The Evolution of Body Size in the Diverse Lesser Apes

by Daniel C. Wawrzyniak

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Sergio Almécija
Assistant Research Professor of Anthropology

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Abstract of Thesis

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The highly specialized locomotor behaviors exhibited by extant hylobatids are generally considered to have evolved alongside a reduction in body size from the last common ancestor of all hominoids. However, among the four currently recognized hylobatid genera there is a greater variation in body size than usually recognized. *Symphalangus* is nearly twice the size of the three smaller genera, creating two discrete morphs of hylobatids. Furthermore, the large array of body mass estimates for putative stem hominoids, as well as a lack of early fossil hylobatids, and the still contentious phylogenetic relationships within this clade make the reconstruction of body size evolution in hylobatids problematic. Within the context of anthropoids, this study models the evolution of body mass in hylobatids and the hominoid last common ancestor. Using a large sample of extant primates, as well as six fossil catarrhines, ancestral body size was estimated under three evolutionary models: maximum-likelihood under constant-variance (cvREML) and multiple-variance Brownian motion (mvREML), and multiple-variance Brownian motion using reversible jump Markov chain Monte Carlo (mvMCMC). As phylogenetic relatedness of fossil taxa is unresolved, and body mass estimates are based on a limited number of specimens, this study tests the impact of their inclusion. The impact of the phylogenetic position of the small-bodied Miocene catarrhine *Pliobates cataloniae* is specifically tested here, by including it as a stem catarrhine, or alternatively as a stem hominoid. Model choice has a larger effect on ancestral body mass predictions here than the inclusion of fossil taxa, or the phylogenetic position of *Pliobates.* Predictions of ancestral body mass are generally consistent across

the three methods, but both multiple-variance models significantly outperformed the constant-variance model, and mvMCMC model outperformed those based on maximum-likelihood. Both the use of multiple-variance models and the inclusion of fossil taxa constrain the impact of the extremely large-bodied great apes on the predictions for hominoid last common ancestor (LCA), Estimates from the mvMCMC model predict a ~19-27 kg hominoid LCA, and a ~8.3-8.8 kg LCA for hylobatids. This is just larger than in *Nomascus*, suggesting that the ~11kg *Symphalangus* is secondarily enlarged, while ~6.9 kg *Hoolock* and especially ~5.5 kg *Hylobates* have continued a trend of reduction since the hominoid last common ancestor. Interestingly, the geographic range of *Symphalangus* falls entirely within the range of *Hylobates*, suggesting that divergence in body size among hylobatids may be coincident with an ecological niche differentiation.

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Chapter 1: Introduction

The family Hylobatidae comprises four extant genera (*Hylobates, Hoolock, Nomascus,* and *Symphalangus*) and 19-20 extant species (Mootnick and Groves, 2005; Anandam et al., 2013; Choudhury, 2013; Roos, 2016; Fan et al., 2017). This lineage diverged from other apes ~19-21 ma (Chatterjee, et al., 2009; Fabre, et al., 2009; Finstermeier, et al., 2013; Carbone et al., 2014; Veeramah et al., 2015; Shi and Yang, 2017), but the most recent molecular studies indicate that the extant members of this speciose clade are the result of a fast adaptive radiation occuring ~5-7.8 ma (Carbone et al., 2014; Veeramah et al., 2015; Shi and Yang, 2017). Hylobatid genera are more genetically distinct than other hominoid taxa, i.e., they exhibit more genetic differentiation than humans and chimpanzees (Roos and Geissmann 2001; Takacs et al. 2005; Whittaker et al. 2007). These gibbons and siamang are recognized at the genus level by the number of diploid chromosomes, each genus having a unique number (van Tuinen and Ledbetter 1983; Prouty et al., 1983; Liu et al., 1987; Wienberg and Stanyon, 1987; Jauch et al. 1992; Groves 2001; Müller et al. 2003; Capozzi et al. 2012; Stanyon, 2013). In addition to being more speciose, hylobatids are also found over a wider range of latitudes than other extant apes (Figure 1B).

While all extant apes are often considered to be adapted to torso-orthograde behaviors and forelimb dominated locomotor behaviors, including suspension (Gebo, 1996; Hunt, 2004; Manfreda et al., 2006; Thorpe and Crompton, 2006; Fleagle, 2013; Hunt, 2016), hylobatids exhibit a number of derived characters of the post-cranium specifically adapted to forelimb suspension and braichiation. These include a highly mobile shoulder girdle; powerful shoulder and elbow flexors; high brachial index (BI)

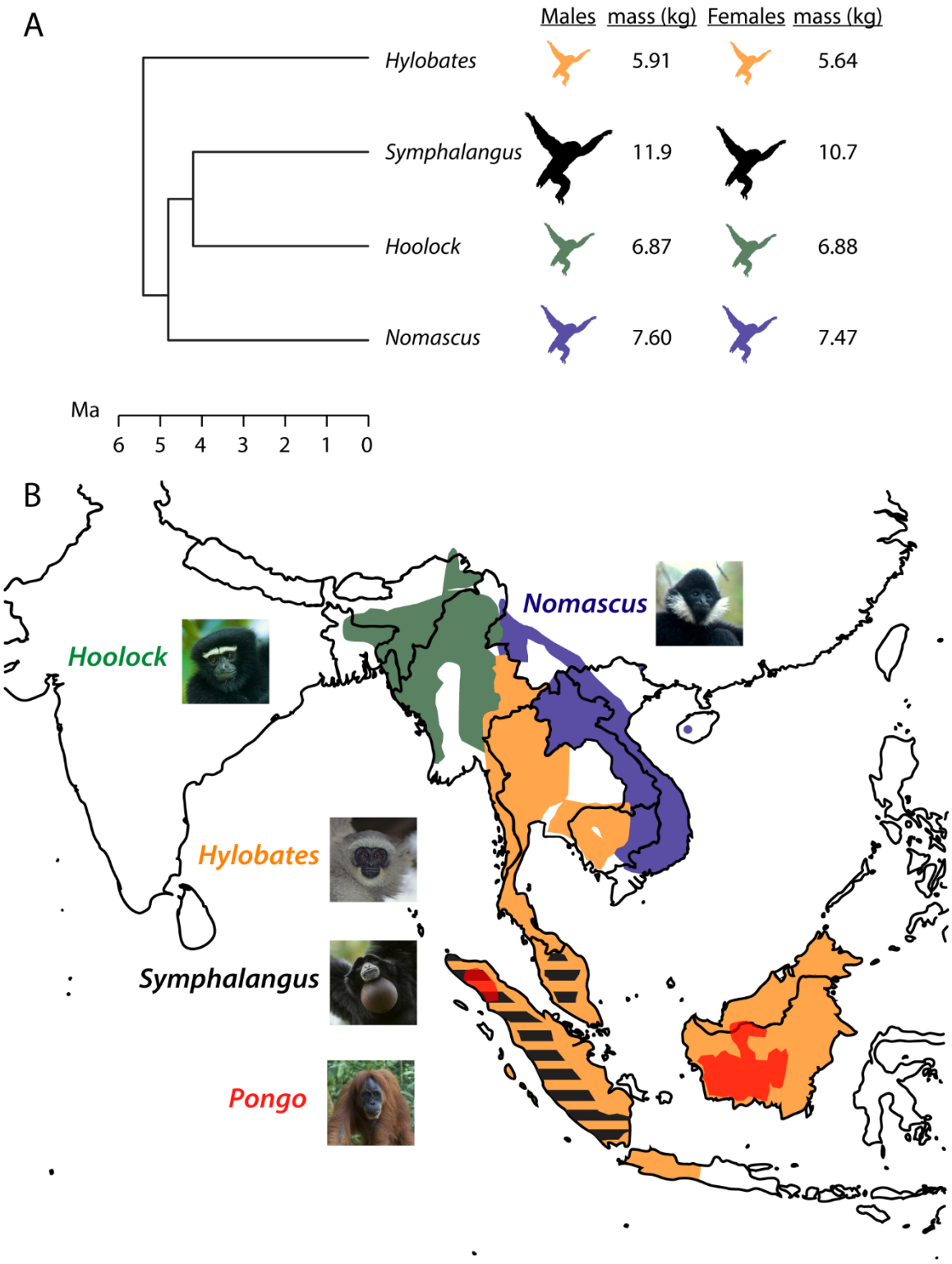

Figure 1. (A) Phylogeny for extant hylobatids and mean body mass of each genus by sex. **(B)** Ranges of extant Asian ape genera (Groves, 2001; Geissmann, 2005; Marshall and Sugardjito, 1986; Thinh, 2010, Which et al., 2010). *Hylobates* = orange; Symphalangus= black (Areas where *Symphalangus* is sympatric with *Hylobates* are indicated by dashed black lines); *Hoolock* = green; *Nomascus* = blue; *Pongo* = red.

and intermembral index (IMI); a highly derived carpus with a ball-and-socket like configuration; a long metacarpus and phalanges (Rose, 1993; Chan, 2008; Milchilsens et al., 2009; Fleagle, 2013). Recent molecular evidence suggests that genes relating to these traits underwent positive selection very early, and that these traits were most likely present in the ancestor to the four extant genera (Carbone et al., 2014). Hylobatids are the most suspensory of all the apes, and are the only true ricochetal brachiators (e.g., Tuttle, 1969; Hunt 2016; Zihlman et al., 2011).

This unique mode of locomotion is possible in part because of hylobatids' small body size (5-12 kg) (Smith and Jungers, 1997; Gordon, 2004; Zihlman et al., 2011) with little to no sexual dimorphism (-2-11%) (Smith and Jungers, 1997; Gordon, 2004). The next smallest ape, the bonobo, is significantly larger with a body mass of ~33 kg for females; female orang-utans, which are most similar to hylobatids in BI and IMI, have a mean body mass of ~36 kg (Gordon, 2004). Because of the disparity in body mass and morphology relative to other living hominds, hylobatids are often treated as a single, small morphotype in comparative studies. Often only one or two genera are represented in these studies (e.g., Chan, 2008; Kivell and Begun, 2007; Spoor et al., 2007; Chan, 2014; Hunt, 2016). This belies the morphological diversity –including body size– of extant hylobatids. For example, the siamang (genus: *Symphalangus*) is more than twice the size (10-12 kg) of the smallest genus, *Hylobates* (5-6 kg) (Gordon, 2004). The remaining genera, *Hoolock* and *Nomascus*, fall between these extremes at 6-7 kg and 7-8 kg repectively (ibid.).

