



Twenty-five well-justified fossil calibrations for primate divergences

Dorien de Vries and Robin M.D. Beck

ABSTRACT

Phylogenies with estimates of divergence times are essential for investigating many evolutionary questions. In principle, “tip-dating” is arguably the most appropriate approach, with fossil and extant taxa analysed together in a single analysis, and topology and divergence times estimated simultaneously. However, “node-dating” (as used in many molecular clock analyses), in which fossil evidence is used to calibrate the age of particular nodes a priori, will probably remain the dominant approach, due to various issues with analysing morphological and molecular data together. Here, we provide a list of 25 well-justified node calibrations for primate divergences, following best practices: 16 within Haplorhini, four within Strepsirrhini, one for crown Primates, and four for older divergences within Euarchontoglires. In each case, we provide a hard minimum bound, and for 22 of these we also provide a soft maximum bound and a suggested prior distribution. For each calibrated node, we provide the age of the oldest fossil of each daughter lineage that descends from it, which allows use of the “CladeAge” method for specifying priors on node ages.

Dorien de Vries. Ecosystems and Environment Research Centre, School of Science, Engineering and Environment, University of Salford, Manchester, UK. (Corresponding author) d.devries@salford.ac.uk @PaleoDorien

Robin M.D. Beck. Ecosystems and Environment Research Centre, School of Science, Engineering and Environment, University of Salford, Manchester, UK. r.m.d.beck@salford.ac.uk @robinmdbeck

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INTRODUCTION

Phylogenies that provide estimates of divergence times between different lineages of organisms (“timetrees”) have the potential to be

extremely useful for answering a wide range of questions relating to evolutionary patterns and processes (Blair Hedges and Kumar, 2009; Ho, 2021). There has been a long history of applying such approaches to primates, for example to identify

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when humans diverged from their closest living relatives (Sarich and Wilson, 1967; Hasegawa et al., 1985; Scally and Durbin, 2012; Schrago and Voloch, 2013; Püschel et al., 2021), to determine when key phenotypic changes (e.g., increases in brain size; Ni et al., 2019; Püschel et al., 2021) occurred, to clarify the timing of significant biogeographical events (e.g., the dispersal of primates to Madagascar and to South America during the Cenozoic; Poux et al., 2005, 2006; Gunnell et al., 2018; Seiffert et al., 2020), and to infer the likely impact of major environmental changes (e.g., shifts in global climate) on primate diversification (Springer et al., 2012; Herrera, 2017; Godfrey et al., 2020).

Calculation of absolute divergence times between lineages usually requires some form of calibration by incorporating known temporal information, and for “deep time” divergences this typically means evidence from the fossil record (Nguyen and Ho, 2020). In a phylogenetic context, arguably the most appropriate approach (at least in principle) is “tip-dating”, in which fossil taxa of known age are incorporated as terminals (“tips”) in the phylogenetic analysis, and this temporal information is used to estimate divergence times at the nodes (Pyron, 2011; Ronquist et al., 2012; O’Reilly et al., 2015; Zhang et al., 2016; Lee, 2020); this approach, in which fossil and extant taxa can be analysed together, has the advantage that topology and divergence times are estimated simultaneously, in the context of a single analysis, and so the relationships of the fossil taxa do not need to be assumed a priori.

However, it seems unlikely that large quantities of molecular data will ever become available for fossil taxa older than a few million years old (Allentoft et al., 2012; Millar and Lambert, 2013; Welker, 2018), and so tip-dating analyses that include fossil taxa will typically require morphological data to inform their evolutionary relationships. This poses several problems. The most widely used model for analysing discrete morphological data (the “Mk” model of Lewis, 2001) makes a number of simplifying assumptions that seem biologically unrealistic (O’Reilly et al., 2015; Wright et al., 2016; Pyron, 2017; Billet and Bardin, 2019; Wright, 2019). Another is that, even for primates (perhaps the most studied of any clade of organisms), morphological datasets are still small in comparison to equivalent molecular datasets, in terms of both taxon and character sampling (Guillerme and Cooper, 2016b). Given that scoring of morphological datasets requires anatomical exper-

tise, considerable amounts of time, and access to widely scattered museum collections or high quality (ideally 3D) images of specimens, it is unlikely that future morphological datasets for primates will ever be sampled as densely in terms of taxa as will current and future molecular datasets. Thus, directly combining a phylogenomic dataset that samples extant primates at the population or sub-population level with a compatible morphological dataset will result in a total evidence dataset in which most extant terminals will lack morphological data (Guillerme and Cooper, 2016a). In addition, phylogenomic datasets for primates can comprise millions of base pairs of sequence data (e.g., Jameson et al., 2011; dos Reis et al., 2018; Vanderpool et al., 2020), while primate morphological datasets typically comprise a few hundred characters (e.g., Rasmussen et al., 2019; Kay et al., 2019; Seiffert et al., 2020; Gilbert et al., 2020), and so combining such datasets will mean that fossil taxa (without molecular data) might end up with >99.99% missing data. The impact of such large amounts of missing data on phylogenetic inference is not fully understood and may not be as severe as might be expected (Wiens et al., 2005; Guillerme and Cooper, 2016a), but nevertheless can still negatively affect accurate inference of topology, support values, and (crucially for the estimation of divergence times) branch lengths (Lemmon et al., 2009; Simmons, 2012, 2014; Xia, 2014).

For these and other reasons (including, we suspect, the relative unfamiliarity to many bioinformaticians of morphological data and of appropriate methods for analysing it), it seems likely that molecular clock analyses, which use molecular data only, will remain the most common approach for inferring divergence times among lineages. In such analyses, fossil taxa for which molecular data are unavailable cannot be included directly as terminals/tips, but instead can be used to calibrate the age of one or more nodes in the phylogeny (“node-dating”; Nguyen and Ho, 2020). Because fossils are assigned a priori to particular nodes under this approach, it is crucial that each calibrating fossil is assigned appropriately, based on the most accurate and up-to-date information (Parham et al., 2012; Marjanović, 2021).

However, as discussed at length by Marjanović (2021), identifying appropriate fossil calibrations is not trivial, and even comparatively recent lists of calibrations (e.g., Benton et al., 2015) now appear to be at least partly out of date. Such issues affect molecular clock analyses of primates. For example, several studies (Perelman et

al., 2011; Meredith et al., 2011; Springer et al., 2012) have used the late Eocene fossil primate *Saharagalago*, which was originally described as a galagid (Seiffert et al., 2003), to place a minimum bound on the age of crown Lorisiformes (= the Galagidae-Lorisidae split). However, a number of subsequent studies - notably, several tip-dating analyses (Herrera and Dávalos, 2016; Gunnell et al., 2018; Seiffert et al., 2020) - have instead placed *Saharagalago* as a stem lorisiform (see summaries in López-Torres and Silcox, 2020; López-Torres et al., 2020), suggesting that it is unsuitable for calibrating the Galagidae-Lorisidae split. Phillips (2016) and Phillips and Fruciano (2018) also found that use of *Saharagalago* for this calibration results in a seeming mismatch in molecular rates, further suggesting this fossil taxon is not a crown lorisiform. Tip-dating may therefore still play a key role in determining divergence times within primates, as part of a two-stage process: tip-dating analyses of smaller (in terms of both taxa and characters) datasets, which ideally use combined morphological and molecular (=total evidence) data and which show good overlap of characters between taxa, can be used to robustly identify fossil taxa suitable for calibrating particular nodes; these calibrations can then be applied to clock analyses of larger, molecular-only datasets.

The way that fossil calibrations are specified in a node-dating analysis is known to have a major impact on the estimated divergence times (Warrack et al., 2012, 2015). Although fossil calibrations have been used to specify normal distributions on the ages of nodes in some studies (e.g., Perelman et al., 2011), it seems more appropriate to view the minimum age of a calibrating fossil as providing a minimum bound on the age of that node (Benton and Donoghue, 2007; Benton et al., 2009; Ho and Phillips, 2009; Parham et al., 2012). Wherever possible, it is appropriate to also specify a maximum bound, otherwise there is no direct constraint on the maximum age of a calibrated node (Phillips, 2016; Marjanović, 2021). If maximum and minimum bounds are specified, then a prior probability distribution between these bounds (and, if these bounds are “soft”, outside them as well) also needs to be specified (Ho and Phillips, 2009). In principle, any distribution could be used, but from a paleontological perspective, perhaps the most defensible are: 1) a uniform distribution, in which there is an equal probability that the divergence occurred at any time between the minimum and maximum bounds, and which appears most appropriate in cases where the fossil

record is known or suspected to be very incomplete, such that the oldest calibrating fossil may in fact substantially postdate the age of the divergence being calibrated; 2) an exponential distribution, in which the probability that the divergence is older than the minimum bound decreases exponentially, and which appears most appropriate in cases where the calibrating fossil is suspected to be very close in time to the actual time of divergences (explained in more detail below; Ho and Phillips, 2009).

Analytical methods for inferring maximum bounds and prior probability distributions on calibrations have been proposed (Marshall, 2008; Wilkinson et al., 2011; Nowak et al., 2013; Matschiner et al., 2017; Matschiner, 2019; Claramunt, 2022), but these often require estimates of parameters such as diversification and/or sampling rates that are not always easy to obtain, even for primates (but see Silvestro et al., 2014; Herrera, 2017; 2019). For this reason, maximum bounds are typically based on somewhat subjective interpretations of available phylogenetic and fossil evidence (as in Benton et al., 2015; Roos et al., 2019; Marjanović, 2021; and most calibrations used by dos Reis et al., 2018). However, dos Reis et al. (2018) based their prior distributions for two nodes - namely the ages of crown Primates and crown Anthroidea - on the analytical estimates of Wilkinson et al. (2011); nevertheless, we note that the maximum bounds of both of these calibrations (88.6 Ma for crown Primates, 62.1 Ma for crown Anthroidea) seem implausibly old based on the fossil record (see our proposed calibrations for both of these nodes below). In turn, this may explain why the Late Cretaceous divergence time for crown Primates estimated by dos Reis et al. (2018; 95% Highest Posterior Density [HPD] interval of 70.0–79.2 Ma) is also strongly incongruent with the fossil record, although their estimate for crown Anthroidea (95% HPD: 41.8–48.3 Ma) is in better agreement with the (very limited) fossil evidence for this node (see “Fossil calibrations” below).

Here, we take these considerations into account to specify an up-to-date set of well-justified fossil calibrations for divergences within Primates, including several entirely new calibrations. In our initial survey of the literature, we identified numerous recent studies that have formally tested the affinities of various fossil primates and relatives using large morphological and total evidence datasets, many of them using tip-dating (e.g., Dembo et al., 2015, 2016; Herrera and Dávalos, 2016; Gun-

nell et al., 2018; Ni et al., 2019; Seiffert et al., 2020; Püschel et al., 2021; Beck et al., 2023). We combined the published evidence regarding the fossil record and phylogeny of primates and other mammals to identify calibrations for 25 nodes: four outside Primates (crown Euarchontoglires, crown Glires, crown Euarchonta and crown Primatomorpha), crown Primates itself, and 20 divergences within crown Primates. This is a >50% increase in the number of calibrations compared to other recent broadscale molecular clock analyses of primates (Perelman et al., 2011; Springer et al., 2012; dos Reis et al., 2018; Vanderpool et al., 2020). For each calibration, we follow the best practices recommended by Parham et al. (2012). We provide a minimum bound for each calibration, based on the minimum age of the calibrating specimen, and for 22 of our 25 calibrations we also provide a maximum bound and a suggested prior probability distribution (either uniform or exponential), based on our interpretation of the available phylogenetic evidence and the relative completeness of the known fossil record. To maximise the utility of our calibration list to other researchers, we also identify the age of the oldest member of the sister lineage of the calibrating fossil taxon, as required by the CladeAge method for inferring divergence times (Matschiner et al., 2017; Matschiner, 2019). Finally, we compare our proposed calibrations with those suggested in other recent studies (in particular, Benton et al., 2009, 2015; dos Reis et al., 2018; Roos et al., 2019), highlight cases in which there are major differences, and further justify our proposals.

METHODS

Identification of Fossil Calibrations

Based on published studies, we identified fossil calibrations for divergences within crown Primates, for crown Primates itself, and for four divergences outside Primates but within Euarchontoglires: crown Euarchontoglires, crown Glires, crown Euarchonta, and crown Primatomorpha. In identifying appropriate fossil calibrations, wherever possible we based our decisions on the results of formal, algorithmic phylogenetic analyses that have robustly tested the affinities of relevant fossil taxa, using the following hierarchy (from what we consider to be the most robust analyses to the least robust analyses): total evidence tip-dating analyses; undated total evidence analyses; undated analyses with a molecular scaffold; morphology-only tip-dating analyses; undated mor-

phology-only analyses (see Beck et al., 2023). In two cases, we propose calibrations that are not based on evidence presented in formal phylogenetic analyses (specifically, crown Haplorhini and crown Papionini); for most of these, we have based our decisions on the presence of one or more morphological synapomorphies that clearly support assignment of that fossil taxon to a particular clade.

We have followed the recommendations of Parham et al. (2012) for “best practices” for fossil calibrations; these include identifying a specific fossil specimen for each calibration, providing a full phylogenetic justification for using a particular fossil taxon (following our general approach listed above), discussing (where relevant) differences between morphological and molecular phylogenetic analyses, giving detailed locality and stratigraphic information for the calibrating specimen, and explaining clearly how this translates to a particular fixed age or age range. Ages are listed according to the degree of precision present in the source publications. For each calibration, we provide a minimum bound, which we argue can reasonably be viewed as “hard” (i.e., zero probability of the divergence being younger than this). For most calibrations, we also propose a maximum bound, which should be viewed as “soft” (i.e., with a small probability that the divergence is older than this). Where we have provided a minimum and a maximum bound, we also propose a prior probability distribution. For most calibrations, we propose a uniform distribution, in which all ages between the minimum and the maximum bounds have equal probability, which we consider to be most appropriate in cases where the fossil record is obviously highly incomplete (Ho and Phillips, 2009). For a few calibrations, however, we consider that the fossil record is sufficiently complete to be relatively confident the true age of divergence is close to the minimum bound. In these cases, we suggest that this should be modelled as an offset exponential distribution, with the minimum bound as the offset, and the shape of the exponential distribution specified such that there is a 5% probability of the divergence being older than the maximum bound (Ho and Phillips, 2009). We propose an exponential distribution for seven nodes: crown Euarchontoglires, crown Glires, crown Euarchonta, crown Primates, crown Cercopithecidae, crown Hominoidea, and crown Hominidae. For each calibrated node, we explain in detail why we consider a uniform or an offset exponential prior distribution to be appropriate.

Our list of a minimum and (where relevant) maximum bound for a calibrated node reflects standard practice in node-dating analyses. However, Matschiner et al. (2017) proposed the “CladeAge” method (see also Matschiner, 2019), in which information about the oldest fossils for particular clades is combined with estimates of sampling and diversification rates to construct prior distributions on the ages of those clades. The simulation study of Matschiner (2019) suggests that the CladeAge method is more robust to model violations than are standard node dating-analyses that use the Fossilised Birth Death (FBD) model (Stadler, 2010; Heath and Huelsenbeck, 2014; Gavryushkina et al., 2014). The CladeAge method requires information on the oldest member of each clade present in a phylogeny, not just the oldest of the daughter clades descending from a particular node (as required in “standard” node-dating). Therefore, to maximise the utility of our calibration list to other researchers, and to allow use of the CladeAge method, for each calibrated node, we provide ages for the oldest member of each daughter lineage descending from that node. It should be noted the CladeAge method also requires estimates of sampling and diversification rates, which we do not give here (such rates can be estimated using programs such PyRate; Silvestro et al., 2014; 2019). Table 1 summarises our full calibration list, including minimum and (where relevant) maximum bounds, suggested prior age distributions, and calibrations in a format suitable for use in the CladeAge method. Figure 1 shows the 25 fossil calibrations in phylogenetic context.

List of Institutional Abbreviations

AUH: Abu Dhabi Islands Archaeological Survey (Abu Dhabi, United Arab Emirates); **CGM:** Cairo Geological Museum (Cairo, Egypt); **DPC:** Duke University Division of Fossil Primates (Durham, North Carolina, USA); **DU/IGM:** Duke University (Durham, North Carolina, USA) and Instituto Nacional de Investigaciones Geologico-Mineras (INGEOMINAS, Bogota, Colombia); **GSP (Y)** and **YGSP:** Yale University (New Haven, Connecticut, USA) and the Geological Survey of Pakistan (Quetta, Pakistan); **GWM:** National Museum of Ethiopia (Addis Ababa, Ethiopia), followed by the collecting area and ‘P’ for palaeontology; **IGM-KU:** Instituto Nacional de Investigaciones Geologico-Mineras (INGEOMINAS, Bogota, Colombia) and Kyoto University (Kyoto, Japan); **IVPP V:** Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China), with ‘V’ being the specimen prefix

of IVPP. **LX,** IVPP’s fossil locality number in the Linxia Basin; **KNM:** National Museums of Kenya (Nairobi, Kenya), with ‘FT’ being the prefix for specimens from Fort Ternan, ‘LU’ being the prefix for specimens from Lukeino, ‘SO’ being the prefix for specimens from Songhor, ‘TH’ being the prefix for specimens from Tugen Hills; **LACM:** Natural History Museum of Los Angeles County (Los Angeles, California, USA); **MGPT-PU:** Museum of Geology and Paleontology of Torino University (Torino, Italy); **OCO:** Orrorin Community Organisation, Kipsaraman Museum (Tugen Hills, Kenya); **RRBP:** Rukaw Rift Basin Project, prefix used by the Tanzania Antiquities Unit (Dar es Salaam, Tanzania); **RZO:** Laboratory of Geology and Paleontology (Thessaloniki, Greece), ‘RZO’ being the prefix used for specimens from locality Ravin des Zouaves 5; **UCMP:** University of California Museum of Paleontology, (Berkeley, California, USA); **UFAC-LPP:** Universidade Federal do Acre Laboratório de Pesquisas Paleontológicas (Acre, Brazil); **UM:** University of Michigan Museum of Paleontology (Ann Arbor, Michigan, USA).

FOSSIL CALIBRATIONS

Crown Euarchontoglires = Euarchonta-Glires split

Calibrating taxon. *Purgatorius mckeeveri*

Specimen. UCMP 150021, an isolated left m2, from Harley’s Point locality in the lowermost part of the Tullock Member of the Fort Union Formation in Montana, USA (Wilson Mantilla et al., 2021).

