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Contextualising primate origins – An ecomorphological framework

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Abstract
Ecomorphology–the characterisation of the adaptive relationship between an organism's morphology and its ecological role–has long been central to theories of the origin and early evolution of the primate order. This is exemplified by two of the most influential theories of primate origins: Matt Cartmill's Visual Predation Hypothesis, and Bob Sussman's Angiosperm Co-Evolution Hypothesis. However, the study of primate origins is constrained by the absence of data directly documenting the events under investigation, and has to rely instead on a fragmentary fossil record and the methodological assumptions inherent in phylogenetic comparative analyses of extant species. These constraints introduce particular challenges for inferring the ecomorphology of primate origins, since morphology and environmental context must first be inferred, before the relationship between the two can be considered. Fossils can be integrated in comparative analyses and observations of extant model species and laboratory experiments of form-function relationships are critical for the functional interpretation of the morphology of extinct species. Recent developments have led to important advancements, including phylogenetic comparative methods based on more realistic models of evolution, and improved methods for the inference of clade divergence times, as well as an improved fossil record. This contribution will review current perspectives on the origin and early evolution of primates, paying particular attention to their phylogenetic (including cladistics relationships and character evolution) and environmental (including chronology, geography, and physical environments) contextualisation, before attempting an up to date ecomorphological synthesis of primate origins.

Keywords
Primates; clade origins; ecology; body size; brain anatomy; evolution.

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1. Introduction

Extant primates are characterised by a number of anatomical features that are, in their majority, not unique to the order, but in combination serve to distinguish them from other mammals (Martin, 1968, 1986, 1990). Those that historically have received the most attention in adaptive terms include increased orbital size and convergence, an opposable hallux, digits lacking functional claws, elongated tarsal bones, reduced relative snout length and increased relative brain size (Martin, 1990; Cartmill, 1992, 2012; Fleagle, 2013; Sussman et al., 2013). Broadly, the most prominent hypotheses of primate origins can be grouped into those that emphasise the importance of locomotor behaviour in shaping the ancestral primate adaptive profile and those emphasising the importance of diet. Although it has been credibly argued that arboreality *per se* is unlikely to have driven the evolution of the ancestral primate adaptive profile (Cartmill, 1972, 1974a, b, 1985, 1992; Kirk et al., 2008), all agree that primates most likely originated in an arboreal context; and most consider the earliest primates to have been small, weighing around 500g at most, and probably substantially less (but see Soligo & Martin, 2006, 2007). Scenarios emphasising the role of locomotion in the origin of primates stress, in particular, the importance of leaping (Szalay & Dagosto 1980, 1988; Dagosto, 1988, 2007; Crompton, 1995, for an added emphasis on nocturnal leaping), while for those emphasising diet, the main proponents have stressed the role of visually directed predation on insects and other prey (Cartmill, 1972, 1974a, b, 1992), or the exploitation of angiosperm products including fruit, flowers, and nectar (Sussman and Raven, 1978; Sussman, 1991; Sussman et al., 2013).

Ecomorphological principles, then, have long been integral to hypotheses of primate origins, as exemplified by two of the most influential hypotheses of primate origins: Matt Cartmill's Visual Predation Hypothesis (Cartmill, 1972, 1974a, b), and Bob Sussman's Angiosperm Co-Evolution Hypothesis (Sussman and Raven, 1978; Sussman, 1991). However, a consensus regarding the ecological significance of inferred ancestral primate traits has proved hard to reach. In this context it is worth questioning whether a polarising discussion aimed at identifying a primary ecological determinant of the ancestral primate niche based on a singular interpretation of anatomical traits can provide a realistic model of primate origins, both because single adaptive features, such as orbital convergence, may equally well serve different functions (Crompton, 1995; Soligo & Martin, 2006), and because the suite of

characters associated with the ancestral primate niche is likely to have evolved in modular fashion (Cartmill, 1972, 2012; Rasmussen, 1990; Bloch et al., 2007; Ravosa & Savakova, 2004; Fleagle 2013), possibly over many millions of years.

Today, most primates are generalists, supplementing a diet of fruit, nectar and/or gum with either animal matter (mostly invertebrates) or leaves for protein (Rowe, 1996; Fleagle, 2013). It is perfectly conceivable that early primates had similarly flexible diets in which case hypotheses seeking to understand the adaptive profile of ancestral primates in the context of derived dietary adaptations may have overestimated the relevance of specific foods, unless it can be argued that they relate to the exploitation of a critical resource. Instead, characters including convergent visual fields, dexterous hands, and grasping feet, may be the consequence of how food items are initially secured, with derived primate morphology reflecting a shift towards manual feeding and derived hand-mouth coordination, rather than dietary specialisation (Soligo & Martin, 2006). The case against a singular dietary specialisation being the key determinant of optical convergence, for example, is supported by data from the lorises, which have the most convergent eyes of any strepsirrhines, yet feed on a range of foods including vertebrates, invertebrates, exudates and nectar; with binocular vision appearing to benefit in particular faunivory and nectarivory (Nekaris, 2014).

Ideally, therefore, hypotheses of form-function relationships in ancestral primates, and of their ecological role, should be verified using a multidisciplinary approach including functional anatomy, palaeoecology, and a broad phylogenetic comparative approach. Here, we present a broad ecomorphological framework for the study of primate origins and provide a brief review of current knowledge, with examples pertinent to an ecomorphological contextualisation of primate origins. We discuss some of the reasons why a consensus on the adaptive origins of the Order has remained elusive, highlighting specific challenges faced by attempts to apply an ecomorphological framework to the past, and suggest some promising avenues for future research.

2. An ecomorphological framework for primate origins

In a palaeontological context, it is important to distinguish between the use of the term ecomorphology as a broad concept aimed at characterising the adaptive relationship between an organism's morphology and its ecological role, from its use to describe methods to infer aspects of palaeoenvironments. In the latter, associations between morphology and habitat preference are documented in extant taxa and form the basis of predictive models that are used to infer aspects of past environments from the morphology of fossil taxa (Andrews & Hixson, 2014), frequently focusing on a single taxon, such as bovids (e.g., Kovarovic & Andrews, 2007), suids (e.g., Bishop et al., 2006), or felids (e.g., Meloro et al., 2013). These approaches are based on the assumption that the functional significance of the morphology they consider is known, that that function translated into corresponding behaviour in the fossil organisms, and that that behaviour was indicative of the environment those fossils occupied.

As a broader concept, ecomorphology encompasses all, or part, of a two-way process: the relationship between morphological and ecological patterns of variation (Winkler, 1988; Bock, 1994; Reilly & Wainwright, 1994). This includes the question of how organism form reflects adaptation to a specific environmental context (i.e., of what functional and biological consequences are facilitated by specific morphologies), but also the question of what consequences specific organisms, as morphological constructs, are having for their

environments' ecological and evolutionary trajectories (i.e., of what ecological role an organism is constrained to fulfil by its phenotype). The changes that organisms effect on their environments and the evolutionary feedback generated by those changes on those organisms are key elements of the concept of niche construction (Odling-Smee, 1988; Odling-Smee et al., 2003). The ecomorphological framework adopted here has been summarised in 5 hierarchical levels of analysis (Reilly & Wainwright, 1994; Figure 1):
1) the description of morphology; 2) the determination of the functional capacity of that morphology; 3) the interpretation of the potential consequences of that capacity for an organism's performance (its fundamental niche); 4) observation of the organism's actual performance (its realized niche); and 5) determination of the fitness consequences of that performance. Transferring this framework into the past, tentatively referred to as the formulation of a palaeo-ecomorphological framework, introduces a number of substantial challenges.

At the first level of analysis, and in the absence of directly ancestral fossils, ancestral morphologies have to be inferred. Uncertainties associated with such inferences vary between characters. For example, all living primates, except for the clearly derived modern humans, have a grasping foot. It seems therefore unproblematic to infer that the last common ancestor (LCA) of living primates also had a grasping foot. In contrast, primate digits end in a variety of keratinous structures ranging from the typical flat nail seen in humans to the fully functional, longitudinally curved and laterally compressed, claws of marmosets, tamarins, and the aye-aye, that are similar to those seen in many other mammals (Le Gros Clark, 1936; Soligo & Müller, 1999; Maiolino et al., 2011, 2012). This raises the legitimate, and functionally important, question of what structures were present in ancestral primates. Similarly, metric variables measured on a continuous scale, such as body mass, typically take on a range of values across a clade of interest, rendering an intuitive, informal estimate of ancestral values unreliable. In these cases, phylogenetically informed average values can be derived and serve in lieu of ancestral values, based on assumptions of evolutionary processes (e.g., Maddison, 1991; Schluter et al., 1997; Felsenstein, 2004; Smaers & Vinicius, 2009). As with models in general, their results can include non-trivial, and sometimes substantial, levels of uncertainty, and their reliability depends to a large extent on the accuracy of their assumptions. Nevertheless, a range of model algorithms exist, making it possible to infer ancestral values, albeit with varying degrees of uncertainty.

Once a probable ancestral morphology or a range of possible morphologies have been inferred, the second level of analysis is required to derive the range of possible functions of those morphologies. This is perhaps the least controversial element of a palaeo-ecomorphological framework. The functional interpretation of past morphologies can to a large extent follow the same protocols as the functional interpretation of the morphology of extant organisms, either by identifying and analyzing suitable extant model organisms with equivalent character expression or through the mathematical modeling of function from morphological form. It amounts to deriving reliably the biomechanical or physiological potential and limitations of a structure. For example, a parsimony reconstruction of the shape of cheirideal appendages in the LCA of extant primates inferred the presence of nails rather than functional claws on all digits (except the second pedal digit, which bore a toilet-claw; Soligo & Müller, 1999). Hypothesized functional benefits of nails in early primates have been hard to substantiate in the context of either pedal or manual grasping (e.g., Cartmill, 1985; Lemelin & Grafton, 1998; Soligo & Martin, 2006; Samaras & Youlatos, 2010). In contrast, it is clear that nails impose a biomechanical constraint compared to claws, as their reduced longitudinal curvature and lateral compression prevents them from penetrating and, hence,

adhering to soft, smooth surfaces; a critical limitation when moving in an arboreal environment, particularly for smaller species, which will more frequently encounter vertical substrates that are too large to embrace and can, hence, only be negotiated with the help of claws or alternative adhesion mechanisms.

