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Pedal grasping in the northern smooth-tailed treeshrew *Dendrogale murina* (Tupaiidae, Scandentia): insights for euarchontan pedal evolution

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Abstract: Pedal grasping evolution in euarchontan mammals is of great importance as it bears on the adaptive significance of specialized hallucal grasping and arboreal niche use related to the group differentiation. Basally divergent arboreal tupaiid treeshrews are very suitable for testing pedal grasping modes and associated substrate correlates and provide insights on euarchontan pedal evolution. For these purposes we filmed wild-caught *Dendrogale murina* from Vietnam and analyzed their foot mechanisms. Our observations showed that hallucal grasp was moderately used and was mainly associated with small and horizontal substrates. Convergent grasp was frequently used on medium-sized and horizontal substrates whereas claws were related to large and vertical substrates. In addition, the foot was frequently inverted and mainly placed in a semiplantigrade position. Inversion and semiplantigrady dominated on small, medium-sized and horizontal substrates but decreased on larger substrates with increased inclinations. The observed pedal mechanism probably represents a derived condition, where hallucal grasping tends to become slightly restrained, compared to the primitive euarchontan (and scandentian) pedal grasping mechanism. Furthermore, it hallmarks an early stage in tupaiid evolution towards a more constrained pedal grasping. This further substantiates pedal grasping plasticity within euarchontan mammals and highlights the strong relation between a hallucal grasping mechanism and the frequent and primary use of small slender substrates.

Keywords: euarchontans; foot grasp; hallux; Tupaiidae; Vietnam.

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Introduction

Grasping extremities are among the defining features of Primates and are central for understanding their origins and early evolution within euarchontan (treeshrews, colugos, primates) mammals (Le Gros Clark 1959, Martin 1990). More particularly, a key feature of primates is a foot specialized for powerful grasping, by opposing and simultaneously flexing the lateral digits against a divergent, adducted and medially rotated hallux (Szalay and Dagosto 1988, Boyer et al. 2007, Sargis et al. 2007). This functional mechanism is particularly important as it facilitates fine branch use in tree crown peripheries and/or the shrub layer, enabling foraging for angiosperm products and/or invertebrates (Cartmill 1972, Sussman 1991, Bloch and Boyer 2002). Within euarchontans, these grasping mechanics, shared by extant and extinct euprimates and fossil carpolestid plesiadapiforms, are functionally related to a short entocuneiform with a saddle-shaped, medially expanded, narrow and ventrally cylindrical distal facet, a robust hallucal metatarsal laterally rotated distally, a flattened and broad proximal hallucal phalanx, and a shallow and broad distal phalanx with a flattened nail (Szalay and Dagosto 1988, Bloch and Boyer 2002, 2007, Sargis et al. 2007). However, while carpolestids bear functional claws in the lateral digits, associated with vertical ranging, extinct and extant strepsirhines possess a hypertrophied peroneal process at the base of the hallucal metatarsal, associated with a buttressing function in leaping and landing (Szalay and Dagosto 1988, Boyer et al. 2007, Sargis et al. 2007, Patel et al. 2015, contra Gebo 1993, 2004).

In contrast, the rest of fossil plesiadapiforms and extant scandentians (families Ptilocercidae and

Tupaiidae) are characterized by an entocuneiform with a relatively large and broad distal facet lacking a medial expansion, a robust hallucal metatarsal lacking the proximal peroneal and medial processes and the strong distal lateral torsion, and a mediolaterally compressed distal hallucal phalanx with a functional claw (Szalay and Dagosto 1988, Bloch and Boyer 2002, 2007, Sargis 2002a; Sargis et al. 2007). This morphology indicates the absence of powerful hallucal grasping and suggests a divergent hallux used in a hook-like grasping manner against the rest of the foot (Jenkins 1974, Sargis 2001, 2002a, Bloch and Boyer 2007). This grasping behavior is exemplified by the arboreal nocturnal pen-tailed treeshrew *Ptilocercus lowii* (Gray, 1848). *Ptilocercus*, the sole representative of the family Ptilocercidae, is a basally divergent scandentian (Le Gros Clark 1926, Butler 1980, Luckett 1980, Szalay and Drawhorn 1980, Szalay and Dagosto 1988, Sargis 2002a,b,c, 2007, Olson et al. 2004, 2005, Roberts et al. 2011), with a mobile tarsus and a divergent hallux of relatively increased mobility at the entocuneiform-metatarsal joint, and an associated intrinsic muscular arrangement that facilitates grasping on small arboreal substrates (Le Gros Clark 1926, Szalay and Drawhorn 1980, Szalay and Dagosto 1988, Emmons 2000, Sargis 2002a,c, Sargis et al. 2007). Analogous grasping behaviors have also been recorded in Eurasian Harvest mice and African dormice (Urbani and Youlatos 2013, Youlatos et al. 2015).

