The evolution of eccrine sweat glands in human and nonhuman primates

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A B S T R A C T

Sweating is an unusual thermoregulatory strategy for most mammals, yet is critical for humans. This trait is commonly hypothesized to result from human ancestors moving from a forest to a warmer and drier open environment. As soft tissue traits do not typically fossilize, this idea has been difficult to test. Therefore, we used a comparative approach to examine 15 eccrine gland traits from 35 primate species. For each trait we measured phylogenetic signal, tested three evolutionary models to explain trait variation, and used phylogenetic models to examine how traits varied in response to climate variables. Phylogenetic signal in traits varied substantially, with the two traits exhibiting the highest values being gland distribution on the body and percent eccrine vs. apocrine glands on the body. Variation in most traits was best explained by an Ornstein-Uhlenbeck model suggesting the importance of natural selection. Two traits were strongly predicted by climate. First, species with high eccrine gland glycogen content were associated with habitats exhibiting warm temperatures and low rainfall. Second, species with increased capillarization were associated with high temperature. Glycogen is a primary energy substrate powering sweat production and sodium reabsorption in the eccrine gland, and increased capillarization permits greater oxygen, glucose and electrolyte delivery. Thus, our results are evidence of natural selection for increased sweating capacity in primate species with body surface eccrine glands living in hot and dry climates. We suggest that selection for increased glycogen content and capillarization may have been part of initial increases in hominin thermoregulatory sweating capacity.

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1. Introduction

Endothermy and high metabolic rate pose hyperthermia risks for mammals (Speakman and Król, 2010a, 2010b), which must minimize metabolic heat production and/or heat gain from the environment. Fur or hair to block solar radiation (Dunbar, 1979; Walsberg, 1988) and behavioral strategies such as sun avoidance (Roberts and Dunbar, 1991; Hill, 2006; Terrien et al., 2011) nocturnality (Haim et al., 2006) and postural changes (Shoshani et al., 1996) are variously employed to minimize environmental heat gain. Endogenous heat production may be minimized through reduction in basal metabolic rate (Cain et al., 2006), sometimes accomplished via tighter coupling of mitochondrial respiration (Nicholls and Locke, 1984), either as short-term acclimation or evolutionary adaptation (Taylor, 2014). Dissipating endogenous heat is most frequently accomplished via panting, increased skin blood flow, and in a small percentage of mammal species, sweating (Bullard et al., 1970; Lieberman, 2015).

Most mammals have two types of sweat glands: apocrine and eccrine. The former are found over the body surface, are associated with a hair follicle and sebaceous gland, and are not principally used in thermoregulation, except in some ungulates (Bullard et al., 1970; Whittow, 1971). In non-primate mammals and strepsirrhine primates, eccrine glands are confined to the friction pads of the hands and feet where they can be high in density and aid in frictional gripping (Adelman et al., 1975). New World monkeys have extended this ability to species with a prehensile tail, while in catarrhines (Old World monkeys and apes, including humans) eccrine glands are distributed over the entire body surface and are employed in thermoregulatory sweating. Eccrine thermoregulatory sweating has been observed in chimpanzees (Hiley, 1976), baboons (Newman et al., 1970; Hiley, 1976), macaques (Lemaire, 1967; Johnson and Elizondo, 1974, 1979), and patas monkeys (Mahoney,

1980; Sato et al., 1990), and eccrine sweating acclimation similar to that in humans has been demonstrated in the Japanese snow monkey (Okuda et al., 1981) and patas monkey (Sato et al., 1990). The ratio of eccrine to apocrine glands varies across catarrhines: chimpanzees and gorillas have an eccrine/apocrine ratio of around 2:1 (Folk and Semken, 1991); in macaques, mangabeys, baboons and gibbons the ratio is about 1:1 (Folk and Semken, 1991); and in humans, nearly all cutaneous glands on the general body surface are eccrine, numbering around 2 million (Kuno, 1956; Montagna, 1962). To our knowledge, there has been no quantitative study examining the potential adaptive function of eccrine glands across primate species.

The evolution of highly derived (Carrier et al., 1984; Jablonski, 2004; Jablonski and Chaplin, 2000; Lieberman, 2015) human eccrine sweating capacity has been linked with other important evolutionary adaptations. Because sweating is made more efficient with near-hairlessness and increased air flow, loss of body hair and adoption of bipedal posture may have been concurrent (Wheeler, 1992), allowing for increased thermal sweating; however, uncertainties regarding the timing of the origins of bipedalism and body hair reduction mean that increased sweating may not have evolved until the genus *Homo* (Lieberman, 2015). Increased sweating capacity likely accompanied expanded foraging in open savanna environments (Harris, 1980; Wheeler, 1984, 1985; Zihlman and Cohn, 1986; Chaplin et al., 1994; Jablonski and Chaplin, 2000). Lieberman (2015) argued that this may have allowed slow and defenseless hominins to forage in midday heat when the threat of predation is reduced. Finally, hominin eccrine sweating may have been driven in part by endurance running (Carrier et al., 1984; Bramble and Lieberman, 2004; Ruxton and Wilkinson, 2011; Lieberman, 2015) an idea supported by the observations that running elicits higher sweat rates than other physical activities in the heat (Torii, 1995) and complete heat acclimatization only occurs with habitual endurance training in hot conditions (Taylor, 2014). If the evolution of human eccrine sweating was indeed tied to climate and physical activity, we may expect to observe similar patterns in other primates. For example, climate variables such as temperature and humidity may correlate with eccrine gland density or other eccrine gland characteristics.

Despite the hypothesized adaptive significance of eccrine sweating in human evolution, we have little knowledge of eccrine gland biology and evolution across primate species. The current body of knowledge regarding comparative eccrine biology of primates is comprised almost entirely of a series of papers on primate skin histology spanning the late 1950s through the 1970s (e.g., Ellis and Montagna, 1962; Arao and Perkins, 1969; Ford and Perkins, 1970; and others - see Supplementary Online Material SOM 1). These papers include comparisons of gland distribution, structure and proportions, and stains estimating the concentrations of various compounds that were common to most histological studies of the mid-20th century. While the eccrine-specific roles of most of these compounds have not been studied, some play a role in metabolism or other processes likely related to sweat production. To our knowledge, Grant and Hoff (1975) are the only researchers to have compiled these and additional skin biology data for comparative analysis, concluding that sweat gland characteristics (apocrine and eccrine) correspond poorly with taxonomic groupings. They noted that the three New World monkeys with tail and/ or body surface eccrine glands - *Lagothrix lagothricha*, *Ateles geof- froyi*, and *Alouatta caraya* - grouped more closely with Old World monkeys and apes, and that this was explained by similar sweat gland and hair follicle characteristics. The causes of this convergent evolution remain unexplored.