At level three, biomechanical and physiological potential are translated to behavioural potential, including the range of possible interactions of an organism with its environment. For example, the presence of claws on all or most digits in a small mammal implies the ability for grappling locomotion, where an animal is able to cling to, and move along steep to vertical substrates, such as smooth tree trunks, by digging the pointed ends of their claws into those substrates. As there would appear to be no reason to think that those claws would prevent the animal also moving along the ground or on less steep to horizontal arboreal surfaces, the potential range of substrates available to such an organism can be interpreted as relatively broad, and to include all surfaces that are soft enough for the claws to penetrate; a factor that can be determined by in-vivo or in-vitro studies. A number of detailed examples of analysis of fossil remains pertinent to levels two and three of the present framework, i.e., to the reconstruction of behaviour in the fossil record, are presented in Plavcan et al. (2002).

In the step from levels 3 to 4, differences between neo- and palaeo-ecomorphological studies become pronounced. Strictly, ecomorphology requires observation of organisms in their natural environment (Bock, 1994). Continuing with the example of a claw-bearing mammal, there are many possible reasons why it might not climb trees despite its claws. There may be nothing of sufficient interest in the trees to justify the energy and time investment of climbing them, exposure on tree trunks may subject them to unsustainable predation risks, or there may simply be no trees where they live. Understanding the translation of an animal's fundamental niche to its realized niche invariably requires data on the environment in which an individual lived and on the behaviours that individual engaged in during its life time, as opposed to the behaviours it potentially could have engaged in based on its anatomy. Data on both can be retrieved from a palaeontological context, but the challenge is identical to that of establishing ancestral primate morphologies; i.e., the absence of directly ancestral fossils and the failure to identify to date the geological context in which those ancestral primates lived. While, technically, elements of the realised niche of a species can be mapped back across phylogenies in the same way as characters discussed in level 1 analyses, the fact that the realised niche depends on variable environmental conditions, and the fact that behaviour is phylogenetically more labile than morphology (Blomberg et al., 2003), renders the reliability of such analyses significantly less predictable.

Finally, at level 5, an organism's realized performance, as expressed through its realized niche, determines its fitness, which is impossible to measure at an individual level in deep time. Here, however, palaeo-ecomorphological studies can provide a different perspective to neo-ecomorphological studies. Correlations between morphological variation, performance and survival, reproductive success or other markers of fitness can be tested and quantified in extant species in order to measure selection on morphological traits (see, Arnold, 1983). However, realistic studies of the relationship between phenotype and fitness in primates can only be conducted on natural populations in the field, require paternity and long-term demographic data, and are correspondingly rare (for examples, see King et al., 2005; Lawler et al., 2005; Leigh et al., 2008; Breuer et al., 2012). In contrast, studies of the past can directly observe (in the case of fossil lineages) or infer (through phylogenetic mapping) the consequences of variable fitness in the form of morphological change through evolutionary time. For example, activity period, whether individuals within a species are primarily active

during the night or during the day, can be observed directly, but can also be highly variable within species, both in primates (Nash, 1986; Bearder et al., 2001, 2006; Fernández-Duque, 2003; Gursky, 2003; Curtis & Rasmussen, 2006; Fernández-Duque & Erkert, 2006; Parga, 2011; Donati et al., 2013) and more generally across mammals (Jacobs, 2013). In cases where individual behavior exhibits substantial plasticity, the fitness consequences of temporal niche adaptation may only become apparent over longer periods of time and across large numbers of individuals, rendering direct measurements of fitness consequences impractical. In contrast, the consequences of variable fitness are expected to shape the relevant anatomical structures and physiological pathways through natural selection. In the case of activity period, the anatomy of the eye, surrounding morphology, and neural correlates can provide direct evidence of variable fitness regimes experienced by evolving lineages (Kay & Kirk, 2000; Heesy & Ross, 2001; Hut et al., 2012). For example, extant tarsiers are primarily nocturnal, but morphological, neurological, and molecular data support the notion that the clade evolved from diurnal ancestors (Ross, 1996; Tan & Li, 1999; Melin et al., 2013; Joffe et al., 2014). Fossil evidence from the Middle Eocene suggests that the enlarged orbits characteristic of extant tarsiers, and associated with nocturnal activity period, had evolved prior to the inferred age of the LCA of crown group tarsiers (Rossie et al., 2006). The combined analysis of fossil evidence and inference of character evolution from extant comparative data therefore strongly suggest that at some point prior to about 45 mya, members of the tarsier stem lineage were subjected to a variable fitness regime that benefitted nocturnal over diurnal individuals.

Additional factors further modulate the interactions between elements of the generalised model presented in Figure 1. Specifically, the fundamental niche of a species (the sum of its performance potential) includes its potential for behavioural and physiological flexibility. Buffering responses to environmental stress can be behavioural, physiological and genetic, with flexibility at one level buffering against change at the next level. High behavioural and physiological flexibility may result in broader geographic distributions and reduced extinction risk as behaviour and physiology buffer against stress induced by environmental variability. In contrast, low behavioural and physiological flexibility results in narrower distributions and increased extinction risk as environmental change is more likely to result in genetic change or extinction (Wennersten & Forsman, 2012; Snell-Rood, 2013). As a consequence, the inference of realised niche from fundamental niche can be expected to be more challenging for species with higher levels of behavioural and physiological flexibiliy. In the absence of direct evidence of ancestral primate behaviour, the most likely source of information on behavioural flexibility will come from comparative analyses of brain anatomy and the phylogenetic mapping of neural characteristics (see section below on *Brain size and anatomy*).

Thus, a comprehensive approach to an ecological contextualisation of primate origins will require: a) knowledge of ancestral primate morphology and of its functional and biological significance, b) knowledge of the environment in which those species lived, and c) an understanding of the interaction between the two. Elements of the ecomorphological framework presented here have frequently been applied to the interpretation of primate origins. However, only a rigorous approach to each level of analysis can result in a probabilistic assessment of the likelihood of specific scenarios of primate origins. In the following we will look in more detail at some of the main themes that require clarification in order to achieve this goal.

3. Contextualising primate origins

3.1 Phylogenetic context

3.1.1 Cladistic relationships and definition of the Order Primates

Accurate hypotheses of the phylogenetic relationships of primates are critical for two reasons: first, in order to define unambiguously the evolutionary process described as 'primate origins' and, second, because an accurate phylogenetic framework is required for accurate inference of character evolution and reconstruction of ancestral character states. Over the last two decades, the increasing availability of molecular data has resulted in growing confidence in estimates of phylogenetic relationships amongst extant mammals. Primates are now generally considered to be part of Euarchonta, a taxon that also includes the extant Orders Scandentia (tree-shrews) and Dermoptera (colugos or flying lemurs). The sister clade to Euarchonta is Glires (Rodentia + Lagomorpha), and together Euarchonta and Glires form Euarchontoglires, one of 4 currently recognised superordinal groupings of extant mammals (e.g., Waddell et al., 1999; Madsen et al., 2001; Murphy et al., 2001; Springer et al., 2004). Relationships within Euarchonta have remained controversial, however, with molecular analyses most frequently implying a dermopteran sister group to primates (e.g., Waddell et al., 1999; Bininda-Edmonds et al., 2007; Janecka et al., 2007, Perelman et al., 2011; dos Reis et al., 2012), or a sister group consisting of Scandentia+Dermoptera (sometimes referred to as Sundatheria; e.g., Murphy et al., 2001; Springer et al., 2003; Nie et al., 2008), the same result as in a recent parsimony analysis of combined phenomic and molecular data (O'Leary et al., 2013). Meanwhile, Scandentia as the sister group to Primates is most commonly supported by morphological data (e.g., Wible & Covert, 1987; Kay et al., 1992; Godinot, 2007). Clearly, the phylogenetic relationships between Dermoptera, Primates and Scandentia cannot be considered resolved yet, with a minority of molecular analyses questioning the monophyly of Euarchonta altogether (Bailey et al. 1992; Porter et al., 1996; Nishihara et al., 2002; Schmitz et al., 2002; Hudelot et al., 2003; Zhou et al. 2015). Within primates, increasingly well-supported phylogenies are readily available for phylogenetic analysis, not least thanks to the on-going work of the 10K Trees Project (Arnold et al., 2010).