Among euarchontan mammals, the *Ptilocercus*-type of opposable non-powerful pedal grasping and its associated morphological correlates, are considered primitive and have preceded the grasping patterns encountered in euprimates and tupaiid scandentians (Szalay and Dagosto 1988, Szalay and Lucas 1996, Sargis 2001, Bloch and Boyer 2007, Sargis et al. 2007). In the arboreal euprimateform lineage, this mechanism evolved into the powerful pedal grasping with the divergent opposable nailed hallux (Bloch and Boyer 2002, Bloch et al. 2007, Sargis et al. 2007). In contrast, increasing terrestriality within the other scandentian family Tupaiidae was coupled with reduced hallucal opposability to loss of grasping in the more terrestrial species (Szalay and Dagosto 1988, Sargis 2001, 2002a). Thus, the arboreal lesser treeshrew *Tupaia minor* (Gunther, 1876) is capable of hypersupinating the foot during descents and of efficient hallucal grasping on small branches, with a relatively restricted abductive capacity at the metatarso-phalangeal joint (Emmons 2000, Sargis 2001, 2002a). The medium-sized scansorial treeshrew *Tupaia glis* (Diard and Duvaucel, 1820) is also capable of foot hypersupination, abduction and plantar flexion, as well as of incipient hallucal grasping, with a restricted abductive capacity at the metatarso-phalangeal joint (Jenkins 1974, Szalay and Drawhorn 1980, Sargis 2002a). Finally, the terrestrial *T. tana* (Raflles, 1821) keeps its limbs extended and digitigrade, seldom uses arboreal substrates and is unable to grasp (Emmons 2000, Sargis 2001). This morpho-behavioral variability (Sargis 2001, 2002a), their early diversification (Bloch et al. 2007, Roberts et al. 2011) and their pivotal role in euarchontan evolution, as a sister group to either dermopterans or primates (Le Gros Clark 1959, Bloch et al. 2007, Bloch and Boyer 2007, Godinot 2007, Sargis et al. 2007, O'Leary et al. 2013), renders scandentians an attractive model for understanding similar shifts between a non-opposable foot and an opposable powerful and non-powerful hallucal grasping foot. Therefore, comparable data on the grasping behavior of basally divergent, more arboreal, representatives of the family Tupaiidae would be valuable for understanding pedal grasping trends and substrate correlates within scandentians and euarchontans. The smooth-tailed treeshrew *Dendrogale* is considered as the most basally divergent tupaiid, having diverged from the rest of the family 34.77 mya (Butler 1980, Luckett 1980, Olson et al. 2004, 2005, Roberts et al. 2011). More particularly, the Northern smooth-tailed treeshrew *Dendrogale murina* (Schlegel and Muller, 1843) is a small (45 g) diurnal treeshrew using the ground and the understory of forests, bushes, savannas and bamboo thickets (Lekagul and McNeely 1977, Timmins et al. 2003, Kvartalnov 2009). The species forages for arthropods at heights ~5 m and in the forest litter, and rarely feeds on fruit or other plant material (Davis 1938, Kvartalnov 2009). On the ground, the animals run, bound and jump between roots and rocks (Kloss 1916, Kvartalnov 2009), whereas on the trees they clamber, climb, and jump between branch and bamboo entanglements (Timmins et al. 2003, Kvartalnov 2009). These behaviors suggest that Northern smooth-tailed treeshrews would be capable of hallucal grasping, but to what extent is unknown. The postcranial morphology and muscular anatomy of *Dendrogale* partly resemble that of *Ptilocercus*, and are functionally associated with forelimb protraction and flexion, hind limb flexion and foot plantar flexion and inversion (Davis 1938, Riesenfeld 1974, Stafford and Thorington 1998, Endo et al. 1999, Sargis 2002a,b). However, *Dendrogale* is more similar to other tupaiids than to *Ptilocercus* (Sargis 2002a,b,c,d). In order to understand foot grasping mechanisms in basally divergent tupaiids, we investigated foot posture, foot position and foot grasping modes of wild-caught *D. murina* in Vietnam. Video analyses of their pedal behavior will provide evidence on rates of hallucal grasping and associated foot postures on different substrates in basally divergent tupaiids and will further help elucidate patterns of hallucal evolution in euarchontans.

