



Original investigation

Integrating locomotion, postures and morphology: The case of the tayra, *Eira barbara* (Carnivora, Mustelidae)

Marcos D. Ercoli^a, Dionisios Youlatos^{b,*}

^a Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, CONICET, IdCyM, Av. Bolivia 1661, Y4600GNE, San Salvador de Jujuy, Jujuy, Argentina

^b Aristotle University of Thessaloniki, School of Biology, Department of Zoology, GR-54124, Thessaloniki, Greece

ARTICLE INFO

Article history:

Received 24 February 2016

Accepted 9 June 2016

Handled by Vera Weisbecker

Available online 11 June 2016

Keywords:

Appendicular skeleton

Eira barbara

Evolution

Mustelidae

Positional behavior

ABSTRACT

Locomotion and postures are key factors to understanding the biology of animals. However, scansorial and arboreal carnivorans remain poorly studied regarding these issues. Herein, we present a behavioral and morphological analysis of the arboreal locomotion of the tayra (*Eira barbara*), a neotropical forest-dwelling mustelid. Data on habitat use and locomotor and postural modes were collected from free-ranging tayras in a terra-firme forest in French Guiana. Additionally, qualitative morphological traits and linear measurements of the girdles and appendicular skeleton were analyzed through comparative anatomical descriptions, univariate tests, and a principal components and discriminant analysis. Tayras frequently used clambering, quadrupedal walking, claw climbing and quadrupedal standing, performed primarily on small and medium, oblique and horizontal branches. Furthermore, our morpho-functional analyses revealed that tayras possess autopodial specializations for navigating on arboreal substrates, while the more proximal elements present features more similar to other terrestrial or scansorial mustelids, and theoretically less modified from the hypothetical weasel-like ancestor of mustelids. This mosaic of morphological features of the tayra, a combination of phylogenetic inertia and ecological signals, very likely evolved to promote the efficient and effective exploitation of diverse habitats and resources in this versatile species.

© 2016 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Locomotion and postures appear to largely contribute to the access and manipulation of food sources, the search for mates, and the escape from predators imposing a decisive effect on the survival of individuals. In this way, any differences in locomotor and postural patterns usually reflect differences in the biology of the animals that exhibit them. On the basis of differences in the overall locomotor behavior (e.g. substrate use), some researchers like Van Valkenburgh (1987) grouped the members of the order Carnivora in three categories. Exclusively terrestrial carnivorans move, forage, feed and rest on the ground. On the other hand, scansorial or semi-arboreal carnivorans spend most of their time on the ground but forage and exploit arboreal food sources. Lastly, arboreal carnivorans rarely use the ground and mainly move, forage and shelter on trees. Compared to terrestrial carnivorans, scansorial and arboreal species exhibit a wider variety of locomotor (e.g. walking, running, clawed climbing, leaping, clambering) and postural (e.g. sitting, crouching, standing, hanging) patterns (Gambaryan, 1974; Taylor, 1989; Hildebrand, 1995). In an effort to scrutinize these variables (posture, agility, gaits), some other researchers (e.g., Gambaryan, 1974; Schutz and Guralnick, 2007; Álvarez et al., 2013) have assayed other categories such as “half-bonders”, “ambulatorials”, “cursorials”, “ricochetals”.

Despite the critical importance of the behavioral studies to understanding ecological and morpho-functional aspects of a species, few studies have focused on the locomotor and postural behavior of carnivorans, especially of scansorial and arboreal species (Taylor, 1970; Trapp, 1972; Laborde, 1986; McClearn, 1992). These studies were qualitative and marked the dominance of quadrupedal walking and standing, claw climbing on vertical trunks and clambering on slender supports for some procyonid and viverrid species (Taylor, 1970; Trapp, 1972; Laborde, 1986; McClearn, 1992; Rozhnov et al., 1992). Such studies are useful in documenting the variety of locomotor and postural patterns of arboreal and scansorial carnivorans, but more detailed quantitative data would help elucidate the adaptive significance of the variety

* Corresponding author.

E-mail addresses: marcosdarioercoli@hotmail.com (M.D. Ercoli), dyoul@bio.auth.gr (D. Youlatos).

of critical and frequent modes that they have evolved in relation to the use of the arboreal habitat.

In an attempt to contribute to the understanding of the associations between skeletal morphology and limb function in carnivorans, we studied the postcranial anatomy of a neotropical mustelid carnivoran, the tayra, *Eira barbara* (Linnaeus, 1758), in association with first-hand preliminary field observations of its locomotor and postural arboreal behavior. Tayras are mainly diurnal, agile, medium-sized (3–7 kg), omnivorous, forest dwelling mustelids which exploit equally the forest floor and the canopy, chasing instead of ambushing their prey, composed mainly of small mammals, other vertebrates and insects (Kaufmann and Kaufmann, 1965; Brosset, 1968; Kavanau, 1971; Bisbal, 1986; Emmons, 1990; Nowak, 1991; Presley, 2000; Bezerra et al., 2009; Wilson and Mittermeier, 2009; Delgado-V et al., 2011; Soley, 2012). Behavioral field observations of tayras are very scarce in the literature. Tayras frequently move with their back arched, can walk, trot and gallop on the ground and can easily claw climb up and down vertical trunks, move on large branches in the same way as on the ground and can clamber or hang by all four limbs from smaller branches when foraging in trees (Kaufmann and Kaufmann, 1965; Brosset, 1968; see also Dagg, 1973; Presley, 2000; Bezerra et al., 2009; Delgado-V et al., 2011; Soley, 2012). The diurnal habits of the tayra allow detailed observations on the time allocated to different patterns of locomotion or postural habits under natural conditions, a prospect difficult to accomplish for many other scansorial carnivorans, which are mainly cryptic and nocturnal.