Phylogenetic justification. *Purgatorius mckeeveri* is the oldest known member of “Plesiadapiformes”, a likely non-monophyletic grade of fossil euarchontans (Silcox et al., 2017). Some phylogenetic analyses focused on deep relationships within Eutheria have recovered *Purgatorius* outside Placentalia (e.g., Wible et al., 2007, 2009; Goswami et al., 2011). However, recent phylogenetic analyses specifically intended to resolve euarchontan relationships consistently place *Purgatorius* and other “plesiadapiforms” within crown Euarchonta, and specifically closer to Primates and Dermoptera than to Scandentia, although the precise affinities of “plesiadapiforms” vary in these analyses (e.g., Bloch et al., 2007; Chester et al., 2015, 2017; Li and Ni, 2016; Ni et al., 2016; Silcox et al., 2017; Gunnell et al., 2018; Morse et al., 2019; Seiffert et al., 2020): different “plesiadapiform” taxa may represent stem members of Primates and/or Dermoptera, or they may fall outside crown Primatomorpha (=Primates+Dermoptera;

TABLE 1. Summary of fossil calibrations proposed here. Values are in millions of years. “CladeAge1” and “CladeAge2” are the ages of the oldest representatives of the two daughter lineages originating after a particular split. See text for full details.

	Clade	Split	Prior distribution	Minimum bound	Maximum bound	CladeAge1	CladeAge2
1	Crown Euarchontoglires	Euarchonta-Glires	offset exponential	65.79	125.816	66.095–65.79	66–62.22
2	Crown Glires	Rodentia-Lagomorpha	offset exponential	62.278	66	66–62.278	66–62.278
3	Crown Euarchonta	Primates-Scandentia	offset exponential	65.79	125.816	66.095–65.79	34
4	Crown Primatomorpha	Primates-Dermoptera	minimum bound only	55.935	NA	56.035–55.935	40.31–40.22
5	Crown Primates	Haplorhini-Strepsirhini	offset exponential	55.935	66.095	56.035–55.935	55.8–55.12
6	Crown Strepsirhini	Lorisiformes-(Lemuriformes+Chiromyiformes)	uniform	36.573	55.8	37.385–36.573	35.102–33.9
7	Lemuriformes+Chiromyiformes	Lemuriformes-Chiromyiformes	uniform	33.9	55.8	35.102–33.9	0.0075
8	Crown Lorisiformes	Lorissidae-Galagidae	uniform	18.5	55.8	22.5–18.5	8.9
9	Crown Lorissidae	Lorissinae-Perodicticinae	uniform	8.9	37.385	8.9	6.1
10	Crown Haplorhini	Anthropoidea-Tarsiiformes	minimum bound only	41	NA	47.8–41	47.8–41
11	Crown Anthropoidea	Catarrhini-Platyrrhini	uniform	33.9	56.035	35.102–33.9	29.68–29.52
12	Crown Catarrhini	Cercopithecoidea-Hominoidea	uniform	25.193	35.102	25.335–25.193	25.335–25.193
13	Crown Cercopithecoidea	Cercopithecoidea-Colobinae	offset exponential	12.47	25.235	12.51–12.47	8.33–7.5
14	Crown Colobinae	Colobini-Presbytini	uniform	8.125	15	8.257–8.125	6.2–5.7
15	Crown Cercopithecoidea	Cercopithecoidea-Papionini	uniform	6.5	15	8.0–6.5	9.3–6.5
16	Crown Papionini	Macacina-Papionina	uniform	5.33	12.51	5.4–5.33	4.2–4.1
17	Crown Cercopithecoidea	uncertain	uniform	6.5	12.51	8.0–6.5	NA
18	Crown Hominoidea	Hominidae-Hylobatidae	offset exponential	13.4	25.235	14.0–13.4	8.2–7.1
19	Crown Hominidae	Homininae-Ponginae	offset exponential	12.3	25.235	12.3	9.937–9.786
20	<i>Homo+Pan</i>	<i>Homo-Pan</i>	uniform	4.631	15	4.799–4.631	0.548–0.272
21	Crown Platyrrhini	Pitheciidae-(Aotidae+Atelidae+Callitrichidae+Cebidae)	minimum bound only	13.363	NA	13.608–13.363	13.183–13.032
22	Crown Pitheciidae	Callicebinae-Pitheciinae	uniform	13.032	34.5	13.183–13.032	13.739–13.032
23	Callitrichidae+Cebidae	Callitrichidae-Cebidae	uniform	13.183	34.5	13.608–13.183	13.183–13.032
24	Crown Cebidae	Cebinae-Saimirinae	uniform	13.032	34.5	13.183–13.032	9.0–4.741
25	Crown Atelidae	Alouattinae-Atelinae	uniform	13.363	34.5	13.608–13.363	7–4.741

Mason et al., 2016) entirely. Definitive stem euarchontans older than *P. mckeeveri* have not been identified. The oldest members of the sister-taxon of Euarchonta, namely Glires, are younger than the oldest known material of *P. mckeeveri* (see “Crown Glires” below). Thus, *P. mckeeveri* is the oldest known taxon that can be used to calibrate the Euarchonta-Glires split.

Hard minimum bound. 65.79 Ma

Soft maximum bound. 125.816 Ma

Suggested prior distribution. Offset exponential

Age justifications. High resolution geochronological data constrains the age of the oldest known material of *Purgatorius mckeeveri* to the early

Puercan (Pu1), chron C29r, and specifically to within ~208 kyr after the K/Pg boundary (Wilson Mantilla et al., 2021). Wilson Mantilla et al. (2021) reported an $^{40}\text{Ar}/^{39}\text{Ar}$ data of a tuff 78 cm located above the Harley’s Point locality, source of our calibrating specimen UCMP 150021, of $65.844 \pm 0.033/0.054$ Ma (with the uncertainty shown as analytical/systematic uncertainty). We thus use a minimum age of 65.79 Ma for this node. A second date from an underlying tuff has an age of $66.052 \pm 0.008/0.043$ Ma, bracketing the age of UCMP 150021 to 66.095–65.79 Ma; we use the maximum age as our soft maximum bound for the age of crown Primates (see below).

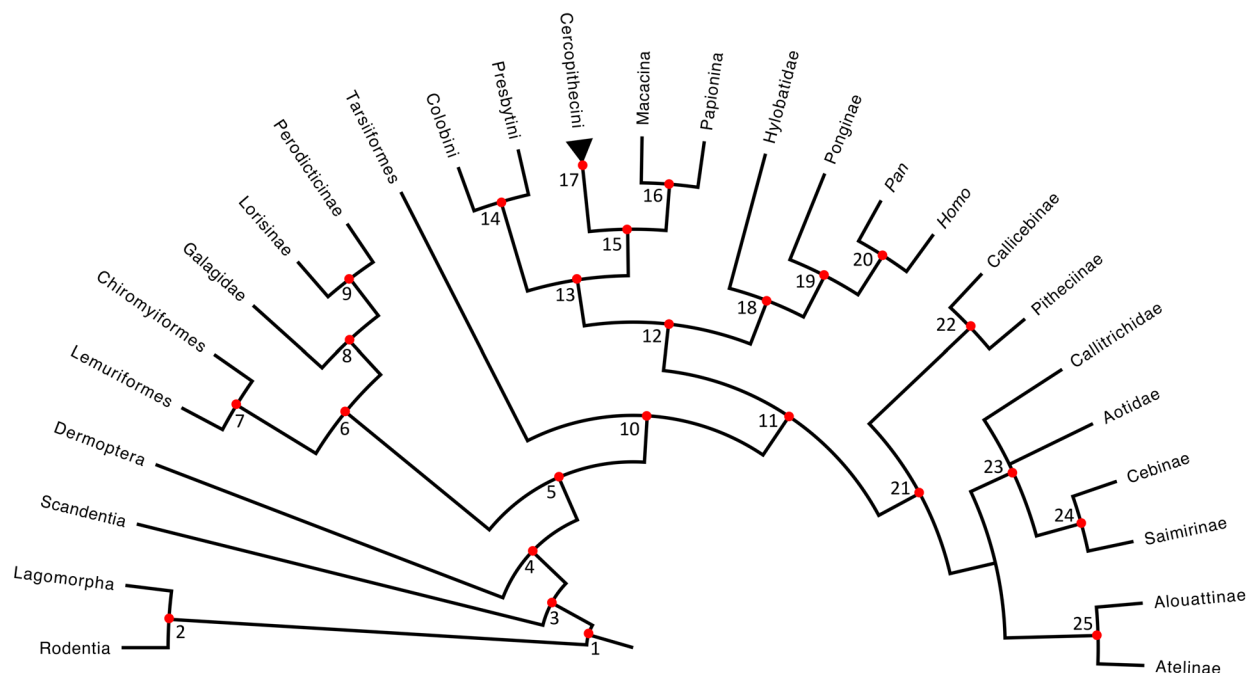


FIGURE 1. The 25 fossil calibrations shown in phylogenetic context. 1 = Crown Euarchontoglires (Euarchonta-Glires split), 2 = Crown Glires (Rodentia-Lagomorpha split), 3 = Crown Euarchonta (Primates-Dermoptera split), 4 = Crown Primatomorpha (Primates-Dermoptera split), 5 = Crown Primates (Haplorhini-Strepsirhini split), 6 = Crown Strepsirrhini (Lorisiformes-[Lemuriformes+Chiromyiformes] split), 7 = Lemuriformes+Chiromyiformes (Lemuriformes-Chiromyiformes split), 8 = Crown Lorisiformes (Lorisidae-Galagidae split), 9 = Crown Lorisidae (Lorisinae-Perodicticinae split), 10 = Crown Haplorhini (Anthropoidea-Tarsiiformes split), 11 = Crown Anthropoidea (Catarrhini-Platyrrhini split), 12 = Crown Catarrhini (Cercopithecoidea-Hominoidea split), 13 = Crown Cercopithecoidea (Cercopithecinae-Colobinae split), 14 = Crown Colobinae (Colobini-Presbytini split), 15 = Crown Cercopithecinae (Cercopithecini-Papionini split), 16 = Crown Papionini (Macacina-Papionina split), 17 = Crown Cercopithecini (uncertain split), 18 = Crown Hominoidea (Hominidae-Hylobatidae split), 19 = Crown Hominidae (Homininae-Ponginae split), 20 = *Homo*+*Pan* (*Homo*-*Pan* split), 21 = Crown Platyrrhini (Pitheciidae-[Aotidae+Atelidae+Callitrichidae+Cebidae] split), 22 = Crown Pitheciidae (Callicebinae-Pitheciinae split), 23 = Callitrichidae+Cebidae (Callitrichidae-Cebidae split), 24 = Crown Cebidae (Cebinae-Saimirinae split), 25 = Crown Atelidae (Alouattinae-Atelinae split).

Placing a maximum bound on the age of Euarchontoglires is difficult because early members of Placentalia, including stem members of Euarchontoglires, probably differed little from stem eutherians in terms of their overall morphology (Bininda-Emonds et al., 2012). This may explain why probable early placentals such as *Purgatorius* (generally accepted as a euarchontan; see above) and *Protungulatum* (often placed within Laurasiatheria, typically close to euungulates; O’Leary et al., 2013) fall outside Placentalia in some phylogenetic analyses (e.g., Wible et al., 2007, 2009; Goswami et al., 2011). We have chosen to use a conservative maximum bound based on the age of well-preserved eutherians from the Yixian Formation such as *Ambolestes*, *Eomaia*, and *Sinodelphys*, which have fallen outside Placentalia in all published phylogenetic analyses to date (e.g., Ji et al., 2002;

Kielan-Jaworowska et al., 2004; Bi et al., 2018). The age of the Yixian Formation has now been constrained to between 125.755 ± 0.061 and 124.122 ± 0.048 Ma, based on U-Pb chemical abrasion-isotope dilution-isotope ratio mass spectrometry (CA-ID-IRMS; Zhong et al., 2021); we use the maximum age of this range (125.816 Ma) as our maximum bound here. However, this is almost certainly highly conservative, as the oldest convincing records of Placentalia are from the earliest Palaeocene (e.g., *Purgatorius mckeeveri*; Wilson Mantilla et al., 2021) or very slightly before (e.g., the latest Cretaceous *Protungulatum coombsi*; Archibald et al., 2011). The putative leptictidan *Gypsonictops* is known from the Late Cretaceous (Campanian-Maastrichtian; Kielan-Jaworowska et al., 2004) but has also been reported from much older, Turonian deposits (Cohen and Cifelli, 2015),

although this material remains to be formally published; if *Gypsonictops* is indeed a leptictidan, and if leptictidans are crown clade placentals, then this would push the origin of Placentalia considerably earlier than the K-Pg boundary. However, this remains uncertain (see Springer et al., 2019; Marjanović, 2021), and the recent study by Velazco et al. (2022) found leptictidans (including *Gypsonictops*) to fall outside Placentalia. The preponderance of current fossil evidence appears to support an origin of Placentalia and of the major placental superorders closer to the K-Pg boundary (see also Budd and Mann, 2022); we explicitly take this into account by proposing that this calibration be modelled as an offset exponential prior distribution. Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 85.9 and 79.7 Ma, respectively.

Additional CladeAge calibration. As discussed above, *Purgatorius mckeeveri* is the oldest known member of Euarchonta. The sister-taxon of Euarchonta is Glires, and the oldest definitive members of Glires (*Heomys* sp., *Mimotona wana*, and *M. lili*) are from the lower part of the Upper Member of the Wanghudun Formation in Anhui Province, China (Li, 1977; see “Crown Glires” below). The lower part of the Upper Member of the Wanghudun Formation is currently interpreted as the Shanguan Stage spanning 66.0–62.278 Ma (Wang, Y. et al., 2019; Speijer et al., 2020). Anagalidans have been suggested to be stem members of Glires (López-Torres and Fostowicz-Frelik, 2018), and the earliest members of this group are from the Lower Member of the Wanghudun Formation (Marjanović, 2021: node 155), thus predating *Heomys* sp., *Mimotona wana*, and *M. lili*. However, the precise relationship of Anagalida to Glires remains to be clearly resolved (López-Torres and Fostowicz-Frelik, 2018), and we note that they fell outside Euarchontoglires in the recent phylogenetic analysis of Asher et al. (2019). In addition, Wang et al. (2019) did not provide separate ages for the Lower Member and the lower part of the Upper Member of the Wanghudun Formation, and so the same age range (66.0–62.22 Ma) would apply even if we elected to use anagalidans for this additional CladeAge calibration.

Comments. The material of *Purgatorius mckeeveri* recently described by Wilson Mantilla et al. (2021) results in a very slightly older minimum on the age of this node than assumed in some previous studies (Benton et al., 2015; Marjanović, 2021). Benton et al. (2009) followed a similar approach to that

used here and based their soft maximum bound on the age of the Yixian eutherians, which were the oldest definitive eutherians known at the time. In their revised list of calibrations, Benton et al. (2015) used the maximum age of an even older eutherian discovered subsequently, namely *Juramaia sinensis* (Luo et al., 2011), to set a maximum bound of 164.6 Ma; however, such a liberal maximum bound is unlikely to place much constraint on the age of this node. By contrast, Marjanović (2021: node 152) proposed a hard maximum bound of 72 Ma on the age of Placentalia, which would force the maximum age of Euarchontoglires (and all other divergences within Placentalia) to be younger than this; however, this very tight maximum bound implicitly endorses an “explosive” model of placental origins, and the validity of this model remains controversial (Springer et al., 2019; but see Budd and Mann, 2022). We prefer to leave this node quite loosely calibrated (although not as loosely as Benton et al., 2015), an approach that we feel is warranted given continuing uncertainty regarding the timing of the origin of Placentalia (Bininda-Emonds et al., 2012; Foley et al., 2016; Springer et al., 2019; Álvarez-Carretero et al., 2022; Budd and Mann, 2022).

Crown Glires = Rodentia-Lagomorpha split

Calibrating taxon. *Heomys* sp.

Specimen. IVPP V4323, a crushed skull without cheek teeth, from the lower part of the Upper Member of the Wanghudun Formation in Anhui Province, China (Li, 1977).

Phylogenetic justification. Recent phylogenetic analyses (Asher et al., 2019; Rankin et al., 2020) support *Heomys* sp. as the earliest known member of Simplicidentata, which includes Rodentia. Of perhaps greatest significance, simplicidentates (including *Heomys* sp.) are characterised by the presence of a single pair of upper incisors, a synapomorphic feature shared by all rodents (Li et al., 2016; Fostowicz-Frelik, 2017, 2020).

Hard minimum bound. 62.278 Ma

Soft maximum bound. 66 Ma

Suggested prior distribution. Offset exponential
Age justifications. IVPP V4323 is from the lower part of the Upper Member of the Wanghudun Formation in Qianshan, Anhui Province (Li, 1977). According to Wang et al. (2019), the Lower Member and lower part of the Upper Member of the Wanghudun Formation can be correlated to the Shanguan Stage, corresponding to the upper-middle part of chron C29r to C27n, which is 66.0 to 62.278 Ma (Wang, Y. et al., 2019; Speijer et al.,

2020); the latter date therefore provides the hard minimum bound for this node.

As summarised by Marjanović (2021: node 155), crown clade Glires (rodents and other simplicidentates; lagomorphs and other duplicidentates) have not been found in the earlier, Lower Member of the Wanghudun Formation (Wang et al., 2016). However, fossil sites from the Lower Member are characterised by a diverse range of anagalidans (anagalids, the pseudictopid *Cartictops*, and the astigalid *Astigale*; Marjanović, 2021: node 155). The affinities of anagalidans are in need of detailed study, but it is widely accepted that they include stem relatives of crown Glires (Meng et al., 2003; Fostowicz-Frelik, 2017; López-Torres and Fostowicz-Frelik, 2018; but see the phylogenetic analysis of Asher et al., 2019). Evidence from their molar structure (including a tendency to hypsodonty) and tooth wear suggests that anagalidans were at least partially herbivorous (Fostowicz-Frelik, 2017), as is also the case for most living and fossil members of crown Glires, and features of the postcranial skeleton indicates that pseudictopids were cursorially adapted, similar to lagomorphs (Rose, 2006). We consider the presence in the Lower Member of the Wanghudun Formation of probable stem Glires (namely anagalidans, including some that were probably ecologically similar to lagomorphs), in combination with the apparent absence of crown Glires, to be reasonable evidence that the Rodentia-Lagomorpha split had not occurred by this time. We therefore propose the maximum age of the Shanghuan Stage (66.0 Ma; Wang, Y. et al., 2019) as the soft maximum bound on this node.

Given our assumption that the absence of crown Glires in the Lower Member of the Wanghudun Formation is not an artefact of incomplete sampling, but that it is an indication that Rodentia-Lagomorpha split had yet to occur, we consider that this calibration is most appropriately modelled using an offset exponential distribution. Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 63.5 and 63.1 Ma, respectively.

