Original Article

The Role of Piloerection in Primate Thermoregulation

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Abstract

The insulating properties of the primate integument are influenced by many factors, including piloerection, which raises the hair and insulates the body by creating motionless air near the skin's surface. The involuntary muscles that control piloerection, the musculi arrectores pilorum (MAP), are mostly absent except on the tail in most strepsirhines, and are entirely absent in tarsiers and some lorisids. The absence of piloerection and the reduced effectiveness of pilary insulation in preventing heat loss affected the evolution of behavior and metabolic thermoregulation in these animals. In lemurs, this situation contributed to the use of positional and social behaviors such as sunning and huddling that help maintain thermal homeostasis during day-night and seasonal temperature cycles. It also contributed in many lemurs and lorises to the evolution of a wide variety of activity patterns and energy-conserving metabolic patterns such as cathemerality, daily torpor, and hibernation. The absence of functional MAP in strepsirhines and tarsiers implies the absence of effective piloerection in early primates, and the reacquisition of whole-body MAP in ancestral anthropoids prior to the separation of platyrrhine and catarrhine lineages.

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In primates, thermoregulation affects behavior and activity levels [Hill et al., 2004; Jablonski et al., 2009], and the requirements of temperature regulation determine dietary caloric requirements and, thus, niche and resource utilization. Primates, like other mammals, regulate body temperature through changes in physiology, mor-

phology, and behavior. Large mammals have smaller surface areas relative to their mass, greater energy reserves as fat, and can have longer coats of hair or fur for insulation. Smaller mammals have larger surface areas relative to their mass, can accommodate only minor energy reserves as stored fat, and cannot grow long coats for insulation. In order to maintain thermal homeostasis, small mammals maintain high rates of activity and food intake; when these conditions cannot be met, they must compensate by hibernation and torpor. Diurnal animals are subject to highly variable temperature regimes as they move in and out of shadows and as the sun traverses the sky. Crepuscular animals experience the highest rates of diurnal thermal variability because the coldest time of the day usually is around dawn and the hottest is in the late afternoon. Nocturnal animals experience a more constant temperature regime. Cathemerality, as an activity pattern, enables the most favorable thermal conditions to be utilized regardless of the solar time or season [Tattersall, 1987; Curtis, 2006].

Animals living in forests, and particularly in low latitude, everwet tropical forests, live under almost constant temperatures [Janzen, 1967]. The climates of the late Cretaceous and early Paleocene, under which many lineages of modern mammals differentiated, were warmer, humid, and less seasonal than those of later epochs [Steuber et al., 2005]. Equable and taxonomically diverse everwet tropical forests of modern aspect existed from equatorial through significantly higher latitudes from the early Paleocene through the early Eocene [Johnson and Ellis, 2002; Archibald et al., 2010], and it is under these conditions that the earliest primates evolved.

Mammals have evolved a wide variety of adaptations to different regimes of environmental temperature, and the nature of these has depended partly on the degree and temporal scale of temperature variation. For small or medium-sized mammals, adaptations to marked diurnal and seasonal temperature fluctuations have involved the evolution of compensatory changes in modes and types of fat storage and pilary insulation, and changes in metabolic rate, and/or activity pattern. Daily or prolonged torpor and hibernation have evolved in many lineages as means of controlling energy expenditure in the face of seasonal changes in climate and food availability. Specific behaviors such as social huddling, nest building, and shelter seeking also appear to have evolved partly or mostly for thermoregulatory purposes.

For most mammals, piloerection is a common method of modifying heat exchange. It is caused by the contraction of the musculi arrectores pilorum or MAP, which are bodies of smooth muscle that extend from the fibrils of the dermis into connective tissue investment of the hair follicle. Innervation to the MAP is supplied by the sympathetic nervous system, and contraction of the muscles is involuntary. Contraction of the MAP elevates the hair and increases the loft of the coat, thereby enhancing its insulative value. In many species, including familiar ones such as dogs, cats, and chimpanzees, raising the hair serves a secondary function of social warning of impending aggression. In mammals such as horses that are well-endowed with MAP, contraction of the muscles raises the effective hair coat depth by 16–32% or by a depth of 0.4–1.4 cm in newborn foals [Cymbaluk, 1994]. The insulating properties of the coat are not determined as much by the intrinsic thermal capacity of the hair itself, but by the layers of motionless air that can be trapped in successive laminations around the body to provide ideal outer insulation [Herrington, 1951]. Piloerection compounds the insulating properties of the hair coat by changing its thickness. It minimizes heat loss primarily through radiation and secondarily through convection, and makes it possible for animals to compensate for moderate cooling of the environ-

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ment without increasing their metabolism. The ability of piloerection to buffer the need for chemical thermoregulation varies according to body size because heat loss and environmental heat gain are proportional to the square of the surface dimensions of the animal under consideration [Herrington, 1951]. Metabolic heat production scales at a similar rate to the volume at the cubed power of the surface dimensions, while surface heat exchange scales according to the Stefan-Boltzmann law, and is proportional to the fourth power of its absolute temperature [Bligh and Johnson, 1973]. Because of the 'surface law', piloerection is especially effective in large mammals (>5 kg), but is less so in small mammals because of their higher surface-to-volume ratio and restriction of the length of the coat covering possible.

The MAP are present and piloerection is possible in most mammals, and these states represent the primitive conditions for Mammalia, based on their presence in reptiles, birds, and in most members of most mammalian orders (table 1; online suppl. table 1; see www.karger.com/doi/10.1159/000355007 for all online suppl. material). In reptiles and birds, homologs of the MAP cause erection of scales and feathers. The absence of MAP in mammals is a derived condition that is most often associated with aquatic, fossorial, or aerial lifestyles. The MAP were lost independently in hairless aquatic mammals (Cetacea), and in three lineages of fur-bearing aquatic species where a protective boundary layer of air cannot be maintained next to the body. These lineages are the eared seals, Otariidae, and otters, Lutrinae, within Carnivora, and the beavers, Castoridae, within Rodentia. The MAP were also lost independently in two lineages of burrowing mammals, namely naked mole rats (Batherygidae) within Rodentia and shrews (Soricidae) within Insectivora (Eulipotyphla). The MAP were also mostly or completely lost in the aerial mammals belonging to Chiroptera and Dermoptera. Very strong MAP confer enhanced pilary insulation in most large terrestrial mammals, but robust MAP also serve as shock absorbers to prevent abrasion in some groups (see online suppl. table 1).