Moreover, *Eira barbara* appears to be a good and interesting case study of a scansorial mustelid. Although it is only present from the Pleistocene or later, in the fossil record (see Cartelle, 1999), the tayra lineage probably diverged much earlier from the other gulonines, very likely during the late Miocene (Eizirik, 2012). This species possibly represents the most basal living member of the subfamily Guloninae, a clade that diverged relatively early during mustelid evolution and contains the mainly scansorial martens and the wolverine (Koepli et al., 2008; Eizirik, 2012). In contrast to living gulonines, the ancestral form of the family Mustelidae has been associated with terrestrial weasel-like forms, predators of fossorial rodents. In relation to this, some morpho-functional aspects of the gulonine gait has been linked to a weasel-like ancestor (Gambaryan, 1974). In general, various postcranial traits have been frequently associated with diverse locomotor and postural patterns (Maynard Smith and Savage, 1956; Ginsburg, 1961; Gambaryan, 1974; Taylor, 1974, 1976, 1989; Jenkins and Camazine, 1977; Savage, 1977; Van Valkenburgh, 1987). More specifically, tayras have been included in several functional comprehensive studies, analysing its appendicular elements by either linear measurements (Yalden, 1970; Holmes, 1980; Van Valkenburgh, 1987; Iwaniuk et al., 2001) or geometric morphometric techniques (Andersson, 2004; Schutz and Guralnick, 2007; Ercoli et al., 2012; Fabre et al., 2013; Ercoli, 2015). All these studies, for virtually all analyzed elements, have identified features that group tayras with arboreal or scansorial carnivorans, whereas some other traits were more linked to terrestrial weasel-like forms (e.g. the cervical and thoraco-lumbar vertebral osteology; Ercoli, 2015). In general, the postcranial morphology of *Eira barbara* is more similar to that of *Martes* and secondarily of *Gulo*, both its closest parents, compared to other scansorial or arboreal musteloids (Holmes, 1980; Fabre et al., 2013; Ercoli, 2015). Compared to other mustelids, the long bones of *Eira barbara* are elongated, the scapula presents a rounded contour, the olecranon is short, the manus is large, with a wrist and intracarpal articulations that allow a great range of movements and mobile phalanges with curved claws, and the ilium forms a low angle with the rest of the pelvic bone, features generally interpreted as related to climbing and fast running abilities (Yalden, 1970; Holmes, 1980; Van Valkenburgh, 1987; Fabre et al., 2013; Ercoli, 2015).

Robust links between morphology and behavior require integrated studies of functional correlates and locomotor and postural modes in free-ranging mammals. The limb movements and frequencies of these modes provide information on frequent and critical functions of postcranial elements, and consequently on the associated anatomical correlates. The combination of morphological functional analyses with quantitative field observations of locomotion and postures further provides a framework for understanding the adaptive significance of morphological complexes and their importance within evolutionary radiations. In this context, the goal of the present report is to investigate, through a comparative analysis, the functional anatomy of postcranial correlates of *Eira barbara*, in association with preliminary quantitative field observations of the locomotion and postures of the species in the wild. This will provide information on the adaptive significance of anatomical complexes and ultimately contribute to the understanding of morphological evolution in mustelid carnivorans.

Material and methods

Field observations

The field study was conducted by one of us (DY) at the 'Station des Nouragues' site (4° 05'N, 52° 40'W) within the Nouragues Reserve in French Guiana. This site represents a 160 ha hilly zone which is mainly characterised by lowland wet high rain forest with patches of transitional, low, liana and pina palm forests. Annual rainfall varies from 3000 to 3250 mm and the mean annual temperature is 26.1 °C. The dominant plant families are the Ceasalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae. The site is described in detail in Bongers et al. (2001).

The data presented here were collected between July and September 1993 (transitional and early dry season; rainfall = 356 mm) during a field study on arboreal mammalian diversity in the site. Forest trails were walked daily in equal parts of morning (6–12 a.m.) and afternoon (12–6 p.m.) shifts. Although, tayras spend most of their time on the ground, this study focuses on arboreal behavior that corresponds mainly to feeding and foraging activities (Emmons, 1990; Nowak, 1991). Whenever a tayra was located on a tree, the animal was followed discreetly from the ground observing its behavior with a pair of binoculars. The focal animal instantaneous sampling method was applied (Martin and Bateson, 1993) using 20-s intervals determined by a stopwatch to record the following variables: (i) estimated height where the animal moved, (ii) estimated height of tree, (iii) branch size, (iv) branch orientation, and (v) locomotor or postural mode. Data collection started as soon as the animal was first spotted on a tree and lasted until the animal was definitely lost from sight.

The height of the location of the animal and the height of the tree were visually estimated with the help of a range finder. Branch size and orientation classes were based on published work on the positional behavior of arboreal primates (Cant et al., 2003). Branch sizes were classified according to a visually estimated diameter (d): (i) Small: $d \leq 2$ cm; (ii) Medium: $2 \text{ cm} < d \leq 10$ cm; (iii) Large: $d > 10$ cm. Branch orientation classes were: (i) Horizontal: angle between 0°–22.5°, (ii) Oblique: angle between 22.5°–67.5°; (iii) Vertical: angle between 67.5°–90°. Locomotor modes were defined as follows: (i) Quadrupedal Walk: slow four-limbed horizontal body displacement on a single branch involving regular swing and stance phases in short strides; (ii) Quadrupedal Run: fast four-limbed horizontal body displacement on a single branch using asymmetrical or irregular gaits; (iii) Clamber: horizontal or diagonal four-limbed body displacement in all directions across multiple diversely oriented branches with irregular limb movements; (iv) Claw Climb: upward and downward vertical climb using the claws; (v) Leap:

gap-crossing mode where propulsion is provided by simultaneous extension of the hind limbs, involving an extended airborne phase. The recorded postural modes were: (i) Crouch: sitting posture where the ischia bear a substantial proportion of body weight and the body is held semi-erect; (ii) Quadrupedal Stance: posture in which the body is supported by all four limbs at a variable crouch and the body is kept parallel to the branch; (iii) Bipedal Stance: forelimb-assisted posture with fully or semi-erect body that is supported by the two hind limbs at variable crouch.

During the surveys, tayras were encountered on three occasions on different locations of the site. Pelage marks suggested that they represented different individuals. As the number of individuals was small and encounters usually lasted less than 30 min each, the collected data were lumped and analyzed together. Data collected by instantaneous sampling are presented in the form of tables where every row corresponds to a different independent instant or count and every column to a specific recorded variable. In order to avoid interdependence between successive counts we retained only every second instant (i.e. i and $i + 2$). After this trimming process, the final sample consisted of a total of 667 locomotor and postural instants. Percentages of different behavioral variables were compared with the log-likelihood ratio G -test using a criterion of $p < 0.05$ (Zar, 1996).