Although sweating is a critical function in the human lineage and sweat gland biology varies across primate species, we have little idea about its potential adaptive function, especially in a comparative context. The purpose of this current study is to examine the evolution of eccrine gland traits across primates using a phylogenetic approach. Specifically, 1) How do eccrine gland traits correlate with phylogeny? 2) Which model of evolution best explains variation in these traits? and 3) Do environmental factors predict eccrine gland trait variation across species? We expect that primate species living in dry, warm environments are associated with biological features of eccrine glands that are related to an increased ability to sweat. As opposed to hard tissue traits, investigating eccrine gland evolution is not possible using the paleontological record because soft tissue and histological characteristics do not readily fossilize. Therefore, using a phylogenetic approach of living species can provide an important framework for understanding the evolutionary context of eccrine gland diversity through time. Ultimately, answering these questions related to eccrine gland evolution across primate species can inform our understanding of humans' unique sweating ability.

2. Methods

2.1. Data sources

Histological and histochemical observations on 35 species - 10 strepsirrhines, 1 tarsier, 13 platyrrhines, and 11 catarrhines - were gathered from 41 publications (SOM 2,3). Of the characteristics described in these sources, 15 were presented in most papers and appeared to have consistent measurement protocols, and were thus amenable for inclusion in the analyses. Suitable variables included two measures of eccrine gland distribution, three histological measures, and 11 histochemical measures. Table 1 summarizes the eccrine characteristics included in our analyses and our coding scheme. The 11 histochemical measures are staining techniques indicating the concentration of enzymes and other compounds. Several of these compounds are involved in metabolism and therefore presumably influence sweating capacity to some degree, but only glycogen has a demonstrated effect on sweating (Shelley and Mescon, 1952; Dobson, 1960; Matsumoto and Ohkura, 1960; Dobson and Abele, 1962; Smith and Dobson, 1966; Sato and Dobson, 1973; Sato, 1977). Degree of capillarization, visualized with an alkaline phosphatase staining technique (Lojda, 1979), may also be expected to have a strong effect on sweat gland function. Greater capillarization would increase blood flow and therefore water, oxygen and fuel substrate delivery and waste removal, thereby enhancing metabolic function. All traits reported in the source papers are semi-quantitative, except for ratio of eccrine to apocrine glands (henceforth referred to as "percent eccrine") and ratio of secretory tubule to excretory tubule length. Where possible we preserved the coding systems reported in the original sources. For example, succinic dehydrogenase activity was scored 0–3, from absent to strongly reactive. For other measures we translated semi-quantitative descriptions into ordered categories, e.g. "absent", "weak", "moderate", and "strong" became 0, 1, 2, and 3, respectively. While data generated from a single source would be ideal, these data were unavailable. That being said, there is an extensive body of research in biology and biological anthropology using comparative data sets where the original data were collected by numerous researchers, often using different methods of quantification (Plavcan et al., 1995; Organ et al., 2011; Wheeler et al., 2011; Pontzer et al., 2014; Kamilar et al., 2015). Our data set has the advantage of being quantified by researchers using the same methods. This is, in effect, a singular research group that quantified the data (Montagna and colleagues). This point is further emphasized by two previous studies that used these and related data for comparative analyses (Grant

Table 1
Eccrine gland traits used in the study.

	Trait	Description/relevance	Coding	n species
Histological characteristics	Eccrine gland distribution	Presence of eccrine glands in different body regions	0 = pes/manus only, 1 = also tail and/or face, 2 = also general body surface	35
	Percent of body surface glands that are eccrine (vs. apocrine)	Percentage of sweat glands on general body surface that are eccrine	Numeric, continuous	35
	Secretory coil:excretory duct, pes and manus	Ratio of secretory coil cross-sectional diameter to excretory duct cross-sectional diameter	1 = 1:1, 2 = 2:1, 3 = 3:1	25
	Presence of dark and clear cells in secretory coil	Distinct cell types discernible through histological staining	0 = two distinct types not present; 1 = two distinct types present	15[a]
Histochemical characteristics	Secretory coil [glycogen]	Primary substrate powering ATPase Na+/K+ pump, required for sweat production and sodium reabsorption	0 = none, 1 = low, 2 = moderate, 3 = high	15[a]
	Secretory coil [alkaline phosphatase]	Membrane-bound enzyme hypothesized to be involved in membrane transport	0 = none, 1 = low, 2 = moderate, 3 = high	14[a]
	Secretory coil [acid phosphatase]	Membrane-bound enzyme found in lysosomes; proxy for lysosome content of tissue	0 = none, 1 = low, 2 = moderate, 3 = high	12[a]
	Secretory coil [phosphorylase]	Glycogen phosphorylase; cleaves glycogen into glucose 1 phosphate, which can become glucose 6 phosphate, a substrate for glycolysis	0 = none, 1 = low, 2 = moderate, 3 = high	15[a]
	Secretory coil [succinic dehydrogenase]	Mitochondrial membrane protein; complex II of the electron transport chain; proxy for mitochondrial content of tissue	0 = none, 1 = low, 2 = moderate, 3 = high	15[a]
	Secretory coil [cytochrome oxidase]	Mitochondrial membrane protein; complex IV of the electron transport chain; proxy for mitochondrial content of tissue	0 = none, 1 = low, 2 = moderate, 3 = high	14[a]
	Secretory coil [monoamine oxidase]	Mitochondrial membrane protein; responsible for oxidative deamination of monoamine neurotransmitters	0 = none, 1 = low, 2 = moderate, 3 = high	12[a]
	Secretory coil [esterase]	Class of enzymes which oxidize lipids; proxy for lipid oxidation potential of tissue	0 = none, 1 = low, 2 = moderate, 3 = high	15[a]
	Nerves [butyrylcholinesterase]	Enzyme which breaks down the neurotransmitter butyrylcholine	0 = none, 1 = low, 2 = moderate, 3 = high	13[a]
	Nerves [acetylcholinesterase]	Enzyme which breaks down the neurotransmitter acetylcholine	0 = none, 1 = low, 2 = moderate, 3 = high	13[a]
	Capillarization, indicated by alkaline phosphatase staining	Number of capillaries supplying the secretory coil	0 = none, 1 = low, 2 = moderate, 3 = high	9[a]

[a] Phylogenetic least squares tests, correlating climate variables with eccrine characteristics, included only species which have eccrine glands on the general body surface and/or prehensile tail.

and Hoff, 1975; Plavcan et al., 1995). Further, continuously measured variables would provide improved statistical power, though we were unable to quantify the variables in this way. Our semi-quantitative approach using ordered traits are commonly used to build robust primate and hominin phylogenies (e.g., Shoshani et al., 1996; Gibbs et al., 2000), as well as research explaining variation in primate trait diversity (Plavcan et al., 1995).