The presence of MAP and piloerection is the ancestral condition for Euarchontaglires [comprising Glires (Rodentia and Lagomorpha) and Euarchonta (Dermoptera, Scandentia, and Primates)]. The ancestral condition for Euarchonta is more difficult to interpret because of the divergent character states present in the crown taxa. In the Tupaiidae, MAP are variably present and weak according to one group of researchers [Montagna et al., 1962], but are absent entirely according to another authority [Sokolov, 1983]. In Dermoptera, they are absent [Sokolov, 1983], but – as noted above – this is almost certainly a derived condition associated with an aerial habitus, as it is in Chiroptera. Among Primates, weak MAP are present on the body and stronger MAP on the tail in most groups except for tarsiers and some lorises, where they are entirely lacking. The presence of weak or vestigial MAP on the body and more prominent and functional MAP on the tail is interpreted as the primitive condition for primates. Therefore, based on the distribution of character states among living Euarchonta, the presence of weak MAP on the body was probably the ancestral state for the group.

Thermoregulation in primates has not been studied extensively because of the difficulty of quantifying parameters of the thermal environment in which primates live [Hill et al., 2004] and because field workers have focused primarily on documenting details of locomotor and social behavior, conservation, and ecology. Our interest in primate thermoregulation arose because of our curiosity about the roles played by the integument and behavior in thermoregulation in ring-tailed lemurs, *Lemur catta*.

Table 1. Distribution of the presence and absence of MAP in extant reptiles, birds, and mammals

Class	Order	Family or higher taxon	MAP coding	MAP
Reptilia	Squamata	All families	1	present
Aves	All orders	All families	1	present
Mammalia	Monotremata	Tachyglossidae	0	absent
	Diprotodontia	Phalangeridae	1	present
	Pholidota	Manidae	0	absent
	Lagomorpha	Leporidae	1	present
		Ochotonidae	1	present
	Rodentia	Bathyergidae	0	absent
		Castoridae	0	absent
		Castoridae	1	present
		Caviidae	1	present
		Chinchillidae	1	present
		Cricetidae	1	present
		Ctenodactylidae	1	present
		Dipodidae	1	present
		Geomyidae	1	present
		Gliridae	1	present
		Heteromyidae	1	present
		Hystricidae	1	present
		Muridae	1	present
		Myocastoridae	1	present
		Sciuridae	1	present
		Spalacidae	1	present
	Macroscelidea	Macroscelidae	0	absent
	Primates	Strepsirhini – Lorisoidea	1	present
		Strepsirhini – Lemuroidea	0	absent
		Tarsiidae	0	absent
		Anthropoidea	1	present
	Scandentia	Tupaiidae	1	present
	Chiroptera	Chiroptera (all families)	0	absent
	Dermoptera	Cynocephalidae	0	absent
	Insectivora	Tenrecidae	1	present
		Erinaceidae	1	present
		Solenodontidae	1	present
		Soricidae	0	absent
		Talpidae	0	absent
		Talpidae	1	present
	Carnivora	Canidae	1	present
		Felidae	1	present
Mammalia	Carnivora	Mustelidae	1	present
		Mustelidae – Lutrinae	0	absent
		Otariidae	0	absent

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Table 1 (continued)

Class	Order	Family or higher taxon	MAP coding	MAP
Mammalia	Carnivora	Ursidae	1	present
		Viverridae	1	present
	Artiodactyla	Bovidae	1	present
		Camelidae	1	present
		Cervidae	1	present
		Giraffidae	1	present
		Moschidae	1	present
		Suidae	1	present
		Tayassuidae	1	present
	Cetacea	Cetacea (all families)	0	absent
	Perissodactyla	Equidae	1	present
		Rhinocerotidae	1	present
	Hyracoidea	Procaviidae	1	present
	Sirenia	Sirenia (all families)	0	absent
	Proboscidea	Elephantidae	0	absent

The presence of MAP and piloerection is denoted by 1 (=present) or 0 (=absent) or by 'present' or 'absent' in the far-right column, respectively. Some mammalian families are listed as having MAP present and absent because some species within them have MAP while others lack them. See online supplementary table 1 for detailed information, including references on non-primates. See text for discussions of the coding of character states in primates and of homoplasy in the presence and absence of MAP and piloerection.

Our preliminary study revealed an unexpected connection between sunning behaviors in *L. catta* and anatomical features of the species' skin and hair [Jablonski et al., 2009]. This study represents an extension of that work and is focused specifically on the role played by the MAP in primate thermoregulation.

Our studies of the skin of *L. catta* [Jablonski et al., 2009] revealed that the torso of the animal is covered with fine, mostly white hair on the venter and coarser, gray and grayish-brown agouti hair on the dorsum. The hairs on the torso are grouped in compound follicles consisting of 6–24 follicles, as noted by Montagna and Yun [1962c] (fig. 1a, b), which exit through a single opening on the surface. The MAP are present on the torso (contra Montagna), but they are sparse and very small relative to the size of the compound follicles with which they are associated. By contrast, the compound follicles of the tail are associated with larger and more abundant MAP (fig. 1c, d). The skin of the ventral torso is black, owing to the high density of melanocytes in the stratum basale of the epidermis and the numerous eumelanin-containing corneocytes in the stratum corneum (fig. 2a). The skin of the dorsal torso is considerably less pigmented (fig. 2b). This is the obverse of the solar exposure pattern.