Morpho-functional study

For the comparative study of postcranial adaptations, we analyzed the skeletons of three adult specimens of *Eira barbara* and of several carnivoran species with known locomotor habits in order to trace qualitative and quantitative differences that could be associated with functional attributes related to terrestrial, scansorial, and arboreal ways of life. Thus, the terrestrial carnivorans examined were: *Conepatus chinga* ($n = 5$), *Galictis cuja* ($n = 5$), *Meles meles* ($n = 2$); Scansorial: *Martes foina* ($n = 4$), *Nasua nasua* ($n = 2$), *Procyon lotor* ($n = 2$); Arboreal: *Arctictis binturong* ($n = 4$), *Nandinia binotata* ($n = 6$), *Potos flavus* ($n = 6$). All the studied skeletons were adult specimens and were housed in the Laboratoire des Mammifères et Oiseaux and the Laboratoire d'Anatomie Comparée, of the Muséum National d'Histoire Naturelle in Paris (MNHN), the División Mastozoología of the Museo Argentino de Ciencias Naturales in Ciudad Autónoma de Buenos Aires (MACN), and the Sección Mastozoología of the Museo de La Plata in La Plata (MLP).

Detailed qualitative comparisons were carried out between these species, which were also completed with metric analyses. Nine linear measurements were taken on the bones of the forelimb of the examined carnivorans: (i) SCH: scapular height, from the glenoid cavity to the vertebral border, (ii) SCW: scapular craniocaudal width, (iii) HW: humeral mediolateral width at midshaft, (iv) HL: humeral length, from the head to the distal edge of trochlea, (v) OL: olecranon length, (vi) UL: total ulnar length, from the proximal olecranon to the styloid process, (vii) BT: distal position of the radial bicapital tuberosity, from the proximal end of radius to the distalmost extension of the tuberosity, (viii) RL: total radial length, (ix) MC3L: metacarpal III length. In addition, ten linear measurements were taken on the bones of the hind limb: (i) ISC: ischial craniocaudal length, (ii) PEL: total pelvic craniocaudal length, (iii) FL: femoral length, from the head to the trochlea, (iv) FW: femoral mid-shaft width, (v) TL: total tibial length, (vi) TPAP: anteroposterior length of the tibial condylar plateau, from the proximal end of the tibial tuberosity to the caudalmost end of the tibial condyles, (vii) TPML: mediolateral width of the tibial condylar plateau, (viii) PCFL: proximal calcaneotalar facet proximodistal length, (ix) CL: calcaneal maximal proximodistal length, and (x) MT3L: metatarsal III length. Finally, we also calculated eleven ratios: SCH/SCW, HW/HL, OL/UL, BT/RL, ISC/PEL, FW/FL, TPAP/TPML, RL/HL, TL/FL, RL/TL, HL + RL/FL + TL. Univariate comparisons between *Eira* and the

Table 1

Frequencies of use of branch size and orientation classes by *Eira barbara* in French Guiana.

Branch Size	Branch Orientation	
	counts	%
Small	275	41.2
Medium	331	49.6
Large	61	9.2
Sample size	667	100.0

Branch Orientation	Branch Orientation	
	counts	%
Horizontal	203	30.4
Oblique	380	57.0
Vertical	84	12.6
Sample size	667	100.0

arboreal, scansorial, and terrestrial groups were performed using non-parametric Mann-Whitney U tests (Zar, 1996), and a criterion of $p < 0.05$ was adopted.

A set of complementary analyses was performed in order to obtain a quantification of the morphological differentiation between compared species and locomotor groups. To an exploratory quantitative approximation of the differentiation between locomotor groups and species, we performed a between-groups Principal Component Analysis (bgPCA; Mitteroecker and Bookstein, 2011). Centered ratios for each species (mean values of each species minus the mean value of the ratio) and for each specimen of *Eira barbara* were projected onto eigenvectors of a morphospace that maximize the differences between *a priori* defined groups (instead of maximizing the differences between samples, as in a standard PCA analysis). These *a priori* defined groups correspond to the three initially defined locomotor groups (i.e., arboreal, scansorial, and terrestrial). To obtain these eigenvectors, the first step was to calculate the mean values of each index for each locomotor group. The eigenvectors were then calculated from the matrix containing the ratios variance/covariance among groups. The factor loadings of each index variable for each PC axis were obtained performing sequential Pearson's Correlations. The femoral trochlea height/weight ratio (FW/FL; see Table 3), was excluded from this analysis as it appeared to deteriorate rather than enhance the group segregation in the morphospace.

Subsequently, we performed a discriminant analysis in order to assess a statistical approximation of the degree of separation among locomotor groups, and to calculate probabilities of classification of the specimens of *Eira barbara* to the predefined locomotor groups. We used only the first two axes of the bgPCA as explanatory variables, because these two axes are sufficient to resume the 100% of the morphological differentiation between any three groups. On the other hand, we used locomotor behavior (with the three locomotor groupings; i.e., arboreal, scansorial, terrestrial) as the categorical variable. The statistical performance of the discrimination of species by groups was accomplished by a cross-validation procedure. Explanatory and discriminant analyses were performed in R 2.14.1 (R Development Core Team, 2013) with the MASS library (Venables and Ripley, 2002).

Results

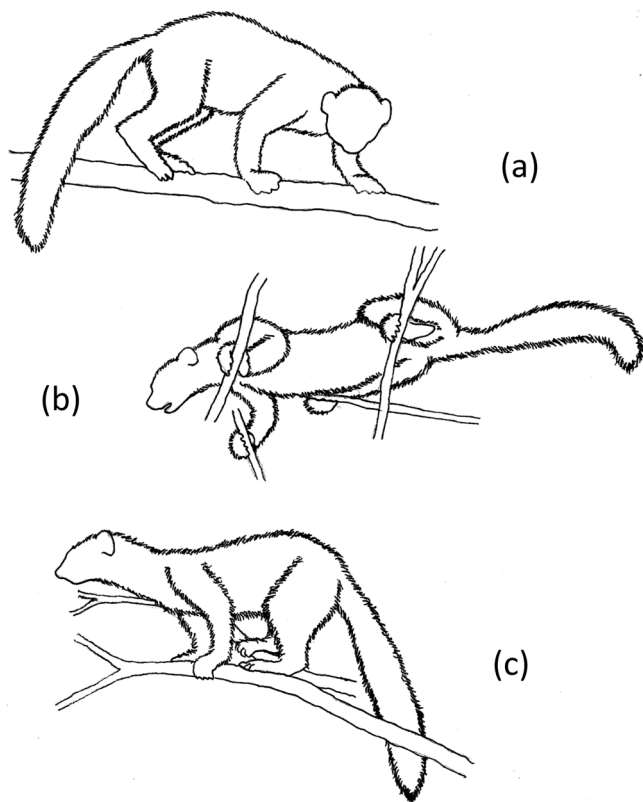
Field observations

Tayras were encountered on three occasions, twice in the afternoon shifts and once in the morning shift. The animals foraged in the canopy at heights ranging between 10m–23 m (median = 20m) on trees with heights between 15 m and 25 m (median = 23m). During arboreal activities the use of medium-sized and small branches was quite frequent and oblique branches were very commonly used (Table 1).

