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Recalibrating the transcriptomic timetree of jawed vertebrates

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Abstract

Molecular divergence dating has the potential to overcome the incompleteness of the fossil record in inferring when cladogenetic events (splits, divergences) happened, but needs to be calibrated by the fossil record. Ideally but unrealistically, this would require practitioners to be specialists in molecular evolution, in the phylogeny and the fossil record of all sampled taxa, and in the chronostratigraphy of the sites the fossils were found in. Paleontologists have therefore tried to help by publishing compendia of recommended calibrations, and molecular biologists unfamiliar with the fossil record have made heavy use of such works. Using a recent example of a large timetree inferred from molecular data, I demonstrate that calibration dates cannot be taken from published compendia without risking strong distortions to the results, because compendia become outdated faster than they are published. The present work cannot serve as such a compendium either; in the slightly longer term, it can only highlight known and overlooked problems. Future authors will need to solve each of these problems anew through a thorough search of the primary paleobiological and chronostratigraphic literature on each calibration date every time they infer a new timetree; over 40% of the sources I cite were published after mid-2016.

Treating all calibrations as soft bounds results in younger nodes than treating all calibrations as hard bounds. The unexpected exception are nodes calibrated with both minimum and maximum ages, further demonstrating the widely underestimated importance of maximum ages in divergence dating.

1 Introduction

Irisarri et al. (2017) inferred a set of timetrees from the transcriptomes of 100 species of gnathostomes (jawed vertebrates) and combinations of up to 30 calibrations from the fossil record. On the unnumbered ninth page of their supplementary information, they described their calibration dates as "five well-accepted fossil calibrations plus a prior on the root" and "24 additional well-established calibration points with solid paleontological evidence". For many of the calibrations, these optimistic assessments are not tenable. Most were taken from secondary or tertiary literature, and so they were – in many cases – outdated by about ten years or more in 2017. Many more have become outdated since then. I have tried to present, and use, the current state of knowledge on each of these calibrations.

2 Materials and methods

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2.1 Calibrations

In the 29 subsections below I discuss the minimum and maximum ages of all 30 nodes used as calibrations by Irisarri et al. (2017), referring to each by clade names and by the node number assigned by Irisarri et al. (2017: especially supp. table 8 and supp. fig. 19), also shown in Fig. 1. The abbreviation Fm stands for Formation; ICS refers to the International Chronostratigraphic Chart v2019/5 (Cohen et al., 2019); Ma is the quasi-SI abbreviation for megayear (million years).

2.1.1 Root node (100): crown group of Gnathostomata (total-group Chondrichthyes – total-group Osteichthyes)

The cladogenesis that created the total groups of Chondrichthyes and Osteichthyes was assigned a minimum age of 421.75 Ma, a remarkably precise date close to the Silurian-Devonian boundary, and a maximum age of 462.5 Ma, which is currently (ICS) thought to lie in the Darriwilian stage of the Middle Ordovician.

The Darriwilian should rather be regarded as the minimum age of this calibration date. While articulated bones and teeth of crown-group gnathostomes – both total-group chondrichthyans (Burrow and Young, 1999) and total-group osteichthyans (Choo et al., 2017, and references therein) – are only known from the Ludfordian (Ludlow, late Silurian) upward, a large diversity of scales that are increasingly confidently assigned to stem-chondrichthyans extends all the way down into the early Darriwilian (Sansom et al., 2012; Andreev et al., 2015, 2016a, b; Žigaitė-Moro et al., 2018; Sansom and Andreev, 2018; and references therein). The Darriwilian is currently thought to have begun 467.3 ± 1.1 Ma ago and to have ended 458.4 ± 0.9 Ma ago (ICS); for the purposes of reducing "the middle part of the Stairway Sandstone" (Sansom et al., 2012: 243) to a single number, the age of 465 Ma should be adequate as a hard minimum age of the gnathostome crown-group.

As a maximum age I cautiously propose the mid-Floian (Early Ordovician) upper fossiliferous level of the Burgess-like Fezouata Shale; at both levels, gnathostomes are absent among the "over 200 taxa, about half of which are soft-bodied" (Lefebvre et al., 2017 "2018": 296). Note that the oldest known hard tissues of vertebrates are Floian in age as well (reviewed by Sansom and Andreev, 2018). The Floian began 477.7 ± 1.4 Ma ago and ended 470.0 ± 1.4 Ma ago (ICS), so I suggest a soft maximum age of 475 Ma for this calibration date.

The minimum and the maximum age proposed here are unexpectedly close together. This may be a sign that one or both is an unduly optimistic assessment of our knowledge of the fossil record – or that the origin of Gnathostomata formed part of the Great Ordovician Biodiversification Event (Sansom et al., 2012; Sansom and Andreev, 2018), which does not seem implausible.

2.1.2 Node 102: crown group of Osteichthyes (Actinopterygii – Sarcopterygii)

Irisarri et al. (2017) assigned a minimum age of 416 Ma and a maximum age of 439 Ma, spanning the Silurian-Devonian boundary, to the cladogenesis that created the osteichthyan crown-group by separating the sister-groups Actinopterygii and Sarcopterygii.

The minimum age of this cladogenesis event depends on the phylogenetic position of the "psarolepids" (Choo et al., 2017) *Guiyu* and *Sparalepis* from the Kuanti [Guandi] Fm of Yunnan, China, which represents an early part of the abovementioned Ludfordian stage (425.6 ± 0.9 to 423.0 ± 2.3 Ma ago: ICS). The "psarolepids" lie either just outside the osteichthyan crown-group or just inside, on the sarcopterygian side of the basal dichotomy (Clement et al., 2018, and references therein). Following the discussions of this issue in Choo et al. (2017), Lu et al. (2017) and Clement et

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al. (2018), and the discussion in Marjanović and Laurin (2019) of the performance of Bayesian inference on the kind of datasets found in vertebrate paleontology, I favor a stem-osteichthyan position for this assemblage over a large number of unexpected reversals to a "placoderm" state.

The oldest known uncontroversial crown-group osteichthyan is the oldest known dipnomorph, *Youngolepis*, as discussed below; following the assignment of *Andreolepis* and *Lophosteus* to the osteichthyan stem (e.g. Botella et al., 2007; Chen et al., 2016), all certain or uncertain actinopterygians are Devonian or younger. Thus, the minimum age for this calibration is the same as that for the next, Node 104.

Likewise, for the same reasons as discussed under Node 104, I cannot assign a maximum age to this divergence other than that for the root node. I recommend against using this cladogenetic event as a calibration date if Nodes 100 and 104 are available.

2.1.3 Node 104: Dipnomorpha – Tetrapodomorpha

The divergence of the sister-groups Dipnomorpha (the lungfish total group) and Tetrapodomorpha (the tetrapod total group) was assigned a minimum age of 408 and a maximum age of 419 Ma.

The minimum age may not contradict the age of the oldest known tetrapodomorph, *Tungsenia*, which is Pragian in age (Lu et al., 2012); the beginning of the Pragian is dated to 410.8 ± 2.8 Ma, its end to 407.6 ± 2.6 Ma (ICS). However, the minimum age is clearly younger than the oldest known dipnomorphs. The oldest known specimens have been referred to *Youngolepis* and come from the lower part of the Xishancun Fm (Zhu and Fan, 1995). This formation is generally (e.g. Choo et al., 2017; Liu et al., 2017 "2018"; and references therein) considered to represent the lower third or less of the Lochkovian stage, its bottom coinciding with the Silurian-Devonian boundary, which is currently dated to 419.2 ± 3.2 Ma (ICS). However, Zhang et al. (2014) placed it in the middle of the immediately preceding Přídolí stage, which began 423.0 ± 2.3 Ma ago (ICS). Needing a single number to summarize this uncertainty, I suggest a hard minimum age of 420 Ma for Node 104, the divergence of Dipnomorpha and Tetrapodomorpha. (This is a revision stratigraphically downward from the 410 Ma recommended by Marjanović and Laurin, 2007.)

A maximum age is difficult to assign. The abovementioned Kuanti Fm, which is universally (Zhang et al., 2014) regarded as representing an early part of the Ludfordian stage which preceded the Přídolí, has yielded several crown-group gnathostomes, but the sample seems too small to tell whether the absence of dipno- and tetrapodomorphs is real. Only one even partial articulated crown-group gnathostome is known from any other Ludfordian site in the world (*Yealepis*, which lies on the chondrichthyan stem: Burrow and Young, 1999). Comparably rich sites older than the Ludfordian have not been discovered. I cannot recommend any particular maximum age for this calibration point, other than by implication the maximum age of the root node (475 Ma, see above).

2.1.4 Node 105: crown group of Tetrapoda (Amphibia – total group of Amniota)

The divergence between the ancestors of lissamphibians and those of amniotes was assigned a minimum age of 330.4 and a maximum of 350.1 Ma.

For a long time, the oldest crown-group tetrapod was thought to be the supposed stem-amphibian *Lethiscus*, which is mid-Viséan in age (Smithson et al., 2012, and references therein; the Viséan lasted from 346.7 ± 0.4 to 330.9 ± 0.2 Ma ago: ICS). More likely, *Lethiscus* and the other aïstopods are rather early-branching stem-tetrapods (Pardo et al. 2017, 2018 "2019"; Clack et al., 2019). Whether *Casineria* from a geographically (southeastern Scotland) and stratigraphically close site (mid-late Viséan: Paton et al., 1999; Smithson et al., 2012) can replace it in that function depends on two unresolved issues: its own phylogenetic position, for which estimates range from very close to

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Amniota (in the tetrapod crown-group) into Temnospondyli (Marjanović and Laurin, 2019, and references therein; Clack et al., 2019); and the controversial phylogenetic position of Lissamphibia in the tetrapod tree (Marjanović and Laurin, 2019; Danto et al., 2019; and references in both), which determines whether the temnospondyls are crown-tetrapods or rather distal stem-group members.

Anderson et al. (2015) reported a number of isolated anthracosaur (embolomere and/or eoherpetid) bones from a mid-Tournaisian site (the Tournaisian preceding the Viséan and beginning at the Devonian/Carboniferous boundary 358.9 ± 0.4 Ma ago: ICS). Whether these are crown-group tetrapods depends on the relative positions of temnospondyls, anthracosaurs and other clades in that region of the tree (Pardo et al., 2018 "2019"; Marjanović and Laurin, 2019; and references in both) in addition to the position of Lissamphibia: even if the lissamphibians are temnospondyls, the anthracosaurs may still be stem-tetrapods.

The same site has yielded tetrapod trackways, some of which are tetradactyl (Smithson et al. 2012, and references therein). Among Paleozoic tetrapods, tetradactyly is only known among "microsaurs" (including lysorophians), scincosaurids, some urocordylids, temnospondyls and *Colosteus*. (Reports of tetradactyl limbs in diplocaulids have been erroneous: Milner, 2019; Marjanović and Laurin, 2019, and references therein.) *Colosteus* and probably (Clack et al., 2019) the urocordylids were stem-tetrapods, but both were fully aquatic, thus unlikely to leave trackways; "microsaurs" and probably scincosaurids were crown-tetrapods, and most were amphibious to terrestrial; temnospondyls spanned the full range of lifestyles, but see above for their phylogenetic position. In short, whether tetradactyl trackways are evidence of crown-group tetrapods in the mid-late Tournaisian remains unclear.

The oldest uncontroversial crown-group tetrapod is thus *Westlothiana* from close to the end of the Viséan (Marjanović and Laurin, 2019, and references therein, especially Smithson et al., 1994, 2012). Other tetrapods from the same site and age may or may not belong to the crown-group: whether the temnospondyl *Balanerpeton* (Milner and Sequeira, 1994; Schoch and Milner, 2014) is a crown-group tetrapod depends on the resolution of the abovementioned controversy about Lissamphibia; likewise, see above on the "anthracosaur-grade" (Marjanović and Laurin, 2019) animals *Silvanerpeton* and *Eldeceeon*; *Kirktonecta* (Clack, 2011) is likely a crown-group tetrapod, but (like *Eldeceeon*) it needs to be fully prepared or μCT-scanned before a confident assessment can be made.

Thus, the hard minimum age may be as young as roughly 335 Ma (mid-late Viséan) or as old as roughly 350 Ma (early-middle Tournaisian) depending on two phylogenetic problems. I have used both in separate analyses to test the sensitivity of the results to this calibration.

The few Tournaisian tetrapod sites discovered so far (Smithson et al., 2012; Anderson et al., 2015; Clack et al., 2016) have not yielded any uncontroversial crown-group tetrapods, temnospondyl bones or temnospondyl footprints; thus, if the temnospondyls are stem-tetrapods, the ages of these sites (up to roughly 350 Ma) may be useful as a maximum age. However, they represent a very small region of the Carboniferous globe, so I continue (Marjanović and Laurin, 2019) to caution against this regardless of the phylogenetic issues. Rather, the richer and better studied Famennian (end-Devonian) record, which has not so far yielded tetrapods close to the crown-group but has yielded more stemward tetrapods and other tetrapodomorphs (Marjanović and Laurin, 2019), should be used to place a soft maximum age around very roughly 365 Ma.

2.1.5 Node 106: Amniota (Theropsida – Sauropsida)

The cladogenesis that separated the total group of mammals (Theropsida: Goodrich, 1916) from the total group of diapsids including turtles (Sauropsida: Goodrich, 1916) was assigned a minimum age of 288 Ma and a maximum age of 338 Ma.

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This minimum age is rather puzzling. I am not aware of any doubts on the membership of *Hylonomus* in Sauropsida since its redescription by Carroll (1964), except the very vague ones presented by Graur and Martin (2004) and taken from even more outdated literature. Because of its late Bashkirian age, this calibration has often been dated to 310 Ma (as discussed by Graur and Martin, 2004). Currently (ICS), the Bashkirian is thought to have ended 315.2 ± 0.2 and begun 323.2 ± 0.4 Ma ago, and the site (Joggins, Nova Scotia) that has yielded *Hylonomus* has been dated to 317–319 Ma (Carpenter et al., 2015); thus, given the fairly highly nested position of *Hylonomus* (Müller and Reisz, 2006; though note that wider amniote phylogeny was not tested), I suggest a hard minimum age of 318 Ma for this calibration.