The sparse distribution and small size of the MAP on the torso of *L. catta*, especially relative to the large size of the compound hair follicles, suggested that the MAP
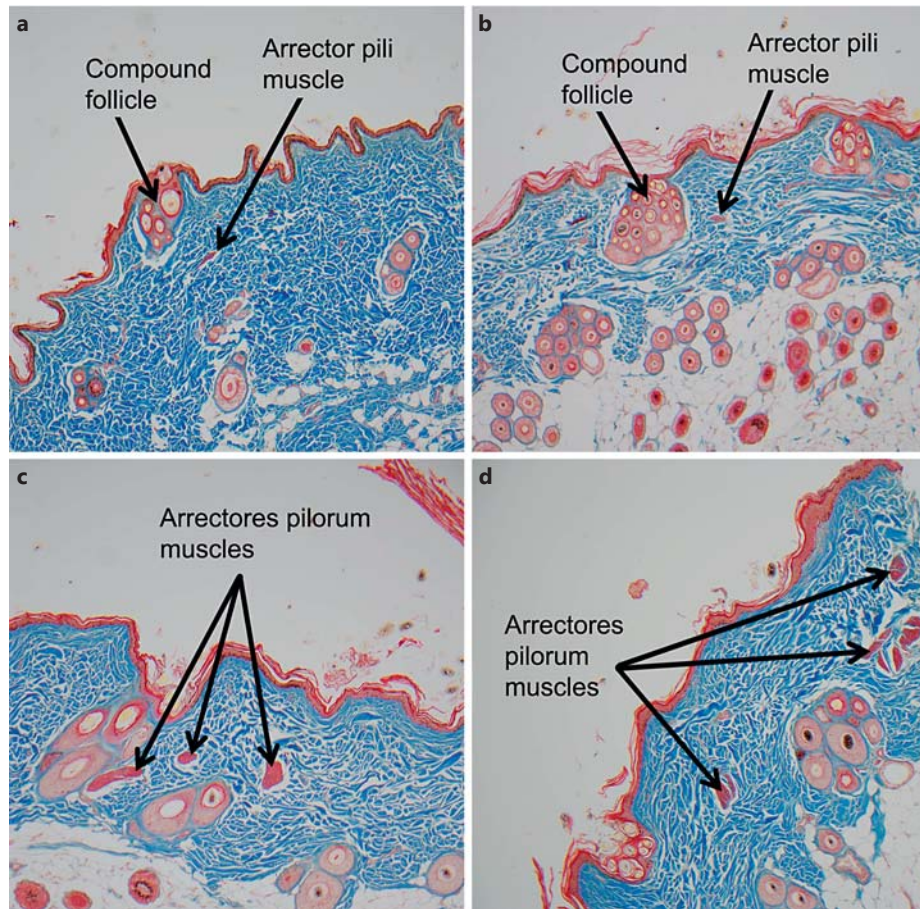
Fig. 1. Photomicrographs of the skin on different regions of the body of *L. catta.* ×10. Compound hair follicles are evident in all regions, but the MAP are sparse, especially on the torso. **a** Ventral torso. **b** Dorsal torso. **c** Ventral tail. **d** Dorsal tail.

are probably non-functional. Therefore, they would have a minimal effect on the thermal characteristics of the hair coat. We inferred, further, that the sunning behavior characteristic of the species was related to the functional absence of MAP and the importance of basking in the sun combined with passive stretching of the skin of the ventral torso in order to maximize warming and reduce the need for chemical thermoregulation on cool mornings [Jablonski et al., 2009]. This finding led us to explore the available information on the presence and nature of the MAP in primates and other mammals, and to speculate on the relationships between the MAP, thermoregulation through metabolism, and behavior in primates.
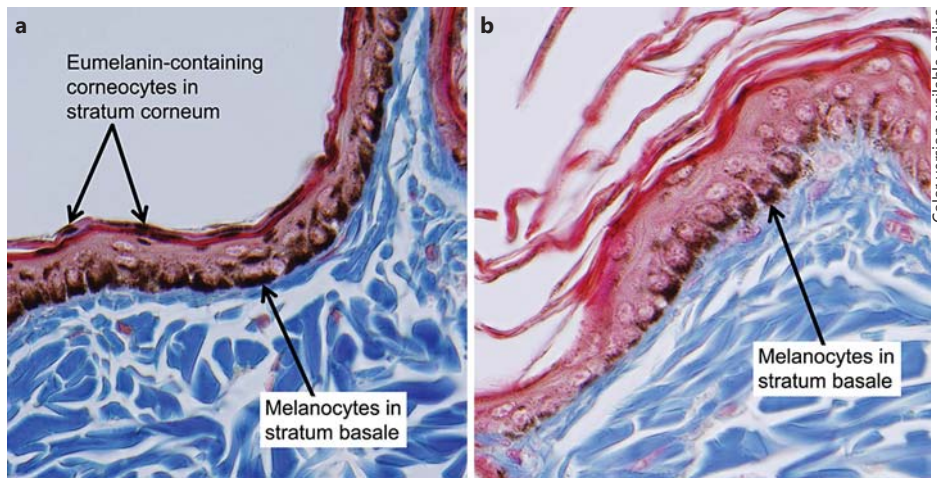
Fig. 2. Photomicrographs of the skin of the torso of *L. catta* to show strong melanization of the skin of the ventral surface (**a**) that underlies the white hair covering the thorax and abdomen, while the skin of the dorsal surface (**b**) is less melanized. ×40.

The MAP in Primates

We surveyed the literature on the primate integument in order to gather information on the status of the MAP, and relied primarily on the descriptive histological studies of William Montagna and colleagues. Our survey of the status of the MAP in primates is presented in table 2.

The distribution of the MAP in primates and their close relatives suggests that the probable ancestral condition in early Primates was the same as in basal Euarchonta, i.e. MAP weak or vestigial on the body and present on the tail. Complete loss of MAP occurred independently in tarsiers and some Lorisidae, and is a derived state. In anthropoids, the MAP are present on all of the non-glabrous skin. In many species of larger platyrrhines and catarrhines, they are described as large and 'strong', especially on the dorsal surface of the trunk. They are generally less prominent in small-bodied callithrichids, but are well developed on parts of the head and distal tail. In figure 2, the distribution of MAP character states in Primates and closely related outgroup taxa was mapped onto a recent and highly supported molecular phylogeny of Primates [Perelman et al., 2011]. Examination of the distribution of MAP character states in figure 3 indicates that most primates retain the probable primitive euarchontan condition of MAP present on body and tail (character states 1, 0), but the size and presumed function of the MAP on the body vary considerably. Dermopterans, tarsiers and some lorisids independently lost MAP entirely (character states 0, 0 in fig. 3), probably for different reasons. Lemurs lost most or all MAP on the body, but retained MAP on the tail (character states 0, 1 in fig. 3).