In terms of postural behavior, quadrupedal stance was the dominant posture (Fig. 1c; Table 2). It occurred almost equally frequently on small and medium-sized branches (52.3% and 46.3% respectively of the quadrupedal stance subsample $n = 231$, $G = 16.6$, $p < 0.001$).

Table 2
Frequencies of use of arboreal locomotor and postural modes by *Eira barbara* in French Guiana.

	counts	%
Locomotor Modes		
Quadrupedal Walk	104	15.6
Quadrupedal Run	31	4.6
Clamber	114	17.1
Claw Climb	81	12.2
Leap	1	0.2
Postural Modes		
Quadrupedal Stance	231	34.6
Bipedal Stance	101	15.1
Crouch	4	0.6
Sample size	667	100.0

**Fig. 1.** Positional modes of Guianan tayras: (a) quadrupedal walk, (b) clamber; (c) quadrupedal stance (drawings from 35 mm photographs).

During this posture, the forelimbs were flexed at the elbow and the arms were slightly abducted (Fig. 1). The forefeet were placed transversely on small branches and were ulnarly deviated on the larger ones. The hind limbs were flexed at the knee joint. The thighs were slightly abducted and the hind feet inverted on the branch. Regarding the other postures, bipedal stance and crouch were not frequently used (Table 2).

Clamber was the most frequent locomotor mode (Table 2). It was primarily used on small branches (87.7% of the clamber subsample, $n = 114$, $G = 177.2$, $p < 0.001$). Limb movements were irregular and cautious and appeared to depend on the location and flexibility of the available branches (Fig. 1b). At higher speeds, tayras were more awkward. The arm and thigh were slightly abducted. The forearms were pronated and flexed at the elbow and were oriented in the sagittal plane. Similarly, the thighs were flexed and feebly abducted, the knee joints were maintained flexed and the hind feet were inverted and supinated.

Quadrupedal walk was less frequent (Table 2). Lateral gaits were used almost exclusively (97.2% of the quadrupedal walk subsample, $n = 104$). Walk occurred mainly on medium-sized branches (75.0% of the quadrupedal walk subsample, $n = 104$, $G = 96.9$, $p < 0.001$). The body was maintained parallel to the branch (Fig. 1a). Strides were short and quick. Arm abduction was minimal. The elbow joints were never fully extended and the forefeet were ulnarly deviated. The knees were mainly flexed while the shanks were kept in the sagittal plane. The hind feet were usually inverted.

Claw climb represented a moderate proportion of the repertoire of tayras (Table 2). It permitted swift vertical ranging between the ground and the canopy, as well as within the canopy. During clawed vertical ascents, the trunk was grasped with the moderately abducted forelimbs and hind limbs, markedly flexed at the elbow and knee joints respectively, keeping the body relatively close to the trunk. The body was propelled upwards by the hind limbs and simultaneous release of the forelimbs to reach a higher handhold, in a bounding manner. Clawed vertical descents were always headfirst and consisted of a series of flexions and extensions of the vertebral column (i.e., vertical looping). The body was kept close to the trunk with all limbs acting as brakes. Both forelimbs and hind limbs were abducted and the hind feet were inverted and hypersupinated.

Comparative descriptions of the appendicular skeleton

This section compares the morphology of selected fore- and hind limb postcranial features of tayra with that of arboreal, scansorial and terrestrial carnivorans in order to identify joint and limb functions related to specific locomotor and postural modes.

The scapular outline in *Eira* is intermediate between rectangular and ellipsoid, similar to that of *Martes*, and scansorial

Table 3

Centered mean values (i.e. mean value of each ratio for each species minus mean value of the ratio) of each ratio for each species used in the between-groups principal components analysis (values for *Eira barbara* are calculated for each specimen).

	SCH/SCW	HW/HL	OL/UJL	BT/RL	ISC/PEL	FW/FL	TPAP/TPML	RL/HL	TL/FL	RL/TL	HL + RL/FL + TL
Comparative sample											
<i>Arctictis binturong</i>	-19.691	-0.566	1.817	2.021	-1.225	0.249	-6.223	-2.398	-8.655	11.955	9.790
<i>Nandinia binotata</i>	-0.667	0.258	2.819	2.934	2.018	0.420	-9.554	-3.109	-0.572	-6.329	-4.733
<i>Potos flavus</i>	-22.109	0.459	-0.511	3.425	-3.900	0.996	-11.122	-1.543	0.286	-0.538	0.602
<i>Conepatus chinga</i>	12.217	1.066	4.311	-5.045	-8.710	1.492	5.863	6.209	7.151	-4.177	-4.777
<i>Galictis cuja</i>	5.554	-0.072	2.668	4.166	2.641	0.039	9.508	-12.478	-2.258	-7.664	-2.136
<i>Meles meles</i>	6.127	1.370	2.731	-1.218	-0.456	0.154	7.549	1.300	-8.965	10.657	6.375
<i>Martes foina</i>	-1.199	-1.401	-2.431	-1.773	-4.018	-1.318	-9.683	-2.600	13.892	-9.230	-3.825
<i>Nasua nasua</i>	-2.844	0.247	2.589	0.216	2.936	-0.222	5.523	2.245	-2.009	1.003	-0.908
<i>Procyon lotor</i>	5.023	-0.998	-4.380	-3.009	2.933	0.029	7.352	21.574	16.012	1.908	-1.713
<i>Eira barbara</i>											
MLP 1013	9.891	-0.631	-3.198	-1.217	3.908	-1.037	-2.414	-3.315	-6.419	0.581	-0.333
MNHN 1985-157	2.879	0.354	-3.134	0.303	0.455	-0.047	1.993	-1.922	-3.369	1.855	1.655
MNHN 1973-148	4.819	-0.086	-3.282	-0.803	3.419	-0.754	1.207	-3.962	-5.095	-0.020	0.004