There appears to be synapsid theropsid material from the same site (Carroll, 1964; Mann et al., in revision). I should also emphasize that the next younger sauropsids and theropsids older than 288 Ma come from several sites in each following geological stage (Moscovian through Artinskian) and represent a considerable diversity; from the Moscovian alone, four sites of successive ages are known that present more or less complete skeletons of uncontroversial amniotes, namely sauropsids closely related to Diapsida and *Hylonomus* (*Anthracodromeus*, *Brouffia*, *Cephalerpeton*, *Paleothyris*), the oldest "parareptile" (*Carbonodraco*) as well as what appears to be the sister-group to most other sauropsids (*Coelostegus*), and, on the theropsid side, ophiacodontid synapsids (*Echinerpeton*; *Archaeothyris* from two sites). This implies ghost lineages for several other amniote clades that might not have lived in coal swamps; several of these show up in the fossil record of the next and last two stages of the Carboniferous, which ended 298.9 ± 0.15 Ma ago (ICS). For more information on the Carboniferous amniote record see Reisz and Modesto (1996: fig. 3), Müller and Reisz (2006), Mann and Paterson (2019) and Mann et al. (2019), the middle two with phylogenetic analyses, and references in all four. Additionally, the oldest known diadectomorphs date from the Kasimovian ("Missourian" in Kissel, 2010) which follows the Moscovian; they may represent the sister-group of Amniota, or they may be non-synapsid theropsids (Marjanović and Laurin, 2019; Klembara et al., 2019; and references in both).

The absence of amniotes (and diadectomorphs) in the Serpukhovian record preceding the Bashkirian should not be given much weight for paleoecological reasons; note that "lepospondyls" like the Viséan *Kirktonecta* and *Westlothiana*, closely related to but outside Amniota, are almost unknown from this age as well (candidates were described by Carroll et al., 1991; Carroll and Chorn, 1995; Lombard and Bolt, 1999). Their absence from the somewhat richer Viséan record (discussed above) suffers in part from the same problem, in part from geographic restrictions. Thus, I refrain from recommending a maximum age other than that of the preceding Node 105, even though such an early age would imply very slow rates of morphological evolution in the earliest thero- and sauropsids.

2.1.6 Node 107: crown group of Diapsida (Lepidosauromorpha – Archosauromorpha); Node 108: Archelosauria (Pan-Testudines – Pan-Archosauria)

The origin of the diapsid crown group by a split into Lepidosauromorpha and Archosauromorpha was assigned a minimum age of 252 Ma and a maximum age of 257 Ma. Ezcurra et al. (2014; correction: The PLOS ONE Staff, 2014) agreed that the oldest unambiguous crown-group diapsid that can be clearly dated is the archosauromorph *Protorosaurus*, which is, however, 257.3 ± 1.6 Ma old as they also discussed. Therefore, they revised the minimum age to 255.7 Ma, the younger end of this confidence interval.

However, like all other phylogenetic analyses of molecular data, Irisarri et al. (2017) found the turtles to be archosauromorphs. If this is correct – note that Irisarri et al. (2017: supplementary table 5) showed that three alternative positions (within Archosauria, as lepidosauromorphs or outside at least the crown-group of Diapsida) are almost equally well supported –, the question whether

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Eunotosaurus is a member of the turtle stem (Schoch and Sues, 2017 "2018", and references therein) becomes relevant, because the earliest occurrence of *Eunotosaurus* is roughly middle Capitanian in age; the Capitanian ended 259.1 ± 0.5 Ma ago and began 265.1 ± 0.4 Ma ago, and further because *Protorosaurus* would almost certainly belong to the archosaur total group and thus calibrate node 108, not 107.

Given that I am trying to date the tree of Irisarri et al. (2017), I set the hard minimum age of Archelosauria (Node 108) as 263 Ma, the approximate midpoint of the Capitanian. But in general I have to, at our current level of understanding, recommend against using either of these two nodes as a calibration. The reason are two major uncertainties about the topology of the phylogenetic tree. First, if *Eunotosaurus* has moved from the "parareptiles" well outside Diapsida to the turtle stem within the crown group of Diapsida, do any other "parareptiles" follow it? The oldest known member of that assemblage comes from the site of Linton in Ohio (Mann et al., 2019), which is about 307–308 Ma old (compare Reisz and Modesto, 1996, and Carpenter et al., 2015), so that should be the minimum age of Archelosauria if all "parareptiles" are archelosaurs; the currently available phylogenies of "parareptiles" (Laurin and Piñeiro, 2018; MacDougall et al., 2019) did not adequately test this question. While Schoch and Sues (2017 "2018") did test the mutual relationships of "parareptiles", *Eunotosaurus* and diapsids and found *Eunotosaurus* nested in the latter, several nodes away from the former, these nodes were very poorly supported. The character and taxon samples of all existing matrices for analyses of amniote phylogeny need to be substantially improved (Ford and Benson, 2018 "2019"; Laurin and Piñeiro, 2018; MacDougall et al., 2019; Mann et al., 2019). Second, I have mentioned the uncertainty over the relationships of lepidosaurs, archosaurs and turtles in the trees of Irisarri et al. (2017); they are large enough that we may look at morphological data as a further source of information, and the available analyses of morphological data (Schoch and Sues, 2017 "2018") have not resolved whether the turtles or the rather long branch of the lepidosauromorphs lies closer to Archosauria.

The maximum age of either node is likewise difficult to narrow down. Uncontroversial diapsids have a notoriously patchy Paleozoic record; the same holds for "parareptiles", which have only two known Carboniferous records so far (Modesto et al., 2015; Mann et al., 2019). I cannot express confidence in a maximum age other than that of Node 106, which I cannot distinguish from the maximum age of Node 105 as explained above. This leaves Node 107 without independent calibrations in the current taxon sample.

2.1.7 Node 109: Archosauria (crocodile total group – bird total group)

The origin of Archosauria by cladogenesis into the total group of crocodiles and birds was given a minimum age of 243 Ma and a maximum age of 251 Ma.

The earliest known archosaur, belonging to the crocodile stem, is *Ctenosauriscus* from just before the end of the Olenëkian (Butler et al., 2011). The age of the Olenëkian/Anisian (Early/Middle Triassic) boundary is given in the ICS as 247.2 Ma without a confidence interval; any such confidence interval cannot be long, however, because an Olenëkian sample has been dated to 247.32 ± 0.08 Ma, while an Anisian sample has been dated to 247.08 ± 0.11 Ma (Maron et al., 2018 "2019"). Given the highly nested phylogenetic position of *Ctenosauriscus* in Archosauria (Butler et al., 2011), I propose 248 Ma as the hard minimum age of this calibration.

I accept the Permian-Triassic boundary (251.902 ± 0.024 Ma: ICS; rounded to 252) as the soft maximum age on the grounds that a major radiation of archosauromorphs at the beginning of the Triassic seems likely for ecological reasons: the Permian record, up to its very end, is full of synapsid theropsids that seem ecologically comparable to Triassic archosaurs, and given the Pangea situation of the time it seems reasonably unlikely that archosaurs existed in unsampled localities. I must

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caution, however, that the fossil record of archosauromorphs and possible archosauromorphs in the four million years of the Triassic preceding the minimum age, and in the Permian, is very patchy, with a poor fit between stratigraphy and phylogeny.

2.1.8 Node 111: Alligatoridae (Alligatorinae – Caimaninae)

The origin of Alligatoridae (the crown group of Brevirostres) by split into Alligatorinae and Caimaninae was given a minimum age of 66 Ma and a maximum age of 75 Ma.

The minimum age would fit well with the finding by Cossette and Brochu (2018) that *Bottosaurus* from the very end of the Cretaceous is a caimanine. Given, however, the limited material and the stratigraphic gap between *Bottosaurus* and the next younger known caimanines, Cossette and Brochu (2018) expressed doubt about the result of their phylogenetic analysis which placed *Bottosaurus* not only within the caimanine crown-group but next to the extant *Paleosuchus*.

If *Bottosaurus* is not an alligatorid at all, the oldest known member is the alligatorine *Navajosuchus* from within the first million years of the Paleocene (Puercan NALMA [North American Land Mammal Age]), translating to a hard minimum age of 65 Ma (Wang et al., 2016, and references therein). The oldest known caimanines (*Protocaiman*, *Eocaiman paleocenicus* and *Necrosuchus*: Bona et al., 2018) follow shortly thereafter (Peligran SALMA [South American Land Mammal Age], 64–63 Ma ago: Woodburne et al., 2014).

Halliday et al. (2013), however, found the Campanian to Maastrichtian *Brachychampsa* to be an alligatorine, as did Arriba et al. (2019) in a less densely sampled analysis of Crocodyliformes; Bona et al. (2018) found it and the newly added Campanian *Albertochampsa* to be caimanines. In either of these cases, the earliest record of an alligatorid is *Brachychampsa sealeyi* from early in the Campanian, which began 83.6 ± 0.2 Ma ago (ICS). These results were not replicated by Lee and Yates (2018) or by Groh et al. (2019), who both found *Brachychampsa* on the brevirostrine stem, not as an alligatorid, and who both did not include *Albertochampsa* in their datasets. I must caution, however, that Groh et al. (2019) found Alligatorinae, and even *Alligator* itself, as a Hennigian comb in which Caimaninae was nested; this result strongly suggests that the character sample was insufficient to resolve Brevirostres.

Given this uncertainty, I have used a hard minimum age of 65 Ma for present purposes, but generally recommend against using this cladogenesis as a calibration for timetrees.

Up to (and including) the Campanian, the record of neosuchians is a surprisingly spotty affair (e.g. Tykoski et al., 2002; Mateus et al., 2018 “2019”). Although a Late Cretaceous age of Alligatoridae (i.e. less than 100.5 Ma: ICS) is likely, I cannot, therefore, assign a maximum age younger than the Triassic/Jurassic boundary, i.e. twice as old (201.3 ± 0.2 Ma: ICS; rounded to 200). Only in the Triassic is the record of ecologically comparable phytosaurs dense enough to really rule out the presence of amphibious crocodylomorphs such as alligatorids. However, I have treated this maximum as hard because the likelihood that the true age approaches it is very low.

2.1.9 Node 113: crown group of Neognathae (Gallanseres – Neoaves)

The last common ancestor of *Anas*, *Gallus* and *Meleagris* on one side and *Taeniopygia* on the other was assigned a minimum age of 66 Ma and a maximum age of 86.5 Ma.

The oldest known crown-group neognath appears to be the presbyornithid stem-anseriform (Elżanowski, 2014; Tambussi et al., 2019) *Teviornis* from somewhere low in the Late Cretaceous Nemegt Fm of Mongolia; it is known only from a carpometacarpus, two phalanges and the distal end of a humerus that all seem to belong to the same right wing (Kurochkin et al., 2002). The most recent

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work on the specimen has bolstered its presbyornithid identity (De Pietri et al., 2016), even though the next younger presbyornithids are middle or late Paleocene (i.e. younger than 61.6 Ma: ICS).

The age of the Nemegt Fm is difficult to pin down; radiometric dating of this or adjacent formations has not been possible, and the only fossils available for biostratigraphy are vertebrates that have to be compared to those of North America where marine correlations and radiometric dates are known. These comparisons favor a vaguely early Maastrichtian age, without ruling out a Campanian component. Magnetostratigraphic evidence was reported in a conference abstract by Hicks et al. (2001); I have not been able to find a follow-up publication. Hicks et al. (2001) stated that the sampled sections from the Nemegt and the conformably underlying Baruungoyot Fm "can be quite reliably correlated to the Geomagnetic Reversal Time Scale […] and clearly lie in the Campanian/Maastrichtian interval that extends from the uppermost part of subchron C33n, through chron 32 into the lower half of chron 31." Where on this scale the Baruungoyot/Nemegt boundary lies was not mentioned. The upper boundary of the Nemegt Fm is an unconformity with a Paleocene formation.

Hicks et al. (2001) also worked on the Late Cretaceous Djadokhta Fm, finding that "a distinct reversal sequence is emerging that allows us to correlate the sections in a preliminary way to the late Campanian through Maastrichtian interval that ranges from C32 to C31." While I have not been able to find a publication by an overlapping set of authors on this finding, it agrees at least broadly with Dashzeveg et al. (2005: 18, 26, 27), whose own magnetostratigraphic work on the Djadokhta Fm indicated "that the sediments were deposited during the rapid sequence of polarity changes in the late part of the Campanian incorporating the end of Chron 33 and Chron 32 between about 75 and 71 Ma […]. However, this tentative correlation to the Geomagnetic Polarity Timescale cannot yet be certainly established." Hasegawa et al. (2008 "2009") disagreed with the stratigraphy by Dashzeveg et al. (2005), but not with their dating.

Most often, the Djadokhta Fm has been thought to underlie the Baruungoyot Fm, but a contact between the two has not so far been identified (Dingus et al., 2008; cited without comment e.g. by Chinzorig et al., 2017); they could be party coeval (references in Hasegawa et al., 2008). Still, it seems safe to say that most of the Nemegt Fm is younger than most of the Djadokhta Fm.

According to Milanese et al. (2018 "2019": fig. 12), the Campanian-Maastrichtian boundary (72.1 ± 0.2 Ma ago: ICS) lies near the end of chron 32. The Djadokhta Fm thus corresponds to the end of the Campanian, the Baruungoyot Fm should have at most the same age, and the youngest magnetostratigraphic sample from the Nemegt Fm, in the earlier half of chron 31, should be about 70 Ma old. Given the stratigraphic position of *Teviornis* low within the formation and its nested phylogenetic position within Neognathae, I propose 71 Ma (within the same subchron as 70 Ma: Milanese et al., 2018: fig. 12) as the soft minimum age of the present calibration.

Should the fragmentary *Teviornis* fall out elsewhere, the minimum age would remain in the Maastrichtian: *Vegavis*, *Polarornis* and *Neogaeornis* seem to be stem-anseriforms as well (Agnolín et al., 2017; Tambussi et al., 2019; though see Mayr et al., 2018), and all three come from the late Maastrichtian (Clarke et al., 2005; Salazar et al., 2010).

As the soft maximum age I tentatively suggest 115 Ma, an estimate of the mid-Aptian age of the (likewise terrestrial) Xiagou Fm of northwestern China, which has yielded a diversity of stem-birds but no particularly close relatives of the crown (Wang et al., 2013; Bailleul et al., 2019; and references therein).