Body size is a critical component of mammalian biology (Damuth and Macfadden, 1990), and has implications for much more than locomotor behaviors. Diet,

life history traits, sexual dimorphism, home range size, behavioral adaptations, and biogeography are just a few examples of components of a primate's biology that are heavily influenced by body size (Fleming, 1973; Jarman, 1974; Emmons et al., 1983; McMahon and Bonner, 1983; Peters, 1983; Schmidt-Nielson, 1984; Damuth and Macfadden, 1990). Hylobatids are unique among anthropoids in that within the family, there are two discrete morphs. The siamang is the sole representative of the large hylobatid morph, with the smallest individuals still being larger than the largest individuals from the three other genera (Smith and Jungers 1997; Gordon, 2004; Geissmann, 1993; Reichard and Preuschoft, 2016) The strepsirrhine family Lorisidae is the only other primate family where this is the case (Nekaris and Bearder, 2011). Given this, several authors have sought to explain why the siamang is so much larger than its sympatric *Hylobates* species (Reichard and Preuschoft, 2016).

Hypotheses for the two discrete morphs of hylobatids

First is adaptation to different habitats. The geographic distribution of *Symphalangus syndactylus* overlaps that of both *Hylobates lar* and *H. agilis*, and spans an elevational range of 0 – 1,100 m (Marshall, 2009). According to Bergmann's rule (Bergmann, 1848), it is predicted that the larger bodied siamang would preferentially exploit cooler, higher elevation habitats within this range, while gibbons would be limited to the lower elevation habitats (Raemaekers, 1984; Reichard and Preuschoft, 2016). However, to date, no empirical evidence has been published in support of this hypothesis. The second hypothesis is that differences in body size are correlated to differences in diet

(MacKinnon and MacKinnon, 1980). The Jarman-Bell principle states that larger bodied mammals will have a poorer quality diet due to a lower metabolism requirement to gut capacity ratio (Bell, 1971; Jarman, 1974; Gaulin, 1979), and it has been shown that larger body size is generally correlated to greater folivory across primates (Clutton-Brock and Harvey, 1977; Gaulin, 1979; Richard, 1985; Harvey et al., 1987). Therefore, this hypothesis predicts that leaves will constitute a larger percentage of the diet for siamangs as compared to the smaller bodied hylobatids. Some support has come from studies showing that the siamang spends more time eating leaves (Chivers, 1974; MacKinnon, 1977; Raemaekers, 1977), and that the colon of the siamang is relatively bulkier and longer than smaller hylobatids (Chivers and Raemakers, 1986). However, subsequent studies have found the hylobatid diet to be more variable, with considerable overlap observed among the diets of the siamang and smaller hylobatids (Gittins, 1982; Oats, 1987; Elder, 2009; Lambert, 2011). The third hypothesis relates to locomotion. This predicts that given the larger body size of the siamang, its postural and locomotor behavior will converge on that of orang-utans (Collis et al., 1999; Hunt 2016), the only other extant ape to share the same habitat (see Figure 1B). Evidence from behavioral studies supports this hypothesis, as siamangs have been observed to do less leaping, and more vertical climbing than smaller hylobatids (Chivers, 1972; Fleagle, 1976; Gittins, 1983; Srikosamatara, 1984; Fan et al., 2013; Hunt, 2016). Finally, the ecological niche differentiation hypothesis (Brown and Wilson, 1956) may explain both diet and locomotion differences (Raemaekers, 1978; Raemaekers, 1984). This hypothesis predicts that the larger, slower siamang will prevail in contest competition, displacing gibbons from preferred feeding sites (Morse, 1974; Maynard Smith, 1982; Abrams, 1983), while

the smaller, more agile gibbons will prevail in scramble competition, reaching preferred feeding sites first. This hypothesis has been supported by observations that siamangs have shorter day ranges and smaller home ranges than sympatric gibbons (MacKinnon and MacKinnon, 1980; Bartlett, 2011).

Despite the body-size diversity within hylobatids, all members of the clade are significantly smaller than all other extant apes. Historically, an apparent lack of small-bodied fossil hominoids from the Miocene (Pilbeam, 1996; Harrison, 2010; Fleagle, 2013; Harrison, 2016) led authors to suggest that extant hylobatids represent a dwarfed lineage (Groves, 1972; Tyler, 1993; Pilbeam, 1996; Reichard et al., 2016), and this is a well-documented phenomenom among other mammal clades (e.g., Foster, 1964; van Valen, 1973; Burness et al., 2001). Assuming that hylobatids are phyletic dwarfs, the most parsimonious explanation for the differences in body size among hylobatids is that the siamang reached some body size optimum, while the remaining three genera continued to evolve smaller body size, with *Hylobates* being the most derived. However, this assumes that *Symphalangus* was the first of the four extant genera to diverge from the other hylobatids.

Recently, the discovery of the small-bodied Miocene catarrhine *Pliobates cataloniae* (Alba et al., 2015) and the advancement of techniques in molecular phylogenetics (e.g., Perelman et al., 2011; Carbone et al., 2014; Veeramah et al., 2015; Shi and Yang, 2017) have complicated the picture. If *Pliobates cataloniae* is a hominoid (Alba et al., 2015; but see Nengo et al., 2017), the hypothesis that hylobatids represent a dwarfed lineage becomes less parsimonious. Multiple small-bodied hominoid lineages could suggest the ancestral hominoids were much smaller than previously predicted, and

extant great apes evolved a large body size much more recently (Grabowski and Jungers, 2017).

Hylobatid phylogeny

The hylobatid phylogeny is far from resolved (Hayashi et al., 1995; Purvis, 1995; Roos and Geissmann, 2001; Raaum et al., 2005; Chatterjee, 2006; Chatterjee et al., 2009; Fabre et al., 2009; Thinh et al., 2010; Chan et al., 2010; Matsudaira and Ishida, 2010; Israfil et al., 2011; Perelman et al., 2011; Chan et al., 2012; Finstermeier et al., 2013; Carbone et al., 2014; Veeramah et al., 2015; Roos, 2016; Shi and Yang, 2017), and may never be, due to issues of rapid diversification and incomplete-lineage sorting (ILS) (Carbone et al., 2014). Prior to the advent of molecular phylogenetics, hylobatids were treated as a single genus (*Hylobates*) (Marshall and Sugardjito 1986; Geissmann 1995; Rowe 1996; Nowak 1999; Groves 2001), or as two genera (*Hylobates* and *Symphalangus*) (Schultz, 1933; Simonetta, 1957; Napier and Napier, 1967) in recognition of the two discrete morphs of the family. The siamang was thought by some to be the first species to diverge, and thereby represent the ancestral condition (Napier and Napier, 1967; Groves, 1972). Even without molecular evidence, there exists evidence against this scenario. Gibbons are known for their complex songs, including duets by breeding pairs. This is thought to be a derived feature of the hylobatids, and the songs of the siamang are more complex than any other hylobatid species (Geissmann, 2002). The siamang is also found at the extreme southern end of the range of asian apes. The origin of extant hylobatids is likely in the northern end of the current distribution of hylobatids

(Chatterjee, 2009), where only members of the extant *Nomascus* and *Hoolock* have been found (Jablonski and Chaplin, 2009), leading other authors to propose that one of these two should occupy the basal position on the hylobatid tree (e.g., Chivers, 1977; Haimoff et al., 1982; Creel and Preuschoft, 1984; Müller et al., 2003).

As it is now clear that hylobatids can be grouped by unique karyotypes (Prouty et al. 1983; Liu et al. 1987; Wienberg and Stanyon 1987; Müller et al. 2003; Stanyon 2013), most authors currently recognize four extant genera: *Hoolock, Hylobates, Nomascus,* and *Symphalangus* (e.g., Roos and Geissmann, 2001; Mootnick and Groves, 2005; Takacs et al., 2005; Chatterjee et al., 2009; Fabre et al., 2009; Chan et al., 2010; Thinh et al., 2010; Israfil et al., 2011; Stanyon, 2013; Carbone et al., 2014; Roos, 2016). However, there still remains disagreement as to the phylogenetic relationships among extant genera (Hall et al., 1998; Roos and Geissmann, 2001; Takacs et al., 2005; Roos et al., 2007; Thinh et al. 2010; Roos, 2016). Studies relying on segments of mitochondrial DNA (mtDNA) have generated an array of results of divergence times as well as topologies (Hayashi et al., 1995; Purvis, 1995; Roos and Geissmann, 2001; Raaum et al., 2005; Chatterjee, 2006; Chatterjee et al., 2009; Fabre et al., 2009; Thinh et al., 2010; Chan et al., 2010; Matsudaira and Ishida, 2010; Israfil et al., 2011; Perelman et al., 2011; Chan et al., 2012; Finstermeier et al., 2013).

Despite this, the three most recent molecular studies using nuclear DNA (nDNA) (Carbone et al., 2014; Veeramah et al., 2015; Shi and Yang, 2017) have all found strongest support for a *Hylobates*(*Nomascus*(*Hoolock*, *Symphalangus*)) topology. These studies also agree on three critical points: a divergence of Hylobatide and Hominidae of

~19-21 Ma; a divergence of the extant genera of hylobatids ~5-7.8 Ma; a rapid diversification of hylobatids combined with a great amount of ILS (ibid.).

Hylobatid fossil record

There are many specimens dating to the Oligocene and early to middle Miocene of Eurasia which were initially considered to be putative fossil hylobatids, or small-bodied stem hominoids by some authors. The current consensus is that these primates (except for *Pliobates cataloniae*) instead represent more primitive stem catarrhines (Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002; Fleagle, 2013; Harrison, 2010, 2016). Indeed, it is difficult to distinguish between fossil hylobatids and stem catarrhines, as they share a relatively short face, globular cranium, simple molars, relatively long and gracile limbs, in addition to small size (Groves, 1972; Szalay and Delson 1979; Andrews et al., 1996; Harrison 2010, 2016; Fleagle, 2013). Stem hominoids can also be difficult to diagnose, as they lack the derived dental features of cercopithecoids and many specimens described as Miocene apes might better be described as non-cercopithecoid catarrhines instead (Fleagle, 2013). Body size estimates for fossil taxa more firmly recognized to be fossil apes in the early Miocene generally exceed the range of extant hylobatids. Estimates for proconsulids range from 15 to at least 35 kg (Harrison, 2010), and multiple members of the Afropithecinae have been estimated at over 40 kg (Fleagle, 2013).

There are only three fossil or subfossil taxa in the record which are generally accepted to be hylobatids, but not attributable to one of the four extant genera (Harrison,

2016; Turvey et al., 2018). These are the late Miocene *Yuanmoupithecus xiaoyuan* (Pan, 2006), the Pleistocene *Bunopithecus sericus* (Matthew and Granger, 1923), and the recently named Holocene *Junzi imperialis* (Turvey et al., 2018). *Yuanmoupithecus*, dated to ~7-9 Ma, is the earliest evidence of the family Hylobatidae in the fossil record and is known only from 13 teeth (premolars and molars) (Pan, 2006). Harrison et al. (2008) and Harrison (2016) show this species to be a stem hylobatid, and not a stem catarrhine, based on dental synapomorphies. However, it differs too much from modern hylobatids to be placed in any extant genus (ibid.).