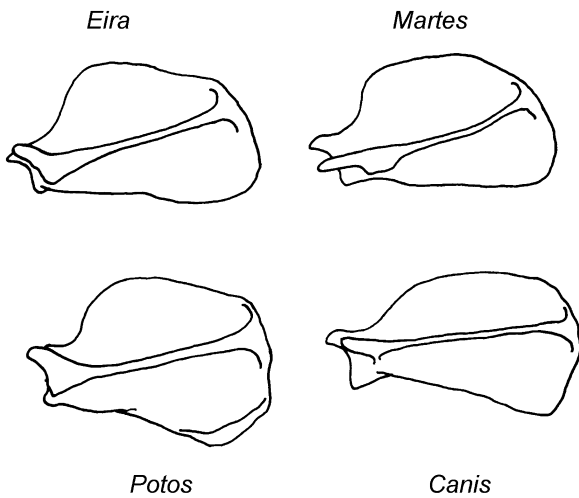


Fig. 2. Lateral view of the scapulae of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

procyonids (Fig. 2), but also similar to the terrestrial mustelid *Galictis*. The scapular form index confirms this similarity that further characterises most quadrupedal mammals (Table 3). This form is intermediate between some terrestrial species (e.g. *Conepatus*) and cursors (e.g. canids) that possess narrower scapulae and that of more specialist climbers (e.g. *Arctictis*, *Potos*) with fan-shaped scapulae (Fig. 2; Table 3, arboreal vs. terrestrial: $z = 3.09$, $p < 0.001$). Arboreal feliforms, like *Nandinia*, possess a morphology intermediate between scansorial and the remaining arboreal forms. Contrary to terrestrial or climber species that frequently perform bounding gaits (e.g. *Martes*, *Galictis* and, in a lesser degree, *Nandinia*), the metacromion process is relatively reduced in *Eira* and other carnivorans of the sample. In *Eira*, as well as in the majority of other scansorial species, and, in a major degree, arboreal ones, the acromion process is ample and tilts cranially with respect to the spine of the scapula. This feature is clearly different from that present in terrestrial species, and in the scansorial bouncer *Martes*, in which this process is more reduced and/or with a lesser tilt. The humeral head of *Eira* is typically located more proximally than the lateral and medial tuberosities, a condition found in many arboreal and scansorial carnivorans (but not present in *Nandinia* and *Martes*; Fig. 3). The deltoid ridge of *Eira* is similar to that of *Martes* in being a

rough, moderately or poorly salient area. This contrasts the prominent ridge of some terrestrial species, like the cursorial *Canis* and the fossorial *Meles*, and the more developed or well defined deltoid crest of the other studied carnivorans (Fig. 3). The humeral shaft of *Eira* is round in section and relatively robust, similar to that of arboreal, scansorial and terrestrial forms (Table 3). On the distolateral surface of the shaft, the supinator crest is relatively well developed in the proximodistal direction, and moderately flares laterally in *Eira* (Fig. 3); while the medial epicondyle is well developed, similar to the majority of other scansorial species. The same structures are typically larger in all the arboreal forms, *Nasua*, and in terrestrial fossorial forms, like *Conepatus* and *Meles*, but poorly developed in the cursorial *Canis* (Fig. 3). The morphology of *Eira* can be considered as intermediate between these two extremes. The distal articulation of the humerus of *Eira*, as well as of all the scansorial and terrestrial non-cursorial forms, including all the mustelid representatives, presents an intermediate morphology. This morphology lies between that of arboreal species, with a particularly reduced trochlea and a rounded capitulum (e.g. *Arctictis*, *Potos*) and of cursorial species, with a widely developed trochlea and a developed and cylindrical capitulum (e.g. *Canis*).

In the ulna, the olecranon process of *Eira* is very similar to that of scansorial species like the mustelid *Martes* and the procyonid *Procyon*, but clearly differs from *Nasua*, in being moderately to poorly developed (Table 3) and oriented slightly anteriorly or straight (Fig. 4). The latter feature is shared by all the studied mustelids irrespective of habits. In arboreal carnivorans analyzed, the olecranon and proximal shaft are oriented further anteriorly, and the olecranon is significantly smaller (Table 3; terrestrial vs. arboreal: $z = -2.23$, $p = 0.0257$). In contrast, it is long, robust and posteriorly oriented in more cursorial species (Fig. 4; Table 3). The entire diaphysis of the arboreal and terrestrial fossorial forms shows ample development, with wide and rough surface on both medial and lateral sides, whereas these surfaces are restrained in other carnivorans, including *Eira*, and extremely reduced, in their distal part, in the terrestrial cursorial *Canis*. On the anterior surface of the distal ulna, *Eira* bears a distinct pronator crest. A similar condition is encountered in most arboreal carnivorans, while cursorial species lack any crest (Fig. 4). The diarthroidal surface is markedly separated from the ulnar diaphysis and styloid process in *Eira* and arboreal forms, is less marked in other scansorial forms, and even less in terrestrial species.

The radial head of *Eira* is elliptical to rounded, with a slightly concave proximal articular surface bearing a small ridge on the

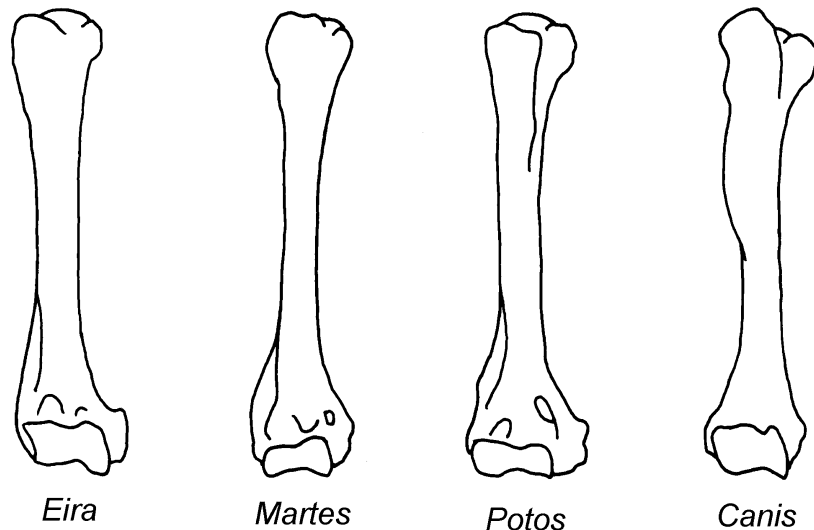


Fig. 3. Anterior view of the humeri of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