Materials and methods

Study animals and experimental setting

The present data derive from the analysis of video recordings of three male (two adult and one subadult) wild-caught Northern smooth-tailed treeshrews *Dendrogale murina* (Schlegel and Müller 1843) from Cat Tien National Park, Vietnam. Both animals were captured at different dates with arboreal live traps and were housed for a week in relatively large outdoor enclosures (1.5 m high×1 m wide×0.80 m deep), topped and surrounded by wire mesh in the Russian-Vietnamese Research Station inside the Park. During captivity, the animals were fed three times per day with arthropods and fruits. After 2 days of accommodation, each single animal was guided to the filming enclosure (0.70 m high×0.30 m wide×0.37 m deep), topped and surrounded by wire mesh, backed by a white non-reflective board and fronted by a glass window. The enclosure contained a variety of available substrates (tree branches) of variable diameters (from ≤2 mm to ≥10 cm) and inclinations (horizontal to vertical), whereupon each treeshrew was able to move freely. Artificial enclosures are always expected to limit positional options of animals. However, the goal of the current study was not to record positional diversity and substrate utilization by treeshrews, but to record foot positioning, posture and grasping modes in relation to substrate size and inclination. For these purposes, the availability of substrate diameters and inclinations was sufficient to guarantee all possible combinations to be tested.

Research on *Dendrogale murina* complied with the guidelines for the treatment of animals in behavioral research (ASAB/ASB 2012). All the experiments with live animals followed Vietnamese laws and were performed under the regulations of the Moscow State University Bioethics Committee adopted in the Russian-Vietnamese Research and Technology Center.

Filming and data collection

For the experimental procedure, we filmed each treeshrew intermittently for 3 h a day during 2 days. During video recording sessions we simultaneously used a digital Casio EX-F1 high-speed camera (300 fps, frame size 512×384 pixels) and a digital Panasonic HDC-SDT750 camera (50 fps, frame size 1920×1080 pixels). After the filming sessions, the animals were returned to their original enclosure and were subsequently released at the place where they were originally captured. The HD digital video files, totaling 18 h of recordings, were subsequently analyzed frame-by-frame on a PC for data collection. Slow motion video files were also used for clarifying foot postures and position and for analyzing the movement of pedal grasping modes. Treeshrews are rapid animals that move with a squirrel-like intermittent locomotor pattern. In order to assure independence of successive sampling events, we used a focal instantaneous sampling at 10-s intervals for recording a selection of variables (Martin and Bateson 1993). The recorded variables were: (a) substrate size categories, divided into small ($d \leq 5$ mm), medium ($5\text{ mm} < d \leq 20$ cm), large ($20\text{ cm} < d \leq 50$ mm) and very large ($d > 50$ mm), were based on average foot length of the study animals (27.5±0.8 mm, n=3); (b) substrate inclination, divided into horizontal (0°–22.5°), oblique (22.5°–67.5°) and vertical (67.5°–90°); (c) foot position, classified as plantigrade (entire plantar side is in contact with the substrate), semiplantigrade (distal tarsus, metatarsals and digits are in contact with the substrate) and digitigrade (only the digits are in contact with the substrate); (d) foot posture, recognized as eversion (foot is placed away from the median plane) and inversion (foot is directed towards the median plane); and (e) pedal grasp, characterized as hallucal (the adducted and apparently medially rotated hallux is opposed to the lateral digits that fully or partly embrace the substrate, Figure 1A), convergent (all digits converge to the median axis of the foot and fully or partially embrace the substrate, Figure 1B) and clawed (claws embedded on the substrate with toes held in an adducted or slightly abducted position, Figure 1C).

Statistical analysis

Each animal was sampled separately, but as the number of sampled individuals was small, we did not analyze their behavior individually in order to assure statistical robusticity. For this reason, we combined together all the individually collected data from every animal for subsequent analysis. In this case, a common problem is the autocorrelation of successive sampling events. Despite the fact that a 10-s interval guarantees independence of successive instants in fast moving animals, we wanted to address any shortcoming of this sort by a trimming procedure (see Youlatos and Samaras 2011). Thus, for the whole dataset we only considered every second bout (b, b+2), deleting each intermediate one (b+1). Following this trimming procedure, we obtained a total of 1542 instants. Differences among frequencies of behaviors within single substrate categories were tested using binomial and

Figure 1: Pedal grasping modes in *Dendrogale murina*: (A) hallucal grasp, (B) convergent grasp and (C) claw grasp.

χ^2 tests, whereas differences among frequencies of behaviors across substrate categories were calculated using log-likelihood G tests. p Values of 0.05 or less were regarded as statistically significant and only those are reported in the results section.

