological adaptations for relatively larger brains in hummingbird skulls. Ecology and Evolution 8: 10482–10488. https://doi.org/10.1002/ece3.4513

Olson EC, Roy SK, Ross LA (1951) *Diplocaulus*: a study in growth and variation. Fieldiana: Geol 11: 57–149. https://doi.org/10.5962/bhl.title.3527

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pardo JD, Szostakiwskyj M, Anderson JS (2015) Cranial morphology of the brachystelechid 'microsaur' *Quasicaecilia texana* Carroll provides new insights into the diversity and evolution of braincase morphology in recumbirostran 'microsaurs'. PLOS ONE 10: e0130359. https://doi.org/10.1371/journal.pone.0130359

Pardo JD, Anderson JS (2016) Cranial morphology of the Carboniferous-Permian tetrapod *Brachydectes newberryi* (Lepospondyli, Lysorophia): new data from µCT. PLOS ONE 11: e0161823. https://doi.org/10.1371/journal.pone.0161823

Pardo JD, Small BJ, Huttenlocker AK (2017a) Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia. Proceedings of the National Academy of Sciences 114: E5389–E5395. https://doi.org/10.1073/pnas.1706752114

Pardo JD, Szostakiwskyj M, Ahlberg PE, Anderson JS (2017b) Hidden morphological diversity among early tetrapods. Nature 546: 642–645. https://doi.org/10.1038/nature22966

Pérez-Ben CM, Schoch RR, Báez AM (2018) Miniaturization and morphological evolution in Paleozoic relatives of living amphibians: a quantitative approach. Paleobiology 44: 58–75. https://doi.org/10.1017/pab.2017.22

Plateau O, Foth C (2020) Birds have peramorphic skulls, too: anatomical network analyses reveal oppositional heterochronies in avian skull evolution. Communications Biology 3: 195. https://doi.org/10.1038/s42003-020-0914-4

Pritchard AC, Sues HD, Scott D, Reisz RR (2021) Osteology, Relationships and Functional Morphology of *Weigeltisaurus jaekeli* (Diapsida, Weigeltisauridae) based on a Complete Skeleton from the Upper Permian Kupferschiefer of Germany. PeerJ 9: e11413. https://doi.org/10.7717/peerj.11413

Pyron RA (2011) Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. Systematic Biology 60: 466–481. https://doi.org/10.1093/sysbio/syr047

Rawson JR, Esteve-Altava B, Porro LB, Dutel H, Rayfield EJ (2022) Early tetrapod cranial evolution is characterized by increased complexity, constraint, and an offset from fin-limb evolution. Science Advances 8: eadc8875. https://doi.org/10.1126/sciadv.adc8875

Reisz RR (1981) A diapsid reptile from the Pennsylvanian of Kansas. Occasional Papers of the Museum of Natural History, University of Kansas 7B: 1–74. https://doi.org/10.5962/bhl.title.8440

Reisz RR, Berman DS (2001) The skull of *Mesenosaurus romeri*, a Small Varanopseid (Synapsida: Eupelycosauria) from the Upper Permian of the Mezen River Basin, Northern Russia. Annals-Carnegie Museum Pittsburgh 70: 113–132. https://doi.org/10.5962/p.215145

Reisz RR, Godfrey SJ, Scott D (2009) *Eothyris* and *Oedaleops*: do these Early Permian synapsids from Texas and New Mexico form a clade? Journal of Vertebrate Paleontology 29: 39–47. https://doi.org/10.1671/039.029.0112

Rieppel O (1992) The skull in a hatchling of *Sphenodon punctatus*. Journal of Herpetology 26: 80–84. https://doi.org/10.2307/1565028

Rieppel O (1996) Miniaturization in Tetrapods: Consequences for Skull Morphology. In: Miller PJ (Ed.) Miniature Vertebrates: The Implications of Small Body Size. Oxford Academic, Oxford, 47–61. https://doi.org/10.1093/oso/9780198577874.003.0003

Rüber L, Britz R, Tan HH, Ng PK, Zardoya R (2004) Evolution of mouthbrooding and life-history correlates in the fighting fish genus Betta. Evolution 58: 799–813. https://doi.org/10.1111/j.0014-3820.2004.tb00413.x

Ruta M, Coates MI, Quicke DL (2003) Early tetrapod relationships revisited. Biological Reviews 78: 251–345. https://doi.org/10.1017/S1464793102006103