In addition to an accurate phylogenetic framework, a prerequisite to any discussion of primate origins is to define clearly both the Order Primates and what is meant by 'origins'. Definition of higher taxonomic groups can be arbitrary, although some criteria are commonly applied. Higher taxonomic units are expected to represent monophyletic groups and/or radiations of species identifiable through a common adaptive profile that distinguishes them from their nearest relatives (Mayr, 1950; Hennig, 1966; Wood & Collard, 1999; Groves, 2001). For the former, the taxon is defined on the basis of a cladistic divergence event. For the latter, it is defined on the basis of a (set of) derived characteristic(s) (apomorphies) considered significant in determining that taxon's overall adaptive profile. Taxa based on adaptive profiles make intuitive sense, especially when viewed through the lens of modern biological diversity, but in most cases their basis eventually disintegrates as new data exposes their defining adaptive profile as the consequence of a mosaic and sequential acquisition of characters over time rather than the wholesale acquisition of an adaptive complex (Cartmill, 2012). Cladistic definition of a taxon can be "node-based" or "stem-based"; i.e., it consists of all the lineages descended from a last common ancestor (LCA) and either excludes or includes some, or all, of the stem lineage leading to that LCA (Groves, 2001; Silcox, 2007; Figure 2). Adherence to the requirement that all taxa be monophyletic, however, means that not all lineages can be classified at all taxonomic levels (e.g., Cartmill, 2002); and if

taxonomic ranks are to reflect the sequence of phylogenetic divergence, one quickly runs out of ranks, in particular when fossil taxa are included (Groves, 2001). Some flexibility may therefore be required to create biologically accurate, yet practical and reasonably stable taxonomies. A crown-based definition of the order primates complies with the monophyly criterion, represents a distinct adaptive profile, and should therefore form the baseline for any further discussions.

A number of radiations documented in the early Cenozoic fossil record are of special interest in the context of a definition of the Order Primates: the Adapiformes, Omomyiformes, and 'plesiadapiforms'. Adapiforms and omomyiforms have the overall adaptive appearance of crown group primates and there is a broad consensus in the literature that they are crown group primates, although there is less agreement on how exactly they are related to the main crown group lineages (Rasmussen, 1994; Miller et al., 2005; Seiffert et al., 2009; Gingerich, 2012, 2015; Fleagle, 2013; Gilbert & Maiolino, 2015). Nevertheless, an alternative interpretation that remains to be fully explored is that adapiforms and omoyiforms are more closely related to each other than to any extant primate lineages and represent a separate radiation, distinct from the strepsirrhine-haplorhine radiation, whose ancestors dispersed into the Western Holarctic around the Palaeocene-Eocene boundary (Martin, 1993; Ross, 2003; Martin et al., 2007). However, the retention in the Order Primates of an adapiform-omomyiform clade that diverged prior to the divergence between crown strepsirrhines and haplorhines is unproblematic, since the Order would remain monophyletic and still represent a distinct adaptive profile. Similarly, in terms of characterising the ecomorphological context of primate origins, it is unlikely that including a basal adapiform-omomyiform clade–as opposed to nesting the two lineages within crown primates–would substantially alter our interpretation of either the adaptive profile or the environmental context of the origins of the Order.

More disruptive for attempts to define the Order Primates, and potentially more relevant to determining the ecomorphological characteristics of primate origins, are the questions of how to classify the plesiadapiforms–a diverse Holarctic radiation of mammals known from the Palaeocene and Eocene (Silcox et al., 2005; Fleagle, 2013)–and their phylogenetic relationships to each other and to crown primates. Plesiadapiforms were traditionally considered a monophyletic stem taxon to Primates, but have since been variably excluded in part or in their entirety from definitions of the Order and were considered by many, during the second half of the 20th century, to be at best of marginal interest to clarifying the adaptive context of primate origins (Martin, 1968, 1990; Cartmill, 1972, 1974a; Beard, 1990, 1993; Kay et al., 1990, 1992). Recently, plesiadapiforms have had a revival of sorts, largely due to the discovery and detailed description of new fossil material, including a number of exceptionally complete specimens (e.g., Bloch & Boyer, 2002; Bloch et al., 2007). While dramatically improving our knowledge of plesiadapiforms through a series of publications, these authors have also sought to re-affirm plesiadapiforms as members of the Order Primates. It is our opinion that this move is premature.

In two influential publications, Bloch and colleagues (Bloch & Boyer, 2002; Bloch et al., 2007) presented the results of cladistic analyses of Euarchonta plus Chiroptera. Analyses were based largely on extinct taxa, only including two extant species of Dermoptera and Scandentia each, and one of Chiroptera for the more comprehensive of the two analyses (Bloch et al., 2007). The 'single most parsimonious' trees reported differed in their details between the publications, but both implied that the taxa traditionally included in 'plesiadapiforms' are paraphyletic (Bloch & Boyer, 2002; Bloch et al., 2007). Specifically, Plesiadapoidea,

consisting of plesiadapids, carpolestids, and saxonellids, are suggested to be more closely related to crown group primates than the other main plesiadapiform clades (Paromomyidae, Microsyopidae, Micromomyidae). The inferred presence of a divergent hallux tipped by a nail in the carpolestid *Carpolestes simpsoni* has been highlighted as particularly relevant in this context (Bloch & Boyer, 2002; Bloch et al., 2007). The relevance of the presence of these traits in *Carpolestes* to interpretations of primate origins may, however, have been overstated, since they are found in several non-primate taxa, including marsupials and rodents (Kirk et al, 2003); and since, according to their own phylogenetic reconstruction, they are unlikely to be shared derived characters of *Carpolestes* and crown group primates (Bloch et al., 2007).

Nevertheless, the consistent association of plesiadapiforms with the crown primate stem lineage and the suggestion that they are paraphyletic has been used to argue against grouping them under a common taxonomic term and in favour of including them in the Order Primates (Silcox, 2007). However, individual nodes were generally poorly supported by those cladistics analyses, with the only node that both contributed to rendering plesiadapiforms paraphyletic and for which support values were reported occurring in a mere 30% of bootstrap replicates (Bloch et al., 2007). This level of 'support' is poor at best and it seems overly optimistic for it to be used to inform taxonomic practice, particularly in view of the problems associated with relying on morphology alone when inferring phylogenetic relationships (see below).

It should also be noted that other analyses continue to return contradicting results. For example, a recent phylogenetic analysis of dental characters in 59 primarily fossil taxa (the extinct omomyiforms, adapiforms, plesiadapiforms, and plagiomenids, plus two species each of extant Scandentia and Dermoptera) returned a single most parsimonious tree with plesiadapiforms most closely allied to Dermoptera and the two, together with Scandentia, forming the sister group of primates represented by omomyiforms and adapiforms (Ni et al., 2010). Finally, it remains the case that nearly all plesiadapiforms are too derived to be considered credible ancestors to crown group primates (Ross, 2003), and interpretation of the group as paraphyletic invokes substantial homoplasy, specifically regarding the characteristic plesiadapiform anterior dentition (Kirk et al., 2003).

More generally, cladistic analyses of large morphological character matrices are a popular means of generating hypotheses of phylogenetic relationships that include fossils. It is important to remember, however, that these analyses routinely contravene the assumptions on which they rely, notably that of character independence, and that there is ample evidence that, while careful selection of morphological characters can help retrieve accurate phylogenies, without a detailed understanding of clade- and character-specific patterns of evolution, their results are often demonstrably wrong (Collard & Wood, 2000; Lockwood et al., 2004; Bjarnason et al., 2011, 2015). This is also illustrated by recent analyses of plesiadapiform and euarchontan relationships where bats (Chiroptera), when included, routinely associate with Dermoptera (Bloch & Boyer, 2002; Silcox et al., 2005; Bloch et al., 2007), a relationship that has been comprehensively rejected by molecular data (e.g., Waddell et al., 1999; Madsen et al., 2001; Murphy et al., 2001; Springer et al., 2004; Bininda-Edmonds et al., 2007). Low clade support in cladistic analyses of fossil taxa has been blamed on the fragmentary nature of fossil specimens (Bloch et al., 2007). This of course is true, but it does not make those inferences more credible, it simply explains why they are not reliable. Clearly, plesiadapiforms may be stem primates, and if they are, they can help clarify the sequence of acquisition of crown primate traits; but at present this has not been established with any

degree of confidence, nor is there strong evidence for either a paraphyletic or monophyletic Plesiadapiformes.

In conclusion, including plesiadapiforms in the Order Primates fails to meet either of the two criteria for higher-level taxonomy listed above. A taxon including plesiadapiforms and crown-group primates clearly would not form a coherent adaptive unit; nor would it describe a clearly defined and well-supported monophyletic clade. It is unhelpful to promote taxonomic frameworks that imply phylogenetic relationships that are, in reality, poorly supported; both because it creates confusion for non-specialists and because poorly supported relationships are bound to be revised in the future and to be subject to different interpretations, resulting in a lack of nomenclatural stability. An appropriate solution to the question of plesiadapiform classification should acknowledge the uncertainties surrounding the cladistic relationships of plesiadapiforms, including the possibility of paraphyly, as well as their probable association with Euarchonta. If the traditional grouping of 'plesiadapiforms' is not monophyletic, the term looses its taxonomic utility, unless it is redefined to include only part of its original diversity. However, given the weak support for paraphyly, we prefer to retain the term as an informal grouping. An outline taxonomy of Euarchonta that reflects current knowledge and is flexible enough to assimilate future evidence without disrupting extant group taxonomy is presented in Figure 3 and adopted for the rest of this paper. Irrespective of taxonomic practice, further improvements of our knowledge of plesiadapiform biology, and of the phylogenetic relationships of plesiadapiforms with each other and with primates, are critical for clarifying the adaptive context and ecomorphological characteristics of primate origins.

Finally, in addition to clarifying phylogenetic relationships and taxonomic practice, it is important, when discussing the ecomorphological context of primate origins, to be clear about the concept of 'origins'. Viewed in the context of the definition of Primates advocated here, the 'origin' of the order can justifiably be considered to coincide with the divergence between the primate crown group and its sister group (i.e., with the root of the stem lineage), with the initial divergence within the crown group (i.e., at the tip of the stem lineage), or with any arbitrarily defined point along the stem lineage (Figure 2). These distinctions are important since, for example, discussions of the time of origins of primates can become unnecessarily confused if the cladistic context is not made explicit. We therefore advocate the use of explicit terminology when referring to elements of clade origins including: *stem-lineage origin*, corresponding to the LCA of the crown group and its sister group; *crown-group origin*, corresponding to the LCA of the crown-group, and *adaptive origins*, when referring to the acquisition of elements of the crown-group's adaptive profile along the stem lineage (Fig. 2).