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2.1.10 Node 117: Testudines (Panpleurodira – Pancryptodira)

The origin of the turtle crown group by split into the pleurodiran and cryptodiran total groups was assigned a minimum age of 210 Ma and no maximum age.

The calibration dates treated above are all too young (some substantially so, others by just a few million years). This one, in contrast, is far too old. It rests on the outdated interpretation of the Norian (Late Triassic) *Proterochersis* as a stem-panpleurodire. With one short series of exceptions (Gaffney et al., 2006, 2007; Gaffney and Jenkins, 2010), all treatments of Mesozoic turtle phylogeny from the 21st century have consistently found *Proterochersis* and all other turtles older than Late Jurassic to lie outside the crown group (Joyce et al., 2016; Sterli et al., 2018; and references therein, in Gaffney and Jenkins, 2010, and in Romano et al., 2014a). The oldest known securely dated crown-group turtle is thus the mid-late Oxfordian stem-panpleurodire *Caribemys* (de la Fuente and Iturralde-Vinent, 2001; Joyce et al., 2016). The Oxfordian ended 157.3 ± 1.0 Ma ago (ICS), so I propose 158 Ma as the hard minimum age for this calibration.

The stem-trionychian cryptodire *Sinaspideretes* (Tong et al., 2013 "2014") may have the same age or be somewhat older. Of the three known specimens, at least one (the exact localities where the type and the other specimen were found are unknown) comes from the Upper (Shang-) Shaximiao Fm (Tong et al., 2013 "2014"), which conformably overlies a sequence of two Middle Jurassic formations and is overlain by two Upper Jurassic formations (Tong et al., 2011 "2012"; Xing et al., 2013), so it should be about Oxfordian to Callovian in age. The biostratigraphic evidence for the age of the Upper Shaximiao Fm is conflicting; there is no consensus on whether it is Middle or Late Jurassic (Xing et al., 2013). It is of course possible that the formation spans both epochs or more with its four members; but Tong et al. (2013 "2014") did not state which member the *Sinaspideretes* specimen in question comes from.

Be that as it may, the unambiguously Middle Jurassic record of turtles very close to but outside the crown group is actually quite rich in Asia (Tong et al., 2011 "2012"; Joyce et al., 2016; and references therein), meaning that at least the observed absence of cryptodires is likely real; combining this with more rootward Middle and Early Jurassic stem turtles from other continents (see Sterli et al., 2018), I suggest a hard maximum age of 175 Ma based on the beginning of the Middle Jurassic (174.1 ± 1.0 Ma ago: ICS).

2.1.11 Node 124: Pleurodira (Pan-Chelidae – Pan-Pelomedusoides)

Citing a source from 2006, the origin of Pleurodira by the cladogenesis that generated Pan-Chelidae (represented by *Phrynops*) and Pan-Pelomedusoides (represented by *Pelusios*) was given a minimum age of 25 Ma and no maximum age.

I have not tried to trace what misunderstanding lies at the root of this perplexing number. Pleurodira has long been known to extend into the Early Cretaceous (reviewed by Pérez-García, 2019); pan-podocnemidids within Pelomedusoides have a particularly rich fossil record. At present, the oldest known pleurodire is the late Barremian pan-podocnemidid *Atolchelys* (Romano et al., 2014a; Ferreira et al., 2018; Pérez-García, 2019), conveniently suggesting a hard minimum age of 125 Ma for this calibration (Romano et al., 2014a; ICS).

Due to the fairly highly nested position of *Atolchelys* within Pleurodira (whether or not it is a bothremydid – Romano et al., 2014a; Cadena, 2015; Ferreira et al., 2018), and due to the somewhat sparse record of stem-pleurodires (from the Late Jurassic onwards: Romano et al., 2014a; Cadena, 2015; Pérez-García 2019), I agree with Irisarri et al. (2017) in not assigning a maximum age other than that of Node 117.

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2.1.12 Node 125: Lepidosauria (Rhynchocephalia – Squamata)

The minimum age of this calibration, given as 238 Ma, has to be slightly revised to 244 Ma (hard) based on *Megachirella*, the oldest known stem-squamate (Renesto and Bernardi, 2013 "2014"; Simões et al., 2018: table S2), which is older than the oldest known rhynchocephalian (238–240 Ma: Jones et al., 2013).

An Early Triassic or perhaps Late Permian maximum age seems reasonable, but, given the rarity of stem-lepidosauromorphs and of Permian diapsids in general, I rather propose to use the ecologically similar small amniotes of Richards Spur (289 ± 0.68 Ma, see Node 107) to support a soft maximum age of 290 Ma.

2.1.13 Node 129: Toxicofera (Pythonomorpha – Anguimorpha incl. Iguanomorpha)

This calibration was given a minimum age of 148 Ma and no maximum age.

The oldest known total-group snake (pythonomorph) is currently the Bathonian ophidian *Eophis* (Caldwell et al., 2015; Martill et al., 2015; by implication Conrad, 2017 "2018"); as the Bathonian began 168.3 ± 1.3 Ma ago and ended 166.1 ± 1.2 Ma ago, i.e. with uncertainty ranges that overlap in the middle (ICS), the suggestion of 167 Ma by Caldwell et al. (2015) is a reasonable hard minimum age for this calibration. The oldest known uncontroversial angui- and iguanomorphs (see below) are considerably younger, and so is the Cretaceous assemblage of marine squamates (mosasaurs, dolichosaurs, pontosaurs etc.) whose positions as angui- or pythonomorphs are controversial.

Given the sparse fossil record of Jurassic squamates, in particular the apparent lack or near-lack of a fossil record for Early Jurassic or Late Triassic squamates (see below), I agree with Irisarri et al. (2017) in not assigning a maximum age other than that for Node 125.

2.1.14 Node 131: Iguania (Chamaeleoniformes – Iguanoidea)

The origin of Iguania, the crown group of Iguanomorpha, by cladogenesis into Chamaeleoniformes and Iguanoidea was assigned a minimum age of 165 Ma and a maximum age of 230 Ma.

Tikiguania was described as a Late Triassic acrodontan (crown-group chamaeleoniform). Not only is it an acrodontan, it is a draconine agamid (Hutchinson et al., 2012); most likely, therefore, the very well preserved isolated lower jaw is not a fossil, but belongs to one of the extant draconine species that live on the site, and fell into the screenwashing sample (Hutchinson et al., 2012).

Bharatagama is known (Evans et al., 2002) from at least 85 maxilla and dentary fragments (with supposed genuine absence of the splenial and supposed fusion of the angular to the dentary) that undoubtedly come from the Upper Member of the Kota Fm in Andhra Pradesh (India), for which, on the balance of conflicting biostratigraphic evidence (Prasad and Manhas, 2007; Prasad et al., 2014), a late Middle Jurassic age seems most likely (notwithstanding the fact that the Lower Member conformably overlies the Dharmaram Fm, which extends down into the Triassic as shown by its phytosaurs and aëtosaurs: Goswami et al., 2016 "2018"). Even so, this age (i.e. 163.5 ± 1.0 Ma or older: ICS) is old enough by comparison to the iguanomorph fossil record and the position of Iguanomorpha in all molecular phylogenies (including Irisarri et al., 2017) that Jones et al. (2013: 15), whose molecular dating found Toxicofera as a whole to be younger than *Bharatagama*, stated: "It is possible that *Bharatagama* represents an early stem crown-group [sic] squamate with a jaw morphology convergent with modern acrodont [= acrodontan] iguanians, or that it belongs to another clade." Simões et al. (2017) cited these doubts without further comment. Evans et al. (2002: 306) listed a number of features shared by acrodontans and sphenodontians; three of these do not occur in the Cretaceous priscagamid stem-chamaeleontiforms, but all are found in *Bharatagama*. Although no

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known sphenodontian is a good match (Evans et al., 2002), I very tentatively suggest that *Bharatagama* could represent a morphologically innovative clade of *Diphydontosaurus*-grade sphenodontians. It would not lie outside the large (Reynoso, 2005, and references therein) sphenodontian morphospace: the shape, size, implantation and attachment of the distal teeth recalls *Clevosaurus* (depicted in Evans et al., 2002), while the shape and size of the mesial teeth is reminiscent of *Sphenovipera* (Reynoso, 2005). Indeed, the one phylogenetic analysis that has ever included *Bharatagama* found it as a rhynchocephalian rather than a squamate, although close to the pleurosaurs (despite the more *Diphydontosaurus*-like plesiomorphic gradient of tooth implantation) and, not surprisingly given the limited material, with weak support (Conrad, 2017 "2018"). In sum, the optimism of Scarpetta (2019) is unwarranted, and the status of *Bharatagama* as a chamaeleoniform is too doubtful for use in calibration.

Xianglong from the Yixian Fm of Liaoning (China), which dates to around the Barremian-Aptian boundary (~ 125.0 Ma: ICS), was described as a chamaeleoniform, possibly an acrodontan (Li et al., 2007). Unfortunately, this rests on very limited evidence, as the one known individual is clearly juvenile and much of the skeleton remains unknown because is covered by exquisitely preserved soft tissue and has not been µCT-scanned (Li et al., 2007; Simões et al., 2017, Scarpetta, 2019, and reference therein).

Daza et al. (2016) briefly described three isolated hindlimbs from Burmese amber (99 Ma old: Daza et al., 2016) as agamids, and a largely complete articulated skeleton as a chamaeleonid. The supposed chamaeleonid later turned out to be an albanerpetid amphibian (Matsumoto and Evans, 2018: 52–53), which may explain the unexpected shape of the palate (Daza et al., 2016: fig. 4K), and the supposed agamids are so incomplete that they probably provide more ecological than phylogenetic information; indeed, the only supposed chamaeleoniform Daza et al. (2016) included in their phylogenetic analysis was the albanerpetid. Therefore, again unlike Scarpetta (2019), I do not think any of these four specimens can be used to calibrate divergence dates.

Priscagamidae is a Campanian clade (from the Djadokhta, Baruungoyot and more or less coeval formations; see above and Borsuk-Białynicka, 1996) of squamates that have usually been considered stem-chamaeleoniforms (most recently found as such by Simões et al., 2018), but have also been found as stem-iguanomorphs (Conrad, 2015, with much denser sampling of early iguanomorphs than Simões et al., 2018).

A consensus now appears to exist (Simões et al., 2015; Conrad, 2015) that Gobiguania (Conrad and Norell, 2007) is a clade of stem-iguanomorphs.

"*Ctenomastax*" Gao and Norell, 2000, a junior homonym of the staphylinid beetle *Ctenomastax* Kraatz in von Heyden, 1870, is likewise known from the Djadokhta and Baruungoyot formations; probably due to the poor preservation of the specimens (Gao and Norell, 2000), it has variously been found as the sister-group of all other chamaeleoniforms (Simões et al., 2015; Reeder et al., 2015) or as a gobiguanian stem-iguanomorph (Conrad, 2015). In the latter case it cannot date the origin of Iguania.

Isodontosaurus, from the Djadokhta Fm and more or less coeval sites, is known from fairly large amounts of material representing much of the skeleton, but its phylogenetic position has been hard to determine (Gao and Norell, 2000); Conrad (2015) found it as a stem-chamaeleoniform iguanian, Reeder et al. (2015) as a gobiguanian.

Alifanov (2013) described *Desertiguana* as a phrynosomatid pleurodontan iguanian based on an almost complete left lower jaw from the Baruungoyot Fm. Curiously, it has been summarily ignored ever since by everyone other than its author (in single-authored publications that do not provide further information), except for a citation as an iguanomorph without any comment by Head (2015).

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Given that Alifanov (2013) also classified three other Djadokhta/Baruungoyot genera otherwise considered gobiguanians as phrynosomatids, I cannot be certain that *Desertiguana* is not a gobiguanian stem-iguanomorph as well.

Equally Campanian or older (summarized in Langer et al., 2019) is the stem-chamaeleoniform *Gueragama* (Simões et al., 2015, 2017). Known from an isolated but largely complete lower jaw, it appears to suffice for setting up a hard minimum age for Iguania at the Campanian/Maastrichtian boundary (72.1 ± 0.2 Ma: ICS), which I round to 72 Ma. I cannot assign a maximum age other than that for Node 125.

Apesteguía et al. (2016) described *Jeddaherdan* from a Cenomanian jaw fragment. Using a dataset entirely restricted to iguanians, their parsimony analysis recovered it as a chamaeleoniform rather than an iguanoid (the only other option) and did not resolve it further until implied weighting was applied, which placed *Jeddaherdan* in a clade with *Gueragama* and the extant agamid *Uromastyx*. Bayesian inference recovered the same content for Uromastyginae, although with rather low support (posterior probability of 0.8). As the authors pointed out, this topology implies that the occurrence of tooth replacement in *Gueragama* is a reversal. Given the very limited material, the taxon sample which presupposes that *Jeddaherdan* is an iguanian, the constraints on the applicability of implied weighting and the poorly understood performance of Bayesian inference with missing data distributed by body part (Marjanović and Laurin, 2019, and references therein), as well as the implications for *Gueragama*, I prefer not to use *Jeddaherdan* to date the origin of Iguania as long as further material has not been discovered.

2.1.15 Node 132: Pleurodonta (Iguanidae + Corytophanidae – Dactyloidae + Phrynosomatidae)

The origin of Pleurodonta, the crown group of Iguanoidea, was given a minimum age of 125 Ma and a maximum age of 180 Ma.

The oldest possible pleurodontan other than the abovementioned *Desertiguana* is, however, *Suzanniwana patriciana* from the Paleocene-Eocene boundary (56.0 Ma ago: ICS). Unfortunately, its phylogenetic position remains unclear: Conrad (2015) stated that *Suzanniwana* was one of the two "taxa with the most volatile positions within this analysis", but only published the Adams consensus of that analysis, which shows *Suzanniwana* as part of a polytomy that also contains Corytophanidae and a clade containing all other extant pleurodontans – whether *Suzanniwana* remains inside Pleurodonta in all of the 98 most parsimonious trees or is placed as the sister-group of Pleurodonta in some could only be determined by repeating the analysis.

The oldest certain pleurodontan is the very highly nested *Afairiguana*, which forms an exclusive clade with the extant *Polychrus* and Dactyloidae in Conrad's (2015) analysis and is 51.66 Ma old (Smith et al., 2008). Followed by the highly nested corytophanid *Babibasiliscus* and the less highly nested corytophanid *Geiseltaliellus* (Conrad, 2015) within the next five million years, it establishes a very tight hard minimum age of 52 Ma for this calibration point.