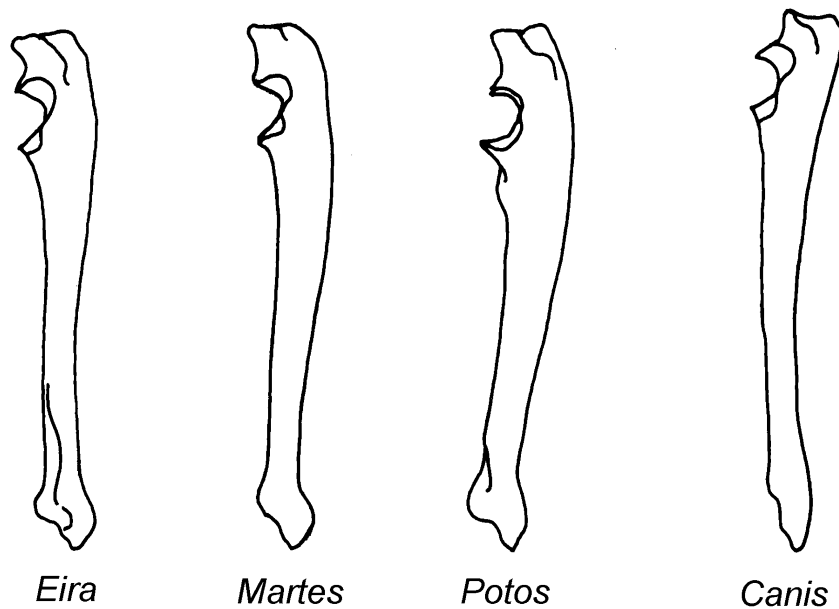


Fig. 4. Medial view of ulnae of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

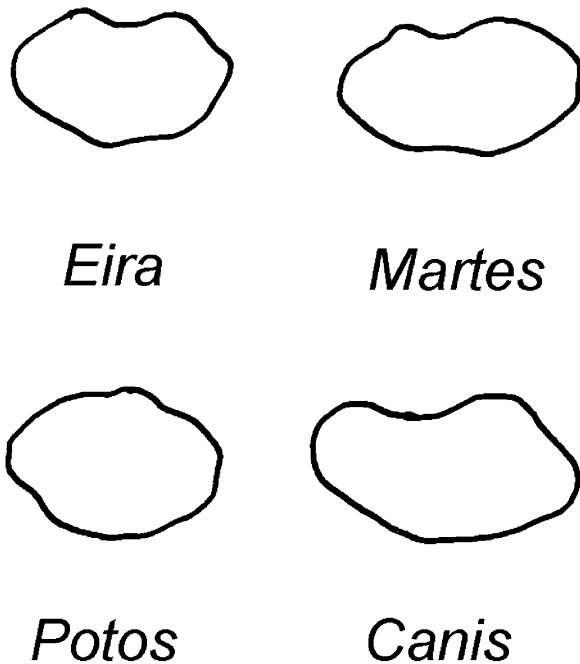


Fig. 5. Outline of the proximal view of the radial head of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

anterior margin, similar to the morphology of most scansorial and arboreal carnivorans (Fig. 5). However, there exists some variation within the scansorial group, with more rounded and smooth heads, similar to arboreal species, as in *Procyon*, and more elliptical and mediolaterally elongated ones, as in *Nasua*. By contrast, terrestrial species possess a mediolaterally extended elliptical to quadrangular head characterised by a deeply excavated proximal articular surface with a conspicuous anterior ridge. The bicapital tuberosity, is relatively distally located in arboreal carnivorans (terrestrial vs. arboreal: $z = -2.48$, $p = 0.0128$), but also in the short-legged terrestrial mustelid *Galictis*, whereas its location is quite variable in other forms, including *Eira* (Table 3).

The forefoot of *Eira* has been already described in detail by Yalden (1970) and Ercoli (2015). The carpal arrangement and intrinsic

articulations of *Eira* include a lateromedially ample proximal carpal series, expanded by a laterally tilted accessory bone and an ample radial sesamoid, and an expanded articular surface without abrupt boundaries in the proximal aspect of the radial bone (which articulates with the radius) and in the proximal surface of the fourth carpal (hamatum) for the ulnar bone. These features have been associated with arboreal tendencies (Yalden, 1970; see also Holmes, 1980). Howell's (1965) metacarpal III/humerus ratio scored a mean of 28% for *Eira*, which is identical to the value of the arboreal plantigrade *Potos*, and similar to the values of plantigrade viverrids (Taylor, 1974). Confirming Ercoli's (2015) observations, we also found a relatively low value of metacarpal III/phalanx III for *Eira*, intermediate between arboreal species, like *Potos* and *Nandinia*, and other gulonines (e.g., *Martes*). There exist some interesting variations in the proportions of metacarpals. Most terrestrial carnivorans tend to possess compact and lateromedially compressed carpal series, and long and more slender metacarpals. On the other hand the arboreal *Potos* and *Arctictis*, as well as *Eira*, possess quite equally developed metacarpals (i.e. the first and fifth metacarpals are not reduced; Fig. 6), while the arboreal *Nandinia* and other scansorial and terrestrial species display significant dissimilarity in metacarpal development.

In the pelvis, the relatively long ischium of *Eira*, is similar to other scansorial species and terrestrial mustelids (Table 3). On the other hand, some arboreal climbers, terrestrial cursors (canids), or ambulatory species (mephitids) possess variably different ischia and our ratio of ischial to pelvic length indicates a wide range of values for each class (Fig. 7; Table 3). The orientation of the plane of the ilium in respect to the ischio-pubic plane is also variable. *Eira* presents an intermediate configuration between bounding species (*Galictis*, *Martes*, and *Nandinia*, with an acute angle between the two planes), while other carnivorans display an angle close to or over 90°. Arboreal and scansorial carnivorans also share a very well developed ischial spine, especially *Potos*, *Nandinia*, *Eira* and *Martes*, and in a lesser degree, *Nasua* and *Procyon*, while this process is typically more reduced in terrestrial species.

The femoral head of *Eira* is similar to *Martes*, in being quite round, hemi-spherical, with transitional limits with the femoral neck (especially at the dorsal aspect), whereas the climbing *Nandinia*, *Potos* and *Arctictis* and procyonids, bear even rounder heads (Fig. 8). In contrast, the femoral head of terrestrial species tends to

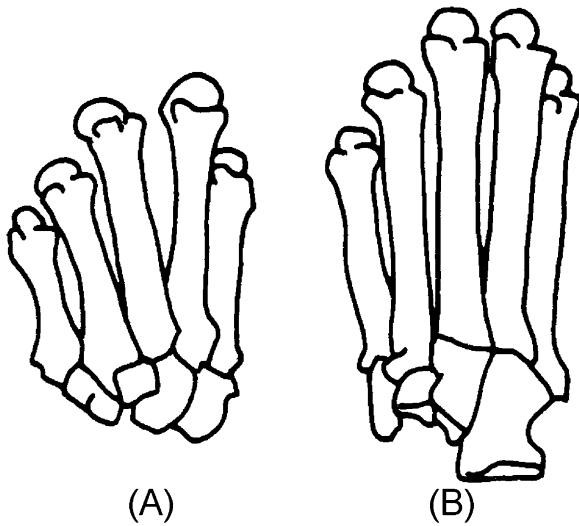


Fig. 6. Dorsal view of distal carpal and metacarpals (A) and distal tarsals and metatarsals (B) of *Eira*.