Primates and many other mammals underwent dramatic evolution and widespread dispersal during the Paleocene-Eocene thermal maximum (PETM) [Lucas, 1998; Storey et al., 2007; Beard, 2008; O'Leary et al., 2013]. Early primates have been

Table 2. Status of the MAP in primates, as compiled from the literature

Family	Genus and/ or species	MAP on body and tail		MAP on tail only		Description	Comments	References	Page
		present/ absent	coding	present/ absent	coding				
Lorisidae	*Perodicticus potto*	Absent	0	Absent	0			Montagna and Ellis, 1959	
Lorisidae	*Arctocebus calabarensis*	Absent	0	Absent	0			Montagna et al., 1966b; Sokolov, 1983	280
Lorisidae	*Nycticebus coucang*	Absent	0	Absent	0			Montagna et al., 1961a	
Lorisidae	*Loris tardigradus*	Present	1	Present	0	Larger follicles only	The larger follicles have a recognizable 'hair bulge' to which are attached the MAP; the small follicles have no muscles	Montagna and Ellis, 1960	21
Galagidae	*Otolemur crassicaudatus*	Present	1	Present	0		The follicles have very poorly developed MAP and many of the smaller ones have none. Muscles are best developed in the larger follicles in the tail	Montagna and Yun, 1962a	152
Galagidae	*Galago demidovii*	Absent	0	Present	1		Present only in the tail	Machida et al., 1966	202
Galagidae	*Galago senegalensis*		0	Present	1		Similar to MAP of lemur, only on the follicles of the tail	Yasuda et al., 1961	145
Lemuridae	*Lemur macaco*	Absent	0	Present	1		None of the follicles, except those of the tail, has well developed MAP	Montagna et al., 1961b	118
Lemuridae	*Lemur catta*	Absent	0	Present	1		MAP present only on the tail	This study	
Lemuridae	*Lemur catta*	Absent	0	Absent	0		Another peculiarity of the hair follicles is the total absence of MAP	Montagna and Yun, 1962c	97
Lemuridae	*Lemur catta*	Absent	0	Present	1		As in adult animals, none of the follicles has a bulge and an MAP except the primary follicles of the skin of the tail	Yun and Montagna, 1964	400
Lemuridae	*Lemur fulvus*	Absent	0	Present	1		As in adult animals, none of the follicles has a bulge and an MAP except the primary follicles of the skin of the tail	Yun and Montagna, 1964	400
Lemuridae	*Lemur mongoz*	Absent	0	Present	1		The follicles have no bulge and no MAP attached to them, except in some of those of the tail	Montagna and Yun, 1963b	373
Tarsiidae	*Tarsius syrichta*	Absent	0	Absent	0		None	Montagna and Machida, 1966	73
Tarsiidae	*Tarsius spectrum*	Absent	0	Absent	0		None	Sokolov, 1983	155
Callithrichidae	*Callimico goeldii*	Present	1	Absent	0		Most developed on tail	Perkins, 1969c	234

Table 2 (continued)

| Family	Genus and/ or species	MAP on body and tail		MAP on tail only		Description	Comments	References	Page
		present/ absent	coding	present/ absent	coding				
Callithrichidae	*Saguinus fuscicollis*	Present	1	Absent	0		The MAP are better developed in the cheek, scalp, back, and tail; in the tail the muscles are larger in the distal than in the proximal part	Perkins, 1966	43
Callithrichidae	*Callithrix argentata*	Present	1	Absent	0	Most developed on tail	An intimate neuropilary relationship exists in all hirsute skin, particularly in the scalp, eyebrow, cheek, chest, belly, back, and tail. Many hairs have an extensive plexus of cholinesterase-positive nerve fibers and nerve endings. Large, tortuous nerves twist and spiral to the level of the MAP, where they terminate; others accompany the muscle, sending branches to the hair follicle nerve end-organ	Perkins, 1969b	365
Callithrichidae	*Callithrix pygmaea*	Present	1	Absent	0	Well-developed	Largest in the tail but all over	Perkins, 1968	352
Callithrichidae	*Saguinus oedipus*	Present	1	Absent	0		MAP are present in all body regions except the facial disk (eyebrow, eyelids, lips, and perialar area), external ears, anogenital skin, and suprapubic region; they are largest in the tail	Perkins, 1969a	15 –16
Cebidae	*Lagothrix lagothricha*	Present	1	Absent	0	Well-developed, large	Large MAP are present, as in the Cercopithecoidea	Perkins, 1975	397
Cebidae	*Lagothrix lagothricha*	Present	1	Absent	0		The follicles have large MAP as do those of the Cercopithecoidea	Machida and Perkins, 1966	312
Cebidae	*Cacajao rubicundus*	Present	1	Absent	0	Dorsum only	MAP are well developed in the back only	Perkins et al., 1968b	59
Cebidae	*Cebus albifrons*	Present	1	Absent	0		MAP are large in the occipital scalp, nape, lumbar back, and tail; in the caudal region the MAP of the proximal tail tend to be somewhat larger than those of the distal tail	Perkins and Ford, 1969	3

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Table 2 (continued)

Family	Genus and/or species	MAP on body and tail		MAP on tail only		Description	Comments	References	Page
		present/absent	coding absent	present/absent	coding absent				
Cebidae	*Ateles geoffroyi*	Present	1	Absent	0		MAP are most developed in the back and tail	Perkins and Machida, 1967	36
Cebidae	*Aotus trivirgatus*	Present	1	Absent	0		About one half the way up the follicle is a conspicuous bulge to which is attached the MAP	Hanson and Montagna, 1962	422
Cebidae	*Saimiri sciureus*	Present	1	Absent	0		The follicles of the tail are equipped with well-developed MAP	Machida et al, 1967	47
Cebidae	*Pithecia monachus*	Present	1	Absent	0		Although their degree of development is nowhere outstanding, MAP are generally larger on the dorsum. However, a hair that is associated with a larger arrector pili muscle (e.g. in the scalp, back or tail) has a somewhat more complex nerve network	Perkins and Ford, 1975	386
Cercopithecidae	*Trachypithecus auratus*	Present	1	Absent	0	Very strong		Machida and Montagna, 1964	444
Cercopithecidae	*Cercocebus atys*	Present	1	Absent	0		Moderately well-developed MAP	Machida et al., 1965	166
Cercopithecidae	*Papio hamadryas anubis*	Present	1	Absent	0		Not mentioned	Montagna and Yun, 1962b	74
Cercopithecidae	*Macaca arctoides*	Present	1	Absent	0	Stout		Montagna et al., 1966a	74
Cercopithecidae	*Macaca mulatta*	Present	1	Absent	0	Strong		Montagna et al., 1964	309
Cercopithecidae	*Macaca nemestrina*	Present	1	Absent	0			Perkins et al., 1968a	76
Cercopithecidae	*Cercopithecus aethiops*	Present	1	Absent	0	Strong	Moderately stout MAP extend from the bulge to the papillary layer	Machida et al., 1964	454
Cercopithecidae	*Cercopithecus mitis*	Present	1	Absent	0	Strong	Moderately stout MAP extend from the bulge to the papillary layer	Machida et al., 1964	
Hominoidea	'Great apes'	Present	1	Absent	0	Large	Widespread	Montagna, 1971	585
Hominidae	*Gorilla* sp.	Present	1	Absent	0	Strong	The large MAP frequently consist of several slips that extend from the bulge to the papillary body	Ellis and Montagna, 1962	84
Hominidae	*Pan troglodytes*	Present	1	Absent	0	Strong	Widespread	Montagna and Yun, 1963a	194
Hominidae	*Homo sapiens*	Present	1	Absent	0	Strong	Widespread	Montagna, 1985	