3.1.2 Character evolution

As the recovery of specimens representing ancestral nodes is highly improbable, the characterisation of evolutionary events will nearly always require some form of inference and, hence, rely on some model assumptions. Specifically, once accurate estimates of phylogenetic relationships are available in the form of phylogenetic trees with reliable branch length estimates, those relationships can be used to infer patterns of character evolution by mapping characters over trees and inferring ancestral character states (e.g., Maddison, 1991; Schluter et al., 1997; Felsenstein, 2004; Smaers & Vinicius, 2009). It can be asked what characters may have changed and how from the root to the tip of the primate stem lineage. Surprisingly few attempts at such formal inference of character evolution pertinent to primate origins have

been made, perhaps because of the continued uncertainties surrounding both the chronological and cladistic context of primate origins and the frequently large confidence intervals associated with such inferences.

To date, the vast majority of comparative analyses that aim to infer ancestral characters are conducted with data from extant species only. This is most likely due to the significant uncertainty that integrating fossils introduces into comparative phylogenetic analyses. These include: a) the inference of biological characters from fragmentary fossils; b) the inference of phylogenetic relationships from fragmentary fossils; c) estimating the age of the fossil; and d) estimating the time of divergence of the fossil lineage from its sister lineage in order to derive branch lengths. Integrating fossils in phylogenetic analysis undoubtedly has the potential to critically improve the reliability of inferred evolutionary scenarios, but only if associated uncertainties are integrated in a probabilistic framework. Otherwise the integration of fossil data simply creates the illusion of an empirically supported scenario.

The characters derived from inferred ancestral anatomy that have traditionally been emphasised as significant to the adaptive profile of ancestral primates translate into animals with an increased field of stereoscopic vision (orbital convergence), an emphasis of visually as opposed to olfactorily guided behaviour (increased orbital size and reduced snout length), grasping feet (opposable hallux), and an emphasis on leaping during locomotion (elongated tarsal bones). Two additional characters have proved particularly difficult to interpret: the absence of functional claws and an increase in brain size. Both, though, may hold critical information for clarifying the context of primate origins, and below we review recent data that may prove pertinent to their interpretation

Nails, claws, and body mass

The functional range of many biomechanical and physiological determinants of species biology is tightly constrained by body mass (Peters, 1983; Schmidt-Nielsen, 1984), to the extent that reliably inferring ancestral primate body mass could significantly impact our understanding of primate origins (Soligo & Martin, 2006). The majority of scenarios of primate origins have assumed that ancestral primates were small, around 500g at most and usually much smaller, as a correlate of having adapted to foraging on small terminal branches (the "small branch niche"; Cartmill 1974; Dagosto 1988; Martin, 1990; Larson et al., 2000; Gebo, 2004). A link between grasping extremities and locomotion on small branches has been comprehensively demonstrated in primates and beyond (Rasmussen, 1990; Lemelin, 1999; Youlatos, 2008; Urbani & Youlatos, 2013); but drawing any kind of conclusion from this observation regarding the likely size of animals in which grasping extremities would have evolved fails to recognise that what represents a small branch is not an absolute, but depends on the size of the animal using it (Soligo & Martin, 2006). In contrast to the obvious benefits of grasping extremities, functional benefits of a reduction of functional claws to nails have proved substantially harder to identify, with behavioural data generally indicating that claws are no hindrance to locomotion and foraging on terminal branches (Cartmill, 1985; Rasmussen, 1990; Youlatos, 2008; Samaras & Youlatos, 2010; Youlatos & Urbani, 2013). To reconcile those two factors, it was proposed that a reduction in the ecological significance of claw-supported locomotion, rather than an adaptive benefit of nails, resulted in the loss of functional claws in the lineage leading to the LCA of crown group primates (Soligo & Müller, 1999; Soligo & Martin, 2006). Specifically, the reduction in the ecological significance of claws was attributed to an increase in body mass and associated increase in physiological cost of claw-supported locomotion with an initial efficiency threshold at around 800g. Evidence

presented in support of this suggestion included, amongst others, a phylogenetic reconstruction of body mass evolution in extant primates and converged on an estimated body mass in the LCA of crown primates of around 1000g (Soligo & Martin, 2006). In contrast, a recent reconstruction that included a number of fossil taxa returned a mean mass estimate of 56g (21-169g), similar to that of the smallest living primates, when assuming a directional model of evolution; directional models having received somewhat better log-likelihood support than non-directional Brownian Motion models (Steiper & Seiffert, 2012). Both those analyses, however, can be challenged. The first (Soligo & Martin, 2006) for not including fossil taxa and for assuming a simple Brownian Motion model of evolution; the second (Steiper & Seiffert, 2012) for including fossil taxa without taking account of the uncertainties inherent in interpretations of the fossil record; and both for not integrating their analyses into a broader mammalian phylogenetic context. Embedding the nodes of interest into a wider clade should improve the reliability of ancestral state estimates, particularly where evolutionary models allow for variable rates to have occurred over the phylogeny since, unlike homogenous rate models, these do not tend to average out bursts of change across several nodes; although this latter point remains to be tested systematically. At present, results of formal phylogenetic reconstructions of ancestral primate body mass must be considered moot; but the increasing availability of comparative data and diversity of models of evolution should help clarify this particular aspect of primate origins in the near future.

Clarifying the phylogenetic trajectory of body size in early primates may also contribute to explaining the increased orbital and optic convergence that has usually been interpreted in light of specific dietary (Cartmill, 1974; Sussman, 1991) or locomotor (Collins 1921; Crompton, 1995) adaptation. Recent studies have emphasised the advantage of binocular vision for filtering information through noisy environments (Changizi & Shimojo, 2008; Otto et al., 2010), implying that early primate environments and, specifically, the need to filter visual information through dense vegetation, may have contributed to shaping ancestral primate visual adaptations. Significantly, the advantage of optical convergence and binocular vision for filtering information through dense leaves is expected to increase with increasing interorbital distance and animal size (Changizi & Shimojo, 2008). The relevance of vegetation density for increasing optical convergence in ancestral primates was consequently questioned on the premise that those animals were "very small" (Heesy, 2009, p. 32); but as has been seen, the common assumption that ancestral primates were very small lacks support (Soligo & Martin, 2006, 2007) and hypotheses of form-function relationships in early primates should clearly not be rejected on that premise alone.

One consequence of a ca. 1000g LCA of crown primates is that extant primate evolution would have included the dwarfing of several major lineages whose members are primarily smaller than this, including callitrichines (marmosets and tamarins), tarsiers, cheirogaleids (mouse and dwarf lemurs), and lorisiforms. This, in fact, is not particularly controversial since dwarfing has been previously proposed for most of those lineages, including the callitrichines (Ford, 1980; Rosenberger, 1984, Sussman & Kinzey, 1984; Martin, 1992), tarsiers (Crompton, 1989; Martin, 1990), and cheirogaleids (Masters et al., 2007, 2014); and the observation that many of the species in these lineages have evolved alternative means of negotiating larger non-horizontal substrates–a key challenge for small arboreal animals–implies independent dwarfing events rather than the persistence of small ancestral size (Soligo & Martin, 2006). Interestingly, recent postcranial finds of *Teilhardina belgica*, a species estimated to have weighed a mere 30-60g, suggest that this early omomyid had fingers of a length similar to those of extant tarsiers (Gebo et al., 2012), raising the possibility

of tarsier-like adaptations in omomyiforms enabling them to cling to larger vertical supports without claws.

New experimental data on the comparative cost of horizontal versus vertical locomotion support the notion of a metabolic efficiency threshold linked to body mass. Specifically, data collected in an innovative study on a number of primate species of different body mass showed that the metabolic cost of vertical climbing was similar to the cost of horizontal walking in small species, but substantially higher in larger species (Hanna et al., 2008; Hanna & Schmitt, 2011). Currently, data for only 6 species are available and the increase of the relative cost of vertical compared to horizontal locomotion is relatively gradual, but the data are compatible with the suggestion of an efficiency threshold between approximately 500-800g (Figure 4), a range that future studies may be able to refine. One possible interpretation of those data is that small body mass would therefore have facilitated the invasion of the small branch niche, since the increase in vertical climbing required to navigate this environment would not have come at additional metabolic cost (Hanna & Schmitt, 2011). This, however, does not explain the associated loss of functional claws. An alternative interpretation that does, is that in a lineage evolving to larger body mass, the increasing cost of vertical climbing compared to horizontal walking would result in a decreased emphasis on claw-supported climbing and the eventual loss of functional claws, implying a LCA of primates that weighed at least between 500-800g in line with earlier suggestions (Soligo & Müller, 1999; Soligo & Martin, 2006). Body mass is known to correlate with the primary source of protein in primate diets and, significantly in the context of earlier hypotheses of primate adaptive origins, these weight estimates lie above 'Kay's threshold', which specifies the upper size limit for primarily insectivorous and the lower size limit for primarily folivorous primates at approximately 500g (Kay, 1984). Primate ancestors weighing more than 500g are, hence, unlikely to have been primarily insectivorous (Soligo & Martin, 2006; Martin et al., 2007).

Brain size and anatomy

Increasing both absolute and relative brain size is commonly interpreted as the result of selection for managing complex social and/or ecological contexts through an increased diversity and complexity of cognitive skills (e.g., Deaner et al, 2007; Dunbar & Shultz, 2007; Reader et al., 2011; Isler & van Schaik, 2014). Large brains, however, are expensive to build and maintain, and their existence has to be explained energetically and ecologically to determine both how the extra costs are met and how the benefits of increased cognitive capacity balance the potential fitness costs of devoting a large amount of metabolic energy to its running (e.g., Aiello & Wheeler, 1995; Martin, 1996; Isler & van Schaik, 2006; Isler et al., 2008; Weisbecker & Goswami, 2010; Barton & Capellini, 2011; van Woerden et al., 2012). This has been formalised explicitly as the expensive brain framework, which states that increasing relative brain size requires an increase in total energy metabolism and/or a reduction of energy allocation to other functions (Isler & van Schaik, 2009).