Bunopithecus sericus was once thought to be a fossil hoolock gibbon (Frisch, 1965). When the extant hoolock gibbon was recognized as a distinct genus, it was included with the fossil species under the generic name *Bunopithecus* (Prouty et al., 1983). Other authors argued that it was most similar to *Nomascus concolor* (Gu, 1989), and suggested it be referred to the junior synonym *Nomascus sericus* (Jabolonski and Chaplin, 2009). The issue of whether or not the fossil species is a member of any extant genus is complicated by an unclear age of the specimens (Harrison, 2016). Several more recent studies have shown that it falls outside the range of variation of modern hylobatids, and therefore probably represents an extinct crown hylobatid (Groves, 2001; Mootnick and Groves, 2005; Ortiz et al., 2015), possibly a sister to *Hoolock* (Harrison, 2016).

Junzi imperialis is known from a partial skull, is just ~2,200-2,300 years old, and has been shown by morphological analysis to be distinct from the four extant genera (Turvey et al., 2018). Destructive testing of the materials was not allowed because its context is an archaeological site. Therefore, molecular evidence is not available for these

specimens, making its phylogenetic position unclear. Regardless of whether this latest discovery should be referred to a new genus or not, it is additional evidence that historical range of hylobatids was much larger than it is today (Jablonski and Chaplin, 2009; Reichard et al., 2016), and several species of hylobatids probably went extinct very recently (Turvey, 2009; Thinh et al., 2016; Turvey et al., 2016).

All three fossil and subfossil hylobatids are known only from China, but evidence for the understanding of hylobatid body size evolution exists elsewhere. The middle Miocene hominoid *Pliobates cataloniae* from Spain, dated to 11.6 Ma and weighing 4-5 kg, does not fall close to the range of body sizes observed in extant great apes (Alba et al., 2015). This recent discovery is of importance to the evolution of hominoid body size, as cladistic analyses have placed this small-bodied primate as either a stem hominoid (Alba et al., 2015), or a stem catarrhine (Nengo et al., 2017), not a hylobatid. Phylogenetic placement of *Pliobates* could have large implications for our understanding of the evolution of body size in the hominoid lineages (e.g., Grabowksi and Jungers, 2017).

Goals of this study

- Compare methods of modeling body mass evolution in anthropoid primates under Brownian motion.
- Predict the body mass of ancestral hominoids, with a focus on the family Hylobatidae.
- Explore how the inclusion of fossil taxa affects ancestral body mass predictions.

- Test the hypothesis that hylobatids represent a dwarfed lineage.

Chapter 2: Materials and Methods

The study of trait evolution is approached here using phylogenetic comparative methods. The main goal of such analyses is to examine how evolution has shaped a trait through time (e.g., Pennell and Harmon, 2013). Despite a recent increase in the number of evolutionary models being used in the literature (Smaers et al., 2016), there are only two frequently used standard models upon which variations are built. These are Brownian Motion (BM) and Ornstein-Uhlenbeck (OU).

In its standard form the constant variance BM (cvBM) model assumes that the rate of evolution is stochastically constant and trait change is proportional to the square root of time (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1985). This creates a model in which the mean rate of change and variance is equal across all branches of the tree. However, the assumption that traits change in proportion to the square root of time and that all branches experience the same rate of change is currently thought to contrast with the way in which traits actually evolve (Harvey and Purvis, 1991). The cvBM model has been modified to incorporate multiple rates of change across the tree. This new multiple variance BM (mvBM) allows for some parts of the tree to experience increased or decreased rates of change in traits and returns estimates for both the rate of change along branches, and the value of traits at internal nodes (O'Meara et al., 2006). BM models typically estimate continuous traits by maximum-likelihood (Felsenstein, 1973). Smaers et al. (2016) introduced a new method for BM models that takes this mvBM a step further by first estimating rates of change along branches using reversible-jump Markov chain Monte Carlo (MCMC), and then reshaping the tree to reflect the variation in rates before again performing MCMC on the modified tree to estimate internal nodes.

OU models incorporate a ‘random walk’ stochastic change of traits with a restraining force which pulls traits toward some optimum (Hansen, 1997). In its simplest single-regime form the OU model can be useful in identifying an adaptive regime of some clade. However, single regime OU models are only applicable to closely related taxa which all fit the same adaptive regime (Harmon et al., 2010; Pennell et al., 2015).

OU models have been expanded to include ‘multi-regime’ models in which parameters vary across the tree (Hansen, 2012). This allows for multiple optima to be identified in different branches and are useful in comparing various evolutionary scenarios (Uyeda and Harmon, 2014). While OU models identify optima in different branches of the tree, they do not predict the ancestral state of traits at nodes. So, while OU models are informative in examining adaptive regimes in extant taxa, their utility in tracking trait changes over time is limited. Hence, OU models are not tested in the current analysis (see Discussion below).

Here, this two-step mvBM simulation using MCMC (mvMCMC) (Smaers et al., 2016) is compared to maximum-likelihood BM (Felsenstein, 1973) methods of body size evolution. Then, ancestral state reconstruction by mvMCMC is used to predict the body mass of ancestral anthropoids at nodes on the phylogenetic tree as well as describe the rate of body size change in lineages. Using a sample of both extant and fossil taxa, we use these methods to investigate the mode and tempo of body size evolution in hominoids, with a focus on the family Hylobatidae.

Species	Mean Male Body Mass (kg)	Mean Female Body Mass (kg)	Reference
Callithrix argentata	0.33	0.36	Smith and Jungers (1997)
Callithrix emiliae	0.313	0.33	Smith and Jungers (1997)
Callithrix humeralifera	0.418	0.426	Smith and Jungers (1997)
Callithrix jacchus	0.362	0.381	Smith and Jungers (1997)
Callithrix mauesi	0.345	0.398	Smith and Jungers (1997)
Callithrix penicillata	0.344	0.307	Smith and Jungers (1997)
Callithrix pygmaea	0.11	0.122	Smith and Jungers (1997)
Leontopithecus chrysomelas	0.62	0.535	Smith and Jungers (1997)
Leontopithecus rosalia	0.663	0.622	Dietz et al., (1994)
Saguinus bicolor	0.431	0.43	Smith and Jungers (1997)
Saguinus fuscicollis	0.328	0.338	Soini (1990)
Saguinus geoffroyi	0.482	0.503	Dawson and Dukelow (1976)
Saguinus leucopus	0.494	0.49	Smith and Jungers (1997)
Saguinus midas	0.535	0.591	Gordon (2004)
Saguinus mystax	0.522	0.545	Gordon (2004)
Saguinus oedipus	0.418	0.404	Smith and Jungers (1997)
Alouatta belzebul	7.27	5.52	Smith and Jungers (1997)
Alouatta caraya	6.42	4.33	Smith and Jungers (1997)
Alouatta palliata	6.96	5.28	Gordon (2004)
Alouatta pigra	11.4	6.43	Smith and Jungers (1997)
Alouatta seniculus	6.66	5.18	Gordon (2004)
Aotus azarai	1.23	1.22	Gordon (2004)
Aotus infulatus	1.19	1.24	Smith and Jungers (1997)
Aotus nancymaae	0.795	0.78	Smith and Jungers (1997)
Aotus vociferans	0.708	0.698	Smith and Jungers (1997)
Ateles belzebuth	8.26	7.88	Smith and Jungers (1997)
Ateles fusciceps	8.89	9.16	Smith and Jungers (1997)
Ateles geoffroyi	7.45	7.64	Schultz (1941)
Ateles paniscus	8.49	8.07	Gordon (2004)
Brachyteles arachnoides	9.42	8.33	Lemos de Sa and Glander (1993)
Cacajao melanocephalus	3.16	2.71	Smith and Jungers (1997)
Callicebus donacophilus	0.991	0.909	Smith and Jungers (1997)
Callicebus hoffmannsi	1.09	1.07	Smith and Jungers (1997)
Callicebus moloch	1.02	0.956	Smith and Jungers (1997)
Callicebus personatus	1.27	1.38	Smith and Jungers (1997)
Callicebus torquatus	1.32	1.16	Gordon (2004)
Cebus albifrons	3.18	2.29	Gordon (2004)
Cebus apella	3.64	2.39	Gordon (2004)

Cebus capucinus	3.66	2.5	Hernandez-Camacho and Defler (1985)
Cebus olivaceus	3.24	2.52	Gordon (2004)
Chiropotes satanas	3.25	3.11	Smith and Jungers (1997)
Lagothrix lagotricha	7.28	7.02	Smith and Jungers (1997)
Pithecia irrorata	2.25	2.07	Smith and Jungers (1997)
Pithecia pithecia	1.94	1.58	Smith and Jungers (1997)
Saimiri boliviensis	1.02	0.75	Gordon (2004)
Saimiri oerstedii	0.897	0.68	Gordon (2004)
Saimiri sciureus	0.92	0.723	Gordon (2004)
Saimiri ustus	0.921	0.799	Smith and Jungers (1997)
Allenopithecus nigroviridis	6.13	3.18	Smith and Jungers (1997)
Cercocebus agilis	9.5	5.66	Smith and Jungers (1997)
Cercocebus atys	11	6.2	Smith and Jungers (1997)
Cercocebus galeritus	9.61	5.26	Gordon (2004)
Cercocebus torquatus	8.01	5.5	Sanders and Bodenbender (1994)
Cercopithecus ascanius	3.7	2.93	Colyn (1994)
Cercopithecus campbelli	4.5	2.7	Smith and Jungers (1997)
Cercopithecus diana	5.2	3.9	Smith and Jungers (1997)
Cercopithecus hamlyni	5.49	3.36	Smith and Jungers (1997)
Cercopithecus lhoesti	5.97	3.45	Smith and Jungers (1997)
Cercopithecus mitis	6.29	3.99	Smith and Jungers (1997)
Cercopithecus neglectus	7.35	4.13	Gordon (2004)
Cercopithecus nictitans	6.67	4.25	Gordon (2004)
Cercopithecus petaurista	4.4	2.9	Smith and Jungers (1997)
Cercopithecus pogonias	4.26	2.9	Gordon (2004)
Cercopithecus wolfi	3.8	2.88	Colyn (1994)
Chlorocebus aethiops	4.94	3.34	Gordon (2004)
Chlorocebus pygerythrus	4.28	2.98	Gordon (2004)
Chlorocebus sabaeus	5.3	3.3	Horrocks (1986)
Erythrocebus patas	12.4	6.5	Smith and Jungers (1997)
Lophocebus albigena	7.79	6.01	Gordon (2004)
Lophocebus aterrimus	7.9	5.64	Colyn (1994)
Macaca arctoides	12.2	8.4	Smith and Jungers (1997)
Macaca assamensis	11.35	6.92	Fooden (1988)
Macaca fascicularis	5.11	3.41	Gordon (2004)
Macaca maura	9.72	6.05	Smith and Jungers (1997)
Macaca mulatta	6.99	4.94	Napier (1981)
Macaca nemestrina	11.2	6.59	Gordon (2004)