If *Desertiguana* is not a pleurodontan, the absence of pleurodontans might suggest a late Campanian maximum age for Pleurodonta. But as this possibility cannot be excluded at present, even apart from unknown geographic or ecological factors that could have kept pleurodontans out of the environments that deposited the Campanian and Maastrichtian formations of Asia and North America, I find myself unable to assign a maximum age other than, again, that for Node 125.

Burbrink et al. (accepted) found extremely short internal branch lengths for the basal radiation of Pleurodonta. Paleoecologically, the recovery phase immediately after the Cretaceous-Paleogene boundary suggests itself as the time of such a radiation. But this idea remains to be tested.

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2.1.16 Node 150: Mammalia

The origin of the crown-group Mammalia by the divergence of Proto- or Yinotheria (Shuotheriidae and Australosphenida) on one side, represented by *Ornithorhynchus*, and a large clade called Theriiformes or Yangotheria, which comprises Theria (to which all extant mammals except the monotremes belong), Spalacotheroidea, Meridiolestida, Dryolestidae, Multituberculata, (Eu)triconodonta and many others, on the other side, was assigned a minimum age of 162.5 Ma and a maximum age of 191.4 Ma.

The phylogenetic position of Haramiyida, a clade that reaches beyond these ages into the Late Triassic, is controversial; of the latest analyses, Huttenlocker et al. (2018) and Zhou et al. (2019: supp. inf. M) have found it just outside Mammalia, but Wang et al. (2019) and Mao et al. (2019: supp. inf.), citing neither of these and clearly not using their findings but using previously unknown data, found them inside.

The oldest uncontroversial mammals are the australosphenidan proto-/yinotherians *Asfaltomylos* and *Henosferus* and the volaticotherian (eu)triconodont *Argentoconodon*, which all come from a level that was originally thought to be high in the Cañadón Asfalto Fm and to be Callovian or even Oxfordian (late Middle or early Late Jurassic) in age, but has more recently been correlated to its very bottom, the transition with the underlying Lonco Trapial Fm (Cúneo et al., 2013), from which three successive (from lowest to highest) U-Pb zircon dates were determined by Cúneo et al. (2013): 178.766 ± 0.23 Ma, 177.37 ± 0.12 Ma and 176.15 ± 0.24 Ma. These are maximum ages in that reworked zircon crystals occur in these lacustrine tuff beds, so that the youngest crystals, from which the cited ages were derived, could still be older than the deposition of the tuff beds themselves; however, given the correlation of the recovered ages with stratigraphic height, and the rarity of older zircons in the oldest and the youngest sample (Cúneo et al., 2013), a large discrepancy is unlikely. Therefore, I recommend a hard minimum age of 179 Ma for this calibration.

The maximum age assigned by Irisarri et al. (2017) may be intended to represent the Sinemurian/Pliensbachian boundary (190.8 ± 1.0 Ma: ICS). Indeed, the Sinemurian record of mammalomorphs (tritylodontids, tritheledontids, *Sinoconodon*, morganucodontans, *Hadrocodium*) from North America, southern Africa and China is fairly rich and diverse, but has not yielded crown-group mammals so far. However, ghost lineages encompassing almost the entire Early Jurassic to the middle of the Middle Jurassic occur for haramiyidans and docodonts, both of which have been found in the Rhaetian and the Bathonian, but not so far in between; and while the Rhaetian and/or possibly Norian *Thomasia* and *Haramiyavia* lie outside the smallest clade of all other haramiyidans, *Tikitherium* is the sister-group of all Jurassic docodonts except the probably Middle Jurassic *Gondtherium* (Zhou et al., 2019: supp. inf. M), requiring two such ghost lineages within Docodonta. All this may be especially relevant if Haramiyida, rather than the Sinemurian *Hadrocodium*, is the sister-group of Mammalia. Currently, the former is recovered by parsimony, the latter by Bayesian analysis of the same matrix (Huttenlocker et al., 2018: extended data fig. 9; Zhou et al., 2019: supp. inf. M), neither option having strong support by its own criteria; for a comparison between the methods as applied to paleontological datasets, see Marjanović and Laurin (2019). Preferring to err on the side of caution, I place the hard maximum age in the Carnian Pluvial Episode 233 Ma ago (Maron et al., 2018 “2019”), which is also substantially older than all possible haramiyidans.

2.1.17 Node 151: Theria (Metatheria – Eutheria)

The origin of Theria by the split into the total groups Metatheria (crown group: Marsupialia) and Eutheria (crown group: Placentalia) was given a minimum age of 124.6 Ma and a maximum age of 138.4 Ma.

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The oldest securely dated eutherian is *Ambolestes* at 126 Ma (Bi et al., 2018). *Juramaia* was originally (Luo et al., 2011) thought to come from the Lanqi Fm, specifically a site variably called Daxigou or Daxishan (Yuan et al., 2013: supp. inf.: 4), which has meanwhile been dated to between 160.889 ± 0.069 Ma and 160.254 ± 0.045 Ma (Jia and Gao, 2019). Meng (2014: 526, 529–530), however, doubted this, called the specimen "floating", and pointed out its great similarity to *Eomaia* in particular (found as its sister-group in the very different matrices of Bi et al., 2018, and Zhou et al., 2019: supp. inf. M; Mao et al., 2019: fig. S9, did find *Juramaia* outside the clade of all other included eutherians, but did not sample *Ambolestes* despite building on the matrix of Bi et al., 2018) and to Barremian–Albian eutherians in general, as well as the long ghost lineages a mid-Oxfordian age for *Juramaia* would create within Eutheria, for Metatheria and for several of the closest relatives of Theria. Bi et al. (2018, 2019) referred to Meng (2014) for this issue but did not try to resolve it. As long as it is not resolved, I much prefer to consider the single *Juramaia* specimen to have been discovered in the Yixian Fm (like *Ambolestes*, *Eomaia* and *Acristatherium*), as suggested by Bi et al. (2019).

Sweetman et al. (2017) described two teeth from the very beginning of the Cretaceous (~ 145 Ma old) as two genera of Late-Cretaceous-grade eutherians, *Durlstotherium* and *Durlstodon*. In view of this limited material, I remain skeptical (see also Bi et al., 2018) and recommend 126 Ma as the hard minimum age for this calibration.

While the oldest uncontested metatherians are only some 110 Ma old (Bi et al., 2018), Mao et al. (2019: fig. S9) have returned *Sinodelphys* (of the same age as *Eomaia* and *Acristatherium*, slightly younger than *Ambolestes*) to its status as the oldest known metatherian. If this holds and if *Juramaia* has the same age instead of being Jurassic, and if further *Durlstotherium* and *Durlstodon* can be disregarded, virtually no ghost lineage is required at the base of Metatheria.

Accepting that *Juramaia* is not from the Lanqi Fm, I propose 160 Ma as the soft maximum age of this calibration, on the grounds that therians or their closest relatives are absent in the Lanqi and the laterally equivalent Tiaojishan Fm, likewise absent in the Kimmeridgian and Tithonian of Portugal and the US (where the Morrison Fm, sampled since the 1860s, extends across several states), and further absent in the end-Tithonian and Berriasian of England despite the diversity of ecologically comparable mammals found there. Given the strong evidence of a Laurasian origin of Theria (e.g. Huttenlocker et al., 2018; Bi et al., 2018), the earliest possible time and place for the origin of Theria that could stay out of the fossil record is therefore Asia after the deposition of the Tiaojishan and Lanqi formations ended in the Oxfordian.

2.1.18 Node 152: Placentalia (Atlantogenata – Boreo(eu)theria); Node 153: Boreo(eu)theria (Laurasiatheria – Euarchontoglires/Supraprimates)

The origin of Placentalia, the crown-group of Eutheria, was given a minimum age of 95.3 Ma and a maximum age of 113 Ma. Its immediate descendant nodes were not constrained.

The minimum age is clearly built on the assumption that the zhelestids are "ungulates", i.e. belong to Placentalia, or perhaps even that the zalambdalestids are related to Glires and therefore belong to Placentalia. For a long time now, every reinvestigation of the anatomy of these Cretaceous animals, and every phylogenetic analysis that sampled Cretaceous eutherians densely (i.e. not including Zhou et al., 2019: supp. inf. M), has found them on the eutherian stem, often not even particularly close to Placentalia (e.g. Novacek et al., 1997; Asher et al., 2005, 2019; Wible et al., 2009; Goswami et al., 2011; Halliday et al., 2015 "2017"; Manz et al., 2015; Bi et al., 2018: fig. 2, SI-1; Wang et al., 2019: ext. data fig. 5; see also Fostowicz-Frelik and Kielan-Jaworowska, 2002).

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A few terminal Cretaceous (late Maastrichtian) eutherians have been attributed to Placentalia in the past. But with *Protungulatum* (Wible et al., 2009; Halliday et al., 2015 "2017", 2019: fig. 1 contrary to the text; Manz et al., 2015: fig. 2a; Wang et al., 2019: ext. data fig. 5; Mao et al., 2019: fig. S9) and *Gypsonictops* (Halliday et al., 2015 "2017", 2019; Bi et al., 2018; Manz et al., 2015: fig. 2; Wang et al., 2019: ext. data fig. 5; Mao et al., 2019: fig. S9) now placed close to but consistently outside Placentalia, *Deccanolestes* – at least if the teeth and the tarsal bones belong together – placed far away (Goswami et al., 2011 [see there also for *Sahnitherium*]; Manz et al., 2015: fig. 2, SI-1; Penkrot and Zack, 2016; Halliday et al., 2019), and the single worn tooth named *Kharmerungulatum*, which had been assigned to Placentalia mostly through comparison to *Protungulatum* in the first place (Prasad et al., 2007), having more recently been found somewhere outside Placentalia as well ("Although none of the strict consensus trees supported the placement of *Kharmerungulatum* within the placental crown group, the limited dental material for this taxon proved insufficient for resolving its phylogenetic relationships, and so it was removed a posteriori from the MPTs to produce the reduced strict consensus trees." – Goswami et al., 2011: 16334), specifically as an adapisoriculid when full molecular constraints were applied by Manz et al. (2015: fig. 2b), the only remaining candidate for a Cretaceous placental is the stylinodontid taeniodont *Schowalteria* (Fox, 2016, and references therein). The phylogenetic position of Taeniodonta remains unknown (Fox, 2016, and references therein); a cryptic statement by Napoli et al. (2017 "2018"), preliminarily placing the group just outside Placentalia in a hand-made supertree for no explicit reason and referring to an ongoing study of eutherian phylogeny by the authors, probably refers to the phylogenetic analysis in Shelley's (2018) doctoral thesis of which only an abstract not mentioning Taeniodonta has been made publicly available (apart from the conference abstract by Püschel et al., 2019, which does not mention Taeniodonta either). Halliday et al. (2015 "2017", 2019) included the early Paleocene *Onychodectes*, the sister-group to all other taeniodonts (Fox, 2016, and references therein), in their analyses, and found it highly nested within Placentalia, but the positions themselves (next to the contemporary palaeanodont, i.e. stem-pholidotan, *Escavadodon*, but rather far from the other palaeanodonts; on the pholidotan stem when a molecular constraint was applied, but on the chiropteran stem otherwise) and the taxon sample (by far the largest sample of Paleocene eutherians so far, but no other taeniodonts and still almost none of the previously proposed closest relatives of the group) cast doubt on this result.

The same reasons make it difficult to decide which of the earliest Paleocene eutherians should be accepted as securely enough identified placentals. But in any case, Williamson et al. (2019: 220) reported that the herbivorous periptychid *Ectoconus*, estimated to have reached about 100 kg, was "present within 0.4 Ma of the K-Pg boundary"; phylogenetic analyses have found it to be not only a placental, but a laurasiatherian – Halliday et al. (2015 "2017"; regardless of constraints) found it and the other periptychids on the pholidotan stem; Halliday et al. (2019), using combined data and maximum likelihood, found a comparable result with much less resolution; Püschel et al. (2019), using a somewhat smaller matrix with, however, a focus on periptychids and new data on them (e.g. Napoli et al., 2017), recovered them as stem-artiodactylomorphs. I therefore suggest 66 Ma, the Cretaceous/Paleogene boundary (66.021 ± 0.081 Ma: Clyde et al., 2016), as the hard minimum age for Node 153, the basal node of Boreoeutheria (a name apparently coined by accident by Murphy et al., 2001) or simply Boreotheria (explicitly coined by Waddell et al., 2001). For Node 152 I cannot recommend a separate minimum age.

Given the continuing worldwide absence of unambiguous placentals in the rich Maastrichtian record (see above as well as Halliday et al., 2016, and Davies et al., 2017) and the absence of even ambiguous ones in the even richer Campanian record (other than three isolated Turonian teeth indistinguishable from both species of *Gypsonictops*: Cohen and Cifelli, 2015; Cohen, 2017), despite the presence of stem-eutherians (all northern continents and India), stem-metatherians (Asia and

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North America), and ecologically comparable spalacotheroids (Asia and North America), meridiolestidans (South America) and haramiyidans (South America, Madagascar, India, Africa), only Antarctica, Australia and New Zealand are left as paleocontinents where Campanian or Maastrichtian placentals could have escaped the fossil record, and they are all unlikely for biogeographical reasons (e.g. Huttenlocker et al., 2018). Therefore, I suggest the Campanian/Maastrichtian boundary, rounded to 72 Ma, as the hard maximum age for Node 152. (I cannot make a separate recommendation for Node 153.) This is more generous than the result of Halliday et al. (2016), 95% of whose reconstructions of the age of Placentalia were 69.53 Ma old or younger. The discrepancy to the published molecular ages (references in Halliday et al., 2016) is most likely due to the effects of body size on rates of molecular evolution (Berv and Field, 2017 "2018"; Phillips and Fruciano, 2018).

2.1.19 Node 154: Carnivora (Feliformia – Caniformia)

The origin of the crown-group Carnivora by the divergence of the sister-groups Feliformia (represented in this matrix by *Felis*) and Caniformia (represented by *Canis*) was assigned a minimum age of 42.8 Ma and a maximum age of 63.8 Ma. Irisarri et al. (2017) justified this by citing the identification of the middle Eocene *Tapocyon* as a caniform by Wesley & Flynn (2003); this should be regarded as rendered obsolete by Spaulding and Flynn (2012) and Solé et al. (2016), who found *Tapocyon* as a stem-carnivoriform in phylogenetic analyses of two successively larger versions of a much larger dataset. The analysis by Tomiya and Tseng (2016) found *Tapocyon* as a feliform, but used a much smaller sample of stem-carnivoriforms and of characters in a misguided (e.g. Kearney and Clark, 2003; Wiens, 2003; Marjanović and Laurin, 2019) attempt to avoid missing data by throwing out known data.