Results

The wild-caught smooth-tailed treeshrews moved freely and used all the available substrates within the filming enclosures. Quadrupedal walk/bound and climb were the more common locomotor modes, followed by leaping and clambering, whereas cling and stand were the main postures. During these activities, the foot mechanisms of *Dendrogale murina* showed significant variation related to substrate size and inclination (Table 1, Figures 2 and 3).

Semiplantigrady was the most frequent foot position on all substrate size and inclination categories (binomial test for each category: $p<0.001$, Figures 2 and 3). Additionally, rates of semiplantigrady decreased significantly when substrate size increased (small vs. large: G=8.7, p=0.013; medium vs. large: G=45.5, $p<0.001$; small vs. very large: G=6.7, p=0.035; medium vs. very large: G=27.9, $p<0.001$; large vs. very large: G=1.5, p=0.043; Table 1, Figures 2 and 3). Moreover, the semiplantigrade foot position dominated on horizontal substrates, but showed significantly lower, but still important, percentages of use on both vertical and oblique branches (horizontal vs. oblique: G=10.6, p=0.002; horizontal vs. vertical: G=7.7, p=0.008; oblique vs. vertical: G=2.2, p=0.034; Table 1, Figures 2 and 3). A digitigrade foot position was never observed.

The foot was mainly inverted on all substrate size categories (binomial test for every category: $p<0.001$; Figures 2 and 3). More precisely, it dominated on small and medium substrates, but decreased significantly on large and very large ones (small vs. large: G=1.7, p=0.421; small vs. very large: G=7.1, p=0.029; medium vs. large: G=17.8, $p<0.001$; medium vs. very large: G=65.9, $p<0.001$; large vs. very large: G=27.5, $p<0.001$), where foot eversion obtained the highest rates (Table 2, Figures 2 and 3). Regarding substrate inclination, foot inversion was dominant on all categories (binomial test for every category: $p<0.001$; Figures 2 and 3), with a significant decrease on vertical substrates (horizontal vs. oblique: G=2.6, p=0.280; horizontal vs. vertical: G=8.4, p=0.015; oblique vs. vertical: G=9.2, p=0.002; Table 2, Figures 2 and 3). Increased eversion on vertical substrates was related to vertical ascents,

Table 1: Percentages of use of different foot positions on different substrate size and inclination categories of *Dendrogale murina* (total n=1542).

Foot position	Substrate size				Substrate inclination		
	Small	Medium	Large	Very large	Horizontal	Oblique	Vertical
Plantigrade	0.0	5.4	33.5	27.3	3.6	28.9	22.5
Semiplantigrade	100.0	94.6	66.5	72.7	96.4	71.1	77.5
Digitigrade	0.0	0.0	0.0	0.0	0.0	0.0	0.0
n	433	441	418	250	484	363	695

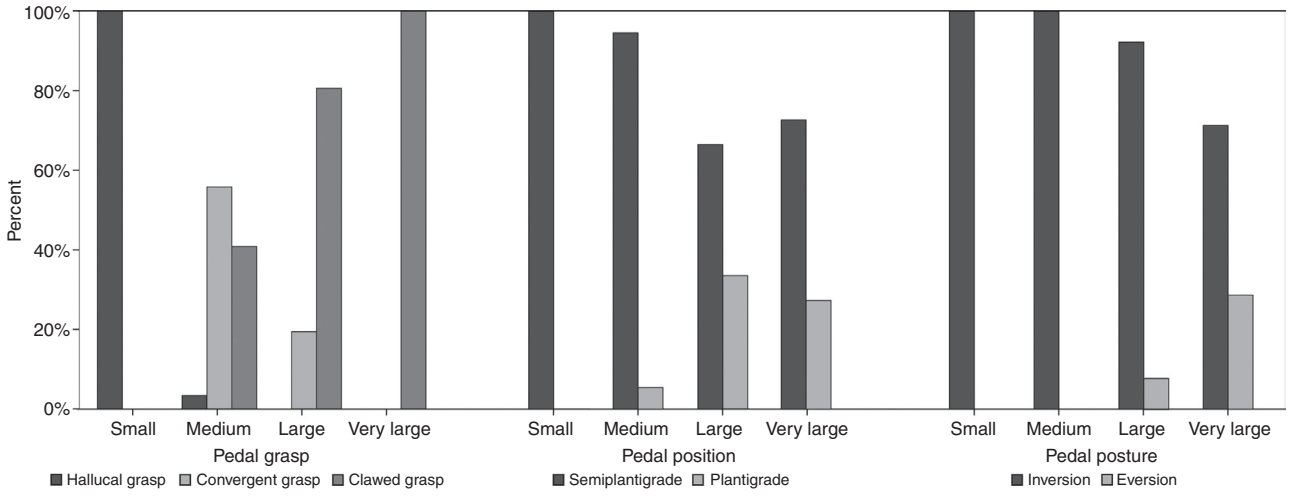

Figure 2: Percentages of use of different categories of substrate size during pedal grasping, pedal position and pedal posture in *Dendrogale murina* (small: d≤5 mm, medium: 5 mm<d≤20 cm, large: 20 cm<d≤50 mm, very large: d>50 mm).