Macaca nemestrina leonina	8.48	4.93	Fooden (1975)
Macaca nigra	9.89	5.47	Smith and Jungers (1997)
Macaca radiata	6.6	3.69	Hartman (1938)
Macaca sinica	5.66	3.3	Cheverud et al. (1992)
Macaca tonkeana	14.9	9	Smith and Jungers (1997)
Mandrillus sphinx	34.4	12.8	Setchell et al. (2001)
Miopithecus talapoin	1.38	1.12	Smith and Jungers (1997)
Papio anubis	23	13.3	Gordon (2004)
Papio cynocephalus	22.3	12	Gordon (2004)
Papio hamadryas	18	10.3	Gordon (2004)
Papio ursinus	29.8	14.8	Smith and Jungers (1997)
Theropithecus gelada	19	11.7	Smith and Jungers (1997)
Colobus angolensis	9.71	7.59	Gordon (2004)
Colobus guereza	13.5	9.2	Smith and Jungers (1997)
Colobus polykomos	9.9	8.3	Smith and Jungers (1997)
Colobus satanas	10.4	7.42	Smith and Jungers (1997)
Colobus vellerosus	8.5	6.9	Smith and Jungers (1997)
Piliocolobus badius	8.3	8.2	Smith and Jungers (1997)
Presbytis comata	6.68	6.71	Smith and Jungers (1997)
Presbytis melalophos	6.59	6.47	Smith and Jungers (1997)
Procolobus verus	4.7	4.2	Smith and Jungers (1997)
Pygathrix nemaeus	11	8.18	Smith and Jungers (1997)
Rhinopithecus roxellana	17.9	11.6	Smith and Jungers (1997)
Semnopithecus entellus	13	9.89	Smith and Jungers (1997)
Trachypithecus cristatus	6.72	5.78	Gordon (2004)
Trachypithecus francoisi	7.7	7.35	Smith and Jungers (1997)
Trachypithecus geei	10.8	9.5	Smith and Jungers (1997)
Trachypithecus johnii	12	11.2	Smith and Jungers (1997)
Trachypithecus obscurus	7.77	6.22	Fooden (1971)
Trachypithecus phayrei	7.93	6.95	Napier (1985)
Trachypithecus pileatus	12	9.86	Smith and Jungers (1997)
Trachypithecus vetulus	8.17	5.9	Smith and Jungers (1997)
Hoolock hoolock	6.87	6.88	Smith and Jungers (1997)
Nomascus leucogenys	7.27	7.65	Geissmann (1993)
Hylobates moloch	6.58	6.25	Smith and Jungers (1997)
Hylobates pileatus	5.5	5.44	Smith and Jungers (1997)
Symphalangus syndactylus	11.79	10.7	Gordon (2004)
Gorilla gorilla gorilla	170.4	71.5	Gordon (2004)

Gorilla beringei graueri	175.2	71	Smith and Jungers (1997)
Gorilla beringei beringei	162.5	97.5	Smith and Jungers (1997)
Homo sapiens	57.4	49.7	Gordon (2004)
Pan paniscus	45	33.2	Smith and Jungers (1997)
Pan troglodytes schweinfurthii	41.4	33.1	Gordon (2004)
Pan troglodytes troglodytes	59.7	45.8	Gordon (2004)
Pan troglodytes verus	46.3	41.6	Smith and Jungers (1997)
Pongo abelii	77.9	35.6	Smith and Jungers (1997)
Pongo pygmaeus	78.5	35.8	Smith and Jungers (1997)

Table 1. Body mass means by sex for extant anthropoid primates used in this study. Reference is the source which originally calculated mean for each sex.

Body mass means and estimates

123 extant (Table 1; Figure 2) and six fossil (Table 2) anthropoid taxa are included in these simulations. Ancestral state reconstructions are made first using only extant taxa, and then again with fossil taxa included. Body mass is predicted over a total of 122 internal nodes for extant taxa, and 128 internal nodes when fossil taxa are included. Body mass means for each sex of extant taxa are drawn from Gordon (2004), the most extensive study on primate body mass to date. Body mass means used here come from both previously published means aggregated in that study (Hartman, 1938; Schultz, 1941; Fooden, 1971, 1975; Dawson and Dukelow, 1976; Napier, 1981; Hernandez-Camacho and Defler, 1985; Napier, 1985; Horrocks, 1986; Fooden, 1988; Soini, 1990; Cheverud et al., 1992; Geissmann, 1993; Colyn, 1994; Sanders and Bodenbender, 1994; Smith and Jungers, 1997; Setchell et al., 2001; Dietz et al., 2003) and means calculated by Gordon (2004) from data in the literature and his own observations. Data from that study were used here because wild populations and large

populations make up the majority of measurements, and wherever possible, equal weight is given to populations, rather than individuals. Hominoids are particularly well sampled, and include three subspecies of *Gorilla* and three of *Pan troglodytes*. Importantly for this study, at least one species mean (for each sex) is available for each of the four genera of extant hylobatids, including data for both species of *Hylobates* present in the phylogeny used here.

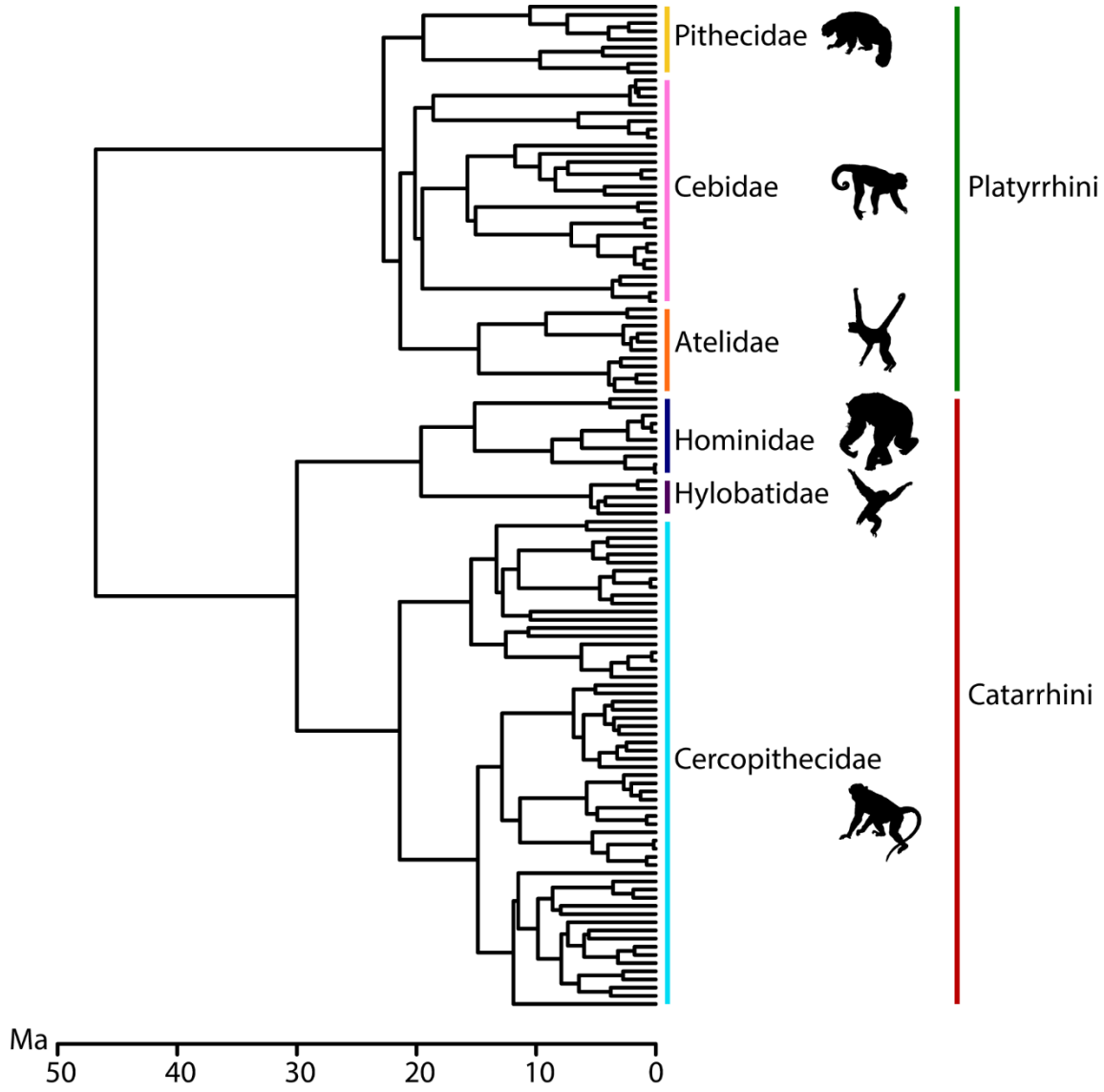

Figure 2. Extant anthropoid primate sample (n=123) and phylogeny used in this study. Parvorder: Platyrrhini (green) n=48; Catarrhini (red) n=75. Family: Pithecidae (yellow) n=9; Cebidae (pink) n=28; Atelidae (orange) n=11; Hominidae (dark blue) n=10; Hylobatidae (purple) n=5; Cercopithecidae (cyan) n=60.

Body mass estimates for fossil taxa are drawn from the literature (Table 2). Due to a lack of female specimens for *Hispanopithecus laietanus* (Alba et al., 2012), ancestral state reconstructions are only conducted for male body mass evolution when fossils are included. Estimates for *Sivapithecus indicus* and *Proconsul africanus* represent and average male body mass for the respective genus. Estimates for smaller-bodied fossil taxa (e.g., *Aegyptopithecus zeuxis; Pliobates cataloniae; Victoriapithecus macinnesi*) are used for male body mass estimates regardless of probable sex of specimens, as smaller-bodied primates are less likely to exhibit sexual dimorphism in body size, and the magnitude of any dimorphism is expected to be slight (Gordon, 2004).