'Comments' are from original sources, except that MAP has been used as an abbreviation throughout. All studies conducted on *Lemur catta* are reported in order to show differences in how the MAP are described and interpreted. Coding: 1 = present, 0 = absent.

found at a wide range of latitudes including far northern sites in Great Britain and Germany, to northern and central China and the northern Great Plains; they were also widespread at equatorial latitudes in Africa [Covert, 2002; Ni et al., 2007]. At the PETM, equable conditions obtained over a wide range of latitudes, and primates lived in hot to warm, humid tropical and paratropical forest biomes. In such environments, animals were probably subjected to very limited ranges of temperature variation (both diurnal and seasonal), and the selection for an increased basal metabolic rate was probably weak [Lovegrove, 2012]. Under these conditions, enhanced pilary insulation for close regulation of the air temperature in the boundary layer close to the skin was probably less important. Mutations leading to the complete or near loss of the MAP probably occurred in stem euarchontans in the late Cretaceous or early Paleocene when temperatures were considerably warmer and daily temperature fluctuations smaller than they are today, even in the tropics. Loss of most MAP may have been under positive selection in order to reduce heat stress, or may have occurred as the result of genetic drift, or in the absence of stabilizing selection. Retention of MAP on the tail in some strepsirhines may have been associated with the importance of the tail in mid-leap maneuvers in some taxa. In galagos and tarsiers, the tail-flick and mid-air rotation of the torso allow the animal to change direction in mid-leap [Crompton and Sellers, 2007; Crompton et al., 2010]. Contraction of the MAP and erection of the hairs on the dorsum of the tail and tail tuft appears to increase air resistance and facilitate braking or a change of direction, working like a sea parachute anchor. Piloerection may also help to resist damage due to abrasion when the tail is being moved during locomotion.

For early primates, the probable absence of functioning MAP except on the tail meant that the roles played by piloerection and pilary insulation in thermoregulation were minimal and that alterations in metabolism and behavior were used instead to maintain thermal homeostasis. Small mammals realize less benefit from piloerection than large mammals, but the absence of any potential for automatic adjustments to the loft of the hair coat in relation to temperature would have meant the evolution of compensatory modes of thermoregulation, including changes in activity patterns, modifications of metabolism, and development of postural and social behaviors favoring conservation of body heat. Many small primates consume diets of high-quality, calorie-dense foods such as insects and gums to maximize metabolic output. In seasonal and energy-limited environments such as Madagascar, lemurs evolved a wide variety of energy-conserving adaptations. Cathemerality buffers animals against the thermal extremes of hot days and cold nights [Tattersall, 1987; Curtis, 2006], and has been suggested as the most likely pattern of activity for the ancestral primate based on short-wave opsin gene sequences [Tan et al., 2005]. For many ancestral primates living in paratropical forests, such as adapiforms living in northern Europe in the early Eocene, cathemerality may have been obligatory due to the vastly varying day lengths at their latitude and the very short period of true darkness (of about 3 h) at midsummer.

Today the most extreme energy-serving adaptations are found in cheirogaleids, and probably not coincidentally, in species of the smallest primate, the mouse lemur *(Microcebus),* where daily torpor is combined with hibernation in the cold and dry season [Schmid and Kappeler, 2005]. In strepsirhines and tarsiers, the limited ability of pilary insulation to buffer animals against environmental temperature fluctuations has led to the evolution of great diversity in activity patterns, metabolic rates, and
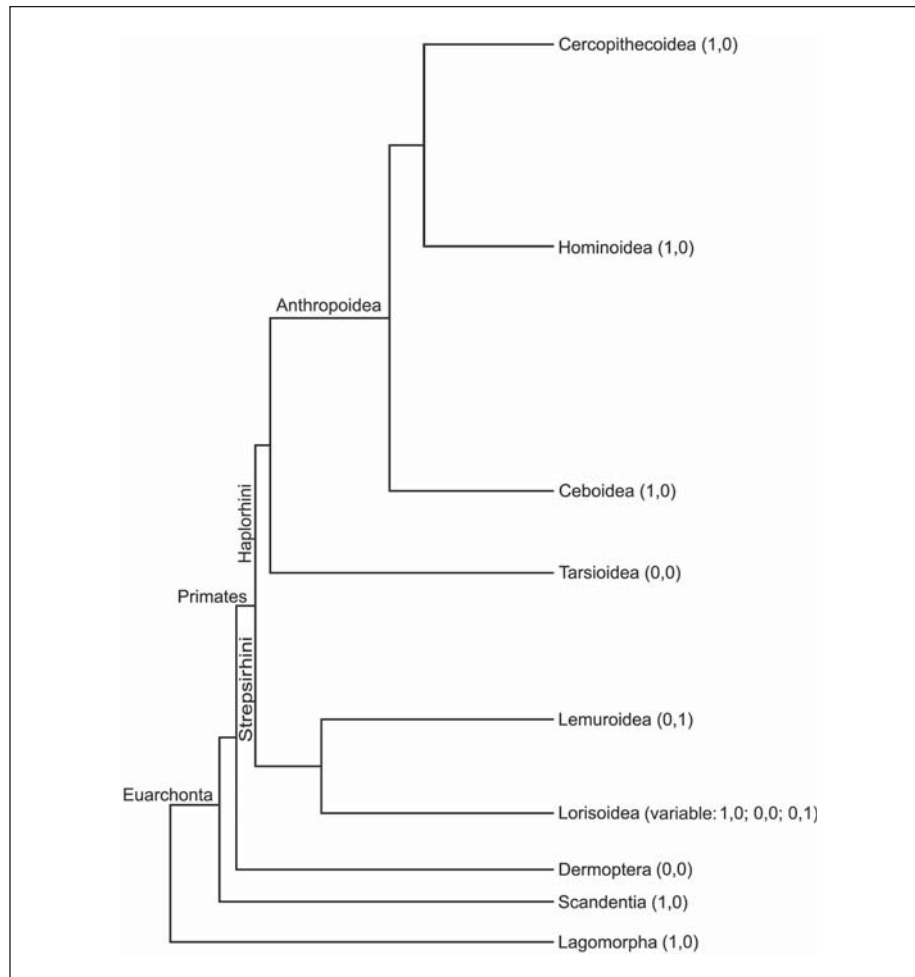
Fig. 3. The distribution of MAP character states in Primates, mapped onto a well-supported molecular phylogeny by Perelman et al. [2011]. The MAP character states given in parentheses after the taxon name follow the coding assigned in table 2: state (1, 0) denotes MAP present on body and tail, and absent on tail only; (0, 1) denotes MAP absent on the body and tail, but present on the tail only, and (0, 0) denotes absent on the body and tail, and absent on the tail only.