possess more abrupt limits and a more medial position in respect with the major axis of the diaphysis, due to a longer neck. The shape and position of the lesser trochanter is variable, even within each locomotor group. The studied terrestrial mustelids present a very posteriorly oriented lesser trochanter (e.g., *Galictis*), while mephitids and canids present a more medially tilted process. Similar to other mustelids, *Eira* possesses a posteromedially tilted lesser trochanter, as is the case of other scansorial mustelids (e.g. *Martes*) and the arboreal *Nandinia*. Finally, many arboreal (*Potos*, *Arctictis*) and scansorial (e.g. procyonids) species, possess a medially tilted lesser trochanter. A common feature to all scansorial and arboreal species, including *Eira*, is that the lesser trochanter is located proximally, near the femoral head (Fig. 8). In *Eira*, the femoral head is slightly more elevated or similar in height in respect to the major trochanter, as is typical of many scansorial and arboreal carnivorans. In contrast, cursorial terrestrial species possess an enlarged proximal trochanter. The femoral shaft of *Eira* is relatively slender, comparable to scansorial carnivorans and differs significantly from the more robust femora of arboreal ones (Table 3; $z = -2.16$, $p = 0.0303$). On the distal femur of *Eira*, the femoral trochlea is rel-

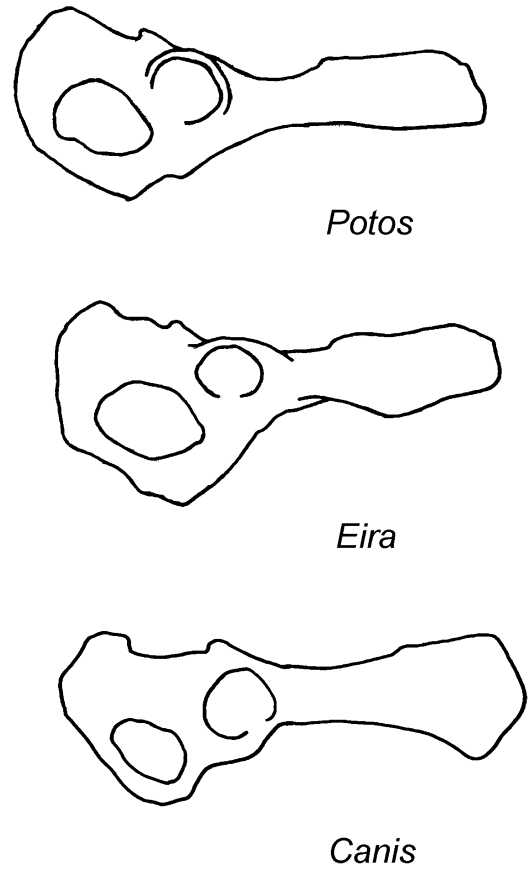


Fig. 7. Lateral view of the bony pelvis of *Potos* (arboreal), *Eira*, and *Canis* (terrestrial).

atively wide with moderately developed ridges similar to other climbing carnivorans (Fig. 8). The arboreal climber *Potos* possesses a much wider and lower trochlea with shallow groove and blunt mediolateral ridges, whereas many terrestrial forms are characterised by high, narrow trochleas with prominent ridges and a deep groove (Fig. 8).

The tibial condylar plateau of *Eira* is moderately craniocaudally deep, a condition similar to that of the other scansorial and terrestrial musteloids analyzed (i.e. *Galictis*, *Meles*, *Nasua*, *Procyon*,

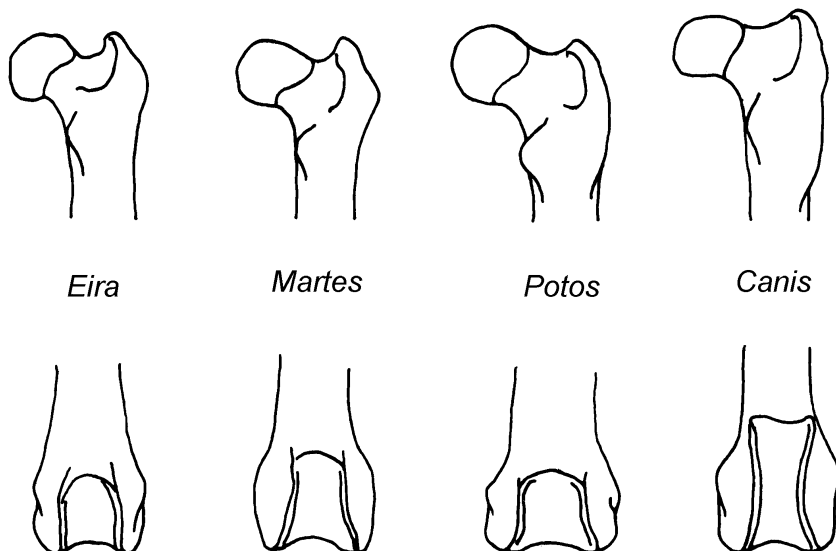


Fig. 8. Posterior view of the proximal femur (top row) and anterior view of the distal femur (bottom row) of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

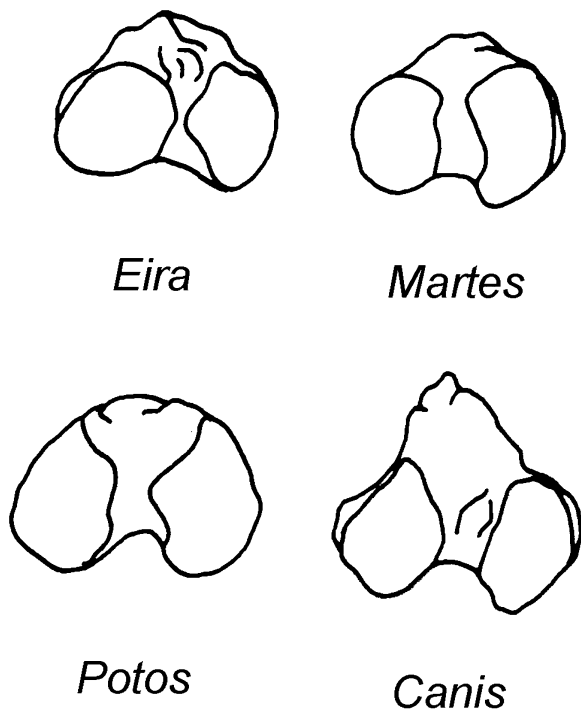


Fig. 9. Proximal view of the tibial plateau of *Eira*, *Martes* (scansorial), *Potos* (arboreal), *Canis* (terrestrial).