We gathered climate data (see SOM 4) for each primate species from PanTHERIA (Jones et al., 2009), including mean temperature, mean annual rainfall, latitude, and actual evapotranspiration (AET). These variables quantify the average values across each species' geographic range. As lower skin temperature/air temperature gradients blunt radiant, convective and evaporative cooling, and high humidity reduces efficiency of sweat evaporation, we may expect selection to favor increased sweating capacity in hot and dry climates where sweating is both more necessary and more efficient. Latitude was included as a proxy for climate seasonality. AET is a measure of ambient temperature and water content (e.g., water in the atmosphere from rain, nearby water sources such as lakes and oceans, and plant evapotranspiration). Climate values associated with *Chlorocebus pygerythrus* were used for *Homo sapiens* as this eastern and southern African habitat approximates the climate of early modern humans (Blumenthal et al., 2017). Climate values associated with *Chlorocebus aethiops* were the mean values across all six *Chlorocebus* species listed in the climate database. We performed this procedure because we did not know the provenance of the *Chlorocebus* used to quantify skin traits.

Our expectation that living primate species traits will be associated with modern climatic variation is the standard approach for comparative biologists and biological anthropologists and has yielded important insights into trait evolution and diversity (Ellis and Montagna, 1962; Roberts and Dunbar, 1991; Kamilar et al., 2015). Of course, this does not exclude the possibility that past climate and other factors may have influenced living species (e.g., Rowan et al., 2016).

2.2. Data analysis

The relationship between trait values and phylogeny, i.e., phylogenetic signal, can be expressed as Blomberg's K, a measure of how observed trait variance differs from variance expected under Brownian motion evolution (see Kamilar and Cooper, 2013 for a thorough treatment of this measure and its applications). Values typically range from zero to one, though can be greater than one. Values approaching zero indicate low phylogenetic signal, i.e., there is a weak relationship between trait similarity and species relatedness. Values approaching one indicate high phylogenetic signal, where closely related species exhibit similar trait values and trait values become more dissimilar between species with increasing phylogenetic divergence. Values greater than one indicate greater trait similarity between related species than would be expected given Brownian evolution. This latter scenario can also be referred to as phylogenetic niche conservatism as defined by Losos (2008). High phylogenetic signal may be indicative of several evolutionary processes (Revell et al., 2008), including limited genetic variation, neutral evolution, stabilizing selection, low rates of evolution, or physiological constraints; low phylogenetic signal typically characterizes adaptation radiations or divergent selection (Kamilar and Cooper, 2013). Phylogenetic signal was estimated using the phylosig function for the phytools package (Revell, 2012).

In part to inform these potential interpretations we used the fitContinuous function for the Geiger package (Harmon et al., 2015) to test three evolutionary models for each trait. In a Brownian motion (BM) model, trait change is proportional to divergence time, and may indicate either genetic drift or multiple and/or changing selection pressures (Freckleton and Harvey, 2006). In the Ornstein-Uhlenbeck (OU) model, a trait evolves through directional selection towards an optimum (Lande, 1976; Felsenstein, 1988; Hansen, 1997); alternatively, variation in the trait may be biologically constrained (Harmon et al., 2010). In an Early Burst (EB) model, trait change is rapid early in time and then slows as time progresses (Harmon et al., 2010) and is characteristic of adaptive radiations (Cooper and Purvis, 2010). We used corrected Akaike Information Criterion (AICc) values to judge which of the three models best fit trait variation, with lower values indicating a better fit. Models within 2 AICc values of the best model are considered equivalently good (Burnham and Anderson, 2002).

Finally, we used the pgls function of the caper package (Orme, 2013) to perform phylogenetic generalized least squares models (PGLS) to examine how climate variables (absolute latitude, log-transformed temperature, rainfall and AET) predicted each eccrine gland trait. For gland distribution, percent eccrine, and pes/manus secretory/excretory ratio, we included any species for which data were available: $n = 35$, 35 and 25, respectively. For dark/clear and histochemical measures we included only species with eccrine glands on the body surface ($n = 9-15$) and included only log temperature and log precipitation as climate variables. We limited the data set for these PGLS analyses because the function of body surface eccrine glands is distinct from those on the pes and manus (thermoregulation vs. frictional gripping), and thus we would not expect pes/manus glands to adapt in response to climate characteristics. We only used two predictors in these latter analyses to reduce the possibility of overfitting the model considering the reduced sample size. All analyses were performed in R (R Development Core Team, 2017).

For all phylogenetic analyses, we used a consensus tree of our study species downloaded from the 10kTrees website with the associated taxonomy from GenBank (Arnold et al., 2010). There were several instances where we had to match an old taxonomic name in the original data papers on skin traits to the GenBank taxonomy-for example, *Lemur mongoz* to *Eulemur mongoz*.

We considered applying a Bonferroni correction (Rice, 1989) to our PGLS models, though decided not to implement this approach. Several authors have recommended not using Bonferroni corrections when statistical power is already low (Moran, 2003; Nakagawa, 2004). Our PGLS analyses have low statistical power due to: small to modest sample sizes (ranging from nine to 15 species for histochemical variables), the reliance on mean climate data across a species' geographic range (as opposed to climate from a specific location where an individual species is found), and dependent variables that are measured semi-quantitatively as opposed to continuously. We used G*Power (Faul et al., 2007, 2009) to calculate the required sample size for a linear model with two predictors and an accepted power of 0.8. We would need a sample size of 31 to detect a large effect size and a sample size of 68 to detect a moderate effect. Therefore, our statistical power is quite low for our PGLS analyses and implementing some form of Bonferroni correction would further decrease our ability to detect a significant effect when one is present.