Species	**Estimated Body Mass**	**FAD (Ma)**	**Body Mass Reference**	**FAD Reference**
Hispanopithecus laietanus	32	9.6	Alba et al. (2012)	Alba et al. (2012)
Sivapithecus indicus	30.5	12.7	Morgan et al. (2015)	Morgan et al. (2015)
Pliobates cataloniae	4.5	9.6	Alba et al. (2015)	Alba et al. (2015)
Proconsul africanus	35	22.5	Harrison (2010); Grabowski and Jungers (2017)	McNulty et al. (2015)
Victoriapithecus macinnesi	3.75	15	Harrison (1989)	Gonzales et al. (2015)
Aegyptopithecus zeuxis	6.78	29.9	Ankel-Simons et al. (1998)	Seiffert (2006)

Table 2. Body mass estimates and FAD (First Appearance Date) for fossil taxa used in this study along with original references for body mass and FAD data.

Phylogenetic trees

The phylogenetic tree of extant primates is the *10ktrees* website consenus tree (Arnold, Matthews and Nunn, 2010). This consenus tree is based on Bayesian inference. The branch lengths and topology for Hylobatidae (Figure 1A) were modified here following a recent study of the gibbon nDNA genome (Shi and Yang, 2017). Shi and

Yang (2017), like other recent nDNA genome studies (e.g., Carbone et al., 2014; Veeramah et al., 2015), finds strongest support for *Hylobates*(*Nomascus*(*Hoolock*, *Symphalangus*)) topology, and a divergence date for extant hylobatid genera of ~5 Ma using non-coding regions. They use a Bayesian MCMC program to analyze 12,413 non-coding loci, making it the most comprehensive hylobatid phylogenetic study to date. The species *Hoolock hoolock* is substituted for *Hoolock leuconedys*, as body mass data is only available for *Hoolock hoolock*, and some authors would consider *Hoolock leuconedys* a sub-species of *Hoolock hoolock*, rather than a separate species (Mootnick and Groves, 2005; Choudury, 2013).

Phylogenetic trees including fossil taxa were constructed using published FADs (First Appearance Dates) (Seiffert, 2006; Alba et al., 2012; Alba et al., 2015; Gonzales et al., 2015; McNulty et al., 2015; Morgan et al., 2015), to which ghost lineages of 1 million years were applied. Topology for these trees was taken from Alba et al. (2015) and Nengo et al. (2017), as these are the most complete and up to date cladistic analyses which include many fossil catarrhines. The two studies agree on the position of all fossil taxa inlcuded here with the exception of *Hispanopithecus laietanus* and *Pliobates cataloniae.* In Nengo et al. (2017) the position of *Hispanopithecus laietanus* is unresolved, because of a trichotomy at the ancestor of the great apes. Alba et al. (2015) places *Hispanopithecus laietanus* as a stem hominid. As this analysis does not allow for trichotomies, *Hispanopithecus* is placed as a stem hominid. Two trees including fossil taxa are constructed to test the effect of the phylogenetic position of *Pliobates cataloniae*; one in which *Pliobates* is positioned as a stem catarrhine (Nengo et al., 2017), and one in which *Pliobates* is positioned as a stem hominoid (Alba et al., 2015). The insertion of a

small-bodied primate close to the ancestor of crown hominoids is expected to have a large effect on the predictions of body size evolution for the clade (e.g., Alba et al., 2015; Grabowski and Jungers 2017).

Ancestral state reconstructions

The phylogenetic comparative approaches employed here include both cvBM and mvBM models as well as maximum-likelihood and MCMC methods for estimating rate of change along branches and trait values at nodes. Ancestral state reconstructions were conducted for each tree under three conditions. All simulations and analyses were implemented in *R* version 3.3.2 (R Core Team, 2016).

The first condition was a cvBM model using maximum-likelihood. This model employed the phylogenetic tree with branch lengths scaled to divergence times (Figure 3A). The maximum-likelihood estimates were calculated with the 'REML' method in the 'ace' function of the 'ape' package (Paradis et al., 2004).

Both maximum-likelihood and MCMC were used to calculate body mass estimates and parameters under a mvBM model. Following the methods in Smaers et al. (2016), rates of phenotypic change were estimated across the phylogenetic tree, branch lengths were rescaled using the 'mvBM' function in the 'evomap' package (Smaers et al., 2016), and estimates of internal nodes were calculated. This approach relaxes the assumption that phenotypic traits evolve at the same rate over all branches of the tree. The maximum-likelihood method was implemented through the 'REML' method of the

'ace' function, both to calculate the rescaled tree (Figure 3B), and to estimate internal node values.

The Bayesian method requires MCMC to be conducted twice; once to estimate rates of trait change over branches, and again to estimate values at internal nodes after branch lengths have been rescaled. MCMC using Bayesian inference was implemented through the function 'anc.Bayes' in the 'phytools' package (Revell, 2012). Ancestral states were sampled from the unmodified tree over 10 million iterations. The first 2,000 estimates were discarded as burn in. Burn in was set high, as the function required many iterations for parameters to normalize with trees consisting of over 100 tips. 10 million iterations resulted in normal distributions of consist estimates and σ^2 values after discarding burn-in. Mean values of σ^2 were then used to rescale branch lengths of the tree with the function 'mvBM' in the package 'evomap' (Figure 3C). A MCMC simulation was then run on the rescaled tree to estimate character values at nodes using the same number of iterations and burn-in runs discarded, resulting in normal distributions of Log-likelihood estimates.

Chapter 3: Results

Model Comparisons

Results of model comparisons and predicted body mass (kg) at major nodes can be found in Table 3. Models using an mvBM framework significantly outperformed the model using standard cvBM. Both mvREML and mvMCMC models produced similar rescaled trees (Figure 3), and second order Akaike information criterion (AICc) estimates for these are much less than that of the cvREML models using branch lengths equivalent to divergence times. AICc estimates are only comparable between models using the same phylogenetic trees (i.e., extant to extant models only; phylogeny I to phylogeny I models only). Models using cvREML and only including data from extant taxa show the greatest differences in predictions. In the cvREML model for male body mass using only data from extant taxa, the crown anthropoid node is significantly higher (18.5 kg) than in all other models (6.4-11 kg). The predictions for crown catarrhines, hominoids, hominids and African apes follow the same pattern for this model. The prediction for African apes (89.7 kg) is so large that both *Pan* (41.4-59.7 kg) and *Homo* (57.4 kg) experience a major decrease in body size from their last common ancestor (71.5 kg). The prediction for male crown hylobatids (11.6 kg) is the size of *Symphalangus* (11.8 kg). Predictions for ancestral body mass for females using mvREML are also generally higher than in mvBM models, but to a lesser degree.

Models using the mvBM framework produced similar predictions for ancestral nodes as well as similar recaled trees. In general, predictions for the nodes of interest here were slightly higher in mvREML models than in mvMCMC models, but only by a

Figure 3. Phylogenetic trees including extant anthropoid primates only used in final ancestral state reconstructions. **(A)** Phylogenetic tree based on Bayesian inference (*10kTrees*) and modified for Hylobatidae following Shi and Yang (2017). Branch lengths scaled to divergence times and used for cvREML method. Rescaled tree branch lengths calculated by mvBM function (Package *evomap*: Smears et al., 2016) using ace (Package *ape*: Paradis et al., 2004) method 'REML' (**(B): mvREML**), and MCMC (**(C): mvMCMC**). Longer branch lengths represent faster rates of change in body mass. **Clade colors follow Figure 2:** Pithecidae = yellow; Cebidae = pink; Atelidae = orange; Hominidae=dark blue; Hylobatidae=purple; Cercopithecidae =cyan.

few kgs for larger estimates, and a few tenths of a kg for smaller estimates. Despite this, AICc estimates were significantly higher for mvREML models (Table 3). AICc weights approach 0 for both cvREML and mvREML methods, while AICc weights for the mvMCMC models approach 1 across all conditions. For this reason, only results from mvMCMC models are presented below and in Figures 4-7.

Ancestral state reconstructions using only extant taxa (Figures 4 and 5)

Female body size evolution (Figures 4A and 5A)

The ancestral anthropoid is predicted to be 7.6 kg. This begins a trend of increasing body size throughout all hominoid lineages with the exception of hylobatids. The ancestral catarrhine is predicted to be 11.7 kg, increasing to 19.2 kg in the ancestral hominoid, 32.4 kg at the ancestral hominid node, and 44.9 kg at the ancestral African ape node. In other primates, the platyrrhines are predicted to experience a general trend of decreasing body size throughout all lineages with the exception of atelids (4.7 kg ancestor). Ceropithecoids are predicted to undergo a slight decrease in body size from the ancestral catarrhine to 7.6 kg for the ancestral colobine and 6.2 kg for the ancestral cercopithecine before both clades begin to diversify.

The ancestral hylobatid is predicted to be 8.4 kg, and remain at 8.4-8.5 kg at the nodes of the *Nomascus-Hoolock-Symphalangus* ancestor, and the *Hoolock-Symphalangus* ancestor. The ancestral *Hylobates* node is predicted to be 6.2 kg.