Additional CladeAge calibration. Our calibrating taxon, *Heomys* sp., is the oldest known stem rodent. The duplicidentates *Mimotona wana* and *M. lili* are from the same deposit as *Heomys* sp. (Li, 1977; Dashzeveg and Russell, 1988; Li et al., 2016). *Mimotona* and other duplicidentates differ from simplicidentates such as rodents and *Heomys* sp. but resemble lagomorphs in retaining two upper incisors (Li et al., 2016; Fostowicz-Frelik, 2020). However, presence of two upper incisors is

plesiomorphic for crown Glires, and so does not by itself constitute evidence that duplicidentates are stem lagomorphs rather than stem Glires. Nevertheless, *Mimotona* does share one distinctive derived dental synapomorphy with lagomorphs that is not seen in rodents or other simplicidentates, namely a longitudinal groove on the labial surface of the anteriormost upper incisor (Li and Ting, 1993; Li et al., 2016). *Mimotona* was also placed as a stem lagomorph in the recent phylogenetic analyses of Asher et al. (2019) and Rankin et al. (2020). Based on this collective evidence, we consider *Mimotona wana* and *M. lili* to be the oldest known stem representatives of Lagomorpha, at 66.0–62.278 Ma, and so provide the second CladeAge calibration for this node.

Comments. Benton et al. (2009) proposed a similar minimum bound for this node as that proposed here, but they proposed a much older maximum bound of 131.5 Ma, based on the maximum age of stem eutherians from the Yixian Formation (see “Crown Euarchontoglires” above). Benton et al. (2015) proposed an even older maximum bound, 164.6 Ma, based on the maximum age of the oldest currently known stem eutherian *Juramaia* (see “Crown Euarchontoglires” above). However, we consider both of these maximum bounds to be unduly conservative given the distinctive craniodental apomorphies of members of crown Glires, and the failure to find such taxa in any mammal-bearing site from the Cretaceous (see also Marjanović, 2021: node 155).

Crown Euarchonta = Scandentia-Primates split

Calibrating taxon. *Purgatorius mckeeveri*

Specimen. UCMP 150021, an isolated lower m2, from Harley’s Point locality in the lowermost part of the Tullock Member of the Fort Union Formation in Montana, USA (Wilson Mantilla et al., 2021).

Phylogenetic justification. Retrotransposon insertions provide statistically significant support for the hypothesis that Primates and Dermoptera form a clade (= Primatomorpha) to the exclusion of Scandentia (Mason et al., 2016; Doronina et al., 2022). Some published analyses examining deep relationships within Eutheria have recovered *Purgatorius* outside Placentalia (e.g., Wible et al., 2007, 2009; Goswami et al., 2011), but all recent published phylogenetic analyses focused on euarchontan relationships have placed *Purgatorius* closer to Primates and/or Dermoptera than Scandentia (Bloch et al., 2007; Ni et al., 2013, 2016; Chester et al., 2015, 2017; Li and Ni, 2016; Gun-

nell et al., 2018; Morse et al., 2019; Seiffert et al., 2020; see “Crown Euarchontoglires” above).

Hard minimum bound. 65.79 Ma

Soft maximum bound. 125.816 Ma

Suggested prior distribution. Offset exponential
Age justifications. In contrast to the craniodentally distinctive early crown members of Glires such as *Heomys* and *Mimotona* (see “Crown Glires” above), the earliest crown euarchontans may have been morphologically little different from stem eutherians (Bininda-Emonds et al., 2012), which might explain why, for example, *Purgatorius* falls outside Placentalia in some published analyses (Wible et al., 2007, 2009; Goswami et al., 2011). For this reason, we use the same minimum and maximum bounds for this node as for Crown Euarchontoglires, and again suggest modelling this as an offset exponential prior (see “Crown Euarchontoglires” above).

Additional CladeAge calibration. The fossil record of Scandentia is sparse. Besides the questionable *Eodendrogale parva* from the middle Eocene (Tong, 1988; Ni and Qiu, 2012), the oldest known scandentian is *Ptilocercus kylin* from the early Oligocene Lijiawa locality, Yunnan Province, China, which has an age estimate of ~34 Ma (Li and Ni, 2016), and represents a second CladeAge calibration for this node. Phylogenetic analyses place *P. kylin* within crown Scandentia, sister to the extant *P. lowii*, suggesting an extensive unsampled history of earlier scandentians.

Comments. Benton et al. (2009) proposed similar minimum and maximum bounds to those used here, whilst Benton et al. (2015) instead suggested a maximum bound of 164.6 Ma based on the maximum age of the oldest currently known stem eutherian, *Juramaia* (see “Crown Euarchontoglires” above). Marjanović (2021) did not calibrate this node.

Crown Primatomorpha = Primates-Dermoptera split

Calibrating taxon. *Teilhardina brandti*

Specimen. UM 99031 (holotype), an isolated m2, from UM locality SC-351 at the head of Big Sand Coulee in the Clarks Fork Basin, Wyoming (Gingerich, 1993a).

Phylogenetic justification. As summarised above (see “Crown Euarchontoglires”), the precise relationships of the various “plesiadapiforms” to the extant primatomorphan orders Primates and Dermoptera differ quite markedly between recent phylogenetic analyses; we therefore consider them unsuitable for calibrating this node. Two groups

with Paleocene representatives, namely plagiome-nids and mixodectids, have been proposed by some authors to be dermopteran relatives (Szalay and Lucas, 1993, 1998; Rose, 2006), but this has been questioned (MacPhee et al., 1989; Yapuncich et al., 2011), and so we have also chosen not to use these to calibrate this node. Instead, we use the oldest well-supported member of crown Primates, the omomyiform *Teilhardina brandti* (Gingerich, 1993a; Rose et al., 2011; Morse et al., 2019) as a necessarily conservative minimum bound.

Hard minimum bound. 55.935 Ma

Soft maximum bound. None

Suggested prior distribution. Not applicable (minimum bound only)

Age justifications. The oldest known material of *Teilhardina brandti*, including our calibrating specimen UM 99031, comes from the Bighorn Basin in Wyoming (Gingerich, 1993a; Smith et al., 2006; Rose et al., 2011; Morse et al., 2019). *T. brandti* material has been reported from various localities in the Bighorn Basin: Big Sand Coulee in the Clarks Fork Basin, a northern sub-basin in the Bighorn Basin (Gingerich, 1993a; Smith et al., 2006), the Willwood Formation (Bown and Rose, 1987), and the Sand Creek Divide and Cabin Fork sections (Rose et al., 2011; Morse et al., 2019). All these localities correlate to the second earliest biozone of the early Eocene, Wasatchian-0 (Wa-0), which follows the brief Wa-M biozone and coincides with most of the Paleocene-Eocene Thermal Maximum (PETM; Rose et al., 2011) which is marked by a global carbon isotope excursion (CIE; Yans et al., 2006). Rose et al. (2011) reported that, based on carbon isotopic stratigraphy, *Teilhardina brandti* appeared only 25 kyr after the onset of the PETM. Using 56.01 ± 0.05 Ma for the start of the PETM (Zeebe and Lourens, 2019), the age estimate of the appearance of *Teilhardina brandti* 25 kyr after this is then 55.985 ± 0.05 Ma, giving a minimum age of 55.935 Ma for UM 99031, which we use as our minimum bound here, and a maximum age of 56.035 Ma.

If the early Palaeocene *Purgatorius* is closer to Primates than to Dermoptera, or vice versa, then it seems likely that the Primates-Dermoptera split could predate the K-Pg boundary; conversely, if *Purgatorius* and other early “plesiadapiforms” are stem rather than crown primatomorphans, then the Primates-Dermoptera split could potentially be close to the Palaeocene-Eocene boundary (the age of the oldest definitive, crown, primates). For

this reason, we have chosen not to propose a soft maximum bound on this node.

Additional CladeAge calibration. The oldest known definitive dermopteran material that we use for the CladeAge calibration of this node is Dermoptera indet. from the Pondaung Formation of Myanmar (Marivaux, Bocat, et al., 2006), which has been radiometrically dated to 40.31–40.22 Ma (Khin Zaw et al., 2014; Jaeger et al., 2019).

Comments. This node does not appear to have been calibrated in recent molecular clock analyses, perhaps because compelling evidence for monophyly of Primatomorpha has only become available comparatively recently (Mason et al., 2016; Doronina et al., 2022).

Crown Primates = Haplorhini-Strepsirrhini split

Calibrating taxon. *Teilhardina brandti*

Specimen. UM 99031 (holotype), an isolated m2, from UM locality SC-351 at the head of Big Sand Coulee in the Clarks Fork Basin, northwestern Wyoming (Gingerich, 1993a).

Phylogenetic justification. *Teilhardina brandti* has been identified as an omomyiform (Gingerich, 1993a; Rose et al., 2011; Morse et al., 2019). Phylogenetic analyses consistently place Omomyiformes generally, and *Teilhardina* specifically, within crown Primates. In these analyses, omomyiforms are usually placed within Haplorhini as stem members of the lineage leading to modern tarsiers (=Tarsiiformes), with which they share large orbit size, elongated tarsals, small body size, an anteriorly positioned foramen magnum indicating a vertical head posture, and shortened crania (Ni et al., 2013, 2016; Gunnell et al., 2018; Morse et al., 2019; Jaeger et al., 2019). Even if *T. brandti* and other omomyiforms are discounted as the oldest crown primates (Godinot, 2015, 2017; Gunnell and Miller, 2018), the oldest known stem strepsirrhine (the 55.8–55.12 Ma old *Donrussellia provincialis*; see below) is only slightly younger than the oldest material of *T. brandti*, and so this would have little impact on the minimum bound of this calibration.

Hard minimum bound. 55.935 Ma

Soft maximum bound. 66.095 Ma

Suggested prior distribution. Offset exponential
Age justifications. The minimum bound is based on the minimum age of the oldest specimen of the oldest crown primate, *Teilhardina brandti* (see “Crown Primatomorpha” above). The maximum bound is based on the maximum age of the oldest specimen of the oldest known plesiadapiform *Purgatorius mckeeveri* (see “Crown Euarchontoglires” above). Although the affinities of *Purgatorius* and

other “plesiadapiforms” vary between analyses, they have not been recovered within crown Primates in any recently published study of which we are aware. A diversity of “plesiadapiforms” are known throughout the Palaeocene (Silcox et al., 2017). At least some of them were likely ecologically similar to early crown primates (Silcox et al., 2017), and they are known from fossil deposits in the same regions (particularly North America) where crown primates are known from younger sites. The presence of “plesiadapiforms” but the absence of ecologically similar crown primates in these Palaeocene sites (several of which are comparatively rich and well-sampled), and the approximately synchronous appearance of members of Haplorhini (*Teilhardina* spp.) and Strepsirrhini (*Donrussellia* spp.) in the earliest Eocene, collectively suggests to us that crown Primates probably originated close to the Palaeocene-Eocene boundary. Based on this, we suggest that this calibration is most appropriately modelled as an offset exponential prior. Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 59.3 and 58.3 Ma, respectively.

Additional CladeAge calibration. We recognise *Teilhardina brandti* as the oldest known haplorhine. Based on current evidence, the oldest known strepsirrhine appears to be the adapiform *Donrussellia*, with three species known from various early Eocene (MP7) sites in Europe (*Donrussellia magna* and *D. provincialis* from France: Godinot, 1978, 1998; and *D. lusitanica* from Portugal: Estravís, 2000). A fourth species, *D. gallica*, is slightly younger (MP8+9; Ramdarshan et al., 2015). Of these, *Donrussellia provincialis* and *D. gallica* have had their phylogenetic affinities formally tested in the context of large scale analyses (e.g., Ni et al., 2013; Morse et al., 2019) and are usually recovered as stem strepsirrhines. *Donrussellia provincialis* is also the best known species, based on multiple dental specimens and an isolated astragalus from the Rians locality (Boyer et al., 2017). We therefore use *D. provincialis* as our additional CladeAge calibration as the oldest known strepsirrhine, with an age range of 55.8–55.12 Ma, based on Solé et al.’s (2015) suggested age for Rians.

Comments. We differ from Benton et al. (2015) and dos Reis et al. (2018), who used *Altiaatlasius koulchii* from the Adrar Mgorn 1 locality, Morocco (Sigé et al., 1990), as the earliest record of crown primates. Adrar Mgorn 1 can be correlated to Chron 24r (Seiffert et al. 2010), which spans the

Paleocene-Eocene boundary, but based on associated fauna of invertebrates and selachians a latest Paleocene age for Adrar Mgorn 1 appears more likely (Gheerbrant 1998; Seiffert et al. 2010). This results in a minimum age of 56.0 Ma for *Altiatlasius koulchii*, based on the age of the end of the Thanetian (Speijer et al., 2020), which is only 0.065 Ma older than the minimum bound we set based on the appearance of *Teilhardina brandti*. However, *Altiatlasius* is of very uncertain phylogenetic relationships: it has been identified as a stem primate (Hooker et al., 1999; Morse et al., 2019), a crown primate of uncertain affinities (Silcox, 2008), a stem tarsiiform (Boyer et al., 2010), a basal haplorhine (Marivaux, 2006; Patel et al., 2012), or a stem anthropoid (Godinot, 1994; Marivaux, 2006; Bajpai et al., 2008; Seiffert et al., 2009; Tabuce et al., 2009; Patel et al., 2012) by different authors. Additionally, Seiffert et al. (2010) note that the morphological variation shown by the upper molars of *Altiatlasius* is problematic, although they still conclude that *Altiatlasius* is more likely to be an anthropoid than a plesiadapiform. Given the uncertainty surrounding its relationships, and the fact its minimum age being very close to that of *Teilhardina brandti*, we do not use *A. koulchii* to calibrate this node.

Benton et al. (2015) used a similar maximum bound to ours, but dos Reis et al. (2018) preferred a much older maximum (88.6 Ma), based on the results of statistical modelling of primate diversification by Wilkinson et al. (2011). In principle, such a quantitative approach is preferable to the admittedly subjective interpretation of the fossil record used here and in most other attempts to identify fossil calibrations for primates. However, we consider a Cretaceous origin for crown Primates to be highly unlikely. Not only is there no record of crown Primates from any Cretaceous site, including the comparatively well-sampled North American record (Kielan-Jaworowska et al., 2004; Wilson, 2014), but a Cretaceous origin for crown Primates would require that all deeper nodes within Euarchontoglires also occurred in the Cretaceous or earlier; there is, however, no record of Cretaceous “plesiadapiforms” either. Furthermore, there does not appear to be a clear explanation why the plesiomorphic “plesiadapiform” *Purgatorius* (a small-bodied [~100g], predominantly insectivorous, arboreal form; Chester et al., 2015; Silcox et al., 2017; Wilson Mantilla et al., 2021) should appear in the fossil record almost immediately after the K-Pg boundary (Wilson Mantilla et al., 2021), but the oldest crown primates, which appear to have been

ecologically broadly similar to *Purgatorius*, appear ~10 Ma later (and approximately simultaneously in North America, Asia, and Europe; Smith et al., 2006; Beard, 2008; Rose et al., 2011) if the lineages leading to *Purgatorius* and crown primates had already diverged in the Cretaceous. Instead, we consider the late Cretaceous and Paleocene fossil record to be sufficiently well sampled to support an origin of crown Primates close to the Palaeocene-Eocene boundary.

Crown Strepsirrhini = Lorisiformes-(Lemuriformes+Chiromyiformes) split

Calibrating taxon. *Saharagalago misrensis*

Specimen. CGM 40266 (type), a lower first molar from the BQ-2 locality in the Fayum region, Egypt (Seiffert et al., 2003).

Phylogenetic justification. Recent phylogenetic analyses of *Saharagalago misrensis* consistently place it as a crown strepsirrhine, typically as a stem lorisiform (Seiffert et al., 2018, 2020; Gunnell et al., 2018). A second taxon from BQ-2, *Karanisia clarki*, is also usually placed as a crown strepsirrhine (Seiffert et al., 2018, 2020; Gunnell et al., 2018; López-Torres and Silcox, 2020), providing further evidence that the Lorisiformes-(Lemuriformes+Chiromyiformes) split predates the age of this locality.

Hard minimum bound. 36.573 Ma

Soft maximum bound. 55.8 Ma

Suggested prior distribution. Uniform

Age justifications. The BQ-2 locality falls in a zone of normal polarity and has been correlated with Chron 17n.1n (Seiffert, 2006; Seiffert et al., 2008), which is currently recognised as spanning 37.385–36.573 Ma (Speijer et al., 2020), resulting in a minimum bound for this node of 36.573 Ma. The maximum bound is based on the maximum age of the earliest well-known stem strepsirrhine, *Donrussellia provincialis* (see “Crown Primates” above), based on the assumption that the divergence of crown Strepsirrhini is unlikely to predate the oldest stem member of the clade. There is a comparatively rich record of stem strepsirrhines from the Eocene in Europe, but the African record is still poorly known, with only three definitive stem strepsirrhines (*Djebelemur*, *Azibius* and *Algeripithecus*) known from the middle Eocene (~48 Ma; Van Couvering and Delson, 2020) of Algeria and Libya (Tabuce et al., 2009; Marivaux et al., 2013), followed by a ~11 million year gap until the probable crown strepsirrhines *Saharagalago* and *Karanisia* from BQ-2 mentioned above. For this reason, we suggest that this calibration be implemented as

a uniform prior between the minimum and maximum bounds.

Additional CladeAge calibration. We accept *Saharagalago* as the oldest known loriform. We consider the oldest well-supported member of the sister-taxon of Loriformes, namely the Chiromyiformes+Lemuriformes clade, to be the stem chiromyiform *Plesiopithecus teras*, from Quarry L-41 in the Fayum region, Egypt (Simons, 1992; Gunnell et al., 2018), which is dated to 35.102–33.9 Ma (Seiffert, 2006; Seiffert et al., 2008; see “Chiromyiformes-Lemuriformes split” below).

Comments. While we have used *Saharagalago* to provide the minimum bound on this node, Benton et al. (2015) instead used *Karanisia clarki* (Seiffert et al., 2003) to provide a minimum bound on the age of this node. In its original description, *Karanisia* was placed as a crown loriform (Seiffert et al., 2003), but its position in subsequent studies has varied, having been found as a stem strepsirrhine, stem loriform, or stem lemuriform (see summary in López-Torres and Silcox, 2020). We therefore prefer to use *Saharagalago*, which has been consistently placed as a loriform in recent analyses, to calibrate this node, as did dos Reis et al. (2018). For the maximum bound, both Benton et al. (2015) and dos Reis (2018) used the age of *Altiatlasius*, which they recognised as the oldest crown primate. However, as already discussed (see “Crown Primates” above), *Altiatlasius* is of uncertain affinities, and we instead use the age of the early stem strepsirrhine, *Donrussellia provincialis*, as our maximum bound here. Nevertheless, the ages of the minimum and maximum bounds proposed here fall closely to those of Benton et al. (2015) and dos Reis et al. (2018).

Chiromyiformes-Lemuriformes split

Calibrating taxon. *Plesiopithecus teras*

Specimen. DPC 12393, a crushed but nearly complete cranium with maxillary dentition from Quarry L-41 in the Fayum Depression, Egypt (Simons, 1992; Simons and Rasmussen, 1994).