Significantly, primate brains may not only be derived in terms of absolute and relative size, but also at the cellular level. Compared to other mammals, primates follow a derived trend towards higher cortical neuron density relative to cortical surface area and mass as a result of derived cellular scaling patterns. Specifically, average neuronal cell mass remains relatively similar across cerebral cortices of different sizes in primates, unlike in other mammals where increases in cerebral cortex size are to various degrees achieved through increases in neuron

size as well as numbers of neurons (Herculano-Houzel, 2011a; Herculano-Houzel et al, 2014; Mota & Herculano-Houzel, 2015). More neurons imply the potential for more complex networks through increased numbers of synapses, dendritic trees and spines and, hence, increased plasticity throughout a lifetime in terms of neural connections and pathways. There is currently a significant lack of inter-specific comparative data for any of these anatomical variables, although smaller cell and larger brain size have been shown to correlate with increased brain complexity in frogs and salamanders (Roth et al., 1994). Genome size is one determinant of cell size, for the simple reason that more DNA results in larger chromosomes that require larger nuclei, and the two are correlated in the optic tectum of frogs and salamanders, implying that genome size may contribute to neuroanatomical variation (Roth et a., 1994). Generally, though, mechanisms and consequences of cell size variation are not fully understood (Ginzberg et al. 2015); but strong indications that cell size is adaptively regulated and the physiological consequences of variable cell size make this an intriguing and promising avenue for future comparative research.

Derived cellular scaling patterns in primates may come at a substantial physiological price. A constant metabolic cost, irrespective of size, has been inferred for neurons across mammals, implying compensatory factors to reduce metabolic costs in larger neurons (Herculano-Houzel, 2011b). In other words, metabolic cost increases linearly with neuron numbers. As a consequence, as they increase in size, primate brains become increasingly more expensive to run compared to equally sized brains in other mammals, peaking in the modern human brain being responsible for 20-25% of total body energetic cost (Mink et al., 1981; Herculano-Houzel, 2011b). These data therefore suggest that in primates more than in other mammals, increasing brain size must be paid for through compensatory mechanisms of redirecting metabolic cost and/or significant improvements in access to resources. The former may explain why the expensive tissue hypothesis (Aiello & Wheeler, 1995) has been difficult to substantiate in other mammals.

Behavioural plasticity is an important potential benefit of increased brain size and is usefully distinguished into developmental and activational behavioural plasticity (Snell-Rood, 2013). Selective pruning of initially overproduced synapses provides a flexible means of establishing adult neural connections and the basis for developmental, or experience-dependent, plasticity in the brain. Comparative data on timing and extent of pruning are limited, but some variation is implied between both cortical regions and mammalian species (Huttenlocher, 1979; Rakic et al, 1986, Bourgeois et al, 1994; Petanjek et al., 2011). This mechanism allows for a degree of neural and behavioural plasticity without having to meet the cost of peak synaptic connectivity through adulthood. In contrast, activational plasticity results from differential activation of the same underlying network and, consequently, relies on the existence of alternative neural pathways and the maintenance of more extensive neural networks (Snell-Rood, 2013). Larger brains, composed of absolutely and relatively larger numbers of neurons, carry the potential for more extensive variation in adult networks, and higher levels of both developmental and activational behavioural plasticity, than smaller brains with fewer neurons. The timing of peak connectivity, and the duration and extent of pruning are likely to have important consequences for determining the extent and relative contribution of both types of behavioural flexibility in adults, as well as for the ensuing metabolic cost. Establishing the genetic basis for variation in cellular scaling and a broader comparative understanding of variation in timing and extent of synaptic connectivity and pruning throughout individual lifetimes could substantially improve our understanding of the role and cost of behavioural plasticity in primate evolution.

Finally, recent data on brain modularity have confirmed that the traditional focus on absolute and relative brain size cannot fully explain neural and, presumably, cognitive phylogenetic variation in primates. First, relative brain size is a construct of two interconnected variables, body size and brain size, both of which are subject to natural selection; with comparative analyses suggesting that, across eutherian mammals, variation in body size is more influential than variation in brain size in determining variation in relative brain size and, hence, that body size may be under higher selective pressure than brain size overall (Smaers et al., 2012). Second, variation in internal organisation, quantified as variation in the relative size of individual brain regions, has been shown to contribute more than relative brain size to overall neural diversity, at least across anthropoid primate evolution (Smaers & Soligo, 2013). This suggests that brain reorganization could be under higher selective pressure than relative brain size, which is likely to result in a higher prevalence of reorganizational changes relative to changes in relative brain size. Recent analysis of the only early cercopithecoid endocast (that of 15 million year old *Victoriapithecus*) confirms the importance of changes in brain organization by suggesting that cerebral complexity preceded enlarged brain size in Old World monkeys (Gonzales et al., 2015).

Primate brain organization comprises several specializations in cortical association networks that are not shared with other mammals. These specializations include the evolution of a dorsolateral prefrontal cortex (Preuss, 1995, Preuss, 2007), lateral ventral and dorsal premotor cortex (Nudo & Masterton, 1990; Preuss et al., 1993), and a distinct pattern of connectivity among the dorsolateral prefrontal cortex, premotor cortex, parietal cortex, temporal cortex, dorsal pulvinar, and the lateral cerebellum (Preuss, 2007). The nature of brain reorganization within primates likely comprised a selective enlargement of cortical association areas relative to primary sensory areas (Van Essen & Dierker, 2007; Avants et al, 2006). Recent work investigating changes in the volume of cortical association areas (prefrontal cortex and parietal cortex) relative to primary sensory areas (striate cortex) indicate that monkeys, great apes and humans constitute three separate grades (Passingham & Smaers, 2014). Similarly, the lateral cerebellar hemisphere, associated with the automation of higher cognitive processes (Koziol et al., 2014), indicates a significant enlargement in hominoids (Smaers, 2014) that is associated with the enlargement of cortical association areas (Smaers et al., 2011, Smaers et al., 2013). Brain reorganization is thus likely to be a crucial feature of primate evolution. Studies focused on capturing the evolutionary pathways of brain organization are providing an increasingly detailed picture of primate brain evolution in deep time, although at present the vast majority of data are limited to anthropoid, and in particular hominoid, primates. Future work should aim to increase the taxonomic scope of comparative data on brain modularity, in particular with respect to strepsirrhine primates, Dermoptera and Scandentia.

There is currently no fossil evidence to suggest a sustained, or lineage-specific increase in relative brain size or neocortex ratio prior to the origin of crown group primates (Gingerich & Gunnell, 2005; Silcox et al., 2009, 2010; Orliac et al. 2014; Long et al., 2015), although the uncertainties associated with estimating body mass from fossil remains pose a significant challenge to accurately inferring relative brain size (Radinsky, 1977; Jerison, 1979). It should also be noted that early Tertiary adapiforms and omomyiforms, while showing expansion of parietal and temporal lobes, appear to have lacked the frontal lobe expansion characteristic of later and living primates (Radinsky, 1967; 1970; Jerison, 1973; Silcox et al, 2010). A domed neocortex and downward shift of the olfactory bulb axis have been proposed as shared derived characters of a plesiadapoid-primate clade, based on their absence in Microsyopidae and Paromomyidae (Orliac et al., 2014). However, since those characters are also present in

both potential primate sister groups (Dermoptera and Scandentia; Orliac et al., 2014), and given the lack of support (outlined earlier) for current hypotheses of plesiadapiform phylogenetic relationships, including for plesiadapiform paraphyly, their evolutionary polarity and, hence, significance remain unclear. Furthermore, comparative cranial and endocranial anatomy supports the notion that plesiadapiforms retained a primarily olfactory sensory ecology, distinct from the derived visually directed sensory ecology of crown group primates (Bloch & Silcox, 2006; Silcox et al., 2009; Orliac et al., 2014).

In summary, current evidence points to changes in brain anatomy being key characters associated with the origin of crown group primates. Those changes are likely to have come at non-trivial metabolic cost and have had to be compensated for by energy trade-offs and/or cognitive benefits translating into significantly improved access to resources or reduced mortality risk. The suggestion that primates as a whole have relatively low daily energy expenditures compared to other mammals (Simmen et al., 2015) specifically implies the existence of behavioural compensatory mechanisms.

The brain determines how an individual perceives its environment, and how it interacts with that environment through its behaviour. Due to its elevated metabolic requirements, the brain also critically constrains an individual's ecological profile. As such, variation in brain anatomy clearly has a central role in determining variation in the nature of interactions between individuals and their environments and, consequently, in characterising the ecomorphological profile of a species. While only minimal information on brain organisation can be extracted from fossil remains, increasingly detailed and sophisticated comparative data are available for extant species. Inferring patterns of evolution of early primate brain anatomy and organisation from those data could prove to be one of the most significant new sources of ecomorphological information relevant to determining the adaptive context of primate origins.