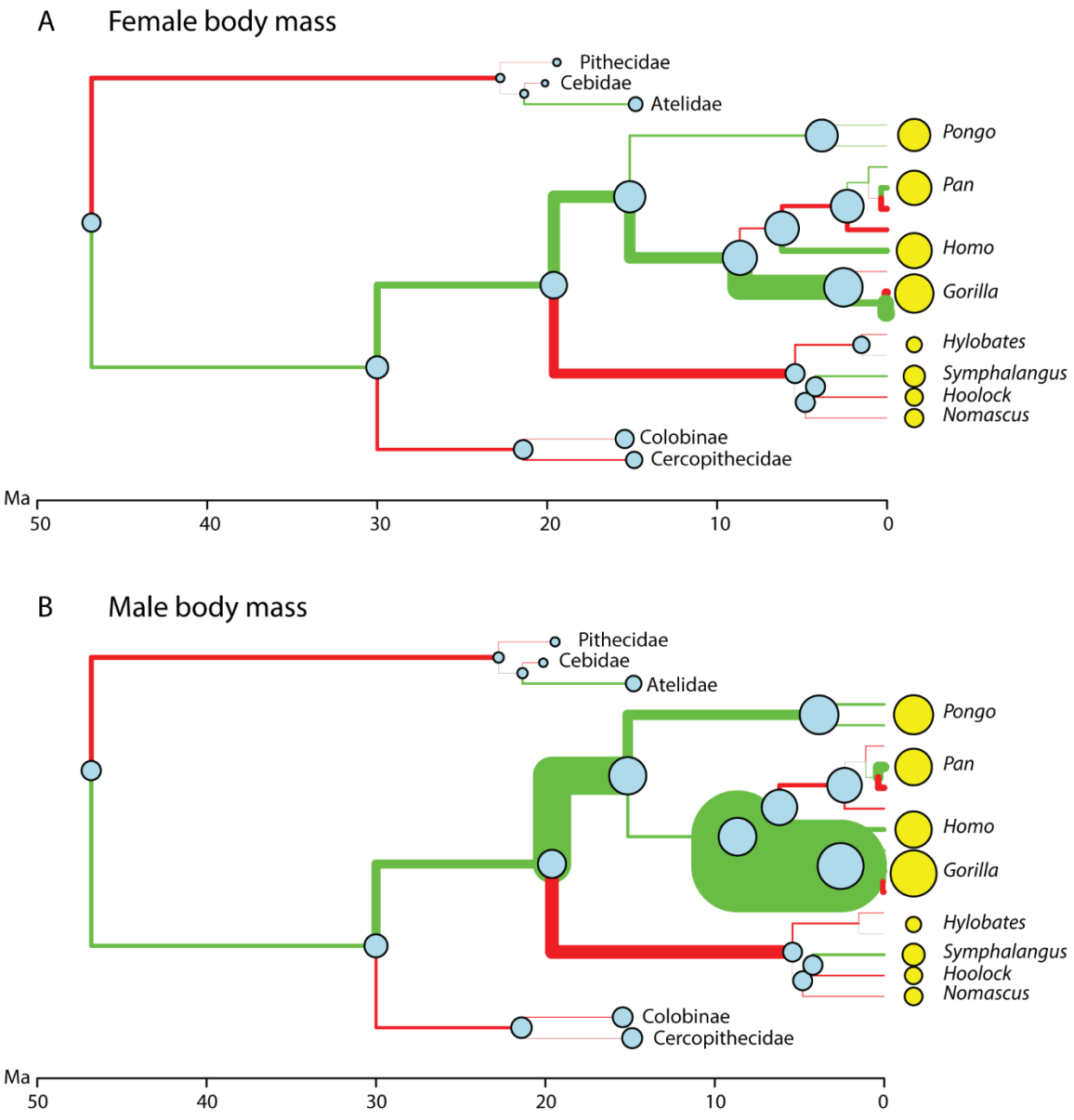

Figure 4. Truncated results of ASR of anthropoid body mass using only extant taxa: **(A) Females**; **(B) Males**. **Node and tip values represented by circles of area = Log2(body mass).** Yellow tip values represent genus mean (by sex) for extant taxa. Blue node values were predicted using mvMCMC method. Branch width represents rate of change; thin branches indicate slow rate of change, and thick branches indicate rapid change. **Green = increase in body mass, Red = decrease in body mass, and Black = < 5% change along branch.**

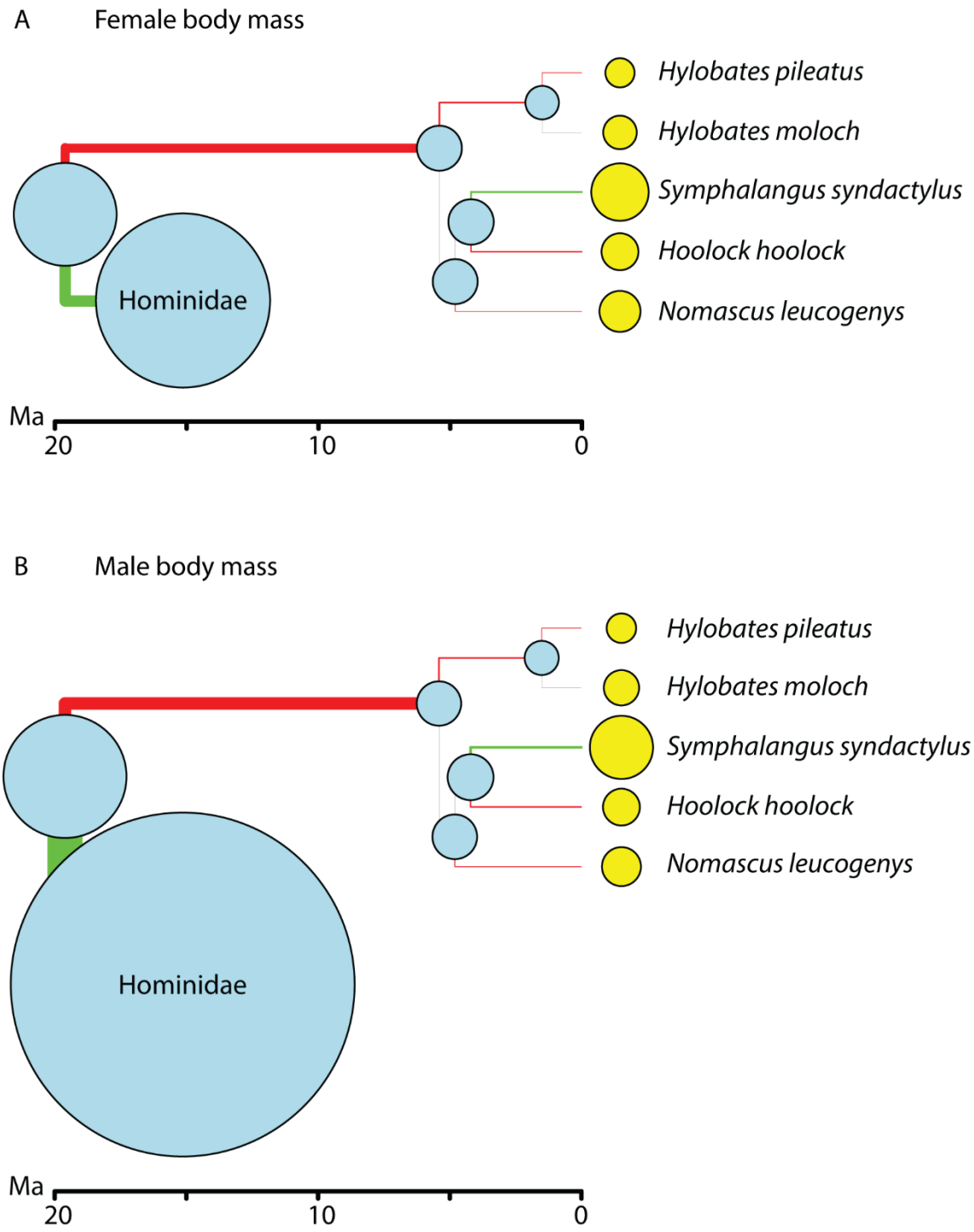

Figure 5. Truncated results of ASR of hylobatid body mass using only extant taxa: **(A) Females**; **(B) Males**. **Node and tip values represented by circles of area = body mass.** Yellow tip values represent species mean (by sex) for extant taxa. Blue node values were predicted using mvMCMC method. Branch width represents rate of change; thin branches indicate slow rate of change, and thick branches indicate rapid change. **Green = increase in body mass, Red = decrease in body mass, and Black = < 5% change along branch.**

Male body size evolution (Figures 4B and 5B)

The ancestral anthropoid is predicted to be 8.6 kg. This begins a trend of increasing body size throughout all hominoid lineages with the exception of hylobatids. The ancestral catarrhine is predicted to be 13.2 kg, increasing to 22.9 kg in the ancestral hominoid, 64.1 kg at the ancestral hominid node, and 67.5 kg at the ancestral African ape node. The ancestral platyrrhine as well as the ancestor for pithecids and cebids is predicted at ~3 kg. Atelids are predicted to experience a body size increase, evolving from a 5.6 kg ancestor. The ancestral cercopithecoid is predicted at 9.9 kg, decreasing slightly to ~9 kg in both colobines and cercopithecines before these clades diversify.

The ancestral hylobatid is predicted to be 8.3 kg, and remain at 8.3-8.6 kg at the nodes of the *Nomascus-Hoolock-Symphalangus* ancestor, and the *Hoolock-Symphalangus* ancestor. The ancestral *Hylobates* node is predicted to be 6.4 kg.

Ancestral state reconstructions with fossil taxa included (Figures 6 and 7)

Phylogeny I - *Pliobates cataloniae* as a stem hominoid (Figures 6A and 7A)

The ancestral anthropoid is predicted to be 6.7 kg. A general increasing trend is observed until the branching of *Pliobates.* The ancestral catarrhine is predicted to be 9.4 kg, increasing to 26.6 kg in the ancestral hominoid. At the node connecting the branch of *Pliobates,* the predicted body mass decreases to 20.9 kg, before beginning an increasing trend again in the non-hylobatid hominoid lineages. Body mass is predicted to be 29.0 kg

at the ancestral hominid node, and 53.9 kg at the ancestral African ape node. The ancestral platyrrhine as well as the ancestor for pithecids and cebids is predicted at 2.4-3 kg. Atelids are predicted to experience a body size increase, evolving from a 5.7 kg ancestor. Similar to predictions for using only extant male data, the ancestral cercopithecoid is predicted at 10.6 kg, decreasing slightly to ~9 kg in both colobines and cercopithecines before these clades diversify.

The ancestral hylobatid is predicted to be 8.5 kg, and remain at 8.5-8.7 kg at the nodes of the *Nomascus-Hoolock-Symphalangus* ancestor, and the *Hoolock-Symphalangus* ancestor. The ancestral *Hylobates* node is predicted to be 6.4 kg.

Phylogeny II - *Pliobates cataloniae* as a stem catarrhine (Figures 6B and 7B)

The ancestral anthropoid is predicted to be 6.4 kg. This again begins a trend of increasing body size throughout all hominoid lineages with the exception of hylobatids. The ancestral catarrhine is predicted to be 8.8 kg, increasing to 29.6 kg in the ancestral hominoid, 31.4 kg at the ancestral hominid node, and 55.8 kg at the ancestral African ape node. The ancestral platyrrhine as well as the ancestor for pithecids and cebids is predicted at 2.4-3 kg. Atelids are predicted to experience a body size increase, evolving from a 5.6 kg ancestor. Similar to results from trees using only extant male data, and phylogeny I, the ancestral cercopithecoid is predicted at 10.3 kg, decreasing slightly to ~9 kg in both colobines and cercopithecines before these clades diversify.

The ancestral hylobatid is predicted to be 8.8 kg, and remain at 8.8-8.9 kg at the nodes of the *Nomascus-Hoolock-Symphalangus* ancestor, and the *Hoolock-Symphalangus* ancestor. The ancestral *Hylobates* node is predicted to be 6.5 kg.