With "*Miacis*" *sylvestris* being recovered even more rootward on the carnivoriform stem than *Tapocyon* by Spaulding and Flynn (2012) and Solé et al. (2016), the oldest securely dated and identified carnivoran specimens belong to the amphicyonid stem-caniform *Daphoenus* and the stem-canid *Hesperocyon* and are about 38 Ma old (Tomiya, 2011, and references therein). *Lycophocyon* could have the same age or be somewhat older (Tomiya, 2011), but unfortunately its phylogenetic position remains uncertain: it was published too late to be included by Spaulding and Flynn (2012), it was not added by Solé et al. (2016), and the much smaller phylogenetic analysis by Tomiya (2011) only resolved its position (as a stem-caniform closer to the crown-group Canoidea than *Daphoenus*) after all post-Paleogene taxa were excluded. Given the uncertainties in both age and phylogenetic position, I provisionally ignore *Lycophocyon* and suggest 38 Ma as the hard minimum age of this calibration.

As a hard maximum age I suggest the Paleocene/Eocene boundary 56.0 Ma ago (ICS), around which there is a very rich record of a range of carnivorous mammals of various sizes and ecologies, including stem-carnivoriforms and many others but not including carnivorans.

2.1.20 Node 155: Euarchontoglires/Supraprimates (Gliriformes – Primatomorpha)

The last common ancestor of mice and men, the first crown-group member of a clade called Euarchontoglires (a name apparently coined by accident by Murphy et al., 2001) or, perhaps less clunkily, Supraprimates (explicitly coined by Waddell et al., 2001), was placed between 61.5 Ma ago and 100.5 Ma ago.

The oldest purported total-group primatomorph (not necessarily total-group primate: Ni et al., 2016) is *Purgatorius coracis*, which is at most 0.4 Ma younger than the 66.0-Ma-old Cretaceous/Paleogene boundary (Fox and Scott, 2011; Scott et al., 2016). However, Halliday et al. (2015 "2017", 2019) found *Purgatorius* outside of Placentalia despite the presence of stem-primates in their analyses.

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When Manz et al. (2015) applied molecular constraints (fig. 2), they did find *Purgatorius* as a total-group primate, though in a strangely nested position when the monophyly of Laurasiatheria was enforced (fig. 2b). Without constraints, the included primatomorphs formed a grade outside most other placentals (and the included laurasiatherians formed a grade outside all other placentals: fig. SI3-1). Note that Halliday et al. (2015 "2017", 2019) scored *Purgatorius* for the tarsal bones that Chester et al. (2015) referred to this taxon (somewhat younger than *P. coracis*); *Purgatorius* is otherwise known exclusively from teeth and lower jaws (Chester et al., 2015; Scott et al., 2016), and Chester et al. (2015) referred the tarsals simply because their size fits and because they show arboreal adaptations which agree with the assumed primate status of *Purgatorius*. Scott et al. (2016: 343) preferred to call these bones "several isolated, possible plesiadapiform tarsals".

Excluding the purgatoriids, the diverse oldest known total-group primatomorphs date, in terms of North American Land Mammal Ages, shortly after the Puercan/Torrejonian boundary (Silcox et al., 2017), which dates to about 64.8 Ma ago (Wang et al., 2016).

On the presumably gliriform side, the oldest known members are anagalidans from the Lower Member of the Wanghudun Fm: the anagalids *Anaptogale*, *Wanogale* and *Chianshania*, the pseudictopid *Cartictops* and the astigalid *Astigale* (Missiaen et al., 2012; Wang et al., 2016; López-Torres and Fostowicz-Frelik, 2018). Their ages are poorly constrained between 66 Ma and about 62.5 Ma, though probably closer to the older end of that range (Wang et al., 2016); López-Torres and Fostowicz-Frelik (2018: fig. 4) illustrated *Anaptogale* as considerably older than *Wanogale* and *Chianshania*, but did not explain why. However, Asher et al. (2019: fig. 4, S5B, supplementary file S4-optimalTrees.nex) found Anagalida in a "primatomorph grade" when using equally weighted parsimony or implied weights with K = 24, as afrotherians with K = 2, and on the placental stem by Bayesian inference; at least in the latter two cases, anagalidans cannot calibrate this node.

Thus, I propose 65 Ma as the hard minimum age of this calibration. As the maximum age, if 66 Ma is deemed too close to the minimum (although there are presently no proposed crown- or even total-group supraprimates from the Cretaceous, despite the abundance of ecologically Glires-like and early-primatomorph-like multituberculates, gondwanatheres and the presence – in India – of ecologically primate-like adapisoriculids), I can only offer the maximum of Node 152 (Placentalia, see above).

2.1.21 Node 157: Marsupialia (Didelphimorphia – Paucituberculata + Australidelphia)

The origin of the metatherian crown-group Marsupialia was given a minimum age of 61.5 Ma and a maximum age of 71.2 Ma.

Eldridge et al. (2019) reviewed this question, and found that the oldest definitive marsupials are only 54.6 Ma old as far as understood today, dating from shortly after the beginning of the Eocene (56.0 Ma ago: ICS). Their phylogenetic and geographic position (total-group australidelphians from Australia) suggests a longer history for Marsupialia, but of the many metatherians known from the Paleocene of South America and from the Late Cretaceous through Miocene of the northern continents, none can currently be shown to belong to the crown-group (Eldridge et al., 2019). I therefore propose 55 Ma as a probably overly strict hard minimum age for this calibration.

Carneiro (2017 "2018"; not cited by Eldridge et al., 2019, whose paper was accepted for publication on 15 January 2018) found the terminal Maastrichtian tooth taxon *Glasbius* from North America as a didelphimorphian marsupial in a phylogenetic analysis (greatly expanded from that of Carneiro and Oliveira, 2017, with the same result, likewise not cited by Eldridge et al., 2019). That analysis, however, implied an extraordinary number of transoceanic dispersals around the Paleocene and – as the Gondwanan metatherians are all Cenozoic, but most Laurasian ones are Mesozoic – a surprisingly

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high rate of survival of metatherians across the Cretaceous/Paleogene boundary. I must suspect that correlation, if not downright redundancy, among mammalian tooth characters has been underestimated once again (e.g. Kangas et al., 2004; Harjunmaa et al., 2014). In earlier analyses, *Glasbius* has been found on the metatherian stem, e.g. by Wilson (2016), whose analysis failed, however, to find Australidelphia as monophyletic despite the morphological and molecular consensus (see Eldridge et al., 2019).

Marsupials, other metatherians and indeed other therians are wholly absent from the Late Cretaceous mammaliform record of South America, which consists instead of gondwanatherian haramiyidans and a very wide variety of meridiolestidan stem-theriiforms. If *Glasbius* is not a marsupial, it can be stated with great confidence that Marsupialia originated in South America (Eldridge et al., 2019, and references therein); if *Glasbius* is a marsupial, North America becomes the obvious candidate, and Didelphimorphia on the one hand and the last few common ancestors of Paucituberculata and Australidelphia on the other hand most likely survived the Cretaceous and immigrated into South America separately. In that case, it is noteworthy that *Glasbius* is the only possible marsupial out of the remarkable diversity of Maastrichtian, Campanian and in some cases yet earlier metatherians known from North America. Rather than the beginning of the Maastrichtian, I propose the beginning of deposition of the Lance and Hell Creek formations, where *Glasbius* has been found, as the hard maximum age for this calibration, which I estimate as 68 Ma.

2.1.22 Node 160: Batrachia (Caudata – Salientia)

The origin of Batrachia by the divergence of the sister-groups Caudata (the salamander total group) and Salientia (the frog total group) was assigned a minimum age of 249 Ma and no maximum age. This was, as usual, done on the basis of *Triadobatrachus*, one of the two oldest known salientians (the other is *Czatkobatrachus*, which is probably early Olenëkian in age: Evans and Borsuk-Białynicka, 2009); all known definitive caudates are much younger. Irisarri et al. (2017) only cited the classic redescription of *Triadobatrachus* from 1989 for this age; more recent stratigraphic work has been reviewed by Ascarrunz et al. (2016: 206–207) and places *Triadobatrachus* either in the late Induan or the very beginning of the Olenëkian. Unfortunately, the precise age of the Induan-Olenëkian boundary remains unclear; the ICS, indirectly citing a source from 2007, places it at "~ 251.2 Ma" without explicit error margins, while Maron et al. (2018 "2019") placed it at "~ 249.7 Ma" based on cyclostratigraphic counting away from the Permian-Triassic boundary, which is exceptionally precisely dated radiometrically. I conclude that 249 Ma is a perfectly adequate hard minimum age for this calibration point.

For a maximum age, I reiterate the suggestion of Marjanović and Laurin (2013b) to use the beginning of Carroll's Gap (see Marjanović and Laurin, 2013a), i.e. the Early Permian record, which has yielded many tetrapods ecologically comparable to batrachians, but no batrachians or albanerpetids (their likely sister-group) so far (e.g. Schoch and Milner, 2014; Glienke, 2015). The abovementioned particularly rich site of Richards Spur, where small terrestrial and possibly amphibious temnospondyls particularly similar to batrachians are very common, is 289 ± 0.68 Ma old (Woodhead et al., 2010), so that 290 Ma may be a defensible soft maximum value. (The value of 275 Ma suggested by Marjanović and Laurin, 2007 and 2013b, is outdated.)

2.1.23 Node 169: crown group of Cryptobranchoidea (Hynobiidae – Pancryptobrancha)

The divergence between the salamander clades Cryptobranchidae (the crown group of the total group Pancryptobrancha: Vasilyan et al., 2013) and Hynobiidae was assigned a minimum age of 145.5 Ma and no maximum age.

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The minimum age, intended to correspond to the Jurassic/Cretaceous boundary (~ 145.0 Ma ago: ICS), constitutes a snapshot in the convoluted history of dating the Jurassic and Cretaceous Konservat-Lagerstätten of northeastern China. None of these sites are now considered Kimmeridgian through Valanginian in age. The oldest sites that have yielded salamanders belong to the abovementioned (see Node 151) Lanqi and Tiaojishan formations; specifically, the abovementioned Daxishan or Daxigou site, which is just over 160 Ma old (see Node 151), has yielded *Linglongtriton* and apparently *Chunerpeton* (Jia and Gao, 2019), and the phylogenetic analysis by Jia and Gao (2019) found the former on the hynobiid stem and the latter as a stem-pancryptobranchan.

However, that analysis, like (to the best of my knowledge) all others that have ever included any Chinese Mesozoic salamanders (references in Jia and Gao, 2019), contains a clear example of what Wiens et al. (2005: title) called "[o]ntogeny discombobulates phylogeny": a clade composed of the extant neotenic non-cryptobranchoid salamander clades, i.e. (Amphiumidae (Sirenidae, Proteidae)), as the sister-group of the non-neotenic ones. Instead, molecular data (e.g. Wiens et al., 2005; Irisarri et al., 2017; Jetz and Pyron, 2018; and references therein) have consistently shown that Sirenidae lies outside the smallest clade formed by all other extant non-cryptobranchoid salamanders (Salamandroidea), as had long been presumed based on other considerations like the retention of external fertilization in sirenids (Reinhard et al., 2013). Likewise, Amphiumidae and Plethodontidae are consistenly sister-groups in phylogenetic analyses of molecular data, rather than Amphiumidae being close to Proteidae or Sirenidae or Plethodontidae being close to Salamandridae (e.g. Rong, 2018) or *Ambystoma* (e.g. Jia and Gao, 2019). This may be particularly relevant because all of the Chinese Mesozoic salamanders are only known from larval or neotenic individuals, or are metamorphic but aquatic (*Pangerpeton*: Wang and Evans, 2006), or combine features expected of different ontogenetic stages (perhaps indicating a less condensed metamorphosis: *Linglongtriton*; also, though found outside Cryptobranchoidea, *Beiyanerpeton*: Gao and Shubin, 2012), or are metamorphic and apparently terrestrial but have not been sufficiently described to be included in a phylogenetic analysis (*Laccotriton*). All known pancryptobranchans except the terminal Paleocene cryptobranchid *Aviturus* (Vasilyan and Böhme, 2012; Vasilyan et al., 2013) have been neotenic or undergone only partial metamorphosis (the extant *Andrias* loses the gills, the gill slits and the coronoid bone, but does not rebuild the palate or grow eyelids); this may attract stem-cryptobranchoids or even some of the more crownward stem-urodeles toward them, even if some (Rong, 2018) or most (Jia and Gao, 2019) end up in the hynobiid total group rather than in Pancryptobrancha. Unfortunately, no phylogenetic analysis has ever included extinct Cenozoic pancryptobranchans together with any Mesozoic salamanders; the overlap between the taxon samples of Vasilyan et al. (2013) and Pearson (2016) or Jia and Gao (2019), as well as all references in all three, is restricted to extant species.

It does not help that the known fossil record of possible hynobiids outside of the mentioned Lagerstätten only begins in the late Miocene and consists entirely of isolated bones (reviewed by Jia and Gao, 2016: 44–45). One possible exception is the metamorphic *Iridotriton*, known from a partial but well preserved skeleton from the early Tithonian (Galli et al., 2018; Maidment and Muxworthy, 2019) Brushy Basin Member of the Morrison Fm (Rainbow Park Microsite, Utah), originally argued to be a non-cryptobranchoid urodele (Evans et al., 2005), more recently found on the hynobiid stem (Jia and Gao, 2019: fig. S6) or in an incompletely resolved position outside the cryptobranchoid crown-group (Pearson, 2016: fig. 4.11), and equipped with a confusing combination of characters (Evans et al., 2005).