Phylogenetic justification. Gunnell et al. (2018) presented compelling morphological evidence that *Plesiopithecus* (and a second taxon, the Miocene *Propotto*) is a stem member of Chiromyiformes (see also comments by Godinot, 2006), which today is represented by a single species, the aye-aye *Daubentonia madagascariensis*. This conclusion is supported by total evidence phylogenetic analyses, with and without the use of a clock model (Gunnell et al., 2018).

Hard minimum bound. 33.9 Ma

Soft maximum bound. 55.8 Ma

Suggested prior distribution. Uniform

Age justifications. *Plesiopithecus teras* comes from Quarry L-41 in the Fayum Depression, Egypt. The age of L-41 has been debated (Gingerich, 1993b; Seiffert, 2006, 2010; Seiffert et al., 2008; Van Couvering and Delson, 2020), but we follow the correlation of L-41 with chron C13r proposed by Seiffert (2006), which is supported by a better statistical fit than the correlations proposed by Kappelman et al. (1992), Gingerich (1993a), and Van Couvering and Delson (2020), and which requires fewer extra, unexplained reversals in the local magnetostratigraphic record (Seiffert et al., 2008, p. 79-81). In addition to the correlation of L-41 with chron C13r, Seiffert (2006) argued that a large unconformity just above the L-41 locality was “likely due to near-coastal erosion associated with the major marine regression that occurred near the Eocene-Oligocene boundary” (see appendix S1 of Sallam and Seiffert, 2016, p. 3) and thus that the L-41 locality predates the Oligocene. Applying the maximum age of chron C13r and the age of the Eocene-Oligocene boundary following Speijer et al. (2020), this results in an age range of 35.102–33.9 Ma for L-41.

Our proposed maximum bound is the same as for crown Strepsirrhini (see above). In particular, *Plesiopithecus* shows a range of unusual chiromyiform specialisations (Godinot, 2006; Gunnell et al., 2018), suggesting that it probably postdates the Chiromyiformes-Lemuriformes split quite considerably, and implying an extensive unsampled ghost lineage. The Oligocene *Bugtilemur mathesoni* from the Bugti Hills, Pakistan, was originally described as a crown lemuriform (Marivaux et al., 2001), but was subsequently identified as an adapiform, and hence a stem strepsirrhine, following the discovery of additional specimens (Marivaux et al., 2006). The 37.385–36.573 Ma old *Karanisia* was placed as a stem lemuriform in the tip-dating analysis of Seiffert et al. (2018), but most other analyses place it as a stem loriform (see summary in López-Torres et al., 2020). Thus, no definitive stem lemuriform fossils are currently known. However, if the Chiromyiformes-Lemuriformes split occurred in mainland Africa, as concluded by Gunnell et al. (2018), then lemuriforms should be expected to be found in the African fossil record. Indeed, Gunnell et al. (2018) implied that the poorly known *Notnamia* from the middle Eocene (~47 Ma; Van Couvering and Delson, 2020) of Namibia (Pickford et al., 2008) might be a stem lemuriform (but see Godinot et al., 2018), although this has not (to our knowl-

edge) been tested via formal phylogenetic analysis. Thus it seems possible that the Chiromyiformes-Lemuriformes split might be much older than 35.102–33.9 Ma. We therefore consider that a uniform age prior is most appropriate for this node.

Additional CladeAge calibration. *Plesiopithecus teras* is the oldest known chiromyiform. The oldest definitive records of the sister clade of Chiromyiformes, Lemuriformes, are subfossil remains from Madagascar, the earliest of which are *Hadropithecus stenognathus*, dating to about 7500 years ago (Burney et al., 2008; Godfrey et al., 2010); this record provides a very young additional CladeAge calibration.

Comments. Benton et al. (2015) and dos Reis et al. (2018) did not calibrate this node.

Crown Lorisiformes = Lorisidae-Galagidae split

Calibrating taxon. *Komba robustus*

Specimen. KNM-SO 501 (holotype), a right mandibular fragment with p4–m2, from Songhor, Kenya (Le Gros Clark and Thomas, 1952).

Phylogenetic justification. A position for *Komba* within crown lorisiforms, as a galagid, receives consistently strong support in recent published phylogenetic analyses (Seiffert et al., 2018, 2020; Gunnell et al., 2018). The older *Saharagalago* (see “Crown Strepsirrhini” above) *Karansia* and *Wadilemur* have been recovered as stem galagids in some analyses, but are placed outside crown Lorisiformes in others (see summaries in López-Torres and Silcox, 2020; López-Torres et al., 2020). Also of note are the findings of Phillips (2016) and Phillips and Fruciano (2018) that use of *Saharagalago* to calibrate the lorisid-galagid split results in extremely high apparent dating error. Using the results of molecular dating analyses to assess the appropriateness of particular fossil calibrations risks circularity, but in this case the strong mismatch in molecular rates found by Phillips (2016) and Phillips and Fruciano (2018) when *Saharagalago* is assumed to be a crown lorisiform, together with the fact that *Saharagalago* falls outside crown Lorisiformes in at least some analyses (Seiffert et al., 2018, 2020; Gunnell et al., 2018), persuades us that *Komba robustus* is a more appropriate calibrating fossil taxon for this divergence.

Hard minimum bound. 18.5 Ma

Soft maximum bound. 55.8 Ma

Suggested prior distribution. Uniform

Age justifications. Species of *Komba* (as well as several other putative galagids that have not had their phylogenetic affinities robustly tested, such as

Progalago spp. and *Mioeuoticus* spp.) are known from multiple early Miocene sites in east Africa (Harrison, 2010a: table 20.2). Although radiometric dates are available for at least some of these sites, including Songhor from where KNM-SO 501 was collected, this dating was done in the 1960s using K-Ar dating (Bishop et al., 1969), and it is in need of verification using more modern techniques (Cote et al., 2018). Songhor is currently recognised as falling within the Legetetian African Land Mammal Age (Van Couvering and Delson, 2020), and so pending new radiometric dating of this site, we use the minimum age of the Legetetian (which spans 22.5–18.5 Ma according to Van Couvering and Delson, 2020) as our minimum bound here, namely 18.5 Ma. Our maximum bound is the same as for crown Strepsirrhini and Chiromyiformes-Lemuriformes (see above).

Given that *Saharagalago*, *Karansia*, and *Wadilemur* have all been recovered as stem galagids in some analyses, it is possible that the galagid-lorisid split predates considerably our proposed minimum bound. For this reason, this calibration is most appropriately modelled as a uniform distribution.

Additional CladeAge calibration. The oldest lorisid that has had its phylogenetic affinities rigorously tested is *Nycticeboides simpsoni*, which is dated to ~8.9 Ma and falls within crown Lorisidae in most recent analyses (see “Crown Lorisidae” below).

Comments. Benton et al. (2015) did not calibrate this node. By contrast, dos Reis et al. (2018) used a similar minimum bound to ours (18 Ma), based on the early Miocene *Mioeuoticus*, which they recognised as a crown lorisid, but a tighter maximum bound (38 Ma) that seems questionable given the possibility that the 37.385–36.573 Ma *Saharagalago* is a crown lorisiform (see above); indeed, we note that their 95% posterior credibility interval for the Lorisidae-Galagidae split (34.1–40.9 Ma) exceeds their proposed maximum bound.

Crown Lorisidae = Lorisinae-Perodicticinae split

Calibrating taxon. *Nycticeboides simpsoni*

Specimen. YGSP 8091 (holotype), a near complete dentition formed by mandibular and maxillary fragments, some skull fragments, and a few post-cranial fragments including a distal humerus, all believed to represent a single individual, from the YGSP 363 locality in the Dhok Pathan Formation, Pakistan (Jacobs, 1981).

Phylogenetic justification. *Nycticeboides simpsoni* closely resembles extant *Nycticebus* species (Jacobs, 1981; MacPhee and Jacobs, 1986; Flynn and Morgan, 2005) and is typically found to be a crown loristine in published phylogenetic analyses: either sister to *Nycticebus* (Seiffert et al., 2015, 2018; Herrera and Dávalos, 2016) or sister to *Loris* (Seiffert et al., 2018). In a few analyses, however, *Nycticeboides* is placed as a stem loristine, outside *Loris+Nycticebus* (Seiffert et al., 2015), or as part of an unresolved polytomy with *Loris* and *Nycticebus* (Seiffert et al. 2010). Regardless, all of these phylogenetic placements support the use of *Nycticeboides* to place the minimum bound for the divergence between Lorisinae and Perodicticinae. An exception to this general pattern is seen in the total-evidence phylogenetic analyses by Seiffert et al. (2018), in which *Nycticeboides* was placed as a stem rather than crown loristid. However, Gunnell et al. (2018) and Seiffert et al. (2020) used morphological matrices that were expanded from Seiffert et al. (2018), and in both of these studies *Nycticeboides* was placed within crown Lorisidae. Morphological synapomorphies that support *Nycticeboides* as a loristine (and hence a crown loristid) are found in its facial, dental, and postcranial morphology (Jacobs, 1981; MacPhee and Jacobs, 1986), and so we are confident in using this taxon to calibrate this node here.

Hard minimum bound. 8.9 Ma

Soft maximum bound. 37.385 Ma

Suggested prior distribution. Uniform

Age justifications. The YGSP 363 (or Y363) locality in the Dhok Pathan Formation, Pakistan, has been argued to be younger than 8 Ma based on dating of older sites in the same section (Tauxe, 1979), and *Nycticeboides* was assigned an approximate age of ~8–7 Ma in its original description (Jacobs, 1981). MacPhee and Jacobs (1986) listed an age of 7.5–7.0 Ma for the holotype based on tracing of the lithologic unit to a measured section dated by Tauxe and Opdyke (1982). However, Flynn and Morgan (2005) subsequently reported an age of 9.1–7.8 Ma for YGSP 363, and this locality is currently believed to be ~8.9 Ma old (L. J. Flynn, pers. comm. 21/01/2021); we use this latter date as our hard minimum bound here.

As discussed above (see “Crown Strepsirrhini” and “Crown Lorisiformes” above), most recent published phylogenetic analyses find that *Saharagalago* and *Karanisia* are stem lorisiforms, and so it seems likely that they predate divergences within the crown lorisiform families Lorisidae and Galagidae. We therefore use the

maximum age of the BQ-2 Quarry (see “Crown Strepsirrhini” above) as our maximum bound here.

There are a number of fossil putative loristids that are older than *Nycticeboides simpsoni*, at least some of which may be members of crown Lorisidae. These include *Mioeuoticus* from the early Miocene (~19–18 Ma) of East Africa (Le Gros Clark, 1956; Leakey, 1962), ?*Nycticebus linglom* from the Miocene (18.0–17.0 Ma or 14.2–12.0 Ma) of Thailand (Mein and Ginsburg, 1997), and an isolated m1 from the middle Miocene (~15.2 Ma) locality Y682 in the Kamli Formation of Pakistan that Flynn and Morgan (2005) identified as *Nycticeboides* sp. We have not used these taxa to inform our proposed minimum bound on this divergence here, because their phylogenetic affinities are either controversial or have not been formally tested; nevertheless, they suggest that the Lorisinae-Perodicticinae split may predate considerably the age of *Nycticeboides simpsoni*, and so a uniform prior distribution on the age of this node seems appropriate.

Additional CladeAge calibration. As summarised above, we consider *Nycticeboides simpsoni* to be the oldest well-supported member of crown Lorisidae. The affinities of most other fossil loristids currently known are controversial or have not been tested via formal phylogenetic analysis. Pickford (2012) described OCO 119'10, a partial rostrum (preserving part of the upper dentition) of a loristid from the Aragai locality in the Lukeino Formation, and tentatively referred this specimen to the extant perodicticine genus *Arctocebus*. Although OCO 119'10 has not been included in a published phylogenetic analysis, its close overall resemblance to *Arctocebus* means that we consider it the oldest definitive perodicticine. The Aragai locality is currently considered to be ~6.1 Ma (Gilbert et al., 2010).

Comments. dos Reis et al. (2018) used a considerably older minimum bound for this divergence of 14 Ma, based on an undescribed genus and species from Fort Ternan in Kenya, which Harrison (2010a) reported “is most similar to *Perodicticus*, and may eventually be referable to the Perodicticinae.” However, pending description of this specimen and formal testing of its affinities, we prefer a younger minimum bound here. The maximum bound of dos Reis et al. (2018) is similar to that used here.

Crown Haplorhini = Anthropeidea-Tarsiiformes split

Calibrating taxon. *Tarsius eocaenus*

Specimen. IVPP V14563, a left premaxillary-maxillary fragment preserving the crown of P3, alveoli for I2, C1, P2, and the mesial roots of P4, from Shanghuang fissure D, near the village of Shanghuang, southern Jiangsu Province, China (Rossie et al., 2006).

Phylogenetic justification. *Tarsius eocaenus* has not, to our knowledge, been included in a comprehensive phylogenetic analysis to formally test its affinities, but its preserved cranial morphology is almost identical to that seen in modern tarsiids, and includes several unusual derived traits (Rossie et al., 2006). Based on this, we are confident that *Tarsius eocaenus* is a definitive tarsiiform. Omomyiiforms, including the oldest known member of this group *Teilhardina brandti*, are typically placed as stem tarsiiforms in recent phylogenetic analyses (see “Crown Primates” above). However, some doubts remain as to whether omomyiiforms are indeed members of the tarsiiform lineage (Godinot, 2015; Gunnell and Miller, 2018).

Based on current evidence, the oldest anthropoids are eosimiids and amphipithecids from the Eocene of Asia (Beard et al., 1994; Beard and Wang, 2004; Marivaux et al., 2005; Seiffert, 2012; Seiffert et al., 2018; Jaeger et al., 2019, 2020). The eosimiid *Eosimias* was placed as a stem haplorhine, rather than an anthropoid, by López-Torres and Silcox (2018), but this study focused on the phylogeny of plesiadapiforms rather than haplorhines. In recent phylogenetic analyses that have been specifically intended to resolve the relationships of haplorhines, however, eosimiids have been consistently placed as stem anthropoids (e.g., Marivaux et al., 2005; Seiffert, 2012; Ni et al., 2013, 2016; Seiffert et al., 2018, 2020; Gunnell et al., 2018; Morse et al., 2019; Jaeger et al., 2019, 2020). The oldest known eosimiid is *Eosimias sinensis*, which, like *Tarsius eocaenus*, is from the Shanghuang fissure fills (Beard et al., 1994; Ni et al., 2020, see Age Justification below); additional eosimiid taxa may be present among the Shanghuang primate material, but they remain unnamed (Gebo et al., 2017).

Older putative records of anthropoids are based on specimens that are much more fragmentary and are correspondingly more equivocal; they include *Altiatlasius koulchii* from the Palaeocene-Eocene of Africa, which is of very uncertain relationships (see “Crown Primates” above), and *Anthrasimias gujaratensis* from the early Eocene of India (Bajpai et al., 2008), the material of which has subsequently been suggested to in fact represent the asiadapid (stem strepsirrhine) *Marcgodinotius*

indicus (Rose et al., 2009, 2018). There is thus an ~8–15 million year gap between the oldest omomyiiform (*Teilhardina brandti*, ~56 Ma; see “Crown Primatomorpha” above) and the oldest definitive tarsiiform (*Tarsius eocaenus*) and oldest widely accepted anthropoid (*Eosimias sinensis*), both of which are 47.8–41.0 Ma old (see Age Justification below). While the primate fossil record is obviously far from complete, the large gap between the oldest omomyiiforms and the oldest tarsiiforms and anthropoids may be an indication that at least some omomyiiforms are stem rather than crown haplorhines; thus, we do not use omomyiiforms to calibrate this node. Although *Tarsius eocaenus* and *Eosimias sinensis* are both from the Shanghuang fissure fillings, the presence of highly distinctive tarsiiform features in *T. eocaenus*, together with the somewhat labile position of *Eosimias* within Haplorhini (López-Torres and Silcox, 2018) means that we use the former as our calibrating taxon here, and use *E. sinensis* for the CladeAge calibration (see below).

Hard minimum bound. 41.0 Ma

Soft maximum bound. None

Suggested prior distribution. Not applicable (minimum bound only)

Age justifications. Five fissures with fills preserving fossil mammals are known from Shanghuang, and these are referred to as fissures A–E. The cranial fragment of *Tarsius eocaenus* that we use as our calibrating specimen is from fissure D (Rossie et al., 2006; see above), but the holotype (IVPP V11030, an isolated right m1) and other dental specimens are known from fissures A and B (Beard et al., 1994). *Eosimias sinensis* is known from two partial right mandibles: the holotype (IVPP V10591) from fissure B, and a referred specimen (IVPP V10592) from fissure A. Fissures D and E have been argued to be older than A–C based on mammalian biostratigraphy (Wang and Dawson, 1994; Beard et al., 1994; Qi et al., 1996; Qi and Beard, 1996; Métais et al., 2004; Rossie et al., 2006). However, Ni et al. (2020) did not recognise different ages for the different Shanghuang fissure fills, assigning all of them to the Irindinmanhan Asian Land Mammal Age, which spans 47.8–41.0 Ma. We therefore assume an age range of 47.8–41.0 Ma for both *Tarsius eocaenus* and *Eosimias sinensis*, and thus a minimum of 41.0 Ma on this node.

Given the uncertainty regarding the affinities of omomyiiforms discussed above, we find it difficult to define an appropriate maximum bound and

associated prior age distribution, and so do not propose these for this node.

Additional CladeAge calibration. As discussed (see Phylogenetic Justification), we recognise *Eosimias sinensis* as the oldest known anthropoid, which therefore represents our additional CladeAge calibration for this node, and which has the same age range (47.8–41.0 Ma) as *Tarsius eocaenus*.

Comments. Although dos Reis et al. (2018) did not discuss omomyiform affinities, it is notable that they chose to specify the minimum bound on crown Haplorhini using *Tarsius eocaenus* (as done here), together with a second fossil tarsiid from China (*Xanthorhysis*), rather than using an omomyiform. Like us, they left the maximum bound on this node uncalibrated.

Crown Anthropoidea = Catarrhini-Platyrrhini split

Calibrating taxon. *Catopithecus browni*

Specimen. DPC 8701, a near complete skull, from Quarry L-41 in the Fayum Depression, Egypt (Simons, 1989, 1990).

Phylogenetic justification. *Catopithecus* has been proposed to be a stem catarrhine, and therefore a crown anthropoid, based on the apomorphic loss of the upper and lower second premolars, and development of a honing blade for the upper canine on a sexually dimorphic lower p3 (Simons and Rasmussen, 1996; Seiffert and Simons, 2001). A stem catarrhine position for *Catopithecus* has been supported by recent phylogenetic analyses focused on relationships within Haplorhini, including those of Ni et al. (2016), Morse et al. (2019), Seiffert et al. (2020), and Beck et al. (2023).