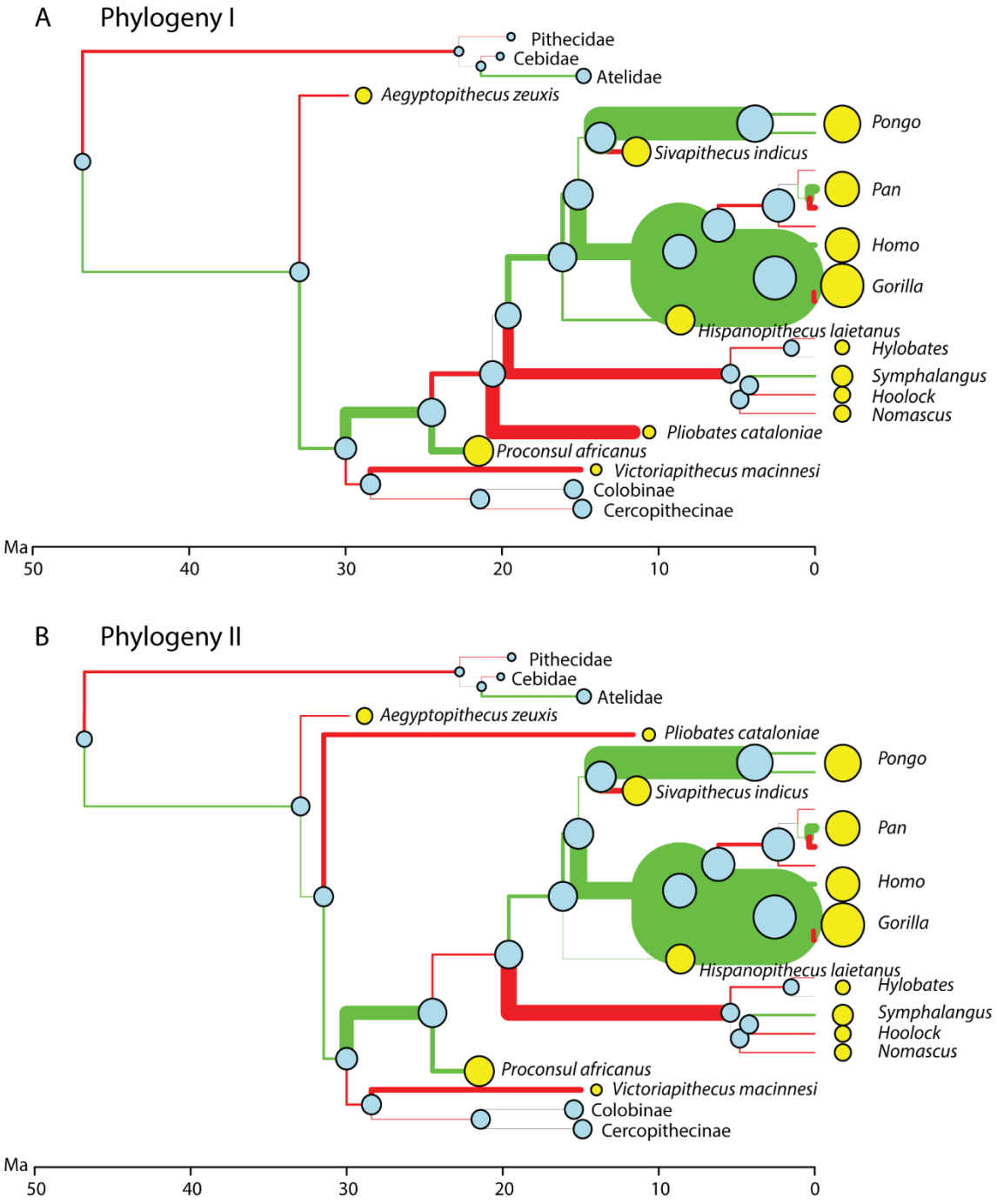

Figure 6. Truncated results of ASR of anthropoid body mass using extant and fossil taxa. **Node and tip values represented by circles of area = Log2(body mass).** Yellow tip values represent genus mean (males) for extant taxa, and species estimates for fossil taxa. Blue node values were predicted using mvMCMC

method. Branch width represents rate of change; thin branches indicate slow rate of change, and thick branches indicate rapid change. **Green = increase in body mass, Red = decrease in body mass, and Black = < 5% change along branch. Phylogeny I (A)** includes *Pliobates cataloniae* as a stem hominoid. **Phylogeny II (B)** includes *Pliobates cataloniae* as a stem catarrhine.

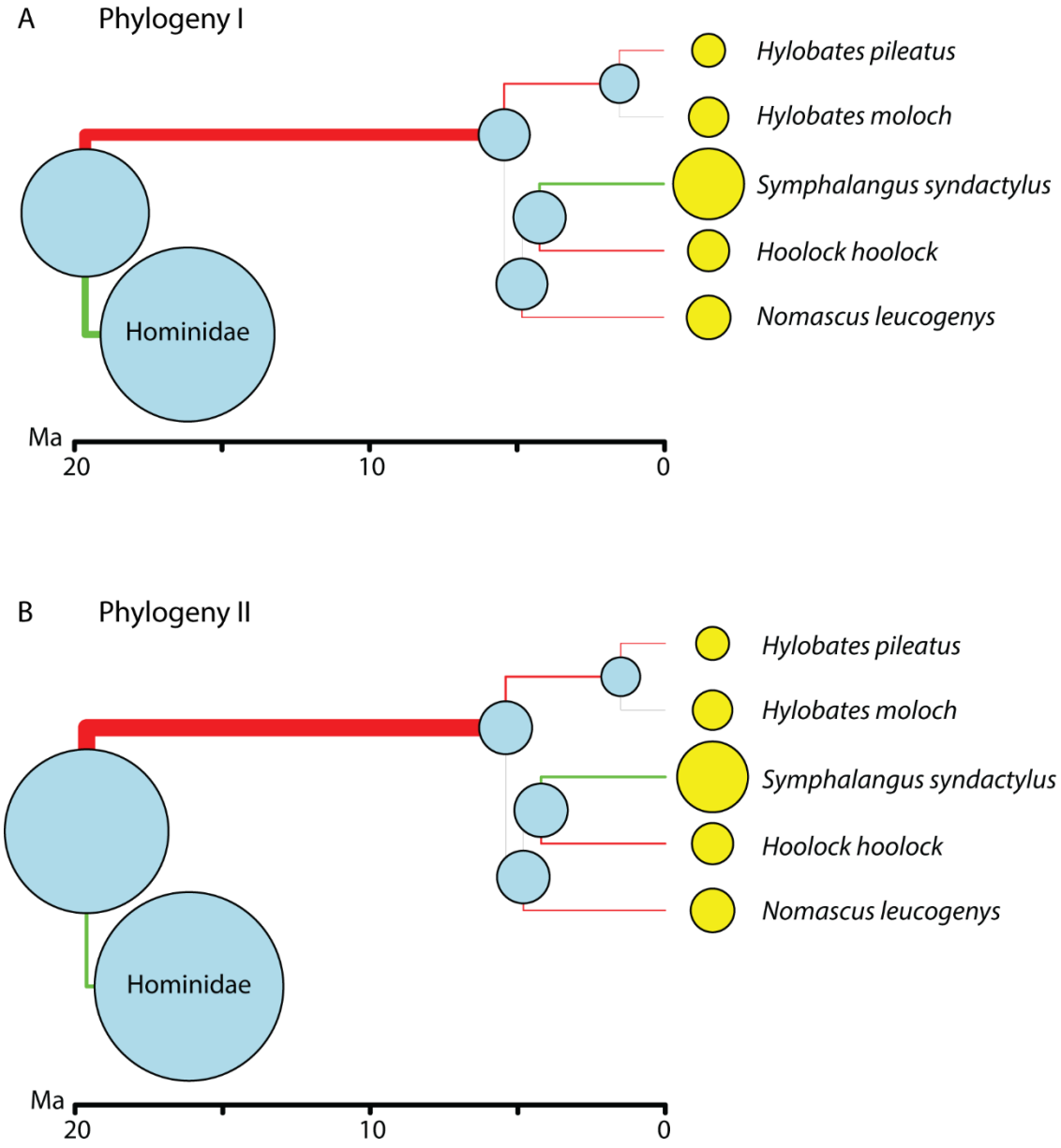

Figure 7. Truncated results of ASR of hylobatid body mass using extant and fossil taxa. **Node and tip values represented by circles of area = body mass.** Yellow tip values represent species mean (males) for extant taxa, and species estimates for fossil taxa. Blue node values were predicted using mvMCMC method. Branch width represents rate of change; thin branches indicate slow rate of change, and thick branches indicate rapid change**. Green = increase in body mass, Red = decrease in body mass, and Black = < 5% change along branch. Phylogeny I (A)** includes *Pliobates cataloniae* as a stem hominoid. **Phylogeny II (B)** includes *Pliobates cataloniae* as a stem catarrhine.

Method	Tree	Sex	$log(L_i)$	$AICc_i$	Δ_i(AICc)	w_i(AICc)	Crown anthropoids	Crown platyrrhines
cvREML	Extant	Female	-845	1694.10	1564.58	0	11	3.4
		Male	-844	1692.10	1555.58	0	18.5	4.6
	Phylogeny I	Male	-886	1776.10	1628.40	0	8.2	3.4
	Phylogeny II	Male	-886	1776.10	1629.60	0	8.1	3.4
mvREML	Extant	Female	-187	382.34	252.81	1.26E-55	8.6	3.1
		Male	-208	424.34	287.81	3.18E-63	10	3.6
	Phylogeny I	Male	-241	490.33	342.63	3.97E-75	7.8	3.3
	Phylogeny II	Male	-235	478.33	331.83	8.79E-73	7.1	3.3
mvMCMC	Extant	Female	-58.4	129.52	0.00	1	7.6	2.6
		Male	-61.9	136.52	0.00	1	8.6	3.2
	Phylogeny I	Male	-67.5	147.69	0.00	1	6.7	3
	Phylogeny II	Male	-66.9	146.49	0.00	1	6.4	3

Table 3. Comparison of models with **ASR values (mass in kg)** at synonymous nodes. cvREML = cvBM model conducted by maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2016). mvREML = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2004). mvMCMC = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and MCMC. **Extant = phylogeny including only extant taxa. Phylogeny I = extant and fossil taxa; *Pliobates cataloniae* is included as a stem hominoid following Alba et al. (2015). Phylogeny II = extant and fossil taxa; *Pliobates cataloniae* is included as a stem catarrhine following Nengo et al. (2017).** $log(L_i)$ = log-likelihood; $AICc_i$ = second order AIC; Δ_i (AICc) = [$AICc_i$ – min(AICc)]; w_iAICc = Akaike weights.