3. Results

3.1. Phylogenetic signal

Eccrine gland distribution ($K = 2.43$, $p = 0.001$) and percent eccrine ($K = 1.87$, $p = 0.001$) displayed very strong phylogenetic signal, with values greater than one (Fig. 1). When viewed on the species phylogeny (Fig. 2), the traits varied across broad taxonomic groups (e.g., catarrhines vs. strepsirrhines), but did not vary within these clades. Presence of dark and clear cells showed moderately strong phylogenetic signal ($K = 0.70$, $p = 0.002$). Secretory-excretory diameter ratio was the only histological trait failing to show significant phylogenetic signal, though this was still moderate ($K = 0.42$, $p = 0.069$). We found a moderate and significant amount of phylogenetic signal in three histochemical traits: secretory coil glycogen concentration ($K = 0.58$, $p = 0.002$; Fig. 3), secretory coil succinic dehydrogenase concentration ($K = 0.46$, $p = 0.047$) and secretory coil monoamine oxidase concentration ($K = 0.66$, $p = 0.001$). All other histochemical characteristics showed weak phylogenetic signal. Plotting histochemical traits onto phylogenies generally revealed recent (family or genus level) similarity with broad differences evident between larger clades (SOM 5).

3.2. Testing evolutionary models to explain trait variation

The Ornstein-Uhlenbeck model best explains evolutionary patterns in five traits and is an equivalent-best for eight additional traits based on AICc values (Table 2). In other words, the OU model best explains the variation observed in 13 of the 15 eccrine gland traits we examined. This includes all of the histological and histochemical traits and none of the eccrine gland distribution variables. In contrast, a Brownian motion model is a best or equivalently-best fit for both eccrine gland distribution traits, and is an equivalent-best fit for five of the histological and histochemical variables based on AICc values. The Early Burst model is an equivalent-best fit for only one trait (eccrine gland distribution), being within 2 AICc values of the Brownian motion model.

3.3. Predicting eccrine gland traits from climate

Based on PGLS analyses and using the 15 species with eccrine glands on the body surface, secretory coil glycogen content was positively associated with $\log_{10}$ temperature ($p = 0.006$) and negatively associated with $\log_{10}$ precipitation ($p = 0.018$; see Table 3). In the nine species with eccrine glands on the body surface and for which information was available, capillarization (as indicated by alkaline phosphatase staining) was positively associated with $\log_{10}$ temperature ($p = 0.024$). $\log_{10}$ precipitation was negatively associated with capillarization at the $p = 0.068$ level. Additional PGLS models predicting eccrine gland traits were significant at the $p > 0.10$ level (see SOM 6). The strength of phylogenetic signal in the PGLS model residuals as measured by Pagel's lambda varied from zero to one.

4. Discussion

We found evidence supporting the idea that body surface eccrine glands evolved to increase sweating in hot and dry environments. In particular, we showed that the eccrine glands of primates in hotter, drier climates tend to have greater glycogen stores and are supplied by more capillaries than are the eccrine glands of primates in cooler and wetter climates (Figs. 3 and 4). These two characteristics have a profound effect on the eccrine glands' capacity to produce sweat. The other histochemical variables included in this study either are only indirectly related to sweat production or mediate small links in the metabolic chain, and increases in these compounds would therefore likely have small effects on sweating capacity. Interestingly, across-species variations in most of these histochemical characteristics are best explained by an OU evolutionary mode, but were not correlated with climate variables. Our relatively small
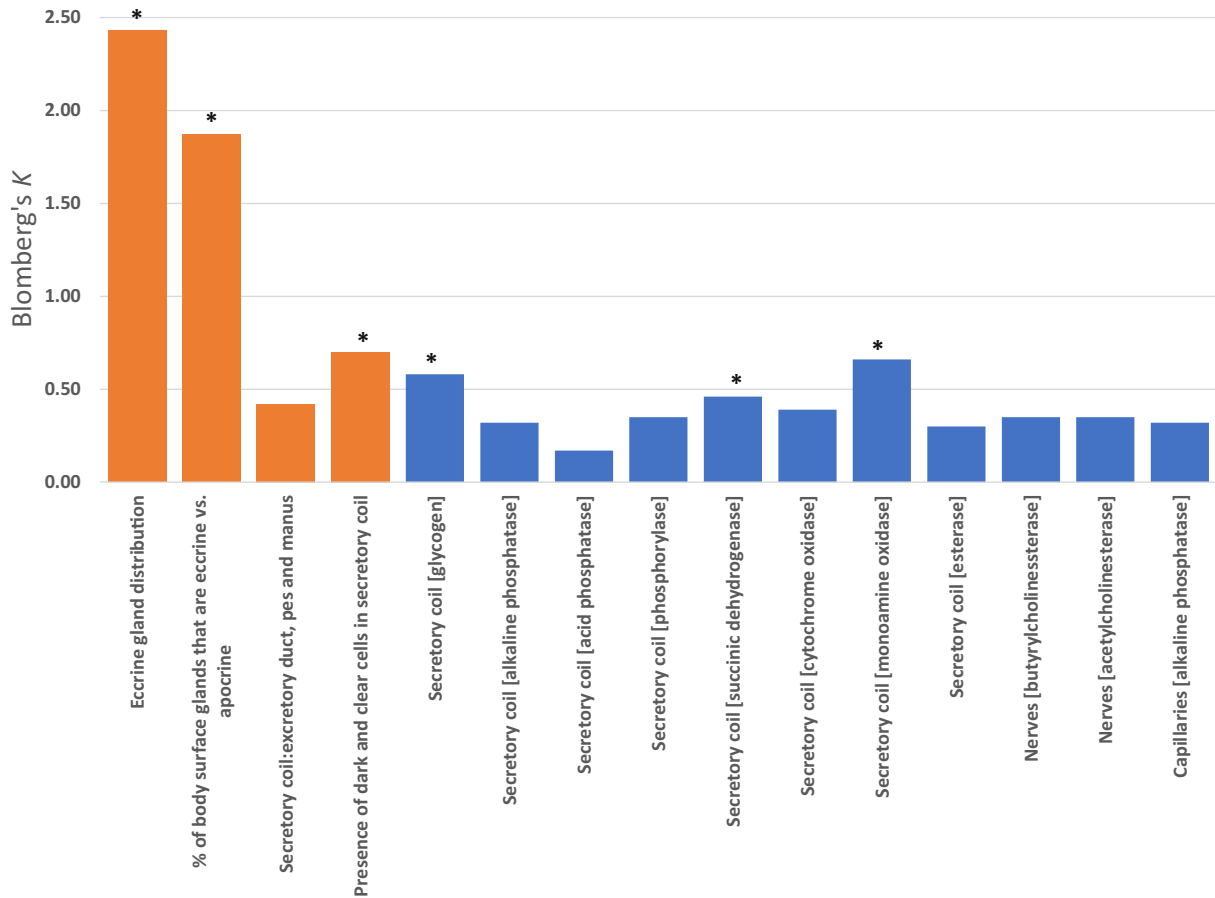
Figure 1. Phylogenetic signal in eccrine characteristics. Histological traits in orange; histochemical traits in blue. *K is significantly greater than 0. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