3. 2 Environmental context

3.2.1 Chronology

The biotic and abiotic environmental context under which a clade emerged can only be taken into account if clade origins and environmental conditions can be correlated chronologically. This remains a major challenge due to a long-standing discrepancy between molecular clock estimates of primate clade origins and the age of the oldest fossil evidence pertaining to that clade. The extent of that discrepancy varies according to clades within primates, but is particularly pronounced for the origin of crown group primates, the time of divergence between haplorhines and strepsirrhines, as well as for the origin of the primate stem lineage, the divergence between primates and their sister group, Dermoptera and/or Scandentia. Both are routinely dated to the Late Cretaceous by molecular data, whereas the fossil record points to a Cenozoic origin (e.g., Martin, 1990, 1993; Tavaré et al, 2002; Martin et al., 2007; Soligo et al., 2007; Wilkinson et al., 2011; Steiper & Seiffert 2012; Fleagle, 2013; Pozzi et al., 2014).

Inferring clade divergence dates from molecular data faces two primary challenges. First, it is now well established that substitution rates vary between lineages and clades and, second, in order to translate relative molecular distances into absolute chronological depth, molecular phylogenies have to be calibrated using evidence from the fossil record. Increasingly sophisticated statistical models are available to address in particular the former (Ho & Duchêne, 2014), but problems with fossil based calibration may be inherently more

challenging than those associated with substitution rate variation, because a fossil can at best provide a minimum age for a lineage, assuming it has been accurately classified and dated, whereas it can never provide direct evidence of the upper age bounds of the lineage it represents. As such, methodological choices with respect to the integration of upper calibration bounds can substantially influence estimates of divergence times, but it is relevant to note that even molecular analyses that date the LCA of most modern orders of placental mammals to the Cenozoic, still infer a Cretaceous date for the LCA of crown group primates (e.g., dos Reis et al., 2012), implying that primates are one of the oldest modern orders of mammals, or that there is something unusual about the primate data.

The fossil record

The fossil record will always be incomplete and include both chronological and geographical gaps. The challenge is to estimate the extent of that incompleteness and its influence on estimates of the time and location of clade diversifications. Probably the most dramatic example of an uncontroversial gap in the primate fossil record is the complete absence of a fossil record for the lemuriform branch of strepsirrhines, bar a number of recently extinct sub-fossil species whose oldest currently documented remains date back to less than 30ky (Crowley, 2010). Yet fossils belonging to the sister group of Lemuriformes, the Lorisiformes, have been recovered from North African deposits dating back to the late Middle or early Late Eocene, depending on stratigraphic interpretation (Seiffert et al., 2003, 2005; Underwood et al, 2013; King et al., 2014), implying a lemuriform ghost lineage of at least 35my.

To date, the fossil record of crown group primates reaches back to the Palaeocene-Eocene boundary, with the oldest potential representative the late Palaeocene *Altiatlasius koulchii* (Sigé et al., 1990). *Altiatlasius* has been variably assigned to omomyiforms, some undetermined primate clade, or plesiadapiforms (Sigé et al. 1990; Hooker et al., 1999; Miller et al., 2005), but has also been considered a stem anthropoid (Godinot, 1994; Bajpai et al., 2008), implying that the tarsier and anthropoid lineages had diverged by the Late Palaeocene. Largely uncontroversial crown group primates are known from the earliest Eocene (Hartwig, 2002; Fleagle, 2013).

Not unexpectedly, given their restricted extant distribution and taxonomic diversity, the fossil record of putative primate sister groups (Dermoptera and Scandentia) is substantially poorer than that of primates. Interpretation of the dermopteran fossil record is complicated by uncertainties surrounding the affinities of two Palaeogene groups of mammals, the Paromomyidae dating back to the Early and the Plagiomenidae dating back to the Middle Palaeocene. Both have at times been associated with Dermoptera as putative stem lineages, but both associations remain controversial (Silcox et al., 2005; Marivaux et al., 2006). Currently, the oldest record of uncontroversial colugos (cynocephalid Dermoptera) stems form the late Middle Eocene of Myanmar (Marivaux et al., 2006). The fossil record of tree shrews is similarly limited, with the only currently recorded pre-Miocene occurrence consisting of fragments of teeth from the Middle Eocene of China (Tong, 1988; Sargis, 2004; Silcox et al., 2005). A direct reading of the fossil record therefore places the origin of crown group primates at, or shortly before, the Palaeocene-Eocene boundary at 56 mya, and the origin of the primate stem lineage at the K/T-boundary, 66 mya, if plesiadapiforms are considered stem primates, or shortly before the origin of crown group primates if they are not.

Explanations for the discrepancy between molecular clock estimates and the fossil record include inaccuracies in estimates of molecular clock rates, a chronological gap in the fossil record of crown group primates of up to several tens of millions of years, or a combination of

the two. Recent developments have seen improvements in the way fossil and molecular data are integrated into the same analytical framework (e.g., Wilkinson et al., 2011; Ronquist et al, 2012). In addition, a recent study has demonstrated that molecular rates of evolution are inversely correlated with body size, and with relative and absolute brain size in primates (Steipert & Seiffert, 2012). Having inferred convergent directional increases in all three size variables across crown group primate lineages from a small ancestor, the study concluded that some of the discrepancy between fossil and molecular data could be explained by a molecular rate slow-down linked to increasing body and brain size (Steipert & Seiffert, 2012). Although these results are dependent on the assumption of a very small LCA of crown primates and of subsequent convergent directional increases in body, brain and relative brain size across primates, assumptions that will benefit from further scrutiny, the integration of biological variables that are known to correlate with molecular rates into analyses of divergence times is clearly a very promising avenue and will undoubtedly help to improve the reliability of estimated times of origins. In the context of this review, however, it is important to note that even with the assumption of a convergent molecular rate slowdown in early crown primate evolution, nearly all generated mean estimates of crown primate origins still pre-dated the K/T boundary (Steipert & Seiffert, 2012). Consequently, if primates did originate in the late Cretaceous, it is important for the likelihood of hypothetical scenarios of primate origins to be considered in the context of late Cretaceous rather than more recent environments.

3.2.2 Geography

If the chronological context of primate origins can be established, the next critical step is to determine the geographical area of origins. The geographical setting has direct implications for general aspects of the ecological conditions under which ancestral primate morphologies evolved including, for example, seasonality in light, temperature and precipitation regimes. If known, it can also be used to infer other aspects of local environments such as vegetation cover, either through interpretation of the palaeobotanical record or through palaeoclimatic reconstructions.

Today, non-human primates are naturally found in Africa, Asia, and South and Central America (Groves, 2005; Fleagle, 2013), but their fossil record also extends to Europe and North America (Szalay & Delson, 1979; Hartwig, 2002). The geographic origin of primates has been difficult to identify (Silcox, 2008). Specifically, attempts at inferring the most parsimonious place of origin are strongly influenced by interpretations of the phylogenetic roots and relationships of fossil taxa. Starting with the origins of the primate stem lineage, both extant Scandentia and Dermoptera have distributions restricted to southern, south-eastern and eastern Asia (Helgen, 2005; Stafford, 2005). The fossil record of Scandentia, while including a wider range than extant species, is also limited to Asia, dating back to the middle Eocene (Sargis, 2004; Ni & Qiu, 2012). The fossil record of undoubted crown-group Dermoptera (Cynocephalidae) is similarly restricted to South Asia, dating back to the Middle Eocene (Marivaux et al., 2006). Glires (rodents and lagomorphs), today, have a global distribution, but the early fossil record of that clade point to Asia as the area of early divergence (Asher et al., 2005; Meng & Wyss, 2005; Rose et al., 2008). In combination, therefore, extant and fossil taxa with firm associations to their extant crown groups tend to point to Asia as the most likely area for the early evolution of Euarchontoglires. This is supported by phylogenetic inferences of ancestral area, which place the last common ancestor of Euarchontoglires and of Euarchonta in Eurasia (Springer et al., 2011).

Consideration of the North American Plagiomenidae, considered by some to be stem-Dermoptera, and of plesiadapiforms complicates interpretations of geographic origins. As discussed above, phylogeny and affiliations of plesiadapiforms remain uncertain. Plesiadapiforms are currently known from North-America, Europe, Asia, and possibly Africa, but with a strong emphasis on North America and Western Europe (Silcox, 2008; Fleagle, 2013). The earliest most primitive putative plesiadapiform taxa (*Pandemonium*, *Purgatorius*, *Ursolestes*) are from the earliest Palaeocene of North America and Canada (Clemens, 2004; Fox et al., 2014, 2015), although another primitive looking plesiadapiform (*Asioplesiadapis*) is known from the early Eocene of China (Fu *et al*., 2002), implying the existence of less derived plesiadapiforms on that continent as well (Silcox, 2008). The results of optimisation of areas of origins over phylogenies can vary substantially depending on data set, phylogeny, and method of analysis (Heesy et al., 2006; Stevens & Heesy, 2006). Inclusion of Plagiomenidae as stem Dermoptera and of plesiadapiforms as paraphyletic stem primates, and coding of groups based on the location of their oldest known record, returns Asia as the most parsimonious area of origin of Euarchontoglires, with subsequent dispersal and initial divergence of plesiadapiforms and primates in North America (Bloch et al., 2007). A similar phylogeny (Plagiomenidae as stem Dermoptera and paraphyletic plesiadapiforms as stem primates), but with character coding based on the total geographic distribution of groups, returned equivocal places of origin for Euarchontoglires and crown group primates, and North America as the most parsimonious place of origin of a clade comprising plesiadapiforms and primates (Silcox, 2008). These results may, however, be influenced by biases in the fossil record and, specifically, by North America having the best-sampled Palaeocene fossil record of any continent (Bloch et al., 2007). In contrast, inclusion of plesiadapiforms as paraphyletic stem dermopterans returned Asia as the most parsimonious area of origin of both Euarchontoglires and crown group primates (Beard, 1998).