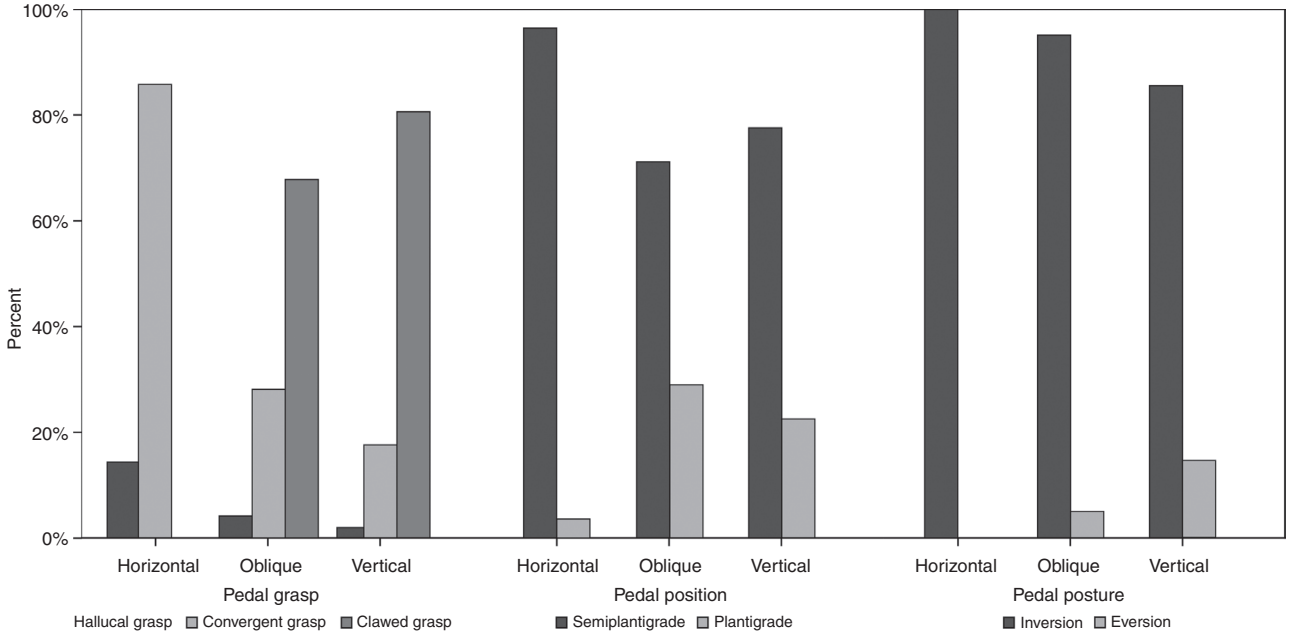

Figure 3: Percentages of use of different categories of substrate inclination during pedal grasping, pedal position and pedal posture in *Dendrogale murina* (horizontal: 0°–22.5°, oblique: 22.5°–67.5°, vertical: 67.5°–90°).

Table 2: Percentages of use of foot postures on different substrate size and inclination categories of *Dendrogale murina* (total n=1542).

Foot posture	Substrate size				Substrate inclination		
	Small	Medium	Large	Very large	Horizontal	Oblique	Vertical
Inversion	100.0	100.0	92.2	71.3	100.0	95.1	85.5
Eversion	0.0	0.0	7.8	28.7	0.0	4.9	14.5
n	433	441	418	250	484	363	695

where the foot was placed in an everted and plantigrade position. In contrast, during vertical descents, the foot was hyperinverted and supinated as in squirrels.