sample size combined with the weak biological relationship to sweating may produce low statistical power to detect a climate effect. Alternatively, non-climatic selective forces and/or non-selective phenomena that we did not examine may play a more important role in driving variation in these traits.

Glycogen content displayed moderate phylogenetic signal and fit best with BM and OU models. These analyses included all species in our data set and thus compared species with eccrine glands on the general body surface with those having eccrine glands on only the friction surfaces. A visual inspection of the trait on our phylogeny (Fig. 3) demonstrates that moderate or high glycogen stores are a common feature of body surface eccrine glands. High glycogen content is observed in many species with body surface eccrine glands, including the three New World monkeys with prehensile tails in our data set. The three macaque species and the gibbon were quantified as having moderate glycogen stores, reflecting the cooler climates of these species. Capillarization showed no significant phylogenetic signal and was best explained by an OU evolutionary model, implying that selection is important for explaining variation in this trait. Although data were available for only nine species with body surface eccrine glands we did detect a statistically significant effect of climate. Hotter climates were associated with increased capillarization while three of the four species with low capillarization live in cool climates.

Eccrine gland glycogen content and capillarization should exert a strong positive effect on sweating capacity. Increases in glycogen storage and capillarization are hallmarks of exercise-induced physiological adaptation in human skeletal muscle (Lamb et al., 1969; Brodal et al., 1977; Ingjer and Brodal, 1978; Saltin and Gollnick, 1983) where the primary challenges to prolonged energy production are substrate availability and oxygen delivery. We suggest that thermoregulatory sweating poses a similar challenge to eccrine glands. Glucose, both from intracellular glycogen and plasma glucose, is a primary substrate for eccrine gland metabolism (Smith and Dobson, 1966; Sato and Dobson, 1973; Sato, 1977), where ATP is needed to drive the Na+/K+ pumps essential to the eccrine glands' main functions of sweat secretion and sodium reabsorption (Sato and Dobson, 1973). Sweating results in glycogen depletion in human (Shelley and Mescon, 1952; Dobson, 1960; Dobson and Abele, 1962) and nonhuman primate glands (Matsumoto and Ohkura, 1960; Smith and Dobson, 1966), and eccrine glands become resistant to glycogen depletion as part of heat acclimation in these taxa (Dobson, 1960), suggesting that increases in glycogen content may be targets of selection in species employing thermoregulatory sweating. We hypothesize that increased capillarization is also selected for in these species. Increased blood supply equates to more water, oxygen and electrolyte delivery and waste removal, permitting increased sweat production. Indeed, even laden glands have insufficient glycogen to supply fuel for prolonged sweating (Sato, 1977); blood glucose is needed as well, and this is delivered via capillaries. As some portion of the metabolism in the gland is aerobic (Sato and Dobson, 1973), insufficiencies in oxygen availability will have a severe limiting effect on gland metabolism and therefore sweat production.

While our results suggest that differences in glycogen content and gland capillarization are targets of selection in primate species
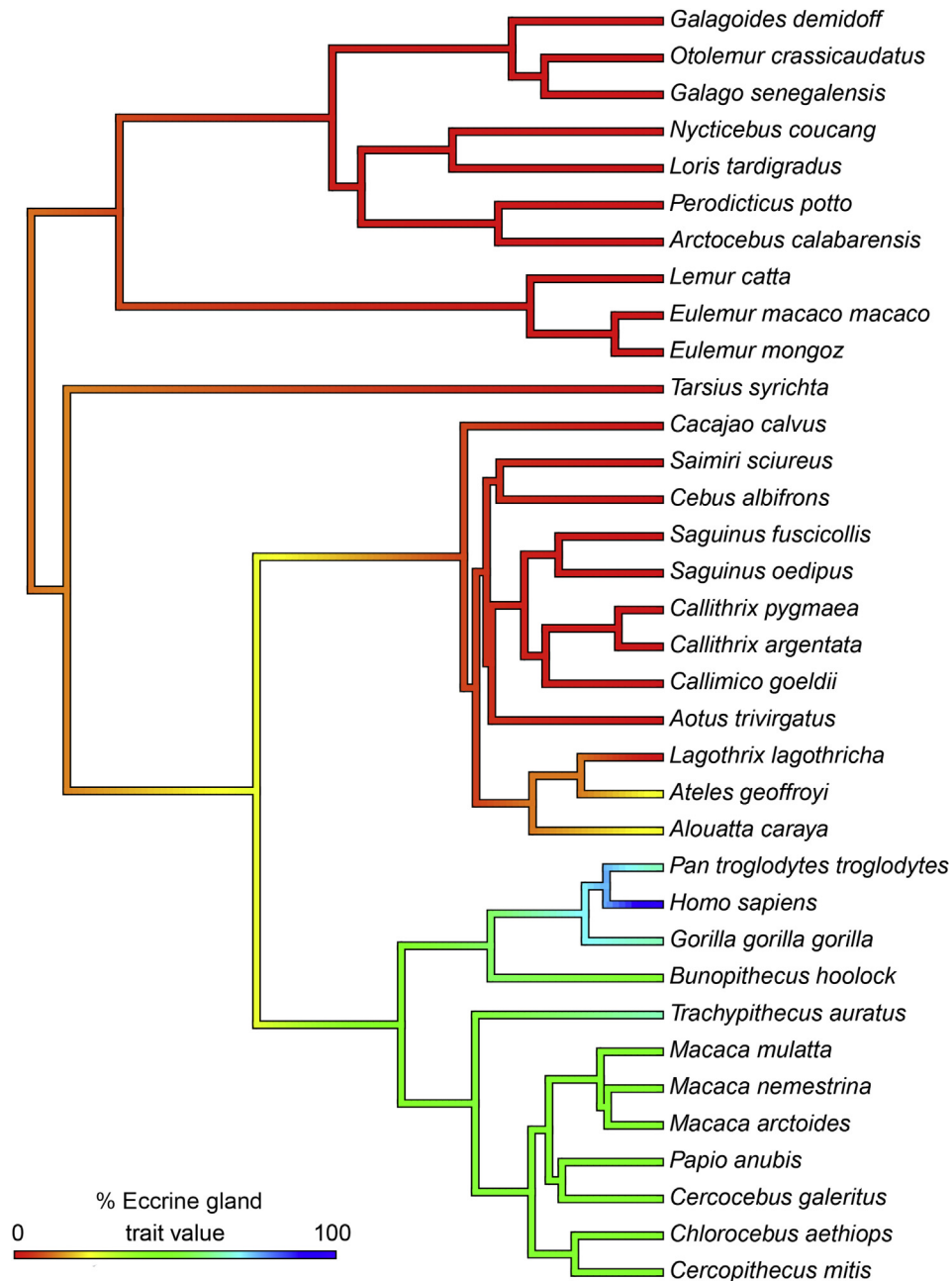
Figure 2. Percentage of body surface sweat glands that are eccrine (vs. apocrine), viewed on a phylogeny showing all species in our data set. Values range from 0% to 100%.