The oldest known fossils considered to be closely associated with crown group primates appear almost simultaneously across the Northern Hemisphere at the Palaeocene-Eocene boundary. Their appearance coincides broadly with the Palaeocene-Eocene Thermal Maximum (PETM), a phase of rapid and massive global warming recorded in both marine and terrestrial deposits (McInerney & Wing, 2011), and their rapid dispersal across the northern hemisphere must have involved high latitude routes made possible by the global greenhouse conditions and the existence of Arctic forests (Harrington et al., 2012). Critically, several major primate lineages may already have been present at that time including potential stem strepsirrhines (represented by adapiforms) in Asia, Western Europe and North America (Gebo, 2002; Rose et al., 2009; Fleagle, 2013), potential tarsiiforms (represented by omomyiforms) in Asia, Western Europe, and North America (Gunnell & Rose, 2002; Fleagle, 2013), as well as potential stem anthropoids in North Africa (Sigé et al., 1990; Godinot, 1994) and India (Bajpai et al., 2008; Kay, 2012). The early omomyiform genus *Teilhardina* has attracted particular interest in the context of early primate dispersal, because it is found across the Holarctic, in Asia, Western Europe, and North America, and detailed stratigraphic and phylogenetic analyses have made it possible to estimate the most likely dispersal sequence (Smith et al., 2006; Beard, 2008a). From those analyses, a general consensus has emerged that the genus originated in Asia, although the sequence of dispersals into Western Europe and North America remains disputed (Beard, 2008b; Gingerich et al., 2008; Rose et al., 2011).

Special consideration has been given to the hypothesis of an origin of Primates (and Euarchonta) on the Indian plate, following its breakaway from mainland Africa and Madagascar in the Cretaceous and prior to its collision with Asia, the so-called Indian Ark

hypothesis (Krause and Maas, 1990; Miller et al., 2005; Martin, 2006). The current location of India as part of Asia means that an Indian plate origin of Euarchonta is compatible with an inferred Eurasian origin based on extant taxa (Springer et al., 2011). A major uncertainty when evaluating the likelihood of an Indian Ark scenario and the potential role of India in early primate evolution and dispersal is the degree of connectivity between the Indian plate and other southern landmasses during the Late Cretaceous and Palaeocene (Ali & Aitchinson, 2008). The sudden appearance of primates across the Northern Hemisphere at the base of the Eocene implies the breakdown of dispersal barriers (Soligo, 2007), which is compatible with an Indian Ark scenario. The presence of *Altiatlasius* in the late Palaeocene of North Africa, however, hints at a more complex dispersal history that could be accounted for by intermittent biotic connectivity between the drifting Indian plate and Africa. There is in fact good evidence from both geology and biogeography for Late Cretaceous connections between the Indian and Afro-Arabian plates from around 70mya (Chatterjee et al., 2013). However, given the length of isolation of the Indian plate from its African origin, an Indian Ark scenario for the origin of Euarchonta may also imply an Indian plate origin of Glires and Euarchontoglires. In this case, the presence of the early Glires taxa *Mimotona* and *Heomys* in the Palaeocene of China (Meng & Wyss, 2005) would imply dispersal from the Indian plate prior to its main connection with Asia. Alternatively, the close association between the sister group of Euarchontoglires, Laurasiatheria, and the Northern Hemisphere, may imply a Laurasian origin with subsequent dispersal of euarchontan ancestors to an isolated Indian or Indo-Malagasy landmass in the Cretaceous. The need for cross-marine dispersal inherent in both those scenarios, however, diminishes their likelihood, and it also remains the case that, to date, no fossils have been described that directly support an Indian origin for euarchontans or primates.

In conclusion, phylogenetic reconstructions tend to favour an Asian origin of Euarchonta and primates, except for those relying heavily on the North American fossil record. The primate fossil record itself does not convincingly eliminate any of North America, Europe, Asia (including India) or Africa from consideration, but environmental considerations place the focus on Africa, India and Asia (see below). The geographically central position of India makes it an attractive proposition as a possible source of dispersal to Africa (*Altiatlasius*, stem strepsirrhines) and the Holarctic via Asia (other anthropoids, tarsiers, omomyiforms, adapiforms), but this will clearly remain speculative unless more relevant fossils are found. In addition to the broader question of the geographic origins of Euarchontoglires outlined above, another issue with an Indian Ark scenario are the plesiadapiforms. If, as many think, plesiadapiforms are stem primates, they would have to have dispersed from the Indian Plate by the beginning of the Palaeocene – some 10 million years before taxa associated with crown group primates. If, as some have suggested, plesiadapiforms are stem primates and paraphyletic, this would imply multiple dispersals during the course of the Palaeocene – which seems improbable. Thus, the likelihood of the Indian Ark scenario hinges not least on the accuracy of inferences of plesiadapiform phylogenetic relationships.

3.2.3 Environments

Today, primates in their vast majority occupy tropical forest habitats and feed on the products of angiosperms (Fleagle, 2013). Reconstruction and interpretation of ancestral primate characteristics are generally compatible with this basic ecological profile and an important consideration, therefore, is whether and where such habitats were available at the inferred time of origins and initial diversification of primates. The Late Cretaceous (Cenomanian to

Maastrichtian; ca. 100-66mya; Gradstein et al., 2012) began with an extreme global warmth period and tropical sea surface temperatures estimated to have exceeded 35˚C (~7–8 °C warmer than today), followed by a cooling trend that reached early Cenozoic levels by the early Campanian, around 80mya (Friedrich et al., 2012). Increasing global rainfall towards the Late Cretaceous and the breakup of earlier prevailing latitudinal desert belts by the Cenomanian may have provided the conditions for a rapid spread and diversification of angiosperms (Chaboureau et al., 2014).

There is a general consensus that angiosperms diversified and came to dominate terrestrial plant diversity during the Cretaceous (Lidgard & Crane, 1988; Crane & Lidgard, 1989; Wing & Boucher, 1998; Cleal et al., 2014), but there is less clarity on when and where typical angiosperm-dominated tropical rainforests first evolved. At present, the earliest strong evidence of tropical rainforest vegetation dates to the earliest Palaeocene of Colorado (Johnson & Ellis, 2002), but some evidence suggests an earlier origin of rainforests. Fossil evidence from southern North America implies a K/T transition from late Cretaceous open forests to early Cenozoic floras resembling modern tropical rainforests, although at least one late Cretaceous assemblage from Kansas has some tropical rainforest characteristics (Wolfe & Upchurch, 1987). Molecular divergence dates and phylogenetic inference of habitat preference of Malphigiales, a highly diverse order of tropical angiosperms and important component of tropical rainforest understory worldwide, imply the existence of closed-canopy, moist, mega-thermal forest habitats in the mid-Cretaceous (Davis et al., 2005). Similarly, molecular divergence dates of Ericales, another diverse and important part of the understory of tropical rainforests also suggest mid-Cretaceous origins (Wikström et al., 2001). Molecular divergence dates and phylogenetic reconstruction of area of origins of rainforest ferns imply a mid-Cretaceous origin of tropical rainforest biomes in Laurasia (Couvreur et al., 2011).

However, early angiosperms are generally reconstructed as having been small and these clades may initially have evolved in forests whose canopies were dominated by large gymnosperms (Davis et al., 2005). The presence of fleshy fruit implies an important role for animal dispersal early in angiosperm diversification (Eriksson et al., 2000a), with a trend towards increased fruit size estimated to have started around 85mya (Eriksson et al., 2000b). Analyses of fossil woods imply that forest canopies became dominated by angiosperms in the Late Cretaceous (Peralta-Medina & Falcon-Lang, 2012) and changes in leaf vein density confirm that by the latest Cretaceous, in the Maastrichtian, angiosperms had evolved to occupy the forest canopy (Feild et al., 2011; de Boer et al., 2012). Finally, a near absence of tree rings in fossil woods from low latitudes (10˚-30˚) imply a Late Cretaceous humid tropical belt that was wider than today (Peralta-Medina & Falcon-Lang, 2012). Within the implied Late Cretaceous tropical zone, fossil angiosperm wood records currently exist for S-America, Africa and the Northern Indian plate (Peralta-Medina & Falcon-Lang, 2012), indicating the possible presence of suitable habitats in those regions. With regard to the Indian Ark Hypothesis, the centre of the Indian plate is estimated to have reached 25˚S by the latest Cretaceous (~70mya) (Chatterjee et al., 2013), well within the inferred humid tropical belt (Peralta-Medina & Falcon-Lang, 2012) and with mean annual precipitation estimated at 20cm/month in the sub-continent's eastern part, higher than at any previous time during the Cretaceous (Chatterjee et al., 2013); and similar to Indonesia today. The rapid northern drift of the Indian plate, taking it from temperate through sub-tropical arid to tropical humid latitudes, combined with its associated anti-clockwise rotation created the basis for substantial plate-wide as well as local environmental variability (Chatterjee et al., 2013), which could in turn have created the conditions for the initial diversification of Euarchonta and any other radiations that may have originated on the sub-continent. By the Palaeocene, tropical

rainforests are inferred to have been present across wide areas of South America, Africa, the Indian plate, and South-East Asia; but also in southern North America and southern Europe (Morley, 2000, 2003).

If early fruit-bearing angiosperms formed an important part of the understory of gymnosperm-dominated forests by the mid-Cretaceous, they may have provided the habitat for early Euarchonta. As angiosperms took over all parts of the tropical rainforest biome, Euarchonta could have diverged into ground- and understory dwelling tree-shrews, and canopy dwelling Dermoptera and Primates, with those two groups evolving alternative strategies (gliding and leaping) for breaching the developing spatial gaps in the tropical angiosperm biome. Current combined evidence implies the likely presence of late Cretaceous tropical rainforest in Asia, S-America, Africa, and on the Indian plate. While failing to constrain the possible regions of origins of primates, it suggests that habitats capable of supporting typical crown group primate ecologies may have been relatively widely distributed by the late Cretaceous.