Ruta M, Coates MI (2007) Dates, nodes and character conflict: addressing the lissamphibian origin problem. Journal of Systematic Palaeontology 5: 69–122. https://doi.org/10.1017/S1477201906002008

Rybczynski N (2000) Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of Eastern Europe. Zoological Journal of the Linnean Society 130: 329–373. https://doi.org/10.1111/j.1096-3642.2000.tb01634.x

San Mauro D, Vences M, Alcobendas M, Zardoya R, Meyer A (2005) Initial diversification of living amphibians predated the breakup of Pangaea. The American Naturalist 165: 590–599. https://doi.org/10.1086/429523

Scherz MD, Hutter CR, Rakotoarison A, Riemann JC, Rödel MO, Ndriantsoa SH, Glos J, Hyde Roberts S, Crottini A, Vences M, Glaw F (2019) Morphological and ecological convergence at the lower size limit for vertebrates highlighted by five new miniaturised microhylid frog species from three different Madagascan genera. PLOS ONE 14: e0213314. https://doi.org/10.1371/journal.pone.0213314

Scheyer TM, Klein N, Evers SW, Mautner AK, Pabst B (2022) First evidence of *Proganochelys quenstedtii* (Testudinata) from the Plateosaurus bonebeds (Norian, Late Triassic) of Frick, Canton Aargau, Switzerland. Swiss Journal of Palaeontology 141: 17. https://doi.org/10.1186/s13358-022-00260-4

Schluter D, Price T, Mooers AØ, Ludwig D (1997) Likelihood of ancestor states in adaptive radiation. Evolution 51: 1699–1711. https://doi.org/10.2307/2410994

Schoch RR (1992) Comparative ontogeny of early Permian branchiosaurid amphibians from southwestern Germany. Developmental stages. Palaeontographica, Abteilung A, Paläozoologie, Stratigraphie 222: 43–83.

Schoch RR (2002) The early formation of the skull in extant and Paleozoic amphibians. Paleobiology 28: 278–296. https://doi.org/10.1666/0094-8373(2002)028%3C0278:TEFOTS%3E2.0.CO;2

Schoch RR (2004) Skeleton formation in the Branchiosauridae: a case study in comparing ontogenetic trajectories. Journal of Vertebrate Paleontology 24: 309–319. https://doi.org/10.1671/1950

Schoch RR, AR Milner (2004) Structure and implications of theories on the origins of lissamphibians. In: Arratia G, Wilson MV, Cloutier R (Eds) Recent advances in the origin and early radiation of vertebrates. Verlag Dr. Friedrich Pfeil, München, 345–377.

Schoch RR, Rubidge BS (2005) The amphibamid *Micropholis* from the Lystrosaurus assemblage zone of South Africa. Journal of Vertebrate Paleontology 25: 502–522. https://doi.org/10.1671/0272-4634(2005)025[0502:TAMFTL]2.0.CO;2

Schoch RR (2009) Evolution of life cycles in early amphibians. The Annual Review of Earth and Planetary Sciences 37: 135–162. https://doi.org/10.1146/annurev.earth.031208.100113

Schoch RR, Witzmann F (2011) Bystrow's Paradox–gills, fossils, and the fish-to-tetrapod transition. Acta Zoologica 92(3): 251–265. https://doi.org/10.1111/j.1463-6395.2010.00456.x

Schoch RR (2013a) How body size and development biased the direction of evolution in early amphibians. Historical Biology 25: 155–165. https://doi.org/10.1080/08912963.2012.724796

Schoch RR (2013b) The evolution of major temnospondyl clades: an inclusive phylogenetic analysis. Journal of Systematic Palaeontology 11: 673–705. https://doi.org/10.1080/14772019.2012.699006

Schoch RR (2014) Amphibian skull evolution: the developmental and functional context of simplification, bone loss and heterotopy. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 322: 619–630. https://doi.org/10.1002/jez.b.22599

Schoch RR, Milner AR (2014) Handbook of Paleoherpetology part 3A2. Temnospondyli I. Verlag Dr. Friedrich Pfeil, München.