living in hot, dry climates, the role of phenotypic plasticity (physiological adaptation to heat stress) is unclear. Unfortunately, the provenance of the primate specimens included in our data set is unknown. Human heat acclimation begins to degenerate just one week after cessation of heat exposure (Taylor, 2006). Therefore, only animals examined quite soon after wild capture, or those kept outdoors in facilities approximating their native climate (i.e., hot), would reflect acclimation to their environment. Even if these animals were unacclimated, this does not preclude the possibility that selection may have favored a more sensitive acclimation response (as opposed to canalized thermoregulatory sweating capacity) in species living in hot and dry environments. Further study using acclimated and unacclimated individuals of the same species could reveal the range of phenotypic plasticity in glycogen content and

capillarization. This would also clarify the degree of plasticity in the other traits reported here, some of which are likely malleable with acclimation, as heat acclimation involves changes in sweat volume per gland, sweat constitution, and gland hypertrophy in primates (Sato et al., 1990) including humans (Taylor, 2006, 2014).

Eccrine gland distribution showed phylogenetic conservatism and fit best with Early Burst and Brownian motion evolutionary models. As a primitive mammalian trait, having eccrine glands confined to the pes and manus is almost certainly the ancestral state for all primates, one retained in all strepsirrhines. Each of the broad clades, strepsirrhines, platyrrhines and catarrhines, differs in gland distribution, and there is limited variation in this trait within these clades. This suggests that gland distribution evolved near the base of each clade but did not subsequently change in any
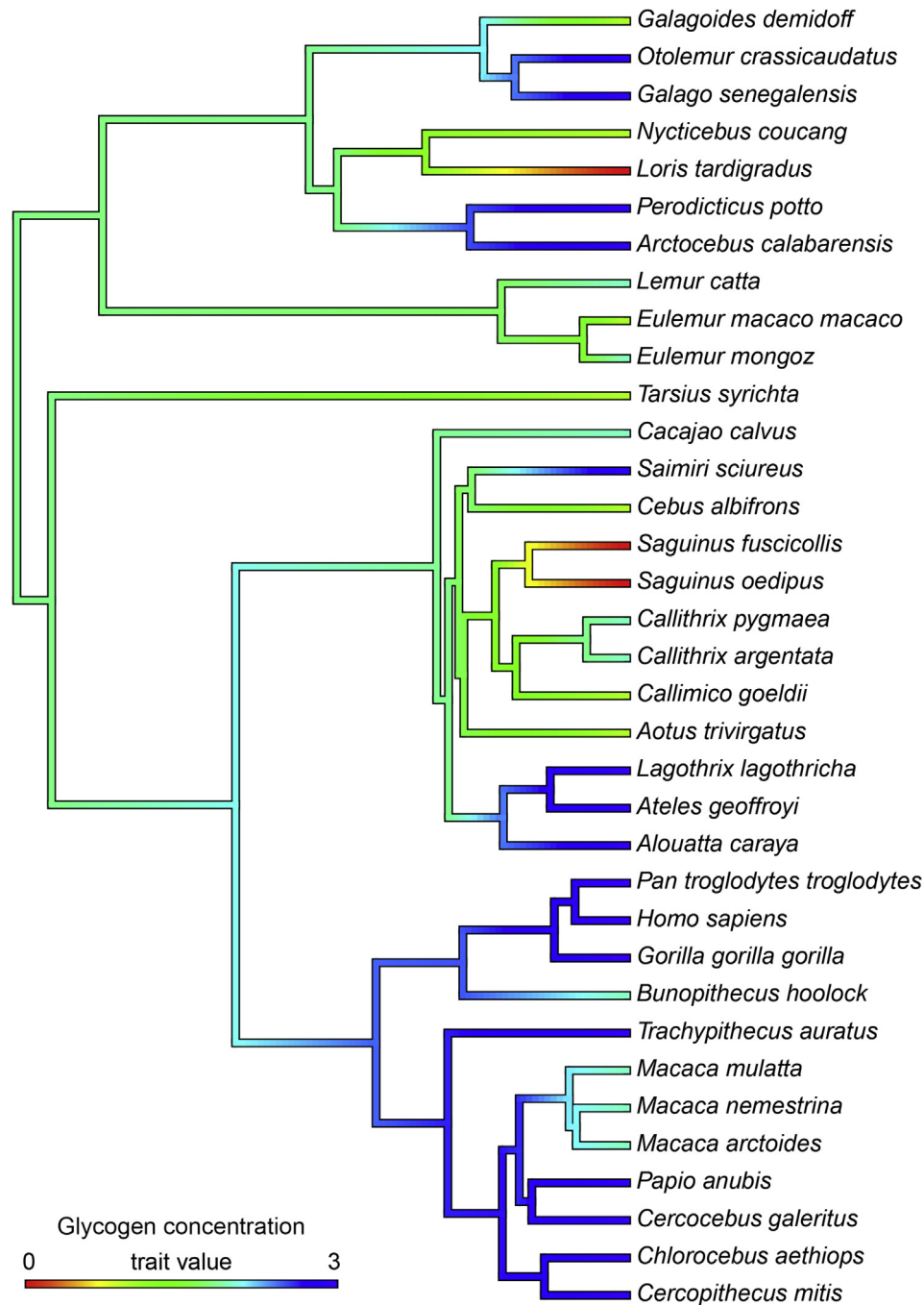
Figure 3. Glycogen content of the eccrine gland secretory coil. Values range from 0 (none) to 3 (high). Note that species shown above *Lagothrix* do not have body surface eccrine glands, so trait values are shown for pes/manus eccrine glands.