Hard minimum bound. 33.9 Ma

Soft maximum bound. 56.035 Ma

Suggested prior distribution. Uniform.

Age justifications. *Catopithecus browni* comes from Quarry L-41 in the Fayum Depression, Egypt, for which we assume an age range of 35.102–33.9 Ma, following Seiffert (2006; see “Chiromyiformes-Lemuriformes split” above). For the maximum bound we use the maximum age of our calibrating specimen of the oldest crown primate, *Teilhardina brandti* (see “Crown Primatomorpha” above).

A few stem anthropoids have been described from African sites that are slightly older than Quarry L-41 (e.g., *Biretia*, *Talahpithecus*), but as yet no definitive crown anthropoids; however, a currently undescribed taxon from the 37.385–36.573 Ma BQ-2 locality may represent a stem

catarrhine (Gunnell and Miller, 2018; E.R. Seiffert, pers. comm. 24/03/2021), which would result in a slightly older minimum bound than that proposed here. In addition, some phylogenetic analyses presented by Jaeger et al. (2019) placed *Aseanpithecus* from the 40.31–40.22 Ma Pondaung Formation of Myanmar within crown Anthropoidea, although Jaeger et al. (2020) subsequently considered this taxon to be “of uncertain familial status”. At present we consider that this calibration is best modelled as a uniform distribution, although we suspect that this divergence is almost certainly closer to the minimum than the maximum bound.

Additional CladeAge calibration. *Catopithecus browni* is the oldest known stem catarrhine. Antoine et al. (2021) recently described highly fragmentary primate teeth from Shapaja, San Martín, Peruvian Amazonia in a site (TAR-21) that they dated to between 33.9 and 34.5 Ma, i.e., the latest Eocene (Antoine et al., 2021). These specimens resemble *Perupithecus ucayaliensis* from the early Oligocene (29.6 ± 0.08 Ma) Santa Rosa Fauna of Peru (Campbell et al., 2021), which is probably a stem platyrrhine (Bond et al., 2015; Kay et al., 2019; Seiffert et al., 2020; Beck et al., 2023), and so we tentatively recognise them as stem platyrrhines as well. However, the reported ages of the Shapaja sites were questioned by Campbell et al. (2021), with these authors concluding that an Oligocene date was more likely. Pending resolution of this issue, we prefer to use the detrital zircon date for the Santa Rosa Fauna, source of *Perupithecus*, as our second CladeAge calibration: this is 29.68–29.52 Ma. *Talahpithecus* from the Dur At-Talah escarpment, central Libya (Van Couvering and Delson, 2020), was recovered as a stem platyrrhine in the phylogenetic analysis of Bond et al. (2015), but its position as sister to *Perupithecus* implies a very complex biogeographical origin for Platyrrhini with multiple crossings of the Atlantic Ocean, and so we do not use *Talahpithecus* as the oldest record of Platyrrhini here.

Comments. Benton et al. (2015) and dos Reis et al. (2018) also used *Catopithecus* to provide a minimum bound on this node. However, both these studies used a more conservative maximum bound than that proposed here. Benton et al. (2015) used 66 Ma, based in part on their identification of *Altiatlasius* as the oldest crown primate and possible crown anthropoid; however, we consider the affinities of *Altiatlasius* to be uncertain (see “Crown Primates” above) and do not use it for calibration purposes. Dos Reis et al. (2018), meanwhile, used a maximum of 62.1 Ma based on the modelling of

primate diversification by Wilkinson et al. (2011), about which we have concerns (see “Crown Primates” above).

Crown Catarrhini = Cercopithecoidea-Hominoidea split

Calibrating taxon. *Rukwapithecus fleaglei*

Specimen. RRBP 12444A (holotype), a right mandible including p4-m3 and part of ascending ramus from Nsungwe 2B, Tanzania

Phylogenetic justification. *Rukwapithecus fleaglei* was consistently recovered as a stem hominoid (within the clade Nyanzapithecinae) in the parsimony and Bayesian phylogenetic analyses of Stevens et al. (2013), indicating that it postdates the Cercopithecoidea-Hominoidea split. Stevens et al. (2013) noted that some nodes within their illustrated phylogeny have low support values, but there are various synapomorphies reported for four nodes leading up to Nyanzapithecinae, and for this subfamily itself. *Rukwapithecus fleaglei* shares two synapomorphies with Miocene and extant hominoids that are not present in cercopithecoids or stem catarrhines: a buccal position of the M2 hypoconulid, and the mesial migration of cusps on the buccal side of lower molars such that the hypoconid is positioned opposite the lingual notch between the metaconid and the entoconid (Stevens et al., 2013).

Hard minimum bound. 25.193 Ma

Soft maximum bound. 35.102 Ma

Suggested prior distribution. Uniform

Age justifications. *Rukwapithecus fleaglei* comes from locality Nsungwe 2B in the Oligocene Nsungwe Formation in southwestern Tanzania (Stevens et al., 2013). The age of the fossil bearing unit is constrained by two volcanic tuffs dated by U-Pb zircon CA-TIMS (U-Pb chemical abrasion thermal ionisation mass spectrometry) at 25.237 ± 0.098 and 25.214 ± 0.021 Ma (Stevens et al., 2013). Taking into account these confidence intervals, the minimum age for this specimen is 25.193 Ma and the maximum is 25.335 Ma. For the soft maximum bound, we use the maximum age of the oldest known probable stem catarrhine, *Catopithecus browni*, from the Quarry L-41 of the Fayum Depression, Egypt (see “Crown Strepsirrhini” above). The late Oligocene record of primates and other terrestrial mammals in Africa is notoriously poor (Kappelman et al., 2003; Wilkinson et al., 2011; Stevens et al., 2013), and for this reason we suggest that this calibration is best modelled as a uniform calibration.

Additional CladeAge calibration. Another fossil species from Nsungwe 2B is *Nsungwepithecus gunnelli*, currently known from a single specimen (RRBP 11178), a left partial mandible with a lower m3 (Stevens et al., 2013). *Nsungwepithecus* was not included in the phylogenetic analyses by Stevens et al. (2013), but the authors reported the presence of numerous lower molar synapomorphies that are shared with “victoriapithecoid” cercopithecoids (“Victoriapithecidae” is a paraphyletic assemblage of stem cercopithecoids in the phylogenetic analyses of Stevens et al., 2013 and Rasmussen et al., 2019), such as deeply incised buccal clefts, a high degree of buccal flare, and the lack of a buccal cingulid. Rasmussen et al. (2019) confirmed the stem cercopithecoid position of *Nsungwepithecus* in their phylogenetic analysis, but they argued that the phylogenetic position of *Nsungwepithecus* should be regarded as tentative until more material is available. We therefore recognise *Nsungwepithecus gunnelli* as the oldest (stem) representative of Cercopithecoidea, with the same age estimate as *Rukwapithecus fleaglei*; 25.335–25.193 Ma.

Comments. Although differing in detail, Benton et al. (2015), dos Reis et al. (2018), and Roos et al. (2019) all proposed very similar minimum and maximum bounds for this node.

Crown Cercopithecidae = Cercopithecinae-Colobinae split

Calibrating taxon. Colobinae gen. et. sp. indet.

Specimen. KNM-TH 48368, an isolated right lower molar (?m3) from the Baringo Paleontological Research Project (BPRP) no. 38 site in the Kabasero type section of the Ngorora Formation, Tugen Hills succession, Kenya (Rossie et al., 2013).

Phylogenetic justification. Phylogenetic analyses by Rossie et al. (2013) consistently placed KNM-TH 48368 as an early colobine, regardless of whether it was coded as an m2 or an m3. KNM-TH 48368 displays a very small but distinct hypoconulid, which is also present in the fossil colobines *Microcolobus* and *Mesopithecus* and many extant colobines (Rossie et al., 2013). Synapomorphies that KNM-TH 48368 shares with extant colobines are: “tall and sharp transverse lophids, reduced basal flare of the crown, a wide and deep median buccal cleft, buccal cusps with a columnar profile and mesial tilt, a long talonid basin relative to overall crown length, and subequal mesial and distal crown breadths” (Rossie et al., 2013).

Hard minimum bound. 12.47 Ma

Soft maximum bound. 25.235 Ma

Suggested prior distribution. Offset exponential
Age justifications. KNM-TH 48368 comes from the Kabasero section of the Ngorora Formation in the Tugen Hills, Kenya (Rossie et al., 2013). 40Ar/39Ar dating of the fossiliferous horizon itself provides an age of 12.49 ± 0.02 Ma for this locality, resulting in a minimum and maximum age for this specimen of 12.47 and 12.51 Ma respectively. The horizon is also bracketed below and above by 40Ar/39Ar dates of 12.56 ± 0.04 Ma and 12.26 ± 0.07 Ma, respectively (Deino et al., 2002; Hill et al., 2002; Rossie et al., 2013). The maximum bound for this node is based on the maximum age of the two oldest known crown catarrhines, namely the stem cercopithecoid *Nsungwepithecus* and stem hominoid *Rukwapithecus* from Nsungwe 2B, Tanzania, with a maximum age of 25.214 ± 0.021 Ma (see “Crown Catarrhini” above).

Between the oldest known stem cercopithecoid *Nsungwepithecus* and KNM-TH 48368, a diverse range of fossil cercopithecoids are known from multiple early and middle Miocene (~22.5–15 Ma; Van Couvering and Delson, 2020) sites throughout Africa, comprising at least nine species-level taxa (Locke et al., 2020, table 1). Not all of these have had their phylogenetic affinities formally tested, but those that have (namely the “victoriapithecids” *Prohylobates*, *Noropithecus*, and *Victoriapithecus*) consistently fall outside crown Cercopithecidae (Miller et al., 2009; Stevens et al., 2013; Rasmussen et al., 2019). The African primate fossil record is sparse between 15 and 6 Ma (Rossie et al., 2013). However, the diversity of stem cercopithecids between 22.5 and 15 Ma (Locke et al., 2020, table 1) and the apparent absence of crown cercopithecids in this same time interval persuades us that this divergence is likely to be close to our minimum bound, and so we propose an offset exponential prior distribution. Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 16.7 and 15.4 Ma, respectively.

Additional CladeAge calibration. KNM-TH 48368 is the oldest known colobine. The oldest known record of Cercopithecinae is possible stem papionin material from the Beticha locality in the Chorora Formation, Ethiopia (Suwa et al., 2015; Katoh et al., 2016). Based on available evidence, we do not consider the Beticha material to be unequivocally papionin (see “Crown Cercopithecinae” below), but we do recognise it as cercopithecine. The Beticha fossil-bearing unit is above a pumiceous tuff that has been dated to 8.18 ± 0.15

Ma by K–Ar dating and 7.86 ± 0.10 Ma by 40Ar–39Ar dating, and below a consolidated tuff dated to 7.67 ± 0.17 Ma by K–Ar dating and 7.82 ± 0.11 Ma by 40Ar–39Ar dating (Katoh et al., 2016). Taking the maximum and minimum bounds for these radiometric dates, this gives an age range of 8.33–7.5 Ma, which we suggest as our additional CladeAge calibration.

Comments. dos Reis et al. (2018) do not calibrate this node, but our maximum and minimum bounds are similar to those proposed by Roos et al. (2019).

Crown Colobinae = Colobini-Presbytini split

Calibrating taxon. *Mesopithecus pentelicus delsoni* (*Mesopithecus delsoni* according to de Bonis et al. 1990; recognised here as subspecies of *Mesopithecus pentelicus* following Alba et al., 2015).

Specimen. RZO 159 (holotype of *Mesopithecus delsoni* according to de Bonis et al., 1990; recognised as a subspecies of *Mesopithecus pentelicus* by Alba et al., 2014a; 2015), a nearly complete adult male mandible, from Ravin des Zouaves-5, Greece.

Phylogenetic justification. *Mesopithecus* has been placed as a member of Presbytini in the few published morphological phylogenetic analyses that have specifically examined this question (Jablonski, 1998; Byron, 2001). However, these analyses have not incorporated molecular data, and that of Jablonski (1998) shows important differences to the current molecular consensus view of relationships within Colobinae. In attempt to remedy this, one of us (RMDB) has undertaken preliminary total evidence analyses combining Jablonski’s (1998) morphological matrix with 55.5 kb of nuclear and mitochondrial DNA sequence data (taken from Springer et al., 2012), using both undated and tip-dating approaches, similar to those used by Beck et al. (2023); these analyses place *Mesopithecus* within Presbytini with strong support (Beck, in prep.). Dental metrics of *Mesopithecus* are more similar to modern presbytins than to colobins (Pan et al., 2004), and mandibular morphology of *Mesopithecus* shows particular similarities to that of the modern presbytin genera *Rhinopithecus* and *Pygathrix* (Jablonski et al., 2020), but these resemblances are only suggestive because they have not been placed in an explicit phylogenetic context.

Some researchers have cited the unreduced pollex of *Mesopithecus* as evidence that it falls outside crown Colobinae, all living members of which are characterised by a reduced-to-absent pollex

(with a greater degree of pollicial reduction in colobins than presbytins; Frost et al., 2015; Alba et al., 2015). However, *Mesopithecus* has been reported to have a slightly reduced pollex (Jablonski et al., 2020; but see Frost et al. 2015), and Jablonski (1998: character 148) specifically included “thumb length” as one of the 455 morphological characters used in her phylogenetic analysis. As noted by Jablonski et al. (see also Nakatsukasa et al., 2010; 2020), pollicial reduction has occurred at least twice within Anthrozoidea, as the pollex is greatly reduced or absent in the platyrrhine atelids *Ateles* and *Brachyteles* (Rosenberger et al., 2008), and we agree with those authors that undue weight should not be placed on a single morphological character, particularly when datasets based on multiple characters are available (Jablonski, 1998; Byron, 2001). We therefore recognise *Mesopithecus* as the earliest definitive presbytin based on the results of published phylogenetic analyses (Jablonski, 1998; Byron, 2001), and our own unpublished work (Beck, in prep.), and therefore suitable for calibrating this node. However, we acknowledge that this relationship warrants further testing, particularly with datasets that include a denser sampling of fossil taxa (*Mesopithecus* is the only fossil taxon included in the dataset of Jablonski, 1998, as used by Beck, in prep.).

Hard minimum bound. 8.125 Ma

Soft maximum bound. 15 Ma

Suggested prior distribution. Uniform

Age justifications. The source of our calibrating specimen, the Ravin des Zouaves-5 locality in Greece, is estimated to date to ~8.2 Ma based on magnetostratigraphic evidence and its correlation to C4r.1r (Sen et al., 2000; Koufos, 2009), which has an age range of 8.257–8.125 Ma (Raffi et al., 2020), of which we use the minimum bound. A *Mesopithecus* specimen from another Greek locality, Nikiti 2, may slightly pre-date this (Koufos, 2016), but its minimum age is also 8.2 Ma. Additionally, the material from Nikiti 2 comprises of one metacarpal and one metatarsal, and we prefer to use the Ravin des Zouaves-5 specimen (which is a near complete mandible) to calibrate this node. A maxillary fragment of *Mesopithecus* has also been reported from Grebeniki 1 (Gremyatskii, 1961), Ukraine, which was originally dated to the early Turolian, specifically zone MN11 (8.8–7.9 Ma, following collated information by Alba et al., 2015). A subsequent faunal correlation analysis by Vangengeim and Tesakov (2013) correlated Grebeniki 1 with the preceding zone MN10 (9.7–8.8 Ma) which would imply an older minimum bound on this

node; however, given the current uncertainty surrounding the age of this site (see Koufos, 2019), we do not use it to calibrate this node.

The oldest stem colobine material is the ~12.5 Ma Colobinae gen. et. sp. indet. from Tugen Hills (Rossie et al., 2013; see “Crown Cercopithecidae” above). However, we have decided against using this material as the basis for our maximum bound due to the poor African record of primates between 15 and 6 Ma (Rossie et al., 2013); instead, we use 15 Ma as our maximum bound, as the better sampled Miocene record prior to this date reveals a diversity of stem cercopithecoids (“victoriapithecids”) but no crown forms (Locke et al., 2020, table 1; see “Crown Cercopithecidae” above). Based on this poor record 15–6 Ma, we suggest modelling this calibration as a uniform prior.

Additional CladeAge calibration. We recognise *Mesopithecus pentelicus delsoni* as the oldest known presbytin (see above). The oldest member of Colobini appears to be an astragalus from the Lukeino Formation, which is ~6.1 Ma (KNM-LU 344, Gilbert et al., 2010). The astragalus displays apparently diagnostic features of Colobini, such as the distinct groove for the flexor tibialis and the lateral suppression of the facet for the lateral calcaneonavicular ligament, making it the oldest fossil specimen identified as exhibiting specific colobin synapomorphies (Gilbert et al., 2010). As far as we are aware, the affinities of KNM-LU 344 have not been tested by formal phylogenetic analysis, but we consider the presence of features that (on current evidence) appear to be synapomorphies of Colobini (Gilbert et al., 2010) to be sufficient to use this specimen to provide the CladeAge calibration for this node. KNM-LU 344 comes from the Aragai site 2/228 near the base of the Lukeino Fm. in Tugen Hills, Kenya (Gilbert et al., 2010). The Lukeino Formation is bracketed between 6.2–5.7 Ma (Deino et al., 2002; Gilbert et al., 2010), and as the Aragai site 2/228 lies near the base of the Lukeino Formation, it was assigned a tentative date of ~6.1 Ma by Gilbert et al. (2010). However, in the absence of specific dating information for Aragai site 2/228, we instead propose the entire age range of the Lukeino Formation of 6.2–5.7 Ma as the CladeAge calibration of this node.

Comments. We refrain from using the ~7 Ma old possible colobin “*Cercopithecoides bruneti*” from Toros-Menalla, Chad, which has been referred to Colobini based on its gracile mandibular morphology and adaptations to at least some degree of terrestrial locomotion (Pallas et al., 2019). The assignment of “*C.*” *bruneti* to the *Cercopithecoides*

genus needs to be further substantiated as “*C*” *bruneti* lacks the distinct mandibular features of Plio-Pleistocene *Cercopithecoides* (i.e., dorsoventrally short and buccolingually broad mandibles; Pallas et al., 2019). Furthermore, although Pallas et al. (2019) identified several dental features in *Cercopithecoides bruneti* that they considered to be “consistent with a Colobini morphology”, they did not clearly identify specific apomorphic features that would support its placement in Colobini.

The study of dos Reis et al. (2018) used the 9.8 Ma colobine *Microcolobus* to provide a minimum bound on this node, but to our knowledge *Microcolobus* has not been demonstrated to be a member of crown Colobinae, and in fact Rossie et al. (2013) found it to be more closely related the older Tugen Hills material than to extant colobines, suggesting that this taxon is more likely to be a stem form. Roos et al. (2019), meanwhile, used *Mesopithecus* to provide a minimum bound on this node in their “calibration set 1”, which is their more restrictive set of calibrations.