Schoch RR, Werneburg R, Voigt S (2020) A Triassic stem-salamander from Kyrgyzstan and the origin of salamanders. Proceedings of the National Academy of Sciences 117: 11584–11588. https://doi.org/10.1073/pnas.2001424117

Schoch RR (2022) Phylogeny of the amphibamiform temnospondyls: the relationship of taxa known by adults, larvae and neotenes. Journal of Systematic Palaeontology 20: 1–30. https://doi.org/10.1080/14772019.2022.2113831

Schoch RR, Witzmann F (2024) The evolution of larvae in temnospondyls and the stepwise origin of amphibian metamorphosis. Biological Reviews 99: 1613–1637. https://doi.org/10.1111/brv.13084

Sefton EM, Bullar B-AS, Mohaddes Z, Hanken J (2016) Evolution of the head-trunk interface in tetrapod vertebrates. eLife 5: e09972. https://doi.org/10.7554/eLife.09972

Sidor CA (2001) Simplification as a trend in synapsid cranial evolution. Evolution 55: 1419–1442. https://doi.org/10.1111/j.0014-3820.2001.tb00663.x

Sigurdsen T, Bolt JR (2010) The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. Journal of Vertebrate Paleontology 30: 1360–1377. https://doi.org/10.1080/02724634.2010.501445

Sigurdsen T, Green DM (2011) The origin of modern amphibians: a re-evaluation. Zoological Journal of the Linnean Society 162: 457–469. https://doi.org/10.1111/j.1096-3642.2010.00683.x

Simoes TR, Caldwell MW, Tałanda M, Bernardi M, Palci A, Vernygora O, Bernardini F, Mancini L, Nydam RL (2018) The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. Nature 557: 706–709. https://doi.org/10.1038/s41586-018-0093-3

Smith-Paredes D, Núñez-León D, Soto-Acuña S, O'Connor J, Botelho, JF, Vargas AO (2018) Dinosaur ossification centres in embryonic birds uncover developmental evolution of the skull. Nature Ecology & Evolution 2: 1966–1973. https://doi.org/10.1038/s41559-018-0713-1

Sookias RB, Dilkes D, Sobral G, Smith RM, Wolvaardt FP, Arcucci AB, Bhullar BAS, Werneburg I (2020) The craniomandibular anatomy of the early archosauriform *Euparkeria capensis* and the dawn of the archosaur skull. Royal Society Open Science 7: 20011. https://doi.org/10.1098/rsos.200116

Strong CR, Scherz MD, Caldwell MW (2022) Convergence, divergence, and macroevolutionary constraint as revealed by anatomical network analysis of the squamate skull, with an emphasis on snakes. Scientific Reports 12: 14469. https://doi.org/10.1038/s41598-022-18649-z

Szostakiwskyj M, Pardo JD, Anderson JS (2015) Micro-CT study of *Rhynchonkos stovalli* (Lepospondyli, Recumbirostra), with description of two new genera. PLOS ONE 10: e0127307. https://doi.org/10.1371/journal.pone.0127307

Tsuji LA (2006) Cranial anatomy and phylogenetic affinities of the Permian parareptile *Macroleter poezicus*. Journal of Vertebrate Paleontology 26: 849–865. https://doi.org/10.1671/0272-4634(2006)26[849:CAAPAO]2.0.CO;2

van Tuinen M, Dyke GJ (2004) Calibration of galliform molecular clocks using multiple fossils and genetic partitions. Molecular Phylogenetics and Evolution 30: 74–86. https://doi.org/10.1016/S1055-7903(03)00164-7

Vallin G, Laurin M (2004) Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. Journal of Vertebrate Paleontology 24: 56–72. https://doi.org/10.1671/5.1

Wake DB (1991) Homoplasy: The Result of Natural Selection, or Evidence of Design Limitations? The American Naturalist 138: 543–567. https://doi.org/10.1086/285234

Wake MH (1993) The skull as a locomotor organ. In: Hanken J, Hall BK (Eds) The Skull. University of Chicago Press, Chicago, 197–240.

Walker W, Bemis W, Liem K, Grande L (2000) Functional Anatomy of the Vertebrates: An Evolutionary Perspective. Third Editon. Harcourt College Publishers, Fort Worth.