meaningful way. The catarrhine shift to more open, hot and semi-arid habitats likely explains proliferation of body surface eccrine glands, but additional factors may have increased thermoregulatory challenges. Catarrhines generally have the greatest body size and brain size/body size ratio of the three major primate clades (Fleagle, 2013), trends that are further exaggerated in hominoids and mirror observed patterns of eccrine gland distribution, including the ratio of eccrine to apocrine glands on the body surface. Larger bodies are less efficient at dissipating heat, a problem exacerbated during physical activity and one that may also impose a reproductive constraint (Speakman and Król, 2010a, 2010b),

increasing selective pressure for thermoregulatory solutions. Haplorrhine mass-adjusted basal metabolic rate is greater than that of strepsirrhines (Pontzer et al., 2014), and body surface hair density appears to scale inversely with body surface area (and therefore roughly with basal metabolic rate) in primates (Schwartz and Rosenblum, 1981), perhaps to aid in evaporative and convective cooling. Larger brains are metabolically expensive (Aiello and Wheeler, 1995) and therefore produce more heat, further compounding the thermoregulatory challenges associated with haplorrhine (and especially catarrhine and hominoid) evolution. Humans' highly derived sweat response, then, is commensurate

Table 2
Evolutionary models used to explain variation in eccrine gland traits.

Variable	Best model	AICc (BM)	AICc (OU)	AICc (EB)	log-lik	σ^2	α
Eccrine gland distribution	EB, BM	44.418	46.813	42.778	−18.001	0.079	−0.043
Percent of body surface glands that are eccrine (vs. apocrine)	BM	289.613	292.012	291.991	−142.619	8.022	NA
Secretory coil: excretory duct, pes and manus	OU	43.520	36.390	46.118	−14.624	0.021	0.051
Presence of dark and clear cells in secretory coil	OU, BM	32.111	32.092	34.511	−12.654	0.008	0.020
Secretory coil [glycogen]	BM, OU	94.577	95.911	96.977	−45.101	0.030	NA
Secretory coil [alkaline phosphatase]	OU	108.092	98.663	110.535	−45.903	0.338	0.163
Secretory coil [acid phosphatase]	OU	95.064	65.948	97.507	−29.545	2.017	2.718
Secretory coil [phosphorylase]	OU	94.077	88.333	96.477	−40.780	0.080	0.062
Secretory coil [succinic dehydrogenase]	BM, OU	45.541	45.722	47.941	−20.583	0.008	NA
Secretory coil [cytochrome oxidase]	BM, OU	19.291	17.681	21.735	−7.439	0.004	NA
Secretory coil [monoamine oxidase]	BM, OU	69.433	70.660	71.911	−32.494	0.020	NA
Secretory coil [esterase]	OU	103.409	90.047	105.810	−41.636	0.174	0.136
Nerves [butyrylcholinesterase]	OU	100.098	92.205	102.577	−42.641	0.204	0.099
Nerves [acetylcholinesterase]	OU	86.604	78.342	89.048	−35.742	0.073	0.062
Capillarization (as indicated by alkaline phosphatase staining)	OU	67.750	61.511	70.542	−27.006	0.212	0.120

Evolutionary parameters (log likelihood, σ^2, α) are shown only for the best-fitting models.
AICc: how well each evolutionary model fits a trait, with lowest values fitting best. Models within 2 values of each other were treated as equivalent.
σ^2: rate of evolution.
α: in an OU model, alpha is the "rubber band parameter" quantifying the strength of attraction towards an optimum trait value. In an EB model, alpha is the rate change parameter; positive values indicate accelerated rate through time and negative values indicate deceleration.

Table 3
Climate variables were $\log_{10}$ transformed before analysis.

Predicting Secretory coil [glycogen] levels					Predicting Capillaries [alkaline phosphatase] levels				
Parameter	Estimate	Std. error	t value	p	Parameter	Estimate	Std. error	t value	p
Intercept	−3.648	2.453	−1.487	0.163	Intercept	−20.978	9.580	−2.199	0.071
Mean precipitation	−0.901	0.330	−2.729	0.018	Mean precipitation	−2.968	1.337	−2.220	0.068
Mean temperature	3.559	1.066	3.338	0.006	Mean temperature	12.619	4.204	3.002	0.024
Full model r^2 = 0.556, p = 0.008, n = 15, Pagel's lambda = 1.00					Full model r^2 = 0.659, p = 0.040, n = 9, Pagel's lambda = 0.00				

with our big brains and bodies and hot/arid evolutionary environment.

The origins of and selective pressures driving the sweating capacity of *H. sapiens* are largely unresolved (Lieberman, 2015). Eccrine glands and body hair do not fossilize, so comparative study of extant species is an important tool with which to investigate these questions. Our results suggest several intriguing hypotheses. First, we provide further evidence that natural selection has favored increased thermoregulatory sweating in some nonhuman primates in hot and arid environments despite the presence of substantial body hair density and length. Therefore, we suggest that this supports the idea that natural selection may have favored initial increases in sweating before the significant body hair reduction that occurred in the hominin lineage. While the timing of body hair reduction is contentious, this would place the origins of expanded sweating capacity with *Australopithecus* or even earlier, as later genera were likely modern human-like in their body hair characteristics (Dávid-Barrett and Dunbar, 2016). Intriguingly, eccrine gland and hair follicle density are inversely associated during development (Kamberov et al., 2015; Lu et al., 2016), providing an elegant mechanism through which selection may simultaneously increase the former and reduce the later. However, given observations of thermoregulatory sweating in (hairy) nonhuman primates, increased sweating capacity in hominins may have occurred via increases in eccrine gland glycogen storage and capillarization, prior to or concurrent with decreasing hair follicle density. Second, increased locomotor activity may not be a prerequisite for thermoregulatory sweating adaptation. Climate appears to be the driving force in our primate sample. Of course, hominin expansion into more open and semi-arid habitats, regardless of timing, is thought to have been accompanied by greater ranging (Wheeler, 1984) and thus

locomotion and climate may have exerted concurrent selective pressures. Full-body eccrine gland distribution and slightly enhanced sweat capacity per gland, perhaps accomplished in part through increases in glycogen and capillarization and driven by climate factors, may have set the stage for enhanced locomotor activity in the genus *Homo*, including long distance walking and running (Lieberman, 2015).