Method	Tree	Sex	Crown catarrhines	Crown hominoids	Crown hominids	Crown African apes
cvREML	Extant	Female	16	26.3	36.2	50.5
		Male	27.6	47.2	66.8	89.7
	Phylogeny I	Male	15	27.5	41.5	81.6
	Phylogeny II	Male	15	32.5	42.7	82
mvREML	Extant	Female	12.5	20.2	33.6	46.3
		Male	14.8	25.4	69.1	75.4
	Phylogeny I	Male	13.8	22.6	37.3	61.5
	Phylogeny II	Male	13.7	28.5	38.5	62.3
mvMCMC	Extant	Female	11.7	19.2	32.4	44.9
		Male	13.2	22.9	64.1	67.5
	Phylogeny I	Male	13.1	21.2	34.4	53.9
	Phylogeny II	Male	13.1	27.3	35.8	55.8

Table 3. Comparison of models with **ASR values (mass in kg)** at synonymous nodes. cvREML = cvBM model conducted by maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2016). mvREML = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2004). mvMCMC = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and MCMC. **Extant = phylogeny including only extant taxa. Phylogeny I = extant and fossil taxa; *Pliobates cataloniae* is included as a stem hominoid following Alba et al. (2015). Phylogeny II = extant and fossil taxa; *Pliobates cataloniae* is included as a stem catarrhine following Nengo et al. (2017).** $\log(L_i)$ = log-likelihood; $AICc_i$ = second order AIC; Δ_i (AICc) = [$AICc_i$ – min(AICc)]; w_iAICc = Akaike weights.

Method	Tree	Sex	Crown hylobatids	*Nomascus-(Symphalangus-Hoolock)* ancestor	*Symphalangus-Hoolock* ancestor	Ancestral *Hylobates*
cvREML	**Extant**	Female	9.4	9.11	9	6.41
		Male	11.6	10.8	10.5	6.9
	Phylogeny I	Male	9.7	9.4	9.4	6.6
	Phylogeny II	Male	10.2	9.7	9.7	6.7
mvREML	**Extant**	Female	8.5	8.5	8.6	6.3
		Male	8.4	8.4	8.6	6.4
	Phylogeny I	Male	8.7	8.7	8.8	6.5
	Phylogeny II	Male	9	8.9	9	6.5
mvMCMC	**Extant**	Female	8.4	8.4	8.5	6.2
		Male	8.3	8.3	8.6	6.4
	Phylogeny I	Male	8.5	8.5	8.7	6.4
	Phylogeny II	Male	8.8	8.8	8.9	6.5

Table 3. Comparison of models with **ASR values (mass in kg)** at synonymous nodes. cvREML = cvBM model conducted by maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2016). mvREML = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and maximum-likelihood method 'REML' in function ace (Package *ape*: Paradis et al., 2004). mvMCMC = mvBM model conducted by rescaling branch lengths using mvBM function (Package *evomap*: Smears et al., 2016), and MCMC. **Extant = phylogeny including only extant taxa. Phylogeny I = extant and fossil taxa; *Pliobates cataloniae* is included as a stem hominoid following Alba et al. (2015). Phylogeny II = extant and fossil taxa; *Pliobates cataloniae* is included as a stem catarrhine following Nengo et al. (2017).** $\log(L_i)$ = log-likelihood; $AICc_i$ = second order AIC; Δ_i (AICc) = $[AICc_i - \min(AICc)]$; w_iAICc = Akaike weights.

Chapter 4: Discussion

Results of model comparisons show that both mvBM methods and the inclusion of fossils constrains early increases in body size. Both mvBM methods result in very similar rescaled trees. Results of ancestral body mass predictions were relatively consistent between phylogenies using mvMCMC. Differences in predictions followed fairly simple patterns. When only extant male body masses were included, predictions were higher at all nodes, with the exception of the platyrrhine clades. Given the extreme nature of the sexual dimorphism of extant great apes (Gordon, 2004), this is hardly unexpected. Interestingly, this did not appear to affect the predictions at previous nodes, as predictions for other hominoid internal nodes were relatively similar throughout all four conditions. Inclusion of *Pliobates cataloniae* as either a stem hominoid or stem catarrhine had the largest and most wide-spread affect on predictions. The only time that predictions along hominoid nodes decrease is when *Pliobates* is included as a stem hominoid. However, even with the inclusion of *Pliobates* as a stem hominoid, none of the internal hominoid nodes drop below a predicted 20 kg, with the exception of the hylobatid lineage. This is still significantly larger than the male siamang, and is good support for the hypothesis that ancestral hominoids were large-bodied, despite the branching of multiple smaller-bodied lineages.

Predictions for ancestral and internal hylobatid nodes are virtually unaffected by the position of *Pliobates* here. All simulations predicted a body mass for the ancestral hylobatid and the nodes of the *Nomascus-Hoolock-Symphalangus* ancestor, and the *Hoolock-Symphalangus* ancestor of 8-9 kg. This robust result indicates that the ancestral

hylobatid body size was likely intermediate between that of *Nomascus* and *Symphalangus*. This predicts that while the hylobatid lineage in general is dwarfed from its hominoid ancestor, *Symphalangus* has experienced an increase in body size since the hylobatid radiation, while the remaining three genera have continued the pattern of decreasing body size. This would also support the idea that *Hylobates* is the most derived in terms of body size. If the ecological niche differentiation hypothesis holds for sympatric *Hylobates* and *Symphalangus*, these results indicate that both genera have undergone body size evolution simultaneously to fill their respective niches.

The overall results of this study are in contrast to those found by Grabowski and Jungers (2017). In their study, the best supported model identified a body mass optima of 6.95 kg for hylobatids. This optima was shared by Atelidae, most of the Cercopithecidae, and some fossil taxa, including *Pliobates cataloniae*. Somewhat surprisingly, they also found that the hominoid last common ancestor (LCA) was predicted to share this regime as well. Grabowski and Jungers (2017) also included a large comparative extant primate sample as well as fossil taxa, and a phylogenetic tree very similar to that referred to in this study as Phylogeny I, with *Pliobates cataloniae* placed as a stem hominoid. The best explanation for the differences in results lies in the different evolutionary modelling approach: while models based on BM make predictions for trait condition at nodes (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1985), OU based models seek to identify trait optima, and group tip taxa based on trait condition and phylogenetic position (Hansen, 1997, 2012). The utility of multi-regime OU models is limited in predicting the condition of nodes, as it seeks to identify where along the tree a regime begins and where it branches to, rather than predict the actual value of the trait at the node (Uyeda and

Harmon, 2014). In Grabowski and Jungers (2017), five of eight identified regimes were composed of members of Hominidae. One contained all strepsirrhines, and most platyrrhines; one was composed only of two species of *Papio*; the final regime is predicted to include the hominoid LCA, as discussed above. While this is useful in identifying lineages that may have experienced similar selective pressures on body size, it does not track the evolution of body size across primate lineages.

The results presented here are robust across mvBM models as well. The difference in rescaled trees produced by the two methods is almost indistinguishable in Figure 3, and choice of the mvREML or mvMCMC model had little affect on node predictions. Clearly, using an mvBM rather than cvBM model is more important to the results than the method of calculation used. This study is a good example of why mvBM models should continue to be selected over cvBM models. The Hominidae show such a dramatic increase in body size over a short time that inclusion of these taxa affect the prediction of trait values back to the most basal nodes (Table 3).

Robust support for using multi-rate evolutionary models to track trait change can be found in Venditti et al. (2011). As here, they identified several clades that experienced extreme changes over relatively short periods of time. Studying the evolution of body size across all mammals, they identified several bursts, including significant increases in the lineages leading to Atelidae and Hominidae. Results here agree, whether fossil taxa are included or not. Primates are also not unique among mammals in their tendency to increase, rather than decrease in body size. There appears to be a directional bias in mammalian evolution towards increases, rather than decreases in body size (Baker et al.,

2015), and the most rapid changes all appear to be toward increasing body size (Venditti et al., 2011).

Here we find that while several primate clades do appear to have undergone some decreases in body size, the only clade to experience a burst toward decreased body size is Hylobatidae. While increases or decreases of a few kilograms in a large-bodied primate such as a gorilla are insignificant, changes of only a few kilograms can have more profound affects on the biology of a small primate (Schmidt-Nielson, 1984). This makes it all the more puzzling that the siamang would then increase body size while other hylobatids continue a decreasing trend. It seems likely that changes in hylobatid body size evolved in response to changes in available niches (Brown and Wilson, 1956). Siamangs are now sympatric with both hoolock gibbons and orang-utans (see Figure 1) as well as cercopithecid monkeys (Reichard et al., 2016). However, we do not know where the Hylobatidae first appeared, and so cannot speculate as to its competition with closely related species.

Despite very different trajectories in body size evolution from a common ancestor, both extant hominids and hylobatids evolved an orthograde body-plan and forelimb dominated locomotor behaviors separately (Fleagle, 2013; Harrison, 2016). It is possible that hylobatid evolution was largely affected by changing climate and the availability of niches as its distribution shifted to its present day status (Reichard and Crossier, 2016). It is known from *Yuanmoupithecus xiaoyuan* that hylobatids reached present day China by at least the late Miocene (~7-9 Ma), and that they were sympatric with larger bodied Asian apes (*Lufengpithecus*) and cercopithecids by that time (Pan, 2006). However, nothing is known about this stem hylobatid's postcranial adaptations at

this critical time period, just before the radiation of the extant genera. Results here suggest that this ancestral hylobatid would have a body mass of approximately 8.5-9 kg, and little to no sexual dimorphism. This small body size appears to have been a key adaptation to this unique clade and may have been key to the survival of its living representatives.

Conclusions

This study provides additional support for the ecological niche differentiation hypothesis for the two discrete morphs of the Hylobatidae. Results of this study predict that neither the large-bodied extant great apes, or the small-bodied extant lesser apes are representative of the hominoid LCA. Instead, both families most likely diverged from a ~20-30 kg ancestor. While the great apes experienced a burst in increased body size, hylobatids experienced a burst in decreasing body size. This rapid trend toward decreasing body size is a rare occurrence in primates, and in mammalian evolution in general. While three genera (*Hylobates, Hoolock*, and *Nomascus*) continued on a trend of decreasing body size, *Symphalangus* secondarily increased body size. Given the rapid diversification of extant hylobatids (Carbone et al., 2014), it is likely that changes in body size for all four extant genera indicate changes in the niches available to small-bodied apes (Reichard and Preuschoft, 2016). Further behavioral studies, particularly those in more northern latitudes, are needed to understand the full range of variation in the diets, habitat exploitation, day range, and home range sizes across extant hylobatids. Only after accumulating more data from extant species, can we test whether the siamang is indeed

occupying a unique niche among hylobatids. Ultimately, though, it will be the discovery of new fossil specimens that will support or refute the findings here of an ~8.5-9 kg ancestor from which the extant genera diverged. What is clear is that the small body size of hylobatids makes them unique among the apes. With the knowledge that one of these unusually small apes most likely experienced a secondary increase in size, the narrative of hylobatid evolution is now certainly more complex than once thought.

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