The maximum bound of 23 Ma proposed for this node by dos Reis et al. (2018) is more conservative than ours and does not appear to take into account the diverse early Miocene record of stem cercopithecoids (see above, Locke et al., 2020). In contrast, Roos et al. (2019) set their maximum bound for this node at 12.5 Ma based on the Kabasero colobine material (Rossie et al., 2013; see “Crown Cercopithecidae” above), which, as discussed above, we consider overly restrictive given the poor African primate record 15–6 Ma (Rossie et al., 2013).

Crown Cercopithecinae = Cercopithecini-Papionini split

Calibrating taxon. Cercopithecini sp. indet

Specimen. AUH 1321, a lower left molar, most likely an m1, from the SHU 2-2 locality in the Baynunah Formation, Abu Dhabi (Gilbert et al., 2014).

Phylogenetic justification. Phylogenetic analyses indicate that AUH 1321 is a crown cercopithecine (Gilbert et al., 2014; Plavcan et al., 2019; see “Crown Cercopithecini” below).

Hard minimum bound. 6.5 Ma

Soft maximum bound. 15.0 Ma

Suggested prior distribution. Uniform

Age justifications. There are no radiometric dates for the SHU 2-2 locality, and so its age estimate is based on geochronological comparisons with Asian and African faunas. These faunal correlations indicate an age between 8.0 and 6.5 Ma, with the most probable age reported as being around

7.0 Ma (Gilbert et al., 2014), but we prefer to use the minimum of this age range as our minimum bound here. As already discussed (see “Crown Cercopithecidae” and “Crown Colobinae” above), a diverse range of stem cercopithecoids, but no crown forms, are known from the early Miocene prior to ~15 Ma (Locke et al., 2020, table 1), with the African fossil record becoming scarce 15–6 Ma (Rossie et al., 2013). A few fossils are known within this interval that may be relevant for calibrating this node, in particular a possible stem papionin from the Beticha locality of the Chorora Formation at 8.33–7.5 Ma (Suwa et al., 2015; Katoh et al., 2016). However, material of this Beticha taxon is extremely fragmentary (Suwa et al., 2015), it has (not to our knowledge) been included in a formal phylogenetic analysis, and Roos et al. (2019) pointed out the difficulty in determining whether it is a stem papionin or stem cercopithecine without lower incisors that might reveal whether or not enamel was present lingually (absence of lingual enamel is the only compelling dental synapomorphy of Papionini). For this reason, we do not use the Beticha taxon to provide our minimum bound.

We use 15.0 Ma as our maximum bound, based on the same reasoning as for crown Colobinae (see “Crown Colobinae” above). Because of the poor fossil record 15–6 Ma, and the possibility of a markedly earlier divergence (based on the Beticha taxon) than specified by our minimum bound, a uniform prior on this calibration seems most appropriate.

Additional CladeAge calibration. We recognise AUH 1321 as the oldest known cercopithecine. Discounting the possible stem papionin from Beticha for the reasons discussed above, we consider the oldest record of Papionini to be the “*Parapapio*” *lothagamensis* material from the Nawata Formation at Lothagam, Kenya (Leakey et al., 2003). Although yet to be rigorously tested by a suitably comprehensive phylogenetic analysis, it is generally accepted that “*Parapapio*” *lothagamensis* is a stem papionin, albeit probably warranting referral to a separate genus (Leakey et al., 2003; Harrison, 2011; Gilbert, 2013; Pugh and Gilbert, 2018). The oldest known material of “*Parapapio*” *lothagamensis* material appears to be from the Lower Nawata Formation (Leakey et al., 2003), the age of which can be constrained based on dated tuffaceous horizons to between ~9.1 ± 0.2 Ma (the youngest age of the underlying Nabwal Arangan Formation) and 6.54 ± 0.04 Ma (the oldest age of the overlying Upper Nawata Formation; McDougall and Feibel,

2003; Brown and McDougall, 2011), giving an age range of 9.3–6.5 Ma for our CladeAge calibration.

Comments. Our minimum bound on this node is the same as that proposed by Roos et al. (2019) in their more conservative “calibration set 2”. By contrast, dos Reis et al. (2018), used a younger minimum bound of 5.0 Ma, based on “*Parapapio*” *lothagamensis*, but this is problematic because the phylogenetic analyses of Gilbert et al. (2014) and Plavcan et al. (2019), although differing somewhat, both place the ~6.5 Ma AUH 1321 within crown Cercopithecini (see below), and so the Cercopithecini-Papionini split must predate this. For a maximum bound, Roos et al. (2019) used the ~12.5 Ma Kabasero colobine material (Rossie et al., 2013; see “Crown Cercopithecidae” above), which, as discussed, we consider overly restrictive given the poor African primate record 15–6 Ma (Rossie et al., 2013). The maximum bound of dos Reis et al. (2018) meanwhile, was 23 Ma, based on the presence of *Kamoyapithecus* (which dos Reis et al., 2018, considered to be hominoid) at ~25 Ma, and the appearance of the stem cercopithecoid *Prohylobates* at 19.5 Ma onwards. Similarly to crown Colobinae (see above), we consider this overly conservative: the diversity of stem cercopithecoids but absence of crown forms in the early Miocene African record prior to ~15 Ma persuades us that the Cercopithecini-Papionini split probably post-dates this.

Crown Papionini = Macacina-Papionina split

Calibrating taxon. cf. *Macaca* sp.

Specimen. MGPT-PU 130508, a partial male cranium, from the Moncucco Torinese locality, Italy (Alba et al. 2014b).

Phylogenetic justification. In a conference abstract, Alba et al. (2014a) reported that MGPT-PU 130508 is “undoubtedly papionin, as evidenced by facial and dental morphology and size”, and that its molars “display the typical generalised papionin morphology that is characteristic of *Macaca*, and their size fits with the upper-most range of *M. sylvanus* subspp.”, and they identified it as cf. *Macaca* sp. A full description of this significant specimen has yet to be published, and it lacks a full phylogenetic context, but based on the information provided by Alba et al. (2014a) we tentatively recognise this as a member of Macacina. In particular, we consider that it provides a more robust basis for calibrating this node than older (~7.0–5.8 Ma) but much more fragmentary remains of ?*Macaca* sp. from Menacer, Algeria (Arambourg,

1959; Delson, 1975), which have been used by some previous authors (see below).

Hard minimum bound. 5.33 Ma

Soft maximum bound. 12.51 Ma

Suggested prior distribution. Uniform

Age justifications. The fossil locality at Moncucco Torinese has been assigned a late Turolian (MN13, late Miocene) age based on its fossil fauna. The presence of an ostracod assemblage assigned to the *Loxocorniculina djafarovi* Zone allows a further refinement of the age to 5.40–5.33 Ma (Alba et al. 2014b), with the minimum age providing our minimum bound.

For a maximum bound, we propose the maximum age of the oldest crown cercopithecoid, namely the Kabasero Colobinae gen. et. sp. indet. material, which is 12.51 Ma (see “Crown Cercopithecidae” above); although the African primate fossil record is poor 15–6 Ma (Rossie et al., 2013), it seems unlikely that the Macacina-Papionina split, which is nested well within Cercopithecidae, would predate the overall oldest crown cercopithecoid record.

We do not use the 7.0–5.8 Ma record of ?*Macaca* sp. from Menacer, Algeria (Arambourg, 1959; Delson, 1975) to calibrate this node (see below), but this record raises the possibility that our minimum bound is relatively conservative; we therefore propose a uniform prior on this calibration.

Additional CladeAge calibration. We consider MGPT-PU 130508 to be the oldest robust record of Macacina. Based on available evidence, we consider the oldest robust record of Papionina to be 4.2–4.1 Ma old specimens from Kanapoi, West Turkana, and Kenya, which have been identified as *Theropithecus* sp. indet. (Frost et al., 2020), and which provide our additional CladeAge calibration.

Comments. Dos Reis et al. (2018) did not calibrate this node. However, Roos et al. (2019) used an older minimum bound on this node of 5.8 Ma in their “calibration set 1” based on ~7.0–5.8 Ma old remains of ?*Macaca* sp. from Menacer, Algeria (Arambourg, 1959; Delson, 1975). Roos et al. (2019) noted themselves that it is unclear whether ?*Macaca* sp. from Menacer falls on the Macacina or the Papionina lineage. More seriously, Jablonski and Frost (2010) observed that there are no features of the ?*Macaca* sp. material from Menacer that would distinguish it from being a stem papionin, as was also noted by Delson (1975, 1980) and Szalay and Delson (1979). We therefore refrain from using this taxon for calibrating this node and instead use the slightly younger cf.

Macaca from Moncucco Torinese discussed above. Roos et al. (2019) also used a comparatively young maximum bound of 8 Ma based on the possible stem papionin from the Beticha locality; we have already discussed the uncertainty surrounding this material (see “Crown Cercopitheci-*nae*” above), and such a tight maximum bound seems unjustified given the comparatively poor record of primates in Africa between 15 and 6 Ma (Rossie et al., 2013).

Crown Cercopithecini

Calibrating taxon. Cercopithecini sp. indet.

Specimen. AUH 1321, a lower left molar (most likely the first molar), from the SHU 2-2 locality in the Baynunah Formation, Abu Dhabi (Gilbert et al., 2014).

Phylogenetic justification. As already mentioned (see “Crown Cercopitheci-*nae*” above), published phylogenetic analyses indicate that AUH 1321 is a crown cercopithecin: it was placed as sister to *Chlorocebus* or *Cercopithecus* in the analysis of Gilbert et al. (2014), but sister to *Miopithecus* or in a polytomous clade with all extant cercopithecin genera except *Allenopithecus* in the analysis of Plavcan et al. (2019). A combination of features makes AUH 1321 most similar to non-*Allenopithecus* cercopithecins, namely a small and narrow molar with low-to-moderately flaring, elongated basin, and a distally expanded lophid (Gilbert et al., 2014). Nevertheless, the variation in the position of AUH 1321 between these analyses means that its precise affinities are unclear. Furthermore, molecular phylogenies support a somewhat different set of relationships within Cercopithecini than do the analyses of Plavcan et al. (2019), in which the deepest split among extant cercopithecins is between *Allenopithecus* and the remaining genera; for example, Perelman et al. (2011) found *Allenopithecus* to be part of a clade that also includes *Chlorocebus* and *Erythrocebus*, whilst dos Reis et al. (2018) recovered an *Allenopithecus*+*Miopithecus* clade. These issues notwithstanding, we consider the phylogenetic analyses of Gilbert et al. (2014) and Plavcan et al. (2019) to collectively comprise sufficient evidence that AUH 1321 post-dates the deepest split within Cercopithecini, and so can be used to provide a minimum bound on this node.

Hard minimum bound. 6.5 Ma

Soft maximum bound. 12.51 Ma

Suggested prior distribution. Uniform

Age justifications. The age of the SHU 2-2 locality, which informs the minimum bound of this node,

is discussed above (see “Crown Cercopitheci-*nae*”). Our maximum bound and suggested prior distribution follow the same logic as for crown Papionini (see above).

Additional CladeAge calibration. Because it is uncertain exactly where AUH 1321 fits within crown Cercopithecini, and because of the incongruence between morphological (Gilbert et al., 2014; Plavcan et al., 2019) and molecular (e.g., Perelman et al., 2011; dos Reis et al., 2018) phylogenies of Cercopithecini, we refrain from suggesting an additional CladeAge calibration for this node.

Comments. This node was not calibrated by Benton et al. (2015), dos Reis et al. (2018), or Roos et al. (2019).

Crown Hominoidea = Hominidae–Hylobatidae split

Calibrating taxon. *Kenyapithecus wickeri*

Specimen. KNM-FT 46a-b (holotype), left maxillary fragment with C1 and P4-M2 present, from Fort Ternan, Kenya (Leakey, 1961).

Phylogenetic justification. *Kenyapithecus* has consistently been referred to as a crown hominoid, and specifically a hominid, by researchers (Pickford, 1985; Kelley et al., 2008; Harrison, 2010b; Alba, 2012) based in particular on the presence of the putative hominid synapomorphy of an anteriorly situated zygomatic root that is relatively high above the alveolar plane. This has been supported by formal phylogenetic analyses focused on hominoid relationships, with *Kenyapithecus* typically recovered as a stem hominid (e.g., Young and MacLachy, 2004; Worthington, 2012; Begun et al., 2012; Pugh, 2022). In contrast, Nengo et al. (2017) and Gilbert et al. (2020) found it to fall within crown Hominidae as a pongine, but we note that these analyses were focused on deeper relationships within Catarrhini, and include relatively limited sampling of hominoids (in contrast to e.g., Pugh, 2022). On available evidence, *Kenyapithecus* is a probable stem hominid, and its position within crown Hominoidea is well supported (but see Benoit and Thackeray, 2017); we consider it the oldest definitive crown hominoid currently known.

Hard minimum bound. 13.4 Ma

Soft maximum bound. 25.235 Ma

Suggested prior distribution. Offset exponential
Age justifications. The minimum age is based on dates of the Fort Ternan fossil locality published by Pickford et al. (2006), who report on whole-rock K/Ar and single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dates of lava flows underlying and overlying the fossil beds at Fort Ternan. The fossil beds at Fort Ternan are estimated

to be 13.7 ± 0.3 Ma (Pickford et al., 2006), giving an age range of 14.0–13.4 Ma, with the minimum age as our hard minimum bound. A second species of *Kenyapithecus*, *K. kizili*, has been described from Paşalar, Turkey (Kelley et al., 2008), which may be slightly older than *K. wickeri* (Roos et al., 2019). However, the age of Paşalar is poorly constrained (Casanovas-Vilar et al., 2011), and we do not use *K. kizili* to inform our minimum bound here. The maximum bound is based on the maximum age of the oldest stem hominoid *Rukwapithecus* (see “Crown Catarrhini” and “Crown Cercopithecidae” above).

In a situation equivalent to that seen in cercopithecoids (see “Crown Cercopithecidae”), the early Miocene African fossil record of Hominoidea is characterised by a diversity of stem taxa (proconsuline and nyanzapithecine “proconsulids”) without any evidence of crown representatives (Harrison, 2010b; Stevens et al., 2013; Nengo et al., 2017; Almécija et al., 2021). We tentatively interpret this as evidence that the Hominidae-Hylobatidae split was probably much closer to our minimum bound than our maximum bound, and so we propose calibrating this divergence with an offset exponential prior distribution. Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 17.4 and 16.1 Ma, respectively.

Additional CladeAge calibration. We consider *Kenyapithecus wickeri* to be the oldest known hominid (stem or crown, see above). For the CladeAge calibration of this node, we conservatively propose the 8.2–7.1 Ma *Yuanmoupithecus xiaoyuan* from the Late Miocene of Yunnan in southern China (Pan, 2006; Gilbert et al., 2020; Ji et al., 2022). Recent published phylogenetic analyses support *Yuanmoupithecus* as a stem hylobatid (Gilbert et al., 2020; Ji et al., 2022). The ~13.8–12.5 Ma *Kapi ramnagarensis* from the Lower Siwaliks of Ramnagar, India, was identified as a stem hylobatid by Gilbert et al. (2020), an inference supported by their phylogenetic analysis. However, *Kapi* is currently known only from a single lower third molar, and the phylogenetic analyses of Ji et al. (2022) found it to be a pliopithecoid or a more primitive stem catarrhine. Based on evidence published to date, we consider the affinities of *Kapi* to be too uncertain for use as a CladeAge calibration, and we instead use the younger *Yuanmoupithecus xiaoyuan*, which is more robustly supported as a definitive hylobatid (Gilbert et al., 2020; Ji et al., 2022).

Comments. Our minimum and maximum bounds are broadly similar to those of Roos et al. (2019). By contrast, Benton et al. (2015) proposed the crown hominid (stem pongine) *Sivapithecus* as the oldest crown hominoid, with a minimum age of 11.6 Ma, and used the age of the earliest anthropoids in the Fayum Depression as their maximum bound; in light of our discussion above, we consider both minimum and maximum bounds proposed for this node by Benton et al. (2015) to be unduly conservative. Dos Reis et al. (2018) did not calibrate this node, but they stated in three separate places that they considered the ~25 Ma old *Kamoyapithecus* to be a “crown hominoid”, a conclusion that they themselves admitted is “controversial”. However, the paper they cited in support of this conclusion, Zalmout et al. (2010), found *Kamoyapithecus* to be a stem (not crown) hominoid, and more distantly related to Hylobatidae+Hominidae than is “Proconsulidae”; table 1 of dos Reis et al. (2018) also lists *Kamoyapithecus* as a stem hominoid, in agreement with current evidence, as summarised above.

Crown Hominidae = Homininae-Ponginae split

Calibrating taxon. *Sivapithecus indicus*

Specimen. (GSP) Y 16075, maxilla (Raza et al., 1983; Kappelman et al., 1991) with the connection between the maxilla and premaxilla partially preserved (Begun, 2015), from locality Y494 from the Chinji Formation, Pakistan (Pilgrim, 1910).

Phylogenetic justification. *Sivapithecus* has been consistently recovered as a pongine in recent phylogenetic analyses (e.g., Begun et al., 2012; Nengo et al., 2017; Gilbert et al., 2020; Pugh, 2022). Y 16075 preserves the derived subnasal anatomy characteristic of modern orangutans (*Pongo* spp.; Kappelman et al., 1991). Isolated teeth from slightly older sites in the Chinji Formation have been referred to *Sivapithecus*, but they lack diagnostic features to support this referral (Kappelman et al., 1991), and so we do not use these for calibration purposes. We note that the slightly older *Kenyapithecus* (see “Crown Hominoidea” above) has been recovered as a pongine in some recent phylogenetic analyses (Nengo et al., 2017; Gilbert et al., 2020), but others place it as a stem hominid (e.g., Young and MacLatchy, 2004; Worthington, 2012; Begun et al., 2012; Pugh, 2022), and so it is not suitable for calibrating this node.

Hard minimum age. 12.3 Ma

Soft maximum age. 25.235 Ma

Suggested prior distribution. Offset exponential

Age justifications. We base our minimum age on the reported age of 12.3 Ma for another site in the mid-Chinji Formation, Y647 (which also preserves *Sivapithecus indicus* specimens), which is stated to be at the same stratigraphic level as Y494 (Morgan et al., 2015); this age is stated to be based on magnetostratigraphy, but Morgan et al. (2015) do not provide further details, and so it should be treated as tentative.