5. Conclusions

Eccrine gland glycogen content and capillarization were highly correlated with climate variables and fit best with an OU evolutionary mode, suggesting selection for increased eccrine function in primates inhabiting hot and dry climates. Eccrine gland distribution and abundance appear to have evolved near the bases of three broad primate clades: strepsirrhines, catarrhines and platyrrhines. Body surface eccrine glands in three platyrrhine species suggests convergent evolution, mirroring a condition otherwise seen only in catarrhines. Observed plasticity in several eccrine traits suggests that selection may operate to heighten the acclimation responses of increased glycogen content and capillarization, while gland distribution measures have evolved as canalized adaptations. We suggest that increases in eccrine function are not dependent upon increased physical activity or reduced body hair. Therefore, enhanced sweating capacity may have evolved in *Australopithecus* or even earlier hominins, driven largely by climate. The additional increase in modern human sweating capacity evolved later, concurrent with long distance walking and running. Elucidating the roles of body hair and physical activity in the thermoregulatory sweating of nonhuman catarrhines could inform our understanding of the evolution of human sweating. To this end, further data are needed regarding nonhuman primate reliance on
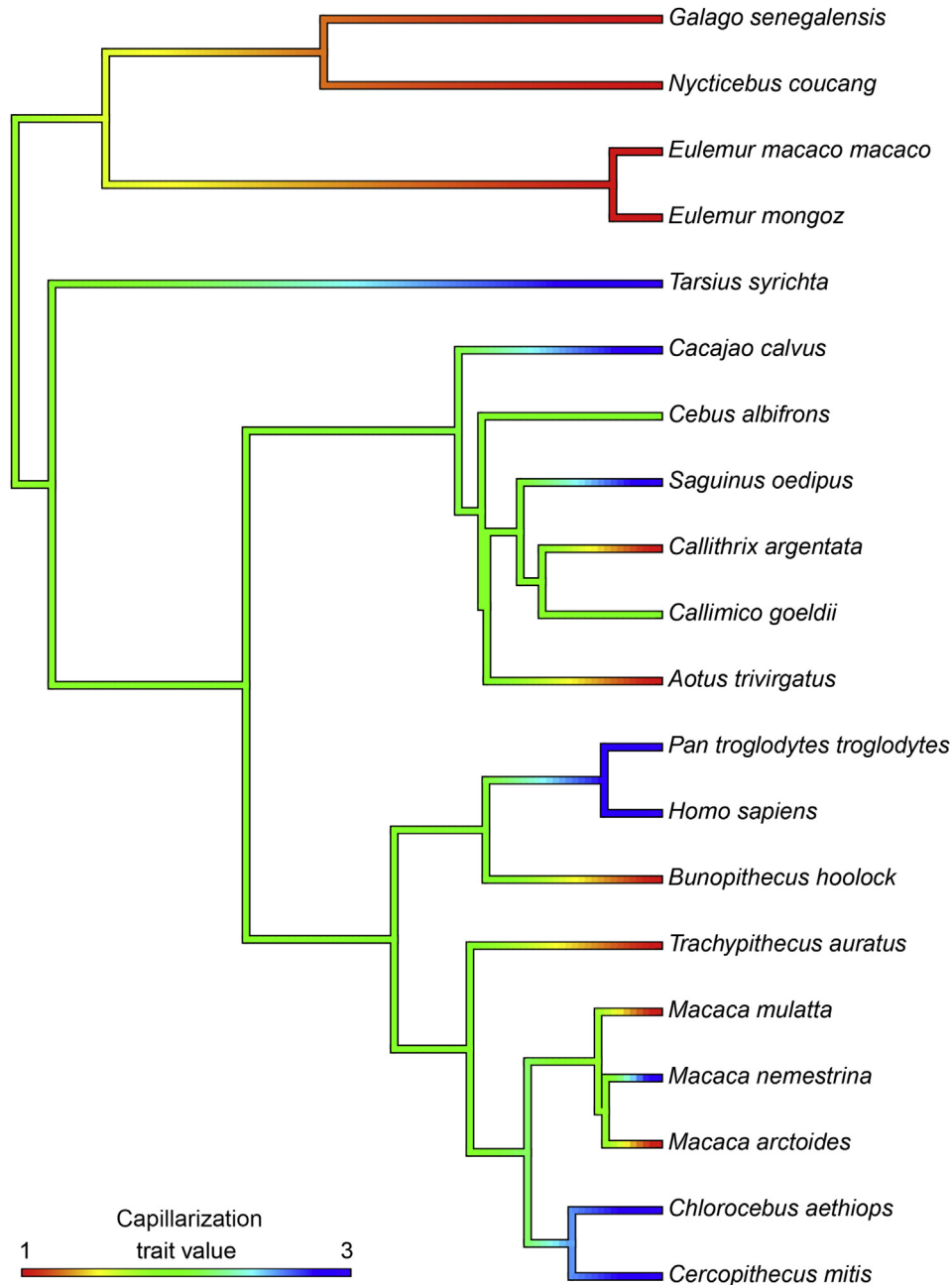
Figure 4. Capillarization of the eccrine gland secretory coil indicated by alkaline phosphatase staining. Values range from 1 (low) to 3 (high). Note that species shown above *Pan* do not have body surface eccrine glands, so trait values are shown for pes/manus eccrine glands.

thermoregulatory sweating, and possible correlations between metabolic heat production (i.e., physical activity level) and eccrine gland glycogen content and capillarization.

Supplementary Online Material

Supplementary online material related to this article can be found at https://doi.org/10.1016/j.jhevol.2017.12.003.

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