



# The evolution of eccrine sweat glands in human and nonhuman primates

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## ABSTRACT

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,

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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 geoffroyi*, 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

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