Wallace RV, Martínez R, Rowe T (2019) First record of a basal mammaliamorph from the early Late Triassic Ischigualasto Formation of Argentina. PLOS ONE 14: e0218791. https://doi.org/10.1371/journal.pone.0218791

Wang W, Shang Q, Cheng L, Wu XC, Li C (2022) Ancestral body plan and adaptive radiation of sauropterygian marine reptiles. Iscience 25: 105635. https://doi.org/10.1016/j.isci.2022.105635

Werneburg R, Witzmann F, Rinehart L, Fischer J, Voigt S (2023) A new eryopid temnospondyl from the Carboniferous–Permian boundary of Germany. Journal of Paleontology 97: 1251–1281. https://doi.org/10.1017/jpa.2023.58

Williston SW (1925) The Osteology of the Reptiles. Harvard University Press. https://doi.org/10.5962/bhl.title.6573

Wilkinson M, Presswell B, Sherratt E, Papadopoulou A, Gower DJ (2014) A new species of striped *Ichthyophis* Fitzinger, 1826 (Amphibia: Gymnophiona: Ichthyophiidae) from Myanmar. Zootaxa 3785: 45–58. https://doi.org/10.11646/zootaxa.3785.1.4

Wiens JJ, Bonett RM, Chippindale PT (2005) Ontogeny discombobulates phylogeny. Systematic Biology 54: 91–110. https://doi.org/10.1080/10635150590906037

Yeh J (2002) The effect of miniaturized body size on skeletal morphology in frogs. Evolution 56: 628–641. https://doi.org/10.1111/j.0014-3820.2002.tb01372.x

Zhang P, Zhou H, Chen YQ, Liu YF, Qu LH (2005) Mitogenomic perspectives on the origin and phylogeny of living amphibians. Systematic Biology 54: 391–400. https://doi.org/10.1080/10635150590945278

Supplementary material 1

Notes and references for presence/absence data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: xlsx

Explanation note: Presence/absence data with notes and references.

Link: https://doi.org/10.3897/fr.27.133803.suppl1

Supplementary material 2

Temnospondyl Hypothesis composite tree

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: tre

Link: https://doi.org/10.3897/fr.27.133803.suppl2

Supplementary material 3

Lepospondyl Hypothesis composite tree

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: tre

Link: https://doi.org/10.3897/fr.27.133803.suppl3

Supplementary material 4

Notes and references for FADs

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: xlsx

Link: https://doi.org/10.3897/fr.27.133803.suppl4

Supplementary material 5

AICs and weights of ARD and ER models in Temnospondyl and Lepospondyl Hypothesis

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: xlsx

Link: https://doi.org/10.3897/fr.27.133803.suppl5

Supplementary material 6

R script

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: R
Explanation note: R Script used for maximum likelihood ancestral state reconstructions.

Link: https://doi.org/10.3897/fr.27.133803.suppl6

Supplementary material 7

TH-LHa data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: csv
Explanation note: Homology Hypothesis A data.

Link: https://doi.org/10.3897/fr.27.133803.suppl7

Supplementary material 8

TH-LHb data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: csv
Explanation note: Homology Hypothesis B data.

Link: https://doi.org/10.3897/fr.27.133803.suppl8

Supplementary material 9

TH-LHc data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis C data.

Link: https://doi.org/10.3897/fr.27.133803.suppl9

Supplementary material 10

TH-LHd data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis D data.

Link: https://doi.org/10.3897/fr.27.133803.suppl10

Supplementary material 11

TH-LHe data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis E data.

Link: https://doi.org/10.3897/fr.27.133803.suppl11

Supplementary material 12

TH-LHf data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis F data.

Link: https://doi.org/10.3897/fr.27.133803.suppl12

Supplementary material 13

TH-LHg data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis G data.

Link: https://doi.org/10.3897/fr.27.133803.suppl13

Supplementary material 14

TH-LHh data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Explanation note: Homology Hypothesis H data.

Link: https://doi.org/10.3897/fr.27.133803.suppl14

Supplementary material 15

FAD data

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: csv

Link: https://doi.org/10.3897/fr.27.133803.suppl15

Supplementary material 16

THa postparietal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl16

Supplementary material 17

THa intertemporal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl17

Supplementary material 18

THa supratemporal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl18

Supplementary material 19

THa tabular

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl19

Supplementary material 20

LHa postparietal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch

Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl20

Supplementary material 21

LHa intertemporal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl21

Supplementary material 22

LHa supratemporal

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl22

Supplementary material 23

LHa tabular

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: pdf

Link: https://doi.org/10.3897/fr.27.133803.suppl23

Supplementary material 24

Alternative transitions

Authors: Kim Julia Kean, Marylène Danto, Celeste Pérez-Ben, Nadia Belinda Fröbisch
Data type: tiff

Link: https://doi.org/10.3897/fr.27.133803.suppl24