Mesozoic pancryptobranchans seem to be represented by a large number of isolated bones from the early Cenomanian through early Campanian of Kazakhstan, Uzbekistan and Tajikistan (Skutschas, 2013) usually grouped as *Eoscapherpeton* and *Horezmia* (but considered two species of

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Eoscapherpeton by Skutschas, 2013). Unfortunately, they have never been included in a phylogenetic analysis outside of Pearson's (2016) doctoral thesis, but the arguments by Skutschas (2013) for referring at least some of the nonoverlapping material to Pancryptobrancha are not easily dismissed. In a Bayesian analysis of a data matrix of morphological data containing extant lissamphibians, the Permian temnospondyls *Doleserpeton* and *Gerobatrachus*, the stem-salientian *Triadobatrachus*, *Eoscapherpeton* and a number of Cretaceous and Cenozoic scapherpetids but no other caudates, Pearson (2016: fig. 4.2) recovered *Eoscapherpeton* as a stem-pancryptobranchan, though with a posterior probability of only 52%; adding further Mesozoic salamanders led to the breakdown of this resolution (Pearson, 2016: fig. 4.12). I therefore tentatively suggest the beginning of the Cenomanian (100.5 Ma ago, given without uncertainty in the ICS), rounded to 101 Ma ago, as the soft minimum age of this calibration for present purposes. Given the great uncertainty, I generally recommend against using this divergence as a calibration date.

It is interesting in this respect that calibrating this node with a minimum age around 160 Ma leads to far too high ages for cladogeneses within Hynobiidae and within Cryptobranchidae, even within *Andrias japonicus* judging by paleogeographic criteria (Matsui et al., 2008).

Like Irisarri et al. (2017), I cannot assign a maximum age other than that of Node 160.

2.1.24 Node 170: Lalagobatrachia/Bombinanura (total group of Bombinatoroidea/Costata – total group of Pipanura); Node 171: Pipanura (total group of Pipoidea/Xenoanura – total group of Acosmanura)

The last common ancestor of Bombinatoroidea or Costata, represented by *Bombina* and *Discoglossus*, and Pipanura, to which all other sampled frogs belong, was assigned a minimum age of 161.2 Ma and no maximum age. Pipanura itself was assigned a minimum age of 145.5 Ma and no maximum age.

Following the finding that *Eodiscoglossus*, to which a Bathonian (Middle Jurassic) species has been referred that forms the basis for the original minimum age, is probably not a costatan (Báez, 2013; Báez and Gómez, 2016, 2019), the oldest lalagobatrachian/bombinanuran is the poorly known *Enneabatrachus* from a site dated to 152.51 ± 0.47 Ma (Trujillo et al., 2015), which has never been included in a phylogenetic analysis. Given, however, the presence of the pipanuran (rhinophrynid or stem-xenoanuran: Henrici, 1998; Gómez, 2016; Aranciaga Rolando et al., 2019) *Rhadinosteus* at the same site as *Iridotriton* (the Rainbow Park Microsite, see Node 169) and as further specimens of *Enneabatrachus*, a hard minimum age of 153 Ma for Pipanura (and Bombinanura by implication), coinciding with the maximum age of the Kimmeridgian/Tithonian boundary (152.1 ± 0.9 Ma: ICS) and constituting a minimal revision of the age proposed by Marjanović and Laurin (2013b), appears safe.

Enneabatrachus, if not *Rhadinosteus*, is at present the oldest securely identified anuran (crown-group salientian). Remarkably, no salientians at all have so far been reported from the Yanliao Biota (Lanqi, Tiaojishan and other formations of approximately Oxfordian age in northeastern China), despite its wealth of salamanders (see Node 169). The stem-salientian record is sparse (Marjanović and Laurin, 2013b; Stocker et al., 2019); the suggestion of a maximum age for Bombinanura of 170 to 185 Ma by Marjanović and Laurin (2013b) is based on the fairly good stratigraphic fit of stem-salientian phylogeny (Marjanović and Laurin, 2007, 2013a: fig. 5, 2013b; Stocker et al., 2019; and references therein), but given its poor geographic coverage, I prefer to follow Irisarri et al. (2017) in not assigning a maximum age other than that of Node 160 for present purposes.

Thus, Node 170 cannot currently be calibrated on its own: its minimum age is that of Node 171, its maximum age is that of Node 160.

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2.1.25 Node 178: Pipidae (Pipinomorpha – Xenopodinomorpha)

The origin of Pipidae (the crown group of Pipimorpha) by the divergence of Pipinomorpha (crown group: Pipinae) and Xenopodinomorpha (crown group: Xenopodinae = *Xenopus* sensu lato) was given a minimum age of 86 Ma and no maximum age.

This cladogenesis is particularly difficult to date from the fossil record because molecular data support Hymenochirini as a member of Xenopodinae, though less strongly than most other parts of the tree (Cannatella, 2015: fig. 1, with a bootstrap support of 71% while other branches have 74%, 93% or 100%, and with a Bayesian posterior probability of 99% while three others have 100%; Irisarri et al., 2017, with a jackknife support of 98% instead of the usual 100%; Jetz and Pyron, 2018: supplementary file amph_shl_new.tre, with a Shimodaira/Hasegawa-like approximate likelihood ratio of 92% instead of the usual 100%), while morphological data have so far only supported Hymenochirini as a member of Pipinae (with a Bayesian posterior probability of 100% in Cannatella, 2015). The only phylogenetic analysis of combined data from pipimorphs yet undertaken (Cannatella, 2015: analysis E1) found almost equal support for both possibilities (bootstrap support of 46% vs. 44%; Bayesian posterior probabilities below 50%), and the winning-sites test could not distinguish between them (p = 1.0: Cannatella, 2015: table 3), although tip-dating with three node calibrations strongly supported the hymenochirins as pipines at the cost of losing a terminal taxon (*Pachycentrata*, see below; Cannatella, 2015: analysis E6).

Using considerably updated and expanded versions of the morphological dataset Cannatella (2015) had used, Gómez (2016), de Souza Carvalho et al. (2019) and Aranciaga Rolando et al. (2019) all found the Cenomanian *Oumtkoutia* (not included by Cannatella, 2015) to be the oldest known pipid; the Cenomanian ended 93.9 Ma ago (ICS). However, while the first of these three phylogenetic analyses found it as a stem-xenopodinomorph, the other two – whose matrices are almost identical to each other, and derived from that of the first with rather few changes – found it as a stem-pipinomorph, and the third cautioned that it may well be a stem-pipimorph because, although Rage and Dutheil (2008) described the material in great detail, it consists entirely of isolated braincases, vertebrae and pelves, and there is some character conflict as *Oumtkoutia* combines a pipinomorph autapomorphy with stem-pipimorph plesiomorphies. The next younger pipid remains *Pachycentrata* of end-Coniacian or Santonian age, found as a stem-hymenochirin by Gómez (2016) but as a stem-pipinomorph by de Souza Carvalho et al. (2019) and Aranciaga Rolando et al. (2019); while the Coniacian ended 86.3 ± 0.5 Ma ago, the Santonian ended only 83.6 ± 0.2 Ma ago (ICS).

Given the presence of *Pipa* in South America but its extant sister-group Hymenochirini in Africa, and further the facts that all known pipomorphs are strictly aquatic and that lissamphibians in general tend to tolerate saltwater poorly, it is tempting to assume that this distribution is due to vicariance and the cladogenesis that separated *Pipa* and the hymenochirins should be dated to the loss of contact between Outer Gondwana (including South America) and Afro-Arabia around the Cenomanian – in other words, a geological event should be used to calibrate this divergence date. If *Pachycentrata* is a stem-hymenochirinomorph, as found by Gómez (2016), this scenario fits the phylogeny beautifully, and neither any overseas dispersal nor any long ghost lineages need to be assumed, as Gómez (2016) pointed out. Contrariwise, if *Pachycentrata* is a stem-pipinomorph, as found by de Souza Carvalho et al. (2019) and Aranciaga Rolando et al. (2019), the fossil record offers no reason to date the origin of Pipinae to the Mesozoic, and the most parsimonious hypothesis becomes that *Pipa* dispersed from Africa to South America together with the platyrrhine monkeys and the caviomorph rodents, perhaps on the same natural raft; de Souza Carvalho et al. (2019: 228) have discussed the possibility of a Paleogene island chain or landbridge on the Walvis Ridge and the Rio Grande Rise at some length.

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On the phylogenies by de Souza Carvalho et al. (2019) and Aranciaga Rolando et al. (2019), the xenopodinomorph fossil record begins only in the late Oligocene (briefly reviewed in Blackburn et al., 2019; see also Gardner and Rage, 2016: 184) rather than the Cenomanian (Gómez, 2016).

As mentioned, the only combined dataset yet brought to bear on this question (Cannatella, 2015: dataset E), which is also the only dataset containing extinct taxa that supports the hymenochirins as pipines, is based on a superseded morphological dataset that lacked *Oumtkoutia* and *Pachycentrata*, not to mention any taxa described since 2007. Given this and the discussion in the preceding paragraphs, it remains unclear whether *Oumtkoutia* is a pipid, and so I can only suggest 84 Ma as a safe hard minimum age for Pipidae.

Any maximum age will have to accommodate the undescribed possible pipid from the Aptian or Barremian of Cameroon (Gardner and Rage, 2016: 177, 179). However, the only maximum age I feel able to propose is much older: the end of deposition of the lake sediments of the Newark Supergroup (Tanner and Lucas, 2015) sometime around the Hettangian/Sinemurian boundary (199.3 ± 0.3 Ma ago: ICS). All known pipimorphs, extant or extinct, have been fully aquatic (reviewed in Cannatella, 2015). The upper formations of the Newark Supergroup, which represent the rift lakes that preceded the opening of the Central Atlantic Ocean between Africa and North America, have yielded whole species flocks of semionotid actinopterygians among other parts of a lake fauna and flora (Olsen, 1988, 2010), and they cover so much space and time that if any aquatic salientians existed in northwestern Pangea during that time, we should expect to have found them – yet, salientians are consistently absent from these sediments (Olsen, 1988). The absence of caudates (Olsen, 1988) may be explained by geography in that that group may have originated in Asia or at least northeastern Pangea. All other Barremian or earlier xenoanurans, however, have so far been found on the Iberian microcontinent or in North America, and the stratigraphic fit of their phylogeny (Gómez, 2016; Aranciaga Rolando et al., 2019) is good enough that if pipids older than *Oumtkoutia* existed, northwestern Pangea is where we should look for them. I therefore propose 199 Ma as the hard maximum age for this calibration.

2.1.26 Node 187: crown group of Chondrichthyes (Holocephali – Elasmobranchii)

The origin of the chondrichthyan crown group was given a minimum age of 410 Ma and a maximum age of 495 Ma.

By current understanding (Frey et al., 2019), the oldest known crown-chondrichthyan is the stem-elasmobranch *Phoebodus fastigatus* from the middle Givetian. The Givetian, part of the Middle Devonian, began 387.7 ± 0.8 Ma ago and ended 382.7 ± 1.6 Ma ago (ICS), so I propose 385 Ma as the hard minimum age of the chondrichthyan crown-group.

Although I cannot assign a maximum age separate from that of the root node (Node 100) to this calibration, no less than ninety million years before the minimum age, I note that this is still twenty million years after the 495 Ma assigned by Irisarri et al. (2017).

2.1.27 Node 188: crown group of Elasmobranchii (Selachimorpha – Batomorpha)

The origin of the elasmobranch crown group by split into Selachimorpha (sharks) and Batomorpha (rays and skates) was given a minimum age of 190 Ma and no maximum age. (Note that the name Neoselachii is consistently treated in the paleontological literature as if defined by one or more apomorphies, not by tree topology; it probably applies to a clade somewhat larger, and possibly much older, than its crown group.)

Any attempt to date this cladogenesis suffers from the fact that the elasmobranch fossil record consists mostly of "the tooth, the whole tooth and nothing but the tooth" (as has often been said about

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the mammalian fossil record); scales and the occasional fin spine do occur, but more substantial remains are very rare. The shape of tooth crowns is naturally prone to homoplasy, the number of characters it offers is easily overestimated due to correlations between them (e.g. Kangas et al., 2004; Harjunmaa et al., 2014; see Node 157), and histological studies, which are needed to determine the states of certain phylogenetically informative characters (e.g. Andreev and Cuny, 2012; Cuny et al., 2017), have not been carried out on all potentially interesting tooth taxa.

Consequently, there is not as much interest in phylogeny among specialists of early elasmobranchs than among specialists of early mammals or early dinosaurs. This goes so far as to affect the use of terminology: Andreev and Cuny (2012) mentioned "stem selachimorphs" in the title of their work, implying that they understood Selachimorpha as a clade name, but quietly revealed it to be the name of a paraphyletic assemblage on p. 263 by stating that bundled enameloid is "diagnostic for Neoselachii exclusive of batomorphs, i.e., Selachimorpha", and their consistent referral of Synechodontiformes (see below) to "Selachimorpha" is not necessarily a referral to the crown group – even though they called bato- and selachomorphs sister-groups in the next sentence.

As if by typographic error, the oldest widely accepted crown-group elasmobranch is not 190 but about 290 Ma old: the oldest fossils referred to the neoselachian *Synechodus* are four teeth of Sakmarian age (referred to *S. antiquus*, whose type tooth comes from the following Artinskian age: Ivanov, 2005; Stumpf and Kriwet, 2019), and the Sakmarian ended 290.1 ± 0.26 Ma ago (ICS). Teeth referred to other species of *Synechodus* range into the Paleocene; *S. antiquus* is the only Permian species (Andreev and Cuny, 2012). The histology of *S. antiquus* remains unknown as of Koot et al. (2014 "2015"); nonetheless, Cuny et al. (2017: 61) regarded *S. antiquus* as "[t]he first proven selachimorph". Rounding up, I therefore tentatively suggest 291 Ma as the soft minimum age of this calibration.

Andreev and Cuny (2012) and Cuny et al. (2017: 69) further suggested that the tooth taxa *Cooleyella* and *Ginteria* could be stem-batomorphs. The oldest known *Cooleyella* specimen dates from around the end of the Tournaisian (Richards et al., 2018), which occurred 346.7 ± 0.4 Ma ago (ICS); *Ginteria* appeared in the following Viséan stage.