abilities to enter and maintain torpor. The absence of MAP also helps to account for why many strepsirhines assume postures that conduce to either heating or cooling, depending on environmental temperatures [Muller, 1985; Morland, 1993; Donati and Borgognini-Tarli, 2006; Snodgrass et al., 2007].

In this context, it is instructive to compare the thermoregulatory behaviors of meerkats *(Suricata suricatta),* of comparable body size (mean weight 800 g [Habicher, 2009]) to many strepsirhines and possessing whole-body MAP. Meerkats live in areas of southern Africa with high diurnal temperature ranges and moderate to high

Chaplin/Jablonski/Sussman/Kelley

Fig. 4. Photographs of a sunning ring-tailed lemur (*L. catta*, **a**) and sunning meerkats (*S. suricatta*, **b**). In *L. catta*, sunning involves passive stretching of the skin of the venter in order to maximize solar exposure of darkly pigmented skin and passive warming of the body. In *S. suricatta*, sunning also involves exposure of the venter to the sun, but occurs along with piloerection so that warmed air is trapped in insulating layers close to the skin's surface. Photograph of *L. catta* by Elizabeth Kelley; photograph of meerkats from http://www.freeimageslive.co.uk/free_stock_image/threemeerkatsjpg.

annual temperature ranges. They engage in a range of thermoregulatory behaviors similar to those of *L. catta*, including sunning and huddling (fig. 4). When cold, meerkats thermoregulate by involuntary piloerection and shivering, and by sunning and huddling; when hot, they pant, lie down in contact with the substrate, and avoid the sun by seeking shade or staying in their burrows [Habicher, 2009]. Meerkats have a 3°C thermal neutral zone but can maintain homeothermy over a much wider range through metabolic and physiological-behavioral adaptations [Habicher, 2009]. When ambient temperatures are below the lower limit of their thermoneutral temperature of approximately 30°C, their body hair is erect regardless of the strength of solar radiation. The animals sunbathe whenever possible. When the temperature is low, sunbathing ceases before the temperature at which piloerection ceases [Habicher, 2009]. The only cold adaptation that enables meerkats to forage on cool to cold and sunless days is piloerection. Piloerection is utilized for up to 86% of the time the animals spend outside [Habicher, 2009]. From this evidence, we infer that the absence of piloerection in small primates appears to have exacted a cost in terms of increased need for chemical thermoregulation and shortened length of the thermal activity window as compared to meerkats and other mammals of comparable size that can piloerect.

Judging from the presence of whole-body MAP in larger Ceboidea, and in Cercopithecoidea, and Hominoidea, MAP were probably reacquired in the ancestor of anthropoids by the later part of the middle Eocene, when the first generally accepted catarrhines are distinguished in the fossil record [Jaeger et al., 2010]. The pattern of

MAP over the surface of the body in many Callithrichidae may be instructive in understanding how MAP were reacquired in anthropoids. In *Saguinus fuscicollis*, MAP are present and better developed on the cheek, scalp, back, and tail; in the tail, the MAP are larger on the distal than on the proximal portion [Perkins, 1966]. In *Saguinus oedipus*, MAP are present on all body regions except the facial disk (eyebrow, eyelids, lips, and perialar area), external ears, anogenital skin, and suprapubic region; they are largest on the tail [Perkins, 1969a]. Reacquisition of MAP may initially have involved selection for the spread of the epidermal follicle stem cell precursors of the MAP over the dorsal surface of the body via cell migration from the neural tube. It is interesting to speculate as to whether the large-bodied subfossil lemurs also reacquired MAP on the torso as part of an adaptation to increased seasonal temperature fluctuations in the Pleistocene. The thermoregulatory stress on smaller-bodied lemurs at that time must have been severe.

Conclusions

Early primates probably had weak or vestigial MAP on the body, but possessed MAP on the tail. This condition persisted in all lemurs and some lorises, and was probably present in the basal haplorhine. The complete loss of MAP in tarsiers is a derived condition. The well-developed MAP of anthropoids is a shared-derived condition probably related primarily to increased body size.

The lack of functional MAP on the body in basal primates probably did not adversely affect the animals living under continuously warm and equable conditions during the PETM, but after that time would have exacted a considerable metabolic cost for maintaining body temperature and/or in restricting the length of time the animals could be actively foraging. The lack of MAP would not be so important for nocturnal or cathemeral animals or for those restricted to tropical or paratropical forests with relatively narrow temperature fluctuations. After the PETM, it is possible that there was strong selection for high-quality diets, with social, physiological, and morphological adaptations to regimes of more extreme daily and seasonal temperature fluctuations. Despite these changes, primates became extinct in non-tropical latitudes by the late Eocene and earliest Oligocene, and it is inviting to speculate that the effective absence of MAP and the ability to piloerect contributed to their demise. In this connection, it is relevant that all primates, even strepsirhines and tarsiers, are more highly encephalized than other mammals of comparable body mass, and so bear the metabolic cost and thermal sensitivity of a relatively larger brain. The evolution of functional, whole-body MAP can thus be seen as a necessary precursor to the development of large-bodied highly encephalized, diurnal primates.