Hallucal grasping was the dominant mode on small substrates, but was weakly used on medium ones and was not observed on larger branches (small vs. medium:

G=59.9, p<0.001; small vs. large: G=87.1, p<0.001; small vs. very large: G=80.3, p<0.001; Table 3, Figures 1A and 2). Additionally, the moderate rates of hallucal grasp decreased significantly as inclination increased (horizontal vs. oblique: G=52.9, p<0.001; horizontal vs. vertical: G=84.3, p<0.001; Table 3, Figure 3). Convergent grasping was very frequent on medium (χ^2 test: p<0.001) and horizontal substrates (binomial test: p<0.001) with significantly lower percentages on larger and more inclined substrates (medium vs. large: G=63.5, p<0.001; medium vs. very large: G=160.4, p<0.001; oblique vs. vertical: G=8.2, p=0.016; Table 3, Figures 1B and 3). Claws were very frequently used on all substrate types, except horizontal and small ones (Table 3, Figures 2 and 3). They were the dominant grip type on large (binomial test: p<0.001) and vertical substrates (χ^2 test: p<0.001; Figures 1C and 3, Table 3), where they assured clinging and vertical progression.

Discussion and conclusions

Smooth-tailed treeshrews, *Dendrogale*, are considered the most basally divergent tupaiids, having diverged from the rest of the family at 34.77 mya (Butler 1980, Luckett 1980, Olson et al. 2004, 2005, Roberts et al. 2011). Their small body mass (~45 g), in combination with several cranial, dental, postcranial characters and mainly arboreal adaptations and behavior indicate their primitive nature (Davis 1938, Butler 1980, Luckett 1980, Szalay and Drawhorn 1980, Szalay and Dagosto 1988, Endo et al. 1999, Sargis 2002a,b,c, Kvartalnov 2009). Therefore, their phylogenetic position is very important for understanding pedal grasping evolution within euarchontan mammals. Our analysis of pedal grasping, position and posture of small-bodied diurnal arboreal Northern smooth-tailed treeshrews (*Dendrogale murina*) showed that the species mainly used a semiplantigrade inverted foot on most substrate categories and displayed a variety of grasping modes in relation to substrate features. Horizontal substrates were handled with a semiplantigrade, inverted and convergently grasping foot (Figure 2). High rates of claw use, increased rates of plantigrady and eversion were associated with vertical substrates (Figure 2). Larger substrates were negotiated with convergent and clawed grasp, and increased rates of plantigrady and eversion (Figure 1). In contrast, smaller substrates were grasped exclusively by the opposable hallux, in association with an inverted and semiplantigrade foot (Figure 1).

Dendrogale murina is an arboreal and semiterrestrial treeshrew that uses both the ground and the trees. When on the forest floor, they forage on and under the litter by running, bounding and jumping between roots and rocks (Kloss 1916, Kvartalnov 2009). A convergent, semiplantigrade and everted foot very likely assures rapid body displacement and foraging on the forest floor. However, even the forest floor may appear irregular and uneven for such a small mammal. In this case, proximal and midtarsal pedal mobility can help adjust the foot on similar irregularities, as is the case for *Tupaia glis* (Jenkins 1974, Schilling and Fischer 1999) and *T. minor* (Sargis 2001). Morphologically, this is supported by the mainly anteroposteriorly oriented calcaneal astragalar facet, the extensive distal articular surface of the calcaneal sustentacular facet, the continuum between the navicular and the sustentacular facet on the plantar surface of the astragalar head, and the round to semitrapezoidal calcaneocuboid joint (Szalay and Drawhorn 1980; Sargis 2002a), This same morphology may also facilitate efficient foot posture, position and grasping on variable, irregular and uneven arboreal substrates (Szalay and Drawhorn 1980, Sargis 2002a). Habitual inversion and a semiplantigrade foot position accommodate a firm hold of the foot on variably oriented slender substrates. Similar substrates abound in entanglements of twigs and bamboo stems, in the understories of forests, bushes, savannas and bamboo thickets, which are frequently exploited by Northern smooth-tailed treeshrews (Lekagul and McNeely 1977, Timmins et al. 2003, Kvartalnov 2009). More proximally, the long tibial crest, the long lesser and the shorter greater femoral

Table 3: Percentages of use of different pedal grasp modes on different substrate size and inclination categories of *Dendrogale murina* (total n=1542).

Pedal grasp	Substrate size				Substrate inclination		
	Small	Medium	Large	Very large	Horizontal	Oblique	Vertical
Hallucal	100.0	3.4	0.0	0.0	14.3	4.1	1.9
Convergent	0.0	55.8	19.4	0.0	85.7	28.1	17.5
Clawed	0.0	40.8	80.6	100.0	0.0	67.8	80.6
n	433	441	418	250	484	363	695

trochanters, and the spatulate ilium, in association with the well-developed mm. gluteus medius and semimembranosus, the long bundles of m. tenuissimus, the two bellies of m. biceps femoris and the strong development of m. gastrocnemius permit frequent hind limb flexion and abduction and foot plantar flexion and inversion (Davis 1938, Endo et al. 1999, Sargis 2002a,b).