Cuny et al. (2017: 21, 69) further pointed out that *Mcmurdodus*, a tooth taxon that first appeared around the Early/Middle Devonian (Emsian/Eifelian) boundary (Burrow et al., 2008), has occasionally been placed within Selachimorpha, even within Hexanchiformes in the selachimorph crown-group (Burrow et al., 2008, and references therein); they very tentatively suggested a stem-selachimorph position. Boisvert et al. (2019) wondered instead if it is a stem-chondrichthyan. The absence of any however tentative suggestions of crown-elasmobranchs before *Mcmurdodus* in the rather rich total-group chondrichthyan microfossil record despite the traditional optimism of paleodontologists may serve as a hard maximum age for this calibration; the ICS places the Emsian/Eifelian boundary at 393.3 ± 1.2 Ma ago, so I suggest 395 Ma.

For purposes beyond the present work, I must recommend against using this divergence to calibrate a timetree for at least as long as the histology of Paleozoic "shark" teeth has not been studied in much more detail in a phylogenetic context. For comparison, the oldest unambiguous records of a crown-group selachimorph belong to the total-group galeomorph *Agaleus* and date from the Hettangian, apparently close to its beginning (Stumpf and Kriwet, 2019, especially fig. 5, and references therein), which was the beginning of the Jurassic and happened 201.3 ± 0.2 Ma ago (ICS). The oldest batoid batomorph is only sightly younger, see Node 192 below.

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2.1.28 Node 192: Batoidea (skates – rays)

The origin of the batomorph crown group, Batoidea, by split into skates (Rajiformes; represented by *Raja* and *Leucoraja*) and rays (taxonomically unnamed; represented by *Neotrygon*) was assigned a minimum age of 176 Ma and no maximum age.

The oldest known batoid is a single rajiform tooth named *Antiquaobatis* from the late Pliensbachian, specifically the *apyrenum* subzone of the *spinatum* ammonite zone (Stumpf and Kriwet, 2019), which is close to the end of the Pliensbachian (Fraguas et al., 2018); that end occurred 182.7 ± 0.7 Ma ago (ICS), so I propose 184 Ma as the hard minimum age for this calibration. (The name should of course have been "Antiquobatis", but must not be amended: ICZN, 1999: Article 32.5.1.)

As a hard maximum age, the Triassic/Jurassic boundary (201.3 ± 0.2 Ma ago: ICS; rounded to 201 Ma) suggests itself for ecological reasons: plesiomorphically, crown-group rays are fairly large marine durophages, a guild formed by the placodont amniotes in the well sampled Middle and Late Triassic.

2.1.29 Node 195: Neopterygii (Holosteomorpha – Teleosteomorpha)

The origin of Neopterygii by cladogenesis into the total groups of Holostei (bowfins – *Amia* – and gars, represented by *Lepisosteus*) and Teleostei (represented by the clupeocephalans *Takifugu* and *Danio*) was given a minimum age of 345 Ma and a maximum age of 392 Ma.

At present, there are only two candidates for Paleozoic neopterygians. One is *Acentrophorus*, "a 'semionotid'-like taxon that desperately requires restudy and formal analysis" (Friedman, 2015: 222; cited as current by Xu, 2019; also Sun et al., 2016) of Wujiapingian age (between 254.14 ± 0.07 Ma and 259.1 ± 0.5 Ma: ICS). The semionotids are stem-members of Ginglymodi, i.e. closer to *Lepisosteus* than to *Amia* (Giles et al., 2017: ext. data fig. 6–8; López-Arbarello and Sferco, 2018; Xu, 2019), but a generic "'semionotid'-like taxon" could easily lie outside Neopterygii. In their in-depth study of neopterygian phylogeny, López-Arbarello and Sferco (2018) did not include *Acentrophorus* or even mention it in the text.

Sun et al. (2016) cited *Archaeolepidotus*, supposedly closely related to *Watsonulus* (see below), together with undescribed specimens as a Changxingian neopterygian (which was originally thought to be Early Triassic, but probably is not according to references in Ronchi et al., 2018). The Changxingian is the stage between the Wujiapingian and the Permian/Triassic boundary (251.902 ± 0.024 Ma ago: ICS). *Archaeolepidotus* does not appear to be well understood; Friedman (2015), Giles et al. (2017), López-Arbarello and Sferco (2018) and Xu (2019) did not mention it, let alone include it in a phylogenetic analysis, and Google Scholar only finds 17 occurrences in the entire literature.

The oldest certain member of Neopterygii is *Watsonulus*, a stem-halecomorph or stem-holosteomorph (Friedman, 2015; Giles et al., 2017: ext. data fig. 6–8; López-Arbarello and Sferco, 2018; Xu, 2019) which comes from the Middle Sakamena Group of Madagascar (López-Arbarello and Sferco, 2018) just like *Triadobatrachus* (see Node 160) and should therefore be around 249 Ma old. I therefore propose 249 Ma as the hard minimum age of Neopterygii.

Assuming from the almost phylogeny-free quantification of the Permo-Triassic fossil record of osteichthyans by Romano et al. (2014b "2016") that at least the Asselian record of actinopterygians is reasonably good, I suggest a soft maximum age for Neopterygii immediately before it, i.e. at the Carboniferous/Permian boundary (298.9 ± 0.15 Ma: ICS), rounded to 299 Ma, which conveniently places it 50 Ma before the minimum age.

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2.2 Analysis methods

Johan Renaudie (Museum für Naturkunde, Berlin) kindly performed the divergence dating using the tree (topology and uncalibrated branch lengths) and the model of evolution (CAT-GTR+Γ) and clock model (lognormal autocorrelated relaxed) inferred by Irisarri et al. (2017) and the data ("nuclear test data set": the variable sites of the 14,352 most complete amino acid positions of their "NoDP" dataset) and the software they used (PhyloBayes, though the latest version, 4.1c: Lartillot, 2015), but the calibrations presented above (all at once, not different subsets).

Above (2.1.4) I describe phylogenetic uncertainty leading to two different minimum ages for the tetrapod crown-group (node 105), 335 Ma and "roughly" 350 Ma. Even when all bounds are treated as soft and the younger age is used for this node, its inferred 95% confidence interval has a younger bound of 346 Ma and an older bound of 366 Ma (Fig. 1, Table 2); therefore, I do not consider it necessary to run a second analysis where the minimum age of this node is set to 350 Ma.

Irisarri et al. (2017) treated all bounds as soft: when the inferred rate variation around a calibrated node was too extreme, that node was allowed to be somewhat younger than its assigned minimum age or somewhat older than its assigned maximum age. (Specifically, 2.5% of the probability mass of the result for each node was allowed to be outside the calibration, meaning 2.5% on each side for calibrations with a maximum and a minimum age.) This is nonsensical for most minimum and arguably even for a few maximum ages. To test the impact of this decision, we ran the analysis twice: with all bounds treated as soft or as hard. Because the results were similar (Fig. 1, Table 2), a separate run with some bounds soft and others hard (as indicated above: 2.1) appears unnecessary.

Having evaluated (2.1) the inherent uncertainty of each calibration before the analyses unlike Irisarri et al. (2017), I did not cross-validate the calibrations. Any "inconsistencies" between the calibrations should be seen as indicating not that the calibrations are wrong, but that the rate of evolution varies substantially across the tree, as already expected from other considerations (e.g. Berv and Field, 2017 "2018").

↓ **Figure 1:** Superimposed timetrees resulting from application of the calibrations described here, with all bounds treated as soft (trees in blue) or all treated as hard (trees in black). The 95% confidence intervals of each node are shown only for hard bounds; they are drawn vertically narrower where the tree is particularly crowded. The calibrations are shown as red arrows horizontally in line with the nodes they apply to; note that the arrow that is almost aligned with the branch of Lalagobatrachia and the one that is almost aligned with the terminal branch for *Silurana* are the maximum and minimum ages of node 178 (Pipidae), the one on the branch for *Siren* applies to node 161 (Urodela), the one on *Iguana* to node 131 (Iguania), and the one on *Pelodiscus* to node 117 (Testudines). The abbreviated genus names are spelled out as clade names; where only one species per genus is sampled, see Irisarri et al. (2017) for full species names. To the extent possible, clade names with node-based definitions are placed close to those nodes, while names with branch-based definitions are shown close to the origin of that branch (i.e. the preceding node if sampled). Period/epoch symbols from oldest to youngest: Cambrian (cut off at 500 Ma), Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Early Cretaceous, Late Cretaceous, Paleogene, Neogene including Quaternary (which comprises the last 2.58 Ma and is not shown separately). Timescale (including colors) from the International Chronostratigraphic Chart, version 2019/05 (Cohen et al., 2019). Node numbers, also used in the text and the Tables, from Irisarri et al. (2017).

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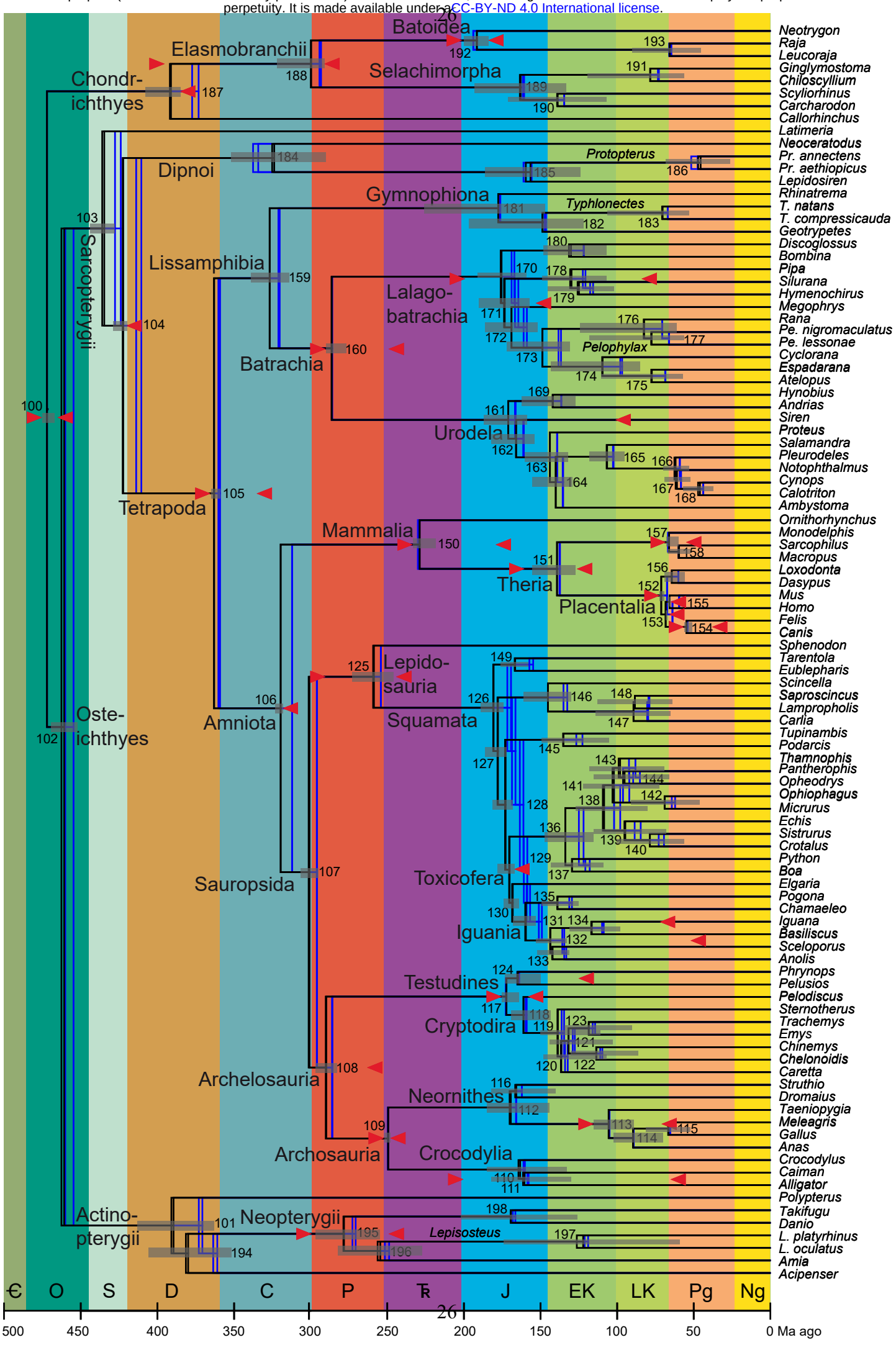

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3 Results and discussion

3.1 Bibliometry

Irisarri et al. (2017: supp. table 8) cited 15 works as sources for their calibrations, six of them compilations made by paleontologists to help molecular biologists calibrate timetrees.

I cite 228 references for calibration purposes. One each dates to 1964, 1988, and 1991, two each to 1994, 1995 and 1996, one each to 1997 and 1998, 3 to 1999, 1 to 2000, 4 each to 2001 and 2002, 1 each to 2003 and 2004, 7 to 2005, 3 to 2006, 7 to 2007, 6 to 2008, 2 to 2009, 5 to 2010, 7 to 2011, 9 to 2012, 15 to 2013, 12 to 2014, 20 to 2015, 25 to 2016, 20 to 2017, 29 to 2018 and 35 to 2019; the accepted manuscript of one more was published in 2019, and one is currently in revision and may be published in 2019 or 2020. None of them are the six compilations cited by Irisarri et al. (2017).

Irisarri et al. submitted their manuscript on 16 September 2016. If we assume that half of the publications cited here that were published in 2016 (rounded up to 13) came out too late to be used by Irisarri et al. (2017), the total proportion of the works cited here that would have been useful to them for calibrating their timetree but were not available amounts to 98 of 228, or 43%. I conclude from this extreme "pull of the recent" that knowledge in this area has an extremely short half-life; calibration dates, therefore, cannot be taken from published compilations (including the present work), but must be checked every time anew against the current primary literature. This is time-consuming even in the digital age, much more so than I expected, and requires reading more works for context than actually end up cited (for some nodes three times as many); but there is no shortcut.

3.2 Results

Treating the bounds of all calibrations as soft (blue trees in Fig. 1) generally results in younger ages (by some 20 Ma in the extreme case of the uncalibrated actinopterygian crown group, node 101, and the minimum-only-calibrated chondrichthyan crown group, 187), sometimes with mean ages younger than the minimum age of the calibration (Fig. 1, Table 2). The only nodes that are found older with soft bounds are three uncalibrated (Dipnoi, *Protopterus*, Lepidosireniformes in one of the two soft-bound runs: nodes 184–186) and, marginally, three fully calibrated nodes (Batoidea, Mammalia, Marsupialia: 192, 150, 157).