We base the maximum bound on the maximum age of the oldest stem hominoid *Rukwapithecus* (see “Crown Catarrhini”, “Crown Cercopithecidae”, and “Crown Hominoidea” above). A potential alternative maximum bound would be to use the maximum age of the oldest hominoid *Kenyapithecus*, which is 14.0 Ma (see Crown Hominoidea above). However, given that a few published analyses have placed *Kenyapithecus* as a crown hominid (Nengo et al., 2017; Gilbert et al., 2020), it may be unduly restrictive to use this taxon to inform our maximum bound. We therefore choose a more conservative approach based on the age of *Rukwapithecus*, as this taxon has been consistently found to be a stem hominoid in recent phylogenetic analyses (see “Crown Catarrhini” and “Crown Cercopithecidae” above). We consider the offset exponential distribution to be most appropriate for this calibration, based on the same arguments given for the crown Hominoidea node (see “Crown Hominoidea” above). Assuming a 5% probability of exceeding the soft maximum bound, this would give a mean and median prior on this divergence of 16.6 and 15.3 Ma, respectively.

Additional CladeAge calibration. We consider *Sivapithecus indicus* to be the oldest definitive pongine. Pugh (2022) presented a series of phylogenetic analyses of Miocene hominoids based on a large (41 taxa, 274 characters) morphological character matrix, using different character coding schemes and analytical methods. Most of these analyses found *Nakalipithecus* (described by Kuni-matsu et al., 2007) to be the oldest (stem) hominine among the taxa included (see Pugh, 2022: figure 5); total evidence tip-dating analysis of the Pugh (2022) matrix in combination with DNA and protein sequence data also strongly supports *Nakalipithecus* as a stem hominine (Beck, in prep.). All known specimens of *Nakalipithecus* are from Upper Member of the Nakali Formation of Kenya, within Chron C5n.1n (Kunimatsu et al., 2007), which is 9.937–9.786 Ma (Raffi et al., 2020), and provides our additional CladeAge calibration here.

Comments. Roos et al. (2019) used *Kenyapithecus wickeri* (with a maximum age of 14.9 Ma) as their maximum bound on this node, on the assumption that it is a stem hominid. The stem hominid position of *Kenyapithecus* has been supported by most recent phylogenetic analyses (e.g., Pugh, 2022), but it was placed as a crown hominid (pongine) by Nengo et al. (2017) and Gilbert et al. (2022), hence our decision to use the maximum age of the oldest stem hominoid *Rukwapithecus fleaglei* (see “Crown Hominoidea” above) for setting the soft maximum bound at 25.235 Ma. Benton et al. (2015), meanwhile, used a maximum of 33.9 Ma based on the age of the oldest known crown anthropoids from the L-41 Quarry of the Fayum Depression, Egypt (see “Crown Anthrozoidea” above), which seems excessively conservative given the diversity of stem hominoids but absence of crown forms in the early Miocene African record (see “Crown Hominoidea” above).

Homo-Pan split

Calibrating taxon. *Ardipithecus ramidus*

Specimen. GWM5sw/P56, a mandibular ramus and partial dentition (p3-m3) from GWM-5sw locality in Gona, Ethiopia (Semaw et al., 2005; Simpson et al., 2019).

Phylogenetic justification. Notable features of *A. ramidus* that appear to be synapomorphies placing it as a member of the *Homo* lineage include the more incisiform canines, an anteriorly located foramen magnum, and a proximal ulnar morphology that is shared with *Australopithecus* species (White et al., 1995, 2009; Suwa, Asfaw, et al., 2009; Suwa, Kono, et al., 2009; but see Harrison, 2010c). This interpretation has been tested in formal phylogenetic analyses by Dembo et al. (2015, 2016), Mongle et al. (2019), Püschel et al. (2021), and Pugh (2022), all of whom recovered *A. ramidus* as a member of the *Homo* lineage. Although *Ardipithecus kadabba* is slightly older than *A. ramidus* (5.8–5.2 Ma, Haile-Selassie, 2001; WoldeGabriel et al., 2001; 2004), we refrain from using this species to calibrate this node as it has not been included in any of these phylogenetic analyses, most likely due to the scarcity of *Ardipithecus kadabba* material. The phylogenetic analyses of Dembo et al. (2015, 2016), Mongle et al. (2019), and Püschel et al. (2021) also placed *Sahelanthropus* (which may be older than *A. ramidus*) closer to *Homo* than to *Pan*, but doubts over the stratigraphic provenance of *Sahelanthropus*, and hence its age, mean that we do not use it as our calibrating taxon here (see “Comments” below).

Hard minimum bound. 4.631 Ma

Soft maximum bound. 15 Ma

Suggested prior distribution. Uniform

Age justifications. The oldest *A. ramidus* localities (GWM-1, GWM-5sw, and GWM-9) have been assigned to the C3n.2r magnetozone (Simpson et al., 2019) which corresponds to an age of 4.799–4.631 Ma (Raffi et al., 2020). Pickford and Senut (2005) reported a ~12.5 Ma isolated lower molar from the Ngorora Formation that they suggested may belong to the *Pan* lineage (but which Kunitatsu et al. (2007) considered resembles *Gorilla*), which raises the possibility that this divergence may be markedly older than our minimum bound. Based on these factors, we take a conservative approach for this node, and use the same 15 Ma maximum bound as for crown Colobinae and crown Cercopithecinae (see above); this was chosen to reflect the generally poor record of primates in Africa 15–6 Ma (Rossie et al., 2013), and the fact that stem hominoids (proconsuline and nyanzapithecine “proconsulids”; see “Hominidae-Hylobatidae split” above) were diverse but crown hominoids were apparently absent in Africa during the early Miocene prior to 15 Ma. For the same reason, we also suggest a uniform bound is the appropriate prior distribution for this node.

Additional CladeAge calibration. We recognise *Ardipithecus ramidus* as the oldest known member of the *Homo* lineage that has a well-constrained age. The fossil record of its sister-clade, the *Pan* lineage, is extremely limited. To date, the oldest fossils are specimens that have been referred to the modern genus *Pan* from the Kapthurin Formation of Kenya (McBrearty and Jablonski, 2005; although this was questioned by Harrison, 2010b, who instead argued that they may belong to *Homo*), the age is constrained by $^{40}\text{Ar}/^{39}\text{Ar}$ dates of 545 ± 3 kyr for deposits underlying the fossils and 284 ± 12 kyr for deposits overlying them (Deino and McBrearty, 2002; McBrearty and Jablonski, 2005). The fossils are located most closely to the underlying deposit, and McBrearty and Jablonski (2005) argued that their age is likely to be close to 0.5 Ma. However, we prefer to use the entire age range (including confidence intervals) for this record, giving an additional CladeAge calibration for this node of 0.548–0.272 Ma.

Comments. Unlike us, Benton et al. (2015), dos Reis et al. (2018), and Roos et al. (2019) all used the age of *Sahelanthropus* to provide a minimum bound on this divergence, although the precise date used varied between these studies: Benton et al. (2015) used 6.5 Ma, Roos et al. (2019) used 6.2

Ma, and dos Reis et al. (2018) used 7.5 Ma. The known cranial morphology of *Sahelanthropus* preserves several apparent synapomorphies shared with members of the *Homo* lineage, to the exclusion of *Pan* (see e.g., Brunet et al., 2002; Zollikofer et al., 2005; MacLatchy et al., 2010; Emonet et al., 2014). Although this interpretation has been questioned by some authors (Wolpoff et al., 2002; Wolpoff and Pickford, 2006), recent phylogenetic analyses by Dembo et al. (2015, 2016), Mongle et al. (2019), and Püschel et al. (2021) have consistently placed *Sahelanthropus* closer to *Homo* than to *Pan*, as the deepest diverging member of the *Homo* lineage among the taxa included in these analyses. However, questions have been raised about the stratigraphic origin of *Sahelanthropus* material (Beauvilain, 2008), and thereby on its reported age of 7.2–6.8 Ma (Lebatard et al., 2008). Ahern (2018) concluded that the fossil material of *Sahelanthropus* is most likely of late Miocene age, but suggested that its age could not be constrained more accurately than 7.5–5.0 Ma based on available data. We accept that *Sahelanthropus* is most likely a member of the *Homo* lineage, but due to the uncertainty surrounding its age we prefer to take a more conservative approach and use the more securely dated *Ardipithecus ramidus* for calibrating this node. However, if more robustly dated *Sahelanthropus* material is reported that predates the age of *A. ramidus*, the minimum age of this calibration will need to be updated.

Orrorin from Kenya, dating to 6.0–5.7 Ma (Senut et al., 2001; Sawada et al., 2002), is another proposed member of the *Homo* lineage that predates *A. ramidus*. Like *Sahelanthropus*, *Orrorin* shares putative *Homo*-lineage synapomorphies with *Ardipithecus*, such as small canines and features hinting at early stages of bipedalism present in the basicranium and lower limb bones (Richmond and Jungers, 2008; MacLatchy et al., 2010; Harrison, 2017). However, to our knowledge, *Orrorin* has not been included in suitably comprehensive, published phylogenetic analyses (such as those by Dembo et al., 2015, 2016; Mongle et al., 2019; Püschel et al., 2021; and Pugh, 2022), that would support its *Homo*-lineage affinity, and so we refrain from using it to calibrate this node.

Benton et al. (2015) proposed a maximum bound of 10 Ma on this node, given that “a range of ape taxa, *Ankarapithecus* from Turkey (10 Ma), *Gigantopithecus* from China (8–0.3 Ma), *Lufengopithecus* from China (10 Ma), *Ouranopithecus* from Greece (~9.3 Ma), and *Sivapithecus* from Pakistan (10–7 Ma) give maximum ages of 10 Ma, early in

the late Miocene, and these deposits have yielded no fossils attributable to either chimps or humans.” Importantly, however, all of these taxa are Eurasian not African, and current evidence supports relatively limited dispersal of hominoids out of Africa (Gilbert et al., 2020). In particular, it seems likely that the split between the *Homo* and *Pan* lineages occurred in Africa (but see Fuss et al., 2018), with members of the *Homo* lineage probably not dispersing out of Africa until the early Pleistocene (Trifonov et al., 2019), and members of the *Pan* lineage apparently never doing so. Thus, the absence of members of the *Homo* and *Pan* lineages in ~10 Ma old Eurasian deposits would still be expected even if the split between these lineages had already occurred by this time, and so there seems no compelling reason to use this as a maximum bound on this node. Roos et al. (2019), meanwhile, assumed a maximum bound of 8 Ma based on the putative stem gorillin *Chororapithecus* (Suwa et al. 2007; Katoh et al. 2016). Dos Reis et al. (2018) also used *Chororapithecus* to provide a maximum bound on this divergence, but assumed a 10 Ma age for *Chororapithecus* based on the initial report by Suwa et al. (2007), whereas its age has now been revised down to 7.5–8.33 Ma (Katoh et al., 2016). Regardless, we consider the use of *Chororapithecus* to inform the maximum bound on this node to be inappropriate, firstly because the phylogenetic position of *Chororapithecus* was found to be unstable by Pugh (2022), secondly because of the ~12.5 Ma potential *Pan* relative described by Pickford and Senut (2005), and thirdly because of the overall poor African record of primates 15–6 Ma (Rossie et al., 2013), as already discussed.

Crown Platyrrhini = Pitheciidae-(Aotidae+Atelidae+Callitrichidae+Cebidae) split

Calibrating taxon. *Stirtonia victoriae*

Specimen. DU/IGM 85-400 (holotype), a right maxilla preserving erupted dP2-dP4 M1-M2, and mineralised but unerupted C1 and P2-P4, from Duke Locality 28, La Venta, Colombia (Kay et al., 1987).

Phylogenetic justification. The total evidence phylogenetic analyses of Beck et al. (2023) identified *Stirtonia* as the oldest well-supported member of crown Platyrrhini. *Stirtonia* was strongly supported as sister to *Alouatta*, within crown Atelidae (Beck et al., 2023). *Cebupithecia* and *Nuciruptor* were both also strongly supported as crown platyrrhines (specifically, stem pitheciines) by Beck et al. (2023), and a partial postcranial skeleton (IGM

184667) that might be referable to one or other of these genera is known from Duke Locality 79 at La Venta (Meldrum and Kay, 1990, 1997; Horovitz, 1999), which lies just below the Chunchullo Sandstone in the La Victoria Formation of the Honda Group (Flynn et al., 1997), and so is slightly older than Duke Locality 28 (Montes et al., 2021). However, in the absence of associated dental material that might clarify to which taxon IGM 184667 belongs, we have not used it for calibration purposes here.

One other candidate for the oldest crown platyrrhine is *Proteropithecia neuquenensis* from the Collón Curá Formation of Argentina, which has been considered by most authors to be a stem pitheciine (Kay et al., 2013; Rosenberger and Tejedor, 2013; Kay, 2015; Tejedor and Novo, 2016; Rosenberger, 2020); however, Beck et al. (2023, table 2) considered the age of this taxon to be poorly constrained to 19.76–10.4 Ma, and so it could potentially be younger than *Stirtonia* and the other La Venta primates (see Beck et al., 2023, table 2). In addition, several of the phylogenetic analyses of Beck et al. (2023) found *Proteropithecia* to be unstable, and these authors noted the possibility that this taxon may in fact be a stem platyrrhine. All older fossil platyrrhines, including *Panamacebus transitus* (which has been found to be a cebid in some other published analyses; Bloch et al., 2016; Kay et al., 2019), were placed outside the crown clade in analyses by Beck et al. (2023).

Hard minimum bound. 13.363 Ma

Soft maximum bound. None

Suggested prior distribution. Not applicable (minimum bound only)

Age justifications. *Stirtonia victoriae* is currently the oldest *Stirtonia* species known, with all known material from Duke Locality 28 within the Cerro Gordo Beds of the La Victoria Formation at La Venta (Guerrero, 1997), approximately 290 m below the stratigraphic level from where specimens of the younger *S. tatacoensis* have been collected (Kay et al., 1987). Guerrero (1993, 1997) and Flynn et al. (1997) indicated that the Cerro Gordo Beds, the overlying Chunchullo Beds, and the underlying San Alfonso Beds all lie within Chron C5ABn (see Montes et al., 2021), which spans from 13.608 to 13.363 Ma (Raffi et al., 2020), with the latter providing our minimum bound.

For less inclusive divergences within crown Platyrrhini (primarily divergences within families; see the calibrations that follow), we have proposed a maximum bound based on the maximum

reported age of the oldest probable stem platyrrhine specimens, which is 34.5 Ma (Antoine et al. 2021, see “Pitheciinae” below for a detailed justification of this), although we note that this date has been questioned (Campbell et al., 2021). The ancestor of crown Platyrrhini was probably a very small (~400g), insectivore-frugivore (Lynch Alfaro, 2017; Silvestro, Tejedor, et al., 2019) that is likely to have been little different morphologically from the specimens described by Antoine et al. (2021). This, together with the overall poor record of platyrrhines, means that it is difficult to rule out an early (pre-Oligocene) origin for crown Platyrrhini on fossil grounds alone; for this reason, we do not propose a maximum bound for this calibration.

Additional CladeAge calibration. *Stirtonia victoriana* is the oldest known atelid (and is, in fact, a crown form, closer to the alouattine *Alouatta* than to atelines), and so is the oldest known member of the Aotidae+Atelidae+Callitrichidae+Cebidae clade. Ignoring *Proteropithecina* for the reasons already discussed, the oldest known member of its sister clade, Pitheciidae, is the crown pitheciid *Cebupithecina sarmientoi*, which is 13.183–13.032 Ma old (see “Crown Pitheciidae” below).

Comments. Benton et al. (2015) did not calibrate this node (or any nodes within Platyrrhini), but dos Reis et al. (2018) proposed a minimum of 15.7 Ma based on the age of *Proteropithecina* reported by Kay et al. (1998); as noted above, the total evidence analyses by Beck et al. (2023) do not unambiguously support *Proteropithecina* as a crown platyrrhine. Dos Reis et al.’s (2018) maximum bound was 33 Ma, based on the age of the oldest crown anthropoid, the stem catarrhine *Catopithecus* (see “Crown Anthropeidea” above). However, if the 34.5 Ma date reported by Antoine et al. (2021) is correct, then the oldest record of probable platyrrhines predates this (although we accept that these are almost certainly stem forms). Overall, we consider the platyrrhine fossil record to be too incomplete to confidently apply a maximum bound on this node.

Crown Pitheciidae = Callicebinae-Pitheciinae split

Calibrating taxon. *Cebupithecina sarmientoi*

Specimen. UCMP 38762 (holotype), a nearly complete skull, mandible, axial skeleton, and limb bones, from the Monkey Beds at La Venta, Colombia (Stirton and Savage, 1951).

Phylogenetic justification. Numerous synapomorphies support *Cebupithecina* as a pitheciine (Stirton and Savage, 1951; Orlosky, 1973; Rosen-

berger, 1979; Kay, 1990), and it has been consistently placed within crown Pitheciidae as a stem pitheciine in phylogenetic analyses (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Ni et al., 2019: fig. S1; Kay et al., 2019). Total evidence phylogenetic analyses by Beck et al. (2023) also support *Cebupithecina* as a stem pitheciine. A second fossil platyrrhine from La Venta, *Nuciruptor rubricae*, has also been consistently placed as a stem pitheciine in published phylogenetic analyses (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019), including the total evidence analyses of Beck et al. (2023). The oldest definitive material of *Nuciruptor* is from the El Cardon Red Beds (C5Ar.2r to C5An.2n Guerrero 1993; 1997; Flynn et al. 1997; as summarised by Montes et al. 2021, figure 3; with ages for these chrons of 12.829–12.272 Ma according to Raffi et al. 2020), which are younger than the Monkey Beds (13.183 to 13.032 Ma, see below). As already discussed (see “Crown Platyrrhini” above), IGM 184667 is a partial postcranial skeleton from Duke Locality 79 at La Venta, which may belong to either *Cebupithecina* or *Nuciruptor* and which predates the Monkey Beds; however, given the uncertainty regarding its taxonomic assignment, we do not consider this specimen further. Also as discussed (see “Crown Platyrrhini” above), the putative pitheciine *Proteropithecina neuquenensis* (Kay et al., 2013; Rosenberger and Tejedor, 2013; Kay, 2015; Tejedor and Novo, 2016; Rosenberger, 2020) was not consistently recovered as a member of this subfamily in the total evidence analyses of Beck et al. (2023). Thus, we have not used *Proteropithecina* to calibrate this node.

Hard minimum bound. 13.032 Ma

Soft maximum bound. 34.5 Ma

Suggested prior distribution. Uniform

Age justifications. The type specimen of *Cebupithecina sarmientoi* comes from the Monkey Beds at La Venta that correspond to Chron C5AAn (Flynn et al., 1997; Kay and Madden, 1997). This interval spans from 13.183 to 13.032 Ma (Raffi et al., 2020), with the latter date providing our hard minimum bound.