This morphology seems to promote the necessary distal mobility that enables the pedal grasping diversity of *Dendrogale murina*. This grasping diversity probably relates to the generalized habits of the species. When on trees, northern smooth-tailed treeshrews climb along large vertical trunks in order to reach, walk on and clamber across clumps of slender bamboo stems and intertwined twigs of trees and bushes while foraging for cryptic arthropods (Timmins et al. 2003, Kvartalnov 2009). Large vertical substrates were handled mainly by claws and, to a lesser extent, a convergent grasp. As the circumference of such substrates is usually wider than the grasping width of the foot, they are impossible to grasp single-footed. In this case, embedded functional claws generally increase the frictional forces against the substrate and apply a firm hold of very wide substrates (Cartmill 1974). The robust metatarsals, the long and curved claws, and the well-developed mm. flexor digitorum superficialis and flexor digitorum longus of *D. murina* may provide the necessary equipment for such postures (Endo et al. 1999). This also allows upward clawed bounding on large vertical trunks enabling rapid vertical shifts within the forest. In addition, vertical descents are facilitated by the hyperabduction of the proximal tarsus in a manner similar to squirrels (Jenkins 1974, Jenkins and McClearn 1984, Sargis 2001). Medium-sized and inclined substrates were usually grasped by a convergent foot, where all digits, including the hallux, converged medially to form a clutch. On these occasions, the hallux is rarely abducted but remains either strongly adducted or slightly divergent on the upper side of the surface of the substrate. The two convergent feet are placed obliquely and laterally upon the substrate and both surround it, securing a double grip that permits a stable posture and safe body displacement (see also Jenkins 1974).

Behavioral observations from the wild report that smooth-tailed treeshrews usually forage on the slender stems of bamboo and in entanglements of twigs and lianas, where cryptic and mobile arthropods usually abound (Kvartalnov 2009). This active behavior requires secure handling and safe navigation upon uneven and unstable substrates, which is apparently achieved by hallucal grasping, assisted by a semiplantigrade and inverted foot. During our observations, the foot was usually used in this manner and the grasp appeared very secure and firm. However, we cannot assess as to whether it could be qualified as powerful. Nevertheless, it was efficient enough to enable the animals to safely handle and easily use small substrates. However, the fact that it was less used on wider substrates probably indicates that its grasping capacity may be restrained and likely limited to substrates that can be wholly surrounded by the grasping foot. If this holds true, grasping performance in the basally divergent tupaiid *Dendrogale murina* is relatively reduced compared to that reported for the more primitive, basally divergent scandentian *Ptilocercus lowii*. In effect, the nocturnal pen-tailed treeshrews are almost exclusively arboreal (Emmons 2000) and are characterized by proficient hallucal grasping on arboreal substrates, and this is supported by their pedal morphology. *Ptilocercus lowii* possesses an entocuneiform with a prominent plantar process and a markedly sellar-shaped distal facet, with a relatively large and broad facet lacking a medial expansion that allows significant hallucal mobility, albeit less than that encountered in euprimates (Szalay and Dagosto 1988, Sargis 2002a,b,c, Sargis et al. 2007). Additionally, the hallucal metatarsal is robust but lacks proximal peroneal and medial processes, denoting an open and mobile joint, and exhibits slight distal torsion, limiting the reorientation of the hallux against the lateral digits (Bloch and Boyer 2002, 2007, Sargis 2002a, Sargis et al. 2007). Finally, the distal hallucal phalanx is mediolaterally compressed and deep, associated with a functional claw (Sargis 2002a, Bloch and Boyer 2007). This morphology indicates efficient but non-powerful hallucal grasping and suggests a divergent hallux used in a hook-like manner against the rest of the foot (Jenkins 1974, Sargis 2001, 2002a, Bloch and Boyer 2007). Unfortunately, despite the body of literature dealing with scandentian hallucal functional morphology, data on the anatomy of the foot of *D. murina* are missing (Szalay and Drawhorn 1980, Szalay and Dagosto 1988, Sargis 2002a,b). This is particularly important, as other tupaiids exhibit reduced hallucal grasping capacity (Jenkins 1974, Sargis 2001). Morphologically, the restricted distal facet of the entocuneiform, the smaller plantar process (also found in *D. melanura*), and the mediolaterally restricted proximal facet of a relatively long hallucal metatarsal suggests reduced proximal hallucal abduction which seems to be regulated more distally, at the metatarsophalangeal joint (Sargis 2002a,b). This condition suggests a secondarily developed grasping ability as it appears to favor a relatively stable hallux contributing primarily to non-arboreal locomotion (Sargis 2002a).