4. Conclusions

With this review, we have aimed to present a brief summary of the elements required for an ecomorphological contextualisation of primate origins. Clearly, we have only been able to address a limited number of relevant aspects of primate anatomy in any detail, and many others will need to be considered for a comprehensive appreciation of primate adaptive origins. Clarification of the evolutionary history of those characters can only come from comparative studies and, as for the example of brain anatomy discussed in detail above, those comparative studies will benefit from an increased resolution of anatomical variation across taxa, and from a formal comparison of different models of evolution. The absence of a pre-Eocene primate fossil record remains a major handicap, but the existing fossil record can, nevertheless, provide important complementary data, as long as the limitations inherent in interpretations of fossil specimens are accounted for, including confidence margins on dating, estimates of phylogenetic relationships, and the inference of biological characters from fossil remains.

An important consideration when studying the evolutionary relationships between form, function and environments in the past, is the potential for behaviour to mitigate the constraining effect of the environment on an organism's ability to realise its fundamental niche and to buffer anatomy against the effects of natural selection. As the main determinant of behavioural flexibility, the brain is central to those processes, and while absolute and relative brain size remain key features of primate evolution, it is now clear that their ecological and evolutionary significance can only be fully understood in light of concurrent organisational and cellular changes. Recent evidence suggests that primates may be derived in aspects of brain anatomy that could have had extensive consequences for both patterns of behavioural flexibility and energy metabolism; but more data are needed to determine the behavioural and evolutionary significance of those observations reliably.

Overall, contextual evidence is compatible with Euarchonta evolving in conjunction with tropical style rainforests on one of the landmasses surrounding the Late Cretaceous Tethys Ocean: the Afro-Arabian, Asian, or Indian plates. Clarification of the physical environment and ecology of ancestral primates is likely to benefit substantially from clarification of the phylogenetic trajectory of ancestral primate body mass. At present most estimates of ancestral

primate body mass in the literature are suggestive rather than the result of formal inference; and the results of the few formal analyses that have been published remain contradictory. A weight of 800g or more, however, would help explain a number of crown primate characteristics that have been difficult to understand when assuming a smaller ancestor, including the loss of functional claws. It would also place the LCA of crown primates above Kay's threshold, implying a limited importance of animal matter in their diet and confirming the possibility of a co-evolutionary relationship with evolving angiosperms as proposed by Sussman's angiosperm co-evolution hypothesis (Sussman and Raven, 1978; Sussman, 1991). Nevertheless, we consider that in light of the dietary flexibility of most modern primates and the likely presence of complex tropical forest environments early in primate evolution, dietary specialisation–whether for visual predation (Cartmill, 1972, 1974a, b) or for angiosperm products (Sussman and Raven, 1978; Sussman, 1991)–may not be the primary force to have driven early primate adaptations. Instead, evolutionary changes in angiosperm and forest physiognomy, and niche partitioning among diversifying Euarchonta could have driven ancestral primates to adapt to locomotion and foraging on the compliant branches of the evolving angiosperm canopies, where dexterity, improved hand-eye coordination, secure pedal grasping, and the ability to bridge gaps through leaping would have benefitted foraging irrespective of diet.

In conclusion, we consider an ecomorphological framework to be ideal for identifying current limitations and to guide future work towards a more integrated contextualisation of primate origins. Throughout this review, we have identified a number of specific avenues of research that we consider to be of particular importance. First, it could prove highly informative to extend the fossil record of crown primates to pre-Eocene deposits; and while this may never happen, corresponding efforts should nevertheless be encouraged. Second, the accuracy of phylogenetic mapping and comparative analyses is already benefiting from the development of more realistic and varied models of evolution, and will benefit further from the integration of fossil data, as long as these also integrate the error margins inherent in interpretations of the fossil record. Finally, we have highlighted the importance of a detailed understanding of the variation and behavioural significance of anatomical characters. Brain anatomy is one example where recent advances are providing us with substantial opportunities, but many other anatomical systems will also benefit from a more detailed characterisation of form, function, and form-function relationships.

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Figures

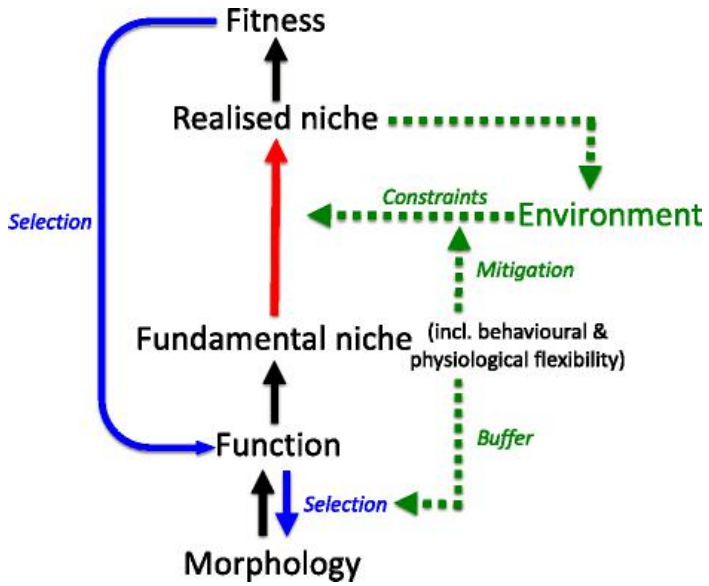

Figure 1. Ecomorphological framework (expanded from Reilly & Wainwright, 1994).

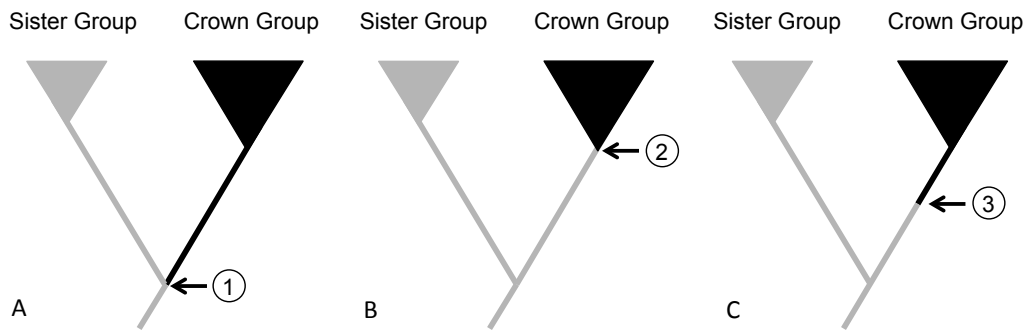

Figure 2. Taxonomic definitions of higher clades and terminology for discussion of clade origins. Clades and lineages to be included in taxon are in black; those to be excluded are in grey. **A**: Stem-based definition; **B**: Crown-based definition; **C**: Apomorphy-based definition (after Silcox, 2007). 1: *stem-lineage origin*, corresponding to the last common ancestor (LCA) of crown-group and sister-group; 2: *crown-group origin*, corresponding to the LCA of the crown-group; 3: *adaptive origins*, when referring to the acquisition of elements of the crown-group's adaptive profile along the stem lineage.

Grandorder Euarchonta
- Euarchonta *incertae sedis* "Plesiadapiformes"†
- Euarchonta *incertae sedis* Plagiomenidae†
  - **Order** Dermoptera
  - **Order** Scandentia
  - **Order** Primates
    - **Suborder** Adapiformes†
    - **Suborder** Omomyiformes†
    - **Suborder** Haplorhini
    - **Suborder** Strepsirrhini

Figure 3. Taxonomic framework for euarchontans. † signifies extinct taxa.

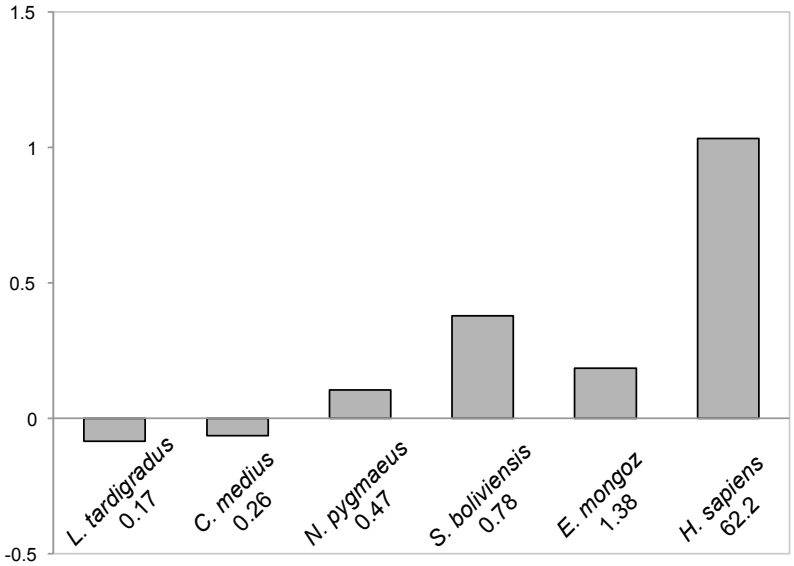

Figure 4. Approximate mean log-transformed ratio of vertical climbing versus horizontal walking costs ($J*kg^{-1}*m^{-1}$) in 6 species of primates ordered by increasing body mass (*Loris tardigradus*, *Cheirogaleus medius*, *Nycticebus pygmaeus*, *Saimiri boliviensis*, *Eulemur mongoz*, *Homo sapiens*; body mass in kg). Data are derived from Hanna et al. (2008) and Hanna & Schmidt (2011). Climbing costs are statistically indistinguishable from walking costs in *Loris*, *Cheirogaleus*, and *Nycticebus* (Hanna & Schmidt, 2011).