References

Archibald SB, Bossert WH, Greenwood DR, Farrell BD (2010). Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* 36: 374–398.

Beard KC (2008). The oldest North American primate and mammalian biogeography during the Paleocene-Eeocene thermal maximum. *Proceedings of the National Academy of Sciences* 105: 3815–3818.

Bligh J, Johnson KG (1973). Glossary of terms for thermal physiology. *Journal of Applied Physiology* 35: 941–961.

Covert HH (2002). The earliest fossil primates and the evolution of prosimians: introduction. In *The Primate Fossil Record* (Hartwig WC, ed.), pp 13–20. Cambridge, Cambridge University Press.

Crompton RH, Sellers WI (2007). A consideration of leaping locomotion as a means of predator avoidance in prosimian primates. In *Primate Anti-Predator Strategies* (Gursky SL, Nekaris KAI, eds.), pp 127–145. New York, Springer.

Crompton RH, Blanchard ML, Coward S, Alexander RM, Thorpe SKS (2010). Vertical clinging and leaping revisited: locomotion and habitat use in the western tarsier, *Tarsius bancanus,* explored via loglinear modeling. *International Journal of Primatology* 31: 958–979.

Curtis DJ (2006). Cathemerality in lemurs. In *Lemurs: Ecology and Adaptation* (Gould L, Sauther ML, eds.), pp 133–157. New York, Springer.

Cymbaluk NF (1994). Thermoregulation of horses in cold, winter weather: a review. *Livestock Production Science* 40: 65–71.

Donati G, Borgognini-Tarli SM (2006). From darkness to daylight: cathemeral activity in primates. *Journal of Anthropological Sciences* 84: 7–32.

Ellis RA, Montagna W (1962). The skin of primates. VI. The skin of the gorilla *(Gorilla gorilla). American Journal of Physical Anthropology* 20: 79–93.

Habicher A (2009). *Behavioural cost minimisation and minimal invasive blood-sampling in meerkats* (S. Suricatta, *Herpestidae*). PhD thesis, University of Cologne.

Hanson G, Montagna W (1962). The skin of primates. XII. The skin of the owl monkey *(Aotus trivirgatus). American Journal of Physical Anthropology* 20: 421–429.

Herrington LP (1951). The role of the piliary system in mammals and its relation to the thermal environment. *Annals of the New York Academy of Sciences* 53: 600–607.

Hill RA, Weingrill T, Barrett L, Henzi SP (2004). Indices of environmental temperatures for primates in open habitats. *Primates* 45: 7–13.

Jablonski NG, Kelley EA, Sussman RW, Chaplin G (2009). A framework for understanding thermoregulation in primates. *American Journal of Physical Anthropology* 138: 206–207.

Jaeger J-J, Beard KC, Chaimanee Y, Salem M, Benammi M, Hlal O, Coster P, Bilal AA, Duringer P, Schuster M, Valentin X, Marandat B, Marivaux L, Metais E, Hammuda O, Brunet M (2010). Late middle Eocene epoch of Libya yields earliest known radiation of African anthropoids. *Nature* 467: 1095–1098.

Janzen DH (1967). Why mountain passes are higher in the tropics. *The American Naturalist* 101: 233–249.

Johnson KR, Ellis B (2002). A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary. *Science* 296: 2379–2383.

Lovegrove BG (2012). The evolution of endothermy in cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biological Reviews* 87: 128–162.

Lucas SG (1998). Fossil mammals and the Paleocene-Eocene series boundary in Europe, North America, and Asia. In *Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records* (Aubry M-P, Lucas S, Berggren WA, eds.), pp 451–500. New York, Columbia University Press.

Machida H, Montagna W (1964). The skin of primates. XXII. The skin of the lutong *(Presbytis pyrrhus). American Journal of Physical Anthropology* 22: 443–451.

Machida H, Perkins EM (1966). The skin of primates. XXX. The skin of the woolly monkey *(Lagothrix lagotricha). American Journal of Physical Anthropology* 24: 309–319.

Machida H, Perkins EM, Giacometti L (1966). The skin of primates. XXIX. The skin of the pigmy bush-baby *(Galago demidovii). American Journal of Physical Anthropology* 24: 199–203.

Machida H, Perkins EM, Hu F (1967). The skin of primates. XXXV. The skin of the squirrel monkey *(Saimiri sciureus). American Journal of Physical Anthropology* 26: 45–53.

Machida H, Perkins EM, Montagna W (1964). The skin of primates. XXIII. A comparative study of the skin of the green monkey *(Cercopithecus aethiops)* and the Sykes' monkey *(Cercopithecus mitis). American Journal of Physical Anthropology* 22: 453–465.

Machida H, Perkins EM, Montagna W, Giacometti L (1965). The skin of primates. XXVII. The skin of the white-crowned mangabey *(Cercocebus atys). American Journal of Physical Anthropology* 23: 165–179.

Montagna W (1971). Cutaneous comparative biology. *Archives of Dermatology* 104: 577–591.

Montagna W (1985). The evolution of human skin(?). *Journal of Human Evolution* 14: 3–22.

Montagna W, Ellis RA (1959). The skin of primates. I. The skin of the potto *(Perodicticus potto). American Journal of Physical Anthropology* 17: 137–161.

Montagna W, Ellis RA (1960). The skin of primates. II. The skin of the slender loris *(Loris tardigradus). American Journal of Physical Anthropology* 18: 19–43.

Montagna W, Machida H (1966). The skin of primates. XXXII. The Philippine tarsier *(Tarsius syrichta). American Journal of Physical Anthropology* 25: 71–83.

Montagna W, Yun JS (1962a). The skin of primates. VII. The skin of the great bushbaby *(Galago crassicaudatus). American Journal of Physical Anthropology* 20: 149–165.

Montagna W, Yun JS (1962b). The skin of primates. VIII. The skin of the anubis baboon *(Papio doguera). American Journal of Physical Anthropology* 20: 131–141.

