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Hallucal grasping behavior in *Caluromys* (Didelphimorphia: Didelphidae): Implications for primate pedal grasping

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ABSTRACT

A key feature in primate evolution is a foot with a divergent opposable hallucal metatarsal bearing a large peroneal process. Extant primates are characterized by a powerful hallucal grasp—an either "euprimate" or "plesiadapoid-euprimate" ancestor acquisition—that facilitates the exploitation of fine branches, an ability that increased the fitness of ancestral euprimates. In this context, the didelphid marsupial *Caluromys* has been used as the extant analog to this primate morphotype stage due to some morphological, ecological, and behavioral features. However, the extent to which and the positional and support contexts in which *Caluromys* uses powerful hallucal grasping are not known. This renders analogies to any mode of "euprimate" or "stem primate" grasping poorly substantiated. The present paper quantifies locomotor and postural behavior, support use, and associated frequencies of hallucal grasping in captive *Caluromys philander* via analysis of video recordings. During locomotion, *Caluromys* primarily used diagonal sequence walk, clamber, and climb, whereas stand, foot-hang, and bipedal stand were the dominant postures. Small, fine, horizontal, and moderately inclined branches were frequently used. Overall rates of "apparently powerful hallucal grasps" were high, but were exceptionally high during clamber, climb, foot-hang, and bipedal stand. Additionally, an "apparently powerful hallucal grasp" was very common upon fine, small, steep, and vertical branches. The extensive use of such powerful hallucal grasping provided stability and safety that enabled *Caluromys* to proficiently utilize fine branches of various orientations. The ability to negotiate such unstable supports, further reflected in foot anatomy, provides evidence that the morphobehavioral complex of *Caluromys* can serve as an extant analog to the plesiadapoid-euprimate ancestor, represented as a terminal branch feeder with effective hallucal grasping.

Introduction

One of the key features that characterize euprimates (Hoffstetter, 1977) is a foot specialized for powerful grasping with a divergent opposable hallux bearing a large peroneal process at the base of metatarsal I (Napier and Walker, 1967). This is particularly important because grasping with a divergent hallux appears to facilitate use of fine branches in either tree crown peripheries or the shrub layer, enabling foraging for angiosperm products and/or invertebrates (Cartmill, 1972; Sussman, 1991; Bloch and Boyer, 2002).

A support is said to be held in a "powerful hallucal grasp" (Sargis et al., 2007) when it is embraced by lateral digits opposed to an adducted and medially rotated hallux (Szalay and Dagosto, 1988). This conjunct adduction and medial rotation of the hallux, albeit decreasing hallucal opposition, can help increase the power of the grasp along with simultaneous digital flexion (Szalay and Dagosto, 1988; Boyer et al., 2007). Until recently, powerful hallucal grasping was morphologically associated with a hypertrophied peroneal process shared by early fossil euprimates and modern strepsirhines (Gebo, 1993, 2004). The tendon of the peroneus longus muscle inserts on this process. A larger process would increase the lever arm contributing to powerful hallucal adduction assisting in grasping (Gebo, 1993). However, recent evidence has shown that this muscle is not important in powerful grasping, which is primarily achieved by the action of flexor digitorum tibialis and adductor hallucis muscles (Szalay and Dagosto, 1988; Boyer et al., 2007).

These findings suggest that a hypertrophied peroneal process cannot account for powerful hallucal grasping, and this bears on the interpretation of the morphotype of stem primates (Bloch et al., 2007) and proposed extant analogs. In Gebo's (2004) synthesis of the stages of early primate evolution, the third stage involved a terminal branch feeder with 'nonpowerful' hallucal grasping and was represented by the didelphid marsupial *Caluromys* as an extant analog. He considered this form to have preceded the evolution of the 'powerfully' grasping hallux with a large peroneal process and nail-bearing digits of euprimates. However, the presence of

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divergent halluces in some arboreal marsupials (Szalay, 1994), arboreal eutherians (Jones, 1953), carpolestid "plesiadapoids" (Bloch and Boyer, 2002), and the disassociation of a large peroneal process from powerful hallucal adduction (Boyer et al., 2007) incited Sargis et al. (2007) to re-evaluate this scenario. Their third stage—characterizing the plesiadapoid-euprimate ancestor—was described as a terminal branch feeder with "powerful" hallucal grasping, a condition retained in fossil *Carpolestes* and represented by the didelphid marsupial *Caluromys* as an extant analog. This interpretation implies that the acquisition of a large peroneal process in the euprimate foot may not represent an adaptive response to a more powerful hallucal grasp than that exhibited by *Caluromys*.

Caluromys, the woolly opossum, has long attracted the interest of students of primate evolution as it appears to converge in the direction of primates: it is highly arboreal, using the terminal and small branches of tree peripheries (Charles-Dominique et al., 1981; Rasmussen, 1990; Julien-Laferrière, 1995; Leite et al., 1996; Grelle, 2003), feeds on ripe fruit and a variety of invertebrates (Atramentowicz, 1988; Julien-Laferrière and Atramentowicz, 1990; Leite et al., 1996), possesses a relatively large brain, large and forward-oriented eyes (Eisenberg and Wilson, 1981; Ravosa and Savakova, 2004), relatively long digits, a long opposable nail-bearing hallux (Szalay, 1994; Lemelin, 1999; Argot, 2002), walks in a diagonal sequence gait (Schmitt and Lemelin, 2002; Lemelin et al., 2003; Delciellos, 2005), exhibits an agile and diverse locomotor and postural behavior (Rasmussen, 1990; Lemelin, 1999; Delciellos, 2005), gives birth to small litters, and shows slow development and metabolic rates similar to that of eutherians (Atramentowicz, 1982; Charles-Dominique, 1983).