Unexpectedly, most nodes with both a minimum and a maximum calibration are found to have the same ages by both methods, unless the constraints are very far apart (Elasmobranchii, 188; Pipidae, 178; Lepidosauria, 125; Neopterygii, 195; but not Batrachia, 160, Mammalia, 150, or the neognath crown group, 113). Although maximum ages evidently play an important role, which I cannot presently explain, in preventing too young results, a maximum without a minimum age (Placentalia: 152) is not sufficient for this effect.

Unconstrained nodes are generally found to have implausibly old ages and large confidence intervals: e.g., the last common ancestor of chickens and turkeys (node 115) is placed around the Cretaceous/Paleogene boundary, with a 95% confidence interval that spans half of each period, and the confidence interval of the avian crown-group (Neornithes, node 112) spans most of the Jurassic, with a younger bound barely younger the age of the distant stem-bird *Archaeopteryx* (just over 150 Ma), while the oldest known crown-birds are less than half as old, about 71 Ma (see 2.1.9). But there are exceptions. Most notably, the squamate radiation is constrained only between the origin of Lepidosauria (node 125, 244–290 Ma; see 2.1.12) and the origin of Toxicofera (node 129, minimum 167 Ma; see 2.1.13), yet it is bunched up around the latter date, unlike in Irisarri et al. (2017) where it

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was more spread out and generally older even though both calibrations were younger; the crucial difference may be that Lepidosauria did not have a maximum age, but this does not explain the very short internodes from Squamata to Iguania in my results.

In part, this may be due to effects of body size (Berv and Field, 2017 "2018"): most sampled squamates are small, while the two sampled palaeognath birds are much larger than all sampled neognaths. This may be supported by the body size increase in snakes: their oldest sampled node (Macrostomata or Afrophidia: 136) as well as the origin of Endoglyptodonta (138) are placed in the Early Cretaceous, while even Late Cretaceous caenophidians (a clade containing Endoglyptodonta) remain unknown, all potential Cretaceous total-group macrostomates are beset with phylogenetic uncertainty, and considerably younger dates were found by Burbrink et al. (accepted) despite the use of a mid-Cretaceous potential macrostomate as a minimum-age-only calibration. Similarly, the fact that the entire confidence interval for Supraprimates (155) is younger than its calibrated minimum age when soft bounds are used may be due to the fact that one of the two sampled supraprimates is *Homo*, the second-largest sampled mammal.

Whelan and Halanych (2016 "2017") found that the CAT-GTR model (at least as implemented in PhyloBayes) is prone to inferring inaccurate branch lengths, especially in large datasets; this may turn out to be another cause of the results described above. The omission of the constant characters from the dataset, intended to speed up calculations (Irisarri et al., 2017), may have exacerbated this problem by leading to inaccurate model parameters (Whelan and Halanych, 2016 "2017").

4 Conflict of Interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

5 Author Contributions

D. M. designed the experiments, gathered the data, interpreted the results, prepared the figure and the tables and wrote the paper.

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Glory to our pirate queen, without whose work this paper would at best have taken a lot longer to write and at worst would have been severely outdated before submission.

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PhyloBayes only runs on Unix systems; Johan Renaudie (Museum für Naturkunde, Berlin) has access to such and kindly performed the time-consuming analyses after expertly overcoming the gaps in the documentation of PhyloBayes.

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Table 1: The first four columns of Irisarri et al. (2017: supplementary table 8), here expanded to five, and the ages recommended here (boldface) or otherwise used for the same calibrations. Dates in parentheses are implied by a preceding (for maximum ages) or following node (for minimum ages) elsewhere in this table. Dashes in the second and third column separate the two branches stemming from the node in question. Hard bounds recommended in the text are marked with an asterisk, but this classification was disregarded in favor of an analysis where all bounds were treated as soft and one where all were treated as hard. See the text for discussion and references.

Node number in Irisarri et al. (2017: supp. table 8, supp. fig. 19)	Description of cladogenesis	Sampled terminal taxa	Minimum age in Irisarri et al. (2017)	Maximum age in Irisarri et al. (2017)	Minimum age recommended here	Maximum age recommended here
100	Root node = crown group of Gnathostomata: total group including Chondrichthyes – total group including Osteichthyes	entire sample	421.75	462.5	**465***	**475**
102	crown group of Osteichthyes: Actinopterygii – Sarcopterygii	entire sample except Chondrichthyes	416	439	(420*)	(475)
104	Dipnomorpha – Tetrapodomorpha	Dipnoi – Tetrapoda	408	419	**420***	(475)
105	crown group of Tetrapoda: Amphibia – total group of Amniota	Lissamphibia – Amniota	330.4	350.1	**335*** (or **350***)	365
106	Amniota: Theropsida – Sauropsida	Mammalia – all other sampled amniotes	288	338	**318***	(365)

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107	crown group of Diapsida: Lepidosauromorpha – Archosauromorpha	Lepidosauria – Testudines, Crocodylia, Neornithes	252	257	(263* or 256* or 307*)	(365)
108	Archelosauria: Pan-Testudines – Pan-Archosauria	Testudines – Crocodylia, Neornithes	–	–	**263*** (or 256* or 307*)	(365)
109	Archosauria: Crocodylotarsi – Avemetatarsalia	Crocodylia – Neornithes	243	251	**248***	252
111	Alligatoridae: Alligatorinae – Caimaninae	*Alligator* – *Caiman*	66	75	65*	200*
113	crown group of Neognathae: Gallanseres – Neoaves	*Anas*, *Gallus*, *Meleagris* – *Taeniopygia*	66	86.5	71	115
117	Testudines: Panpleurodira – Pancryptodira	*Phrynos*, *Pelusios* – all other sampled turtles	210	–	**158***	**175***
124	Pleurodira: Pan-Chelidae – Pan-Pelomedusoides	*Phrynops* – *Pelusios*	25	–	**125***	(175*)
125	Lepidosauria: Rhynchocephalia – Squamata	*Sphenodon* – Squamata	238	–	**244***	**290**
129	Toxicofera: Anguimorpha + Iguanomorpha – Pythonomorpha	snakes – their sister-group	148	–	**167***	(290)

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131	Iguania: Pleurodonta – Acrodonta	*Iguana*, *Basiliscus*, *Sceloporus*, *Anolis* – *Pogona*, *Chamaeleo*	165	230	**72***	(290)
132	Pleurodonta: Iguanidae + Corytophanidae – Phrynosomatidae + Dactyloidae	*Iguana*, *Basiliscus* – *Sceloporus*, *Anolis*	125	180	**52***	(290)
150	Mammalia	*Ornithorhynchus* – Theria	162.5	191.4	**179***	233*
151	Theria: Metatheria – Eutheria	Marsupialia – Placentalia	124.6	138.4	**126***	160
152	Placentalia: Atlantogenata – Boreo(eu)theria	*Loxodonta*, *Dasypus* – *Felis*, *Canis*, *Homo*, *Mus*	95.3	113	(66*)	**72***
153	Boreo(eu)theria: Laurasiatheria – Euarchontoglires/Supraprimates	*Felis*, *Canis* – *Homo*, *Mus*	–	–	**66***	(72*)
154	Carnivora: Feliformia – Caniformia	*Felis* – *Canis*	42.8	63.8	**38***	**56***
155	Euarchontoglires/Supraprimates	*Homo* – *Mus*	61.5	100.5	**65***	(72*)
157	Marsupialia	*Monodelphis* – *Macropus*, *Sarcophilus*	61.5	71.2	**55***	**68***
160	Batrachia: Salientia – Caudata	Anura – Urodela	249	–	**249***	**290**

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169	crown group of Cryptobranchoidea: Hynobiidae – Pancryptobrancha	*Hynobius* – *Andrias*	145.5	–	101	(290)
170	Bombinanura: total group including Bombinatoroidea – total group including Pipanura	*Bombina*, *Discoglossus* – all other sampled frogs	161.2	–	(153*)	(290)
171	Pipanura: total group including Pipoidea – total group including Neobatrachia	*Pipa*, *Hymenochirus*, *Silurana* – their sister-group	145.5	–	**153***	(290)
178	Pipidae	*Pipa* – *Silurana*, *Hymenochirus*	86	–	**84***	199*
187	crown group of Chondrichthyes (Holocephali – Elasmobranchii)	*Callorhinchus* – Elasmobranchii	410	495	**385***	(475)
188	Neoselachii (Selachimorpha – Batomorpha)	sharks – rays	190	–	**291**	395*
192	Batoidea (Rajiformes – all other rays)	*Neotrygon* – *Raja*, *Leucoraja*	176	–	**184***	**201***
195	Neopterygii (total group of Holostei – total group of Teleostei)	*Lepisosteus*, *Amia* – *Takifugu*, *Danio*	345	392	**249***	299

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Table 2: The ages found by Irisarri et al. (2017: supplementary table 9: last three columns) when all calibrations were used, and the results obtained here with the updated calibrations. All are rounded to whole Ma. Asterisks indicate where the (rounded) results with soft bounds exceed the calibration constraints (younger than the minimum for younger bounds and mean ages, older than the maximum for older bounds except that of node 155, which is younger than the minimum age). Irisarri et al. (2017) treated all bounds as soft.

	Irisarri et al. (2017)			Results with soft bounds			Results with hard bounds		
Node number	Mean age	younger bound of 95% CI	older bound of 95% CI	Mean age	younger bound of 95% CI	older bound of 95% CI	Mean age	younger bound of 95% CI	older bound of 95% CI
100	460	452	465	472	466	475	473	467	475
101	393	383	403	370	340	400	389	363	413
102	437	431	440	454	440	466	461	452	469
103	426	420	431	424	407	437	435	428	444
104	412	408	418	410*	394*	424	423	420	429
105	341	331	350	359	346	366	363	359	365
106	289	283	296	312*	300*	322	320	318	323
107	257	256	257	296	286	305	301	295	307

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108	254	253	256	286	277	294	290	283	297
109	243	242	245	249	248	252	250	248	252
110	120	90	162	160	131	182	164	133	185
111	71	66	75	158	129	179	161	130	182
112	137	111	173	166	148	184	169	144	185
113	83	70	87	105	87	116*	105	89	115
114	63	47	73	89	71	104	89	70	102
115	16	8	25	65	52	82	66	52	81
116	92	66	130	162	144	181	166	140	182
117	224	211	234	172	164	176*	172	164	175
118	206	184	221	159	143	168	161	143	169
119	168	133	188	134	111	148	139	111	150
120	155	117	176	132	108	146	136	107	148
121	127	90	150	127	104	142	132	103	144

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122	95	63	124	109	85	127	113	86	130
123	78	45	107	114	91	132	118	90	134
124	192	167	211	164	151	172	165	150	173
125	239	233	244	254	244	268	259	246	273
126	199	190	208	169	153	182	181	174	189
127	195	185	204	166	150	179	178	172	186
128	187	177	196	161	144	173	173	168	181
129	182	173	192	158*	141*	170	170	167	178
130	181	172	190	157	140	168	168	164	176
131	166	159	175	149	131	161	160	153	168
132	137	124	151	134	115	146	143	133	153
133	127	111	142	133	113	145	142	131	152
134	130	115	145	108	86	125	116	98	131
135	128	104	143	129	108	143	139	125	149

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136	94	72	119	122	103	140	134	115	147
137	88	66	112	118	98	136	129	109	143
138	64	40	91	98	76	121	108	80	127
139	47	26	72	84	65	109	94	68	115
140	11	4	25	69	53	93	78	56	100
141	46	25	72	92	69	115	102	72	122
142	27	13	49	62	42	82	69	46	91
143	39	21	64	88	66	111	98	69	118
144	22	11	42	85	63	108	95	66	115
145	179	167	190	122	98	141	135	115	149
146	156	136	172	132	110	148	145	130	161
147	57	34	77	79	58	102	89	65	114
148	44	24	65	79	57	101	88	64	113
149	165	146	181	155	136	168	166	158	176

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150	165	161	172	230	217	237	229	218	233
151	138	136	140	137	126	156	139	127	155
152	94	91	96	67	61*	72	71	69	72
153	89	85	92	64*	58*	68	68	67	68
154	61	53	65	54	48	57*	54	51	56
155	79	71	84	59*	53*	64*	66	65	67
156	91	87	94	60	52	67	64	56	69
157	68	62	72	66	61	69*	66	60	68
158	50	38	60	60	53	67	60	52	67
159	315	300	328	321	297	334	327	314	339
160	307	290	323	286	274	292*	286	277	290
161	202	173	237	166	152	185	171	159	187
162	192	163	226	161	146	180	166	154	182
163	177	146	210	139	127	157	144	132	160

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164	168	137	199	135	122	153	140	129	155
165	117	86	143	102	90	115	107	95	118
166	92	62	117	59	49	68	62	53	70
167	77	49	101	58	49	67	62	52	69
168	53	30	74	43	34	54	47	37	57
169	162	134	196	136	119	157	142	127	162
170	201	170	232	167	151*	185	175	159	191
171	192	161	224	164	149*	183	173	157	190
172	186	154	218	159	141	179	169	152	186
173	155	123	186	136	118	164	149	131	172
174	105	71	140	96	79	135	110	85	143
175	94	62	127	68	54	99	77	57	110
176	70	33	110	70	56	113	83	61	124
177	54	22	89	66	53	107	78	56	118

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178	156	119	189	120	98	142	130	107	149
179	144	106	177	115	92	137	125	102	145
180	160	125	194	122	100	141	130	107	148
181	213	162	255	177	148	241	178	147	226
182	155	105	195	147	117	212	149	122	197
183	36	12	65	67	47	107	70	53	106
184	223	165	279	334	295	363	324	290	352
185	78	48	107	155	124	177	160	124	186
186	6	2	15	47	26	65	47	26	68
187	414	402	428	377*	350*	402	392	385	408
188	293	256	332	294	282*	314	300	291	322
189	202	140	269	160	131	190	163	133	193
190	156	92	223	134	104	167	139	107	171
191	98	50	168	72	53	112	78	56	119

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192	207	172	262	194	184	201	192	184	200
193	76	42	110	66	49	95	65	45	90
194	380	370	390	361	331	390	380	352	406
195	345	338	352	270	250	295	279	255	297
196	330	319	340	249	222	278	256	227	282
197	55	18	91	121	57	168	126	59	174
198	277	244	297	166	126	209	169	126	202

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