Montagna W, Yun JS (1962c). The skin of primates. X. The skin of the ring-tailed lemur *(Lemur catta). American Journal of Physical Anthropology* 20: 95–117.

Montagna W, Yun JS (1963a). The skin of primates. XV. The skin of the chimpanzee *(Pan satyrus). American Journal of Physical Anthropology* 21: 189–203.

Montagna W, Yun JS (1963b). The skin of primates. XVI. The skin of *Lemur mongoz. American Journal of Physical Anthropology* 21: 371–381.

Montagna W, Machida H, Perkins EM (1966a). The skin of primates. XXVIII. The stump-tail macaque *(Macaca speciosa). American Journal of Physical Anthropology* 24: 71–85.

Montagna W, Machida H, Perkins EM (1966b). The skin of primates. XXXIII. The skin of the angwantibo *(Arctocebus calabarensis). American Journal of Physical Anthropology* 25: 277–290.

Montagna W, Yasuda K, Ellis RA (1961a). The skin of primates. III. The skin of the slow loris *(Nycticebus coucang). American Journal of Physical Anthropology* 19: 1–21.

Montagna W, Yasuda K, Ellis RA (1961b). The skin of primates. V. The skin of the black lemur *(Lemur macaco). American Journal of Physical Anthropology* 19: 115–129.

Montagna W, Yun JS, Machida H (1964). The skin of primates. XVIII. The skin of the rhesus monkey *(Macaca mulatta). American Journal of Physical Anthropology* 22: 307–319.

Montagna W, Yun JS, Silver AF, Quevedo WC (1962). The skin of primates. XIII. The skin of the tree shrew *(Tupaia glis). American Journal of Physical Anthropology* 20: 431–439.

Morland HS (1993). Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs *(Varecia variegata variegata).* In *Lemur Social Systems and Their Ecological Basis* (Kappeler PM, ed.), pp 193–203. New York, Plenum Press.

Muller EF (1985). Basal metabolic rates in primates: the possible role of phylogenetic and ecological factors. *Comparative Biochemistry and Physiology Part A: Physiology* 81: 707–711.

Ni X, Beard KC, Meng JIN, Wang Y, Gebo DL (2007). Discovery of the first early Cenozoic euprimate (Mammalia) from inner Mongolia. *American Museum Novitates* 3571: 1–11.

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo Z-X, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AL (2013). The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339: 662–667.

Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, Moreira MAM, Kessing B, Pontius J, Roelke M, Rumpler Y, Schneider MPC, Silva A, O'Brien SJ, Pecon-Slattery J (2011). A molecular phylogeny of living primates. *PLoS Genetics* 7: e1001342.

Perkins EM (1966). The skin of primates. XXXI. The skin of the black-collared tamarin *(Tamarinus nigricollis). American Journal of Physical Anthropology* 25: 41–69.

Perkins EM (1968). The skin of primates. XXXVI. The skin of the pigmy marmoset – *Callithrix (=Cebuella) pygmaea. American Journal of Physical Anthropology* 29: 349–364.

Perkins EM (1969a). The skin of primates. XL. The skin of the cottontop pinché *Saguinus (=Oedipomidas) oedipus. American Journal of Physical Anthropology* 30: 13–27.

Perkins EM (1969b). The skin of primates. XLI. The skin of the silver marmoset – *Callithrix (=Mico) argentata. American Journal of Physical Anthropology* 30: 361–387.

Perkins EM (1969c). The skin of primates. XXIV. The skin of Goeldi's marmoset *(Callimico goeldii)*. *American Journal of Physical Anthropology* 30: 231–249.

Perkins EM (1975). Phylogenetic significance of the skin of New World monkeys (order Primates, infraorder Platyrrhini). *American Journal of Physical Anthropology* 42: 395–423.

Perkins EM, Ford DM (1969). The skin of primates. XXXIX. The skin of the white-browed capuchin *(Cebus albifrons). American Journal of Physical Anthropology* 30: 1–12.

Perkins EM, Ford DM (1975). The skin of primates. XLII. The skin of the silvered sakiwinki *(Pithecia monachus). American Journal of Physical Anthropology* 42: 383–393.

Perkins EM, Machida H (1967). The skin of primates. XXXIV. The skin of the golden spider monkey *(Ateles geoffroyi). American Journal of Physical Anthropology* 26: 35–43.

Perkins EM, Arao T, Dolnick EH (1968a). The skin of primates. XXXVII. The skin of the pig-tail macaque *(Macaca nemestrina). American Journal of Physical Anthropology* 28: 75–83.

Perkins EM, Arao T, Uno H (1968b). The skin of primates. XXXVIII. The skin of the red uacari *(Cacajao rubicundus). American Journal of Physical Anthropology* 29: 57–79.

Schmid J, Kappeler PM (2005). Physiological adaptations to seasonality in nocturnal primates. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (Brockman DK, van Schaik CP, eds.), pp 129–155. New York, Cambridge University Press.

Snodgrass JJ, Leonard WR, Robertson ML (2007). Primate bioenergetics: an evolutionary perspective. In *Primate Origins: Adaptations and Evolution* (Ravosa MJ, Dagosto M, eds.), pp 703–737. New York, Springer.

Sokolov VE (1983). *Mammal Skin*. Berkeley, University of California Press.

Steuber T, Rauch M, Masse J-P, Graaf J, Malkoc M (2005). Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. *Nature* 437: 1341–1344.

Storey M, Duncan RA, Swisher CC III (2007). Paleocene-Eocene thermal maximum and the opening of the northeast Atlantic. *Science* 316: 587–589.

Tan Y, Yoder AD, Yamashita N, Li W-H (2005). Evidence from opsin genes rejects nocturnality in ancestral primates. *Proceedings of the National Academy of Sciences* 102: 14712–14716.

Tattersall I (1987). Cathemeral activity in primates: a definition. *Folia Primatologica* 49: 200–202.

Yasuda K, Aoki T, Montagna W (1961). The skin of primates. IV. The skin of the lesser bushbaby *(Galago senegalensis). American Journal of Physical Anthropology* 19: 23–33.

Yun JS, Montagna W (1964). The skin of primates. XX. Development of the appendages in *Lemur catta* and *Lemur fulvus*. *American Journal of Physical Anthropology* 22: 399–401.