It is uncertain to what extent these morphological attributes related to restrained hallucal divergence and

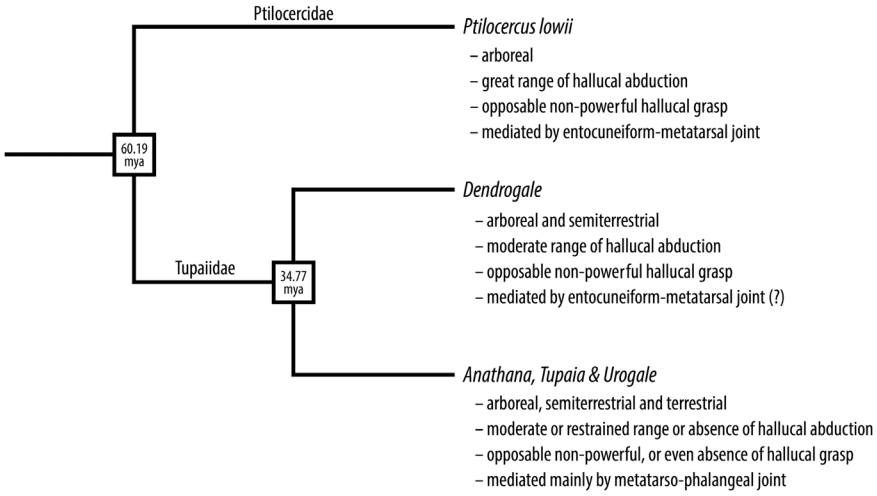

Figure 4: Behavior, range of hallucal abduction, grasping capacity, and the way it is mediated of *Ptilocercus lowii*, *Dendrogale murina* and the rest of tupaiid scandentians plotted on the tree proposed by Roberts et al. (2011) on the phylogenetic relationships of Scandentia.

grasping are found in *Dendrogale murina*. Their basally divergent phylogenetic position within the family Tupaiidae (Olson et al. 2004, 2005, Roberts et al. 2011), small size (Davis 1938, Sargis 2002b), primarily arboreal habits (Kvartalnov 2009), and hallucal grasping capacity, as demonstrated in the present study, suggest that smooth-tailed treeshrews should demonstrate a more derived intermediate pedal morphology towards a certain degree of hallucal stability. Besides, a similar degree of intermediate morphology is also evident in some morphological features of the fore- and hind limb, such as the carpus, pelvis, proximal femur, proximal tibia, tarsus, and metatarsals, which are related to arboreal habits and are reminiscent of those of *Ptilocercus*, whereas others indicate affinities with the other, more terrestrially adapted, tupaiids (Davis 1938, Riesenfeld 1974, Endo et al. 1999, Sargis 2002a,b,c,d). In this way, we assume that *Ptilocercus lowii* of the primitive family Ptilocercidae represents an ancestral condition (within euarchontans and consequently scandentians) with increased hallucal abduction mediated mainly by the entocuneiform-metatarsal joint (Figure 4). Accordingly, we consider that *D. murina* probably represents an early stage in the evolution of the family Tupaiidae, where the primitive *Ptilocercus*-like non-powerful hallucal grasping tends to become slightly restrained (Figure 4). In this condition, the primitive wide range of rotations in hallucal abduction, as observed in *Ptilocercus*, are now limited in a way to permit effective grasping of small branches, whereas wider substrates require a safer convergent grasp engaging both feet and even the functional claws. In this way, hallucal grasping in *D. murina* may not be as effective but is likely homologous to that of *P. lowii*. More derived tupaiids, which tend to become more terrestrial, exhibit even more restricted hallucal grasping ability at the level of the entocuneiform-metatarsal joint, but compensate on the abductive motion of the metatarso-phalangeal joint (Sargis 2002a, Figure 4). In this way, the grasping mechanism of *D. murina* may likely be analogous to that exhibited in the other tupaiids, in which, hallucal grasping may represent a secondary adaptation (see Sargis 2002a). However, a thorough study of the pedal anatomy of *D. murina* will surely shed more light on scandentian hallucal grasping evolution, and its plasticity within euarchontan evolution. In all cases, this further highlights the strong relation between a hallucal grasping mechanism and the frequent and primary use of small slender substrates (Byron et al. 2015, Youlatos et al. 2015). This substantiates the pivotal role and importance of pedal grasping evolution and plasticity for the diversification of the euarchontan groups that subsequently led to primates.

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