The total evidence tip-dating analysis of Beck et al. (2023) suggest that the most recent common ancestor of crown Platyrrhini is ~21–27 Ma old, but according to this analysis the oldest definitive crown platyrrhines (including *Cebupithecina*) are some 10–15 Ma younger; all fossil platyrrhines older than ~14 Ma were placed outside the crown. Thus, the early stages of the evolution of crown Platyrrhini appear to be currently unsampled, prob-

ably because they occurred in northern South America, where the fossil record for this time period remains poor (although ongoing research is starting to improve this; e.g., Antoine et al., 2012, 2017; Bond et al., 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019). For this reason, we suggest a conservative maximum bound of 34.5 Ma, based on the maximum reported age of the oldest platyrrhine specimens from TAR-21 site, Shapaja, Peru (Antoine et al., 2021). The TAR-21 specimens appear to be highly plesiomorphic, and similar to the better preserved *Perupithecus* (Antoine et al. 2021; Bond et al. 2015), which has been dated to 29.6 ± 0.08 Ma (Campbell et al., 2021). Campbell et al. (2021) questioned the late Eocene age for TAR-21, and presented tip-dating analyses of fossil rodents suggesting an Oligocene age for this and other Shapaja sites. However, pending confident resolution of this issue, we prefer to take a conservative approach and use the maximum age for TAR-21 reported in the literature (i.e., from Antoine et al., 2021) as the maximum bound of this calibration. Given the obvious incompleteness of the fossil record, we also suggest that this should be modelled as a uniform distribution. We propose the same maximum bound and uniform prior distribution for all other divergences within Platyrrhini.

We note here that, whereas we use the age of TAR-21 reported by Antoine et al. (2021) to inform our soft maximum bound for crown Pitheciidae, we did not use it to inform our alternative CladeAge calibration for crown Anthropea (= age of oldest probable platyrrhines; see above), because of the question marks raised by Campbell et al. (2021). This may appear inconsistent, but in fact reflects key differences between “standard” node dating and the CladeAge method. “Standard” node dating uses bounds and associated distributions that are specified a priori as age priors; these may be deliberately chosen to be very broad/conservative to reflect uncertainty in the fossil record, and may not be tied to the ages of specific fossils (for example, a geological boundary might be specified as a maximum bound). By contrast, the CladeAge method uses first occurrence ages of specific fossil taxa and estimates of diversification and fossil sampling rates to calculate prior distributions analytically, without user-specified bounds (Matschiner et al., 2017; Matschiner, 2019). Thus, accurate, and ideally tightly constrained, estimates of the ages of specific fossil occurrences is likely to be important for successful implementation of the CladeAge method. Given the different interpreta-

tions of Antoine et al. (2021) and Campbell et al. (2021), it is not clear that the age of TAR-21 can be tightly constrained on current published evidence; thus, it can be used to inform a (deliberately conservative) maximum bound, but is of less use for the CladeAge method. Instead, we used the relatively tightly constrained (and as-yet unchallenged) detrital zircon date published by Campbell et al. (2021) for the Santa Rosa fauna (from which the holotype and only known fossil of the probable early platyrrhine *Perupithecus* has been recovered) for the alternative CladeAge calibration for crown Anthropea.

Additional CladeAge calibration. We recognise *Cebupithecia sarmientoi* as the oldest stem pitheciine. The fossil taxon *Miocallicebus villaviejai* has been described as being dentally similar to, but much larger than, *Callicebus sensu lato* (= the currently recognised modern callicebine genera *Callicebus*, *Plecturocebus*, and *Cheracebus*; Takai et al., 2001; Kay, 2015; Byrne et al., 2016). The only known specimen (IGM-KU 97001) is a partial maxilla preserving only a single fully intact tooth (M2), which is heavily worn, and its affinities have not been tested via formal phylogenetic analysis. Nevertheless, we consider the available evidence sufficient to recognise *Miocallicebus* as a fossil callicebine, and so we propose it as an additional CladeAge calibration here. IGM-KU 97001 comes from the Bolivia Site at La Venta, which is just above the Tatacoa Beds, towards the top of the La Victoria Formation. According to Guerrero (1993, 1997) and Flynn et al. (1997), the base of the Tatacoa Beds is within Chron C5ABr, whilst the top of the La Victoria Formation is within Chron C5AAn (as summarised by Montes et al. 2021, figure 3). Following Raffi et al. (2020), this gives an age range of 13.739–13.032 Ma for *Miocallicebus villaviejai*, which we use as our CladeAge calibration for the oldest record of Callicebinae.

Comments. This node was not calibrated by Benton et al. (2015) or by dos Reis et al. (2018).

Callitrichidae-Cebidae split

Calibrating taxon. *Lagonimico conclucatus*

Specimen. IGM 184531 (holotype), a crushed skull with partial upper dentition present and a near complete mandible with most of the mandibular dentition from Duke University/INGEOMINAS locality 90 in the Victoria Formation, La Venta, Colombia (Kay, 1994).

Phylogenetic justification. *Lagonimico* shares a number of dental synapomorphies with extant (crown) callitrichids (Kay, 1994: table 7), and recent

phylogenetic analyses consistently place it as a stem callitrichid (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019). Beck et al. (2023) found a similar result in their tip-dating analysis, with *Lagonimico* being strongly supported as sister to crown callitrichids, and so it is suitable for calibrating this divergence.

Analyses by Beck et al. (2023) as well as several others (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019) suggest that two other taxa from La Venta - *Mohanamico hershkovitzi* (Luchterhand et al., 1986) and '*Aotus*' *dindensis* (originally described as an aotid; Setoguchi and Rosenberger, 1987; see also Ni et al., 2019 fig. S1) - may also be stem callitrichids, but both are from the Monkey Beds, which are stratigraphically younger than Duke University/INGEOMINAS locality 90 (Guerrero, 1993, 1997; Flynn et al., 1997, see below).

Hard minimum bound. 13.183 Ma

Soft maximum bound. 34.5 Ma

Suggested prior distribution. Uniform

Age justifications. Duke University/INGEOMINAS locality 90, source of IGM 184531, is located stratigraphically between the overlying Tatacoa Beds and underlying Chunchullo Beds of the Victoria Formation (Guerrero, 1993, 1997; Kay, 1994, table 7; Flynn et al., 1997). According to Guerrero (1993, 1997) and Flynn et al. (1997), the base of the Tatacoa Beds is within Chron C5AAr, whilst the Chunchullo Beds are entirely within Chron C5ABn, as are the Cerro Gordo Beds that underlie them (see Montes et al., 2021). Thus, Duke University/INGEOMINAS Locality 90 must be younger than the base of Chron C5ABn, and older than the top of Chron C5AAr, which gives an age range of 13.608 to 13.183 Ma (Raffi et al., 2020), with the latter providing our minimum bound.

Given the poor fossil record of crown Platyrrhin, we once again suggest a conservative maximum bound of 34.5 Ma for this node, based on the maximum reported age of the oldest probable platyrrhine specimens described to date (Antoine et al., 2021), and a uniform prior distribution (see "Crown Pitheciidae" above).

Additional CladeAge calibration. *Lagonimico conclucatus* is the oldest known callitrichid. The sister taxon of Callitrichidae is either Cebidae, Aotidae, or Cebidae+Aotidae, as the precise relationships of *Aotus* have proven difficult to resolve (Osterholz et al., 2009; Perez et al., 2012; Valencia et al., 2018; Schrago and Seuánez 2019; Wang et al., 2019; Vanderpool et al., 2020; Beck et al., 2023). Considering the fossil record of cebids and

aotids together, the oldest well-supported representative of either family is *Neosaimiri*, which has been consistently proposed to be closely related to the modern *Saimiri* from its original description by Stirton (1951) and onwards (e.g., Rosenberger et al., 1991; Takai, 1994). Congruent with this, recent phylogenetic analyses support *Neosaimiri* as a crown cebid, sister to *Saimiri* (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023). The oldest *Neosaimiri* material, including the holotype UCMP 39205, comes from the Monkey Beds in the Villavieja Formation (see "Crown Cebidae" below), which ranges from 13.183 to 13.032 Ma (see "Crown Pitheciidae" above), and this age range provides our additional CladeAge calibration.

Comments. This node was not calibrated by Benton et al. (2015) or by dos Reis et al. (2018).

Kay (2015) discussed records of two possible crown callitrichids from La Venta: an isolated upper incisor (IGM-KU 8402) and a lower fourth premolar (IGM-KU 8403) from the Monkey Beds that Setoguchi and Rosenberger (1985) tentatively referred to *Micodon kiotensis* (see also Rosenberger et al., 1990); and the holotype of *Patasola magdalenae* (IGM 184332), a partial lower jaw preserving the deciduous premolars and the molars from the stratigraphically older Duke Locality 40 (Kay and Meldrum, 1997), which is in the interval between the overlying Chunchullo Beds and underlying Cerro Gordo beds (and so appears to fall within Chron C5ABn; Guerrero, 1993; 1997; Flynn et al., 1997; as summarised by Montes et al., 2021, figure 3). However, as discussed by Setoguchi and Rosenberger (1985), Rosenberger et al. (1990), and Kay and Meldrum (1997), the evidence for referring GM-KU 8402 and 8403 to Callitrichidae (whether stem or crown) is weak, and this proposed relationship has not been tested via formal phylogenetic analysis. By contrast, Kay and Meldrum (1997) did formally test the relationships of *Patasola* via maximum parsimony analysis of 55 dental characters and found that it fell within crown Callitrichidae. However, the overall topology for extant callitrichids recovered by Kay and Meldrum (1997) is highly incongruent with molecular data (e.g., Garbino and Martins-Junior, 2018). Given this incongruence, which is likely to have a major impact on the polarities of the dental characters used by Kay and Meldrum (1997) to place *Patasola*, we do not consider the phylogenetic analysis of Kay and Meldrum (1997) to be strong evidence that *Patasola* is a crown callitrichid and

this age range provides our additional CladeAge calibration.

Crown Cebidae = Cebinae-Saimirinae split

Calibrating taxon. *Neosaimiri fieldsi*

Specimen. UCMP 39205 (holotype), comprising a left hemi-mandible preserving p2-m2, and a right hemi-mandible preserving i2-m2, from UCMP locality V4517 in the Monkey Beds of the Villavieja Formation at La Venta, Colombia (Stirton, 1951).

Phylogenetic justification. As already discussed (see “Callitrichidae-Cebidae split” above), *Neosaimiri* has been consistently identified as a close relative of the extant saimirine genus *Saimiri* since its original description. Indeed, Rosenberger et al. (1991) concluded that *Neosaimiri* could be synonymised with *Saimiri*, although Takai (1994) argued that the two genera should be maintained as distinct. Regardless, a close relationship between *Neosaimiri* and *Saimiri* to the exclusion of *Cebus*, within crown Cebidae, has been a consistent feature of recent published phylogenetic analyses (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023). The ~20.9 Ma old *Panamacebus transitus* has also been placed within crown Cebidae in some published phylogenetic analyses (Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019), but it fell outside crown Platyrrhini in the total evidence tip-dating analysis of Beck et al. (2023), and we do not use this taxon for calibrating purposes here.

Hard minimum bound. 13.032 Ma

Soft maximum bound. 34.5 Ma

Suggested prior distribution. Uniform

Age justifications. As already discussed (see “Crown Pitheciidae” above), the age of the Monkey Beds at La Venta can be constrained to between 13.183 and 13.032 Ma. We propose the same maximum bound and uniform prior distribution as for crown Pitheciidae and the Callitrichidae-Cebidae split (see above).

Additional CladeAge calibration. As discussed, we consider *Neosaimiri fieldsi* to be the oldest well-supported saimirine. If *Panamacebus* is discounted, the oldest well-supported member of Cebinae is *Acrecebus fraileyi* (Kay and Cozzuol, 2006), which has been placed sister to *Cebus* in most recent published phylogenetic analyses (Kay, 2015; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023). *Acrecebus fraileyi* is known from a specimen, LACM 134880 (a left M2) from locality LACM 5158 (“Bandeira”), Solimoes Formation, Acre River, Acre, Brazil. The age of the Acre vertebrate fauna of the Solimoes Formation

has been controversial and remains poorly constrained (Cozzuol, 2006). The Patos locality, which is near the Bandeira locality (Negri et al., 2010), has recently been proposed to be no older than 7 Ma based on palynological data (Leite et al., 2021). However, in the absence of more precise stratigraphic evidence, we follow Kay and Cozzuol (2006) in assigning the Acre vertebrate fauna to the Huayquerian SALMA. Following the age justification outlined in Beck et al. (2023) and below, we apply a conservatively wide estimate of 9.0–4.741 Ma to the Huayquerian SALMA, which is to be used as the CladeAge calibration for this node. Age estimates for the Huayquerian SALMA include 9.0–5.28 Ma (Prevosti et al., 2013; Tomassini et al., 2013) and 9.0–6.8 Ma (Flynn and Swisher, 1995). However, Prevosti et al. (2021) reported an 40Ar/39Ar date from the lower “Ireanean” fauna at Quequén Salado River - which shows similarities to Huayquerian faunas - of 5.17 +/- 0.08 Ma, i.e., younger than previously proposed minimum bounds for the Huayquerian. We therefore use a more conservative minimum bound of 4.741 Ma based on the median maximum age of the Monte Hermoso fauna (Prevosti et al., 2021), which is the type fauna of the Montehermosan SALMA that follows the Huayquerian.

Comments. This node was not calibrated by Benton et al. (2015), but dos Reis et al. (2018) also used *Neosaimiri* to provide a minimum bound for this node. In addition, dos Reis et al. (2018) specified a maximum bound of 18 Ma based on *Soriacebus*, which they considered to be the oldest known atelid. It is not clear to us how the oldest record of Atelidae would directly inform the likely maximum age of crown Cebidae, and dos Reis et al. (2018) acknowledged that *Cebus-Saimiri* split might in fact be as old as 20–21 Ma, based in part on the age of *Panamacebus*, which has been found to be a crown cebid in several published analyses (Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019). However, numerous phylogenetic analyses place *Soriacebus* as a stem platyrrhine (Kay, 2015; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023), and *Panamacebus* was also placed outside crown Platyrrhini in the total evidence tip-dating analysis of Beck et al. (2023). Thus, neither *Soriacebus* nor *Panamacebus* are of direct relevance for informing the maximum bound of this node. In any case, we consider that the very limited platyrrhine record means that a much more conservative maximum bound is appropriate for divergences within crown Platyrrhini (see “Crown Pitheciidae” above).

Crown Atelidae = Alouattinae-Atelinae split**Calibrating taxon.** *Stirtonia victoriae*

Specimen. DU/IGM 85-400 (holotype), a right maxilla preserving erupted dP2-dP4 M1-M2, and mineralised but unerupted C and P2-P4, from Duke Locality 28, La Venta, Colombia (Kay et al., 1987).

Phylogenetic justification. Several authors have noted that *Stirtonia* shares numerous dental similarities (at least some of them derived) with the modern genus *Alouatta* (Stirton, 1951; Rosenberger, 1979; Setoguchi et al., 1981; Kay and Cozzuol, 2006), and a *Stirtonia+Alouatta* clade has been recovered in several recent phylogenetic analyses (Kay and Cozzuol, 2006; Bloch et al., 2016; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023).

Hard minimum bound. 13.363 Ma

Soft maximum bound. 34.5 Ma

Suggested prior distribution. Uniform

Age justifications. See “Crown Platyrrhini” above for discussion of the age of *Stirtonia victoriae*.

Additional CladeAge calibration. *Stirtonia victoriae* is the oldest known alouattine. Kay and Cozzuol (2006) named *Solimoaea acrensis* based on an isolated left m1 (the holotype, UFAC-LPP 5177) and an isolated right maxillary fragment preserving P3-4 (UFAC-LPP 5178) from the Patos locality (equivalent to LACM 4611) in the Solimoes Formation and identified it as an ateline. They also carried out a four different maximum parsimony analyses based on 57 dental characters (although only 25 of these were parsimony informative; Kay and Cozzuol, 2006, table 1) and using a molecular scaffold that was based on the studies of Meireles et al. (1999 a; 1999 b) but which is still in agreement with current molecular evidence (e.g., dos Reis et al., 2018): in all four analyses, *Solimoaea* formed a clade with living atelines, with moderate-to-high (57-86%) bootstrap support depending on the analysis. Kay (2015) subsequently stated that he considered *Solimoaea* to be specifically related to *Lagothrix* within crown Atelinae, although Kay and Cozzuol (2006) found that *Solimoaea* fell outside crown Atelinae in three out of four of their phylogenetic analyses. Rosenberger et al. (2015) argued that *Solimoaea* is more likely an alouattine, and cast doubt on whether the holotype m1 and the referred maxillary fragment represent the same taxon. However, in the absence of formal phylogenetic analysis supporting alternative relationships for *Solimoaea*, we tentatively accept it as the oldest known ateline. Based on palynological evidence, the Patos locality is 7 Ma or younger (Leite et al.,

2021); given that we accept a Huayquerian age for the Acre vertebrate fauna as a whole (see “Crown Cebidae” above) to which we apply a conservatively wide estimate of 9–4.741 Ma, we assign *Solimoaea acrensis* an age range of 7–4.471 Ma for our additional CladeAge calibration.

Comments. This node was not calibrated by Benton et al. (2015), but dos Reis et al. (2018) used *Stirtonia* as the basis for a minimum bound of 12.8 Ma for this node. In addition, dos Reis et al. (2018) specified a maximum bound of 18 Ma, based on the assumption that the “divergence of atelids is unlikely to have occurred before the first appearance of the potential stem or crown atelid *Soriacebus* at 18 Ma” (dos Reis et al., 2018: 611). However, as already noted (see “Crown Cebidae”), several recent phylogenetic analyses have placed *Soriacebus* as a stem platyrrhine rather than an atelid (Kay, 2015; Marivaux et al., 2016; Kay et al., 2019; Beck et al., 2023), and so it is inappropriate to inform a maximum bound on this node. For reasons already discussed, given the extremely limited platyrrhine fossil record, we prefer a much more conservative maximum bound for divergences within Platyrrhini, based on the maximum proposed age for the oldest known platyrrhines (34.5 Ma; Antoine et al., 2021; see “Crown Pitheciidae” above for a full justification of this).

CONCLUSION

Marjanović (2021) noted that compendia of fossil calibrations quickly go out of date, due both to the discovery of new fossils and to reinterpretation and reanalysis of those already known. However, the impact of this on analyses that need to use fossil calibration information can (we hope) be lessened by careful consideration of the appropriate prior distribution for each calibrated node, to adequately reflect our current uncertainty and to take into account the likely impact of future discoveries. For example, it is certainly possible, or even probable, that crown primates that are slightly older than *Teilhardina brandti* will be discovered, but we think it highly unlikely that they will be found earlier than the K-Pg boundary, an assumption that is taken into account by our suggested prior distribution on the age of crown Primates. Thus, we expect that improvements in the primate fossil record will lead to tighter constraints on the ages of particular nodes (mainly due to older minimum bounds), but not ones that actively conflict with those proposed here. In turn, revisions to this list should lead to more precise, but not contradictory, estimates of divergence times in future node-dating analyses.

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