All of these morphological, ecological, and behavioral characters have formed the basis for using *Caluromys* as the adaptive analog of the terminal branch feeder capable of powerful hallucal grasp. Limited behavioral (Rasmussen, 1990; Lemelin, 1999; Lemelin et al., 2003; Delciellos, 2005) and morphological observations (Grand, 1983; Szalay, 1994; Lemelin, 1999; Argot, 2002) appear to support this. However, the extent to which *Caluromys* uses "powerful hallucal grasping" and within what specific support and positional contexts is not known, rendering an analogy with any mode of "euprimate" or "stem primate" (Bloch et al., 2007) grasping poorly substantiated. For instance, it is possible that "powerful hallucal grasps" are differentially used when the availability of different support sizes varies. Moreover, the "power" or effectiveness of such hallucal grasps may further vary depending on the positional diversity and profile compared to that of a euprimate. The goal of this paper is to provide quantitative data on hallucal grasping modes during locomotion and postures, and frequency of use of various postures and supports by woolly opossums, *Caluromys philander*, in captivity. If *Caluromys* frequently utilizes behaviors and supports of particular diameters and inclinations that require what appear to be powerful hallucal grasps, this would suggest that *Caluromys* accurately represents an extant analog of the plesiadapoid-euprimate ancestor as characterized by Sargis et al. (2007).

Materials and methods

The present data derive from the analysis of video recordings of two adult male and two adult female captive *Caluromys philander* from French Guiana. The animals were housed in enclosures (2.5 m high × 2 m deep × 2.5 m wide) topped by wire mesh and fronted by a glass window in the Laboratoire d'Ecologie Générale at Brunoy, France, under a 12L:12D light regime. Each enclosure contained a variety of branches of various diameters and orientations upon which the animals moved freely. However, provided supports in a cage were expected to limit positional options of the animals. The estimate of their availability would allow for a controlled test of support preference or avoidance. For these reasons, I calculated the number and length of all available supports and subsequently estimated the availability of different support size categories. The quantification showed that the different size categories of available branches (see Table 1 for definitions) were more or less equally represented in the enclosure (fine: 29.2%, small: 27.7%, medium: 20.4%, and large: 22.7%). Preference or avoidance of these categories was then estimated by the Jacobs' D value (Jacobs, 1974):

$$D = U - A/U + A \ - 2U^{*}A$$

where U is proportion of use and A is proportion of availability. Values of the index range from −1, depicting strong avoidance, to +1, showing strong preference; values around 0 are considered as neutral.

The animals moved freely on the available supports within the enclosure. In addition, they were provided with small pieces of fruit that were placed at the extremities of fine branches during three

Table 1

Recorded variables of the positional behavior of *Caluromys philander*. Definitions of modes adapted from Hunt et al. (1996) for primates

Diagonal sequence walk	Body displacement along single horizontal or oblique branch using quadrupedal diagonal sequence couplets walking gait (Schmitt and Lemelin, 2002; Lemelin et al., 2003)
Clamber (up, horizontal, down)	Body displacement in various directions using multiple branches and an irregular quadrupedal gait and limb movements
Climb (up, down)	Upward or downward body displacement along single steep or vertical branches using a regular quadrupedal gait with digital grasping
Bridge	Crossing short gaps whilst keeping at least three limbs anchored
Suspensory	Below-branch quadrupedal locomotion involving inverted lateral walk and inverted clamber
Leap	Horizontal body displacement that incorporates a significant brief or long airborne phase
Sit	Above-branch crouched bipedal posture with only the feet touching the branch
Stand	Above-branch quadrupedal posture with semi-extended or crouched limbs
Bipedal	Above-branch bipedal posture with semi-extended or extended feet allowing rotatory movements of the body
Cantilever	Feet anchor the lower body to a branch of various orientations while the trunk is rapidly extended keeping the forelimbs extended
Foot-hang	Below-branch suspensory posture with the feet supporting the body; the tail may or may not be used
Tail-hang	Below-branch suspensory posture with only the tail supporting the body
Fine branch	Diameter < 1 cm
Small branch	Diameter 1–2 cm
Medium branch	Diameter 2–4 cm
Large branch	Diameter >4 cm
Unnatural	Wire mesh, nest box
Ground	Enclosure floor
Horizontal	Within ±22.5° to horizontal
Moderate	Between 22.5–45°
Steep	Between 45–67.5°
Vertical	Within ±22.5° to vertical
Convergent hand grasp	Grasp where all digits converge to the median axis of the hand
Zygodactylous hand grasp	Grasp between digits II and III
Apparently-powerful hallucal grasp (Fig. 1)	Firm and secure pedal grasp where the adducted and apparently medially-rotated hallux is opposed to the lateral digits that fully or partly embrace the branch; the proximal foot is usually elevated from the branch
Nonpowerful hallucal grasp	Pedal grasp where the divergent hallux is somewhat opposed to the lateral digits that partly encircle the branch; plantar surface of the foot either loosely placed or gently held upon the branch