Conepatus, and to lesser degree *Martes*; Fig. 9; Table 3). On the other hand, arboreal climbers like *Potos*, and to a lesser degree *Nandinia* and *Arctictis*, possess a flattened and mediolaterally wide plateau marking a significantly lower ratio (Table 3; arboreal vs. scansorial: $z=2.08$, $p=0.0372$). In contrast, cursorial and, in a lesser degree, other terrestrial carnivorans possess a craniocaudally deep tibial condylar plateau with a marked tibial (patellar) tuberosity (Fig. 9; Table 3, terrestrial vs. arboreal: $z=4.16$, $p<0.0001$). Furthermore, *Eira* and all the scansorial and arboreal species studied shared the presence of a well developed scar for the medial collateral ligament.

On the dorsal surface of the talus in *Eira*, as well as in other non cursorial-forms, the lateral trochlear crest is higher than the medial one (Fig. 10). In arboreal climbers (*Potos*) the talar trochlea wedges more distinctly proximally contrasting that of cursorial *Canis*, marked by two equally high parallel ridges (Fig. 10). The trochlear groove of *Eira* is moderately deep similar to other scansorial and arboreal carnivorans (e.g., *Arctictis*, *Martes* and procyonids), and intermediate between the shallower trochlea of terrestrial musteloids (especially *Conepatus*), and the deeper trochlea of cursorial *Canis*. The talar neck in *Eira* is moderately medially deviated, similar to other musteloids, and relatively longer, similar to other scansorial mustelids, but not to scansorial procyonids. On the other hand, arboreal climbers possess a similar or even more marked projection and medial deviation of the talar neck, whereas cursorial carnivorans are distinguished by a very weak medial deviation (Fig. 10). In *Eira*, the ectal surface is ample, and the sustentacular surface is very convex and tilts medially. A similar condition is encountered in other scansorial and arboreal species, exacerbated in *Nandinia* and procyonids, but especially in *Potos*. Contrary to that, the ectal surface of terrestrial forms is less ample and the sustentacular surface is flatter and ventrally orientated, facing fully ventrally in canids and mephitids.

On the dorsal surface of the calcaneus of *Eira*, the proximal calcaneotalar facet is proximodistally elongate, a condition similar to other carnivorans (Fig. 10), except of the cursorial species (i.e. *Canis*). On the distal calcaneus, the calcaneocuboid facet of *Eira* is dorsoplantarly low, shallow, and faces mainly distodorsally

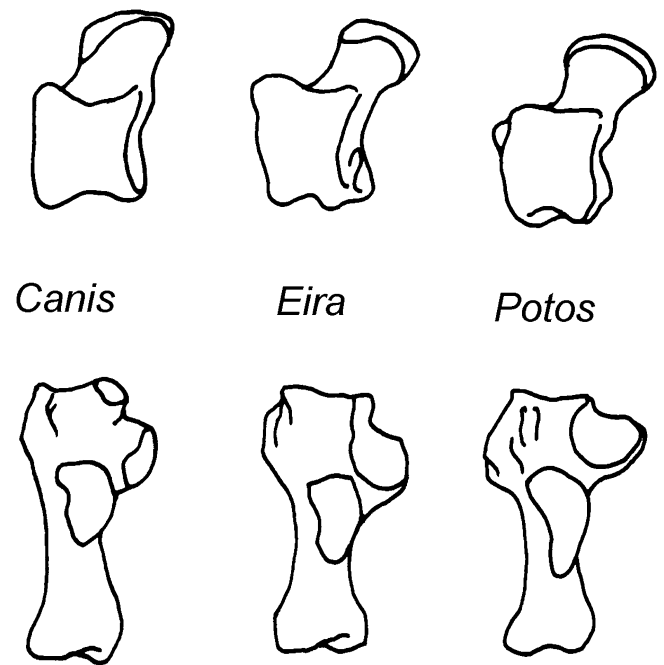


Fig. 10. Dorsal view of the tali (top row) and calcanei (bottom row) of *Canis* (terrestrial), *Eira*, and *Potos* (arboreal).

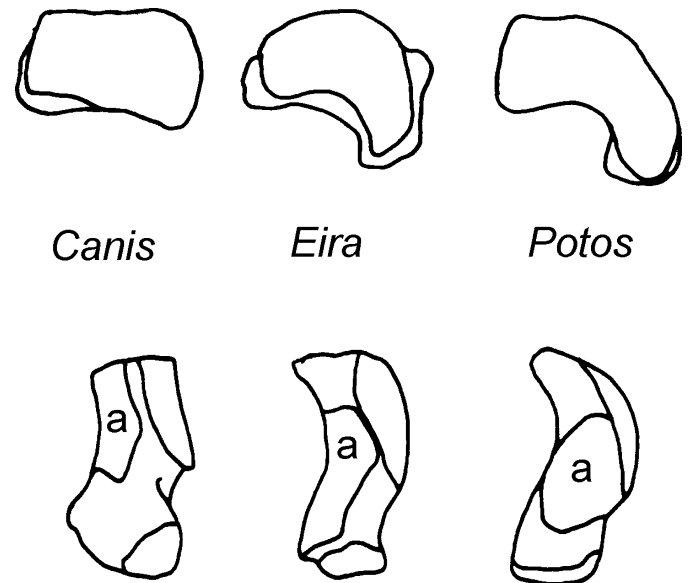


Fig. 11. Proximal view of the cuboidocalcaneal facet on the proximal surface of the cuboid (top row) and lateral view of the naviculocuboid facet (a) on the lateral surface of the navicular (bottom row) of *Canis* (terrestrial), *Eira*, and *Potos* (arboreal).

(Fig. 11). The facet articulates with the corresponding proximal cuboid facet that is equally low, smoothly convex, and presents a lateroplantar extension yielding an asymmetrical outline. The trochlear process, on the laterodistal region of the calcaneum is well developed in *Eira*, a typical feature of other musteloids, present in all the scansorial and arboreal carnivorans analyzed, and variable in terrestrial ones.

The naviculocuboid facet of *Eira*, on the lateral surface of the navicular, is extensive and located in the middle of the bone (Fig. 11). *Potos* bears a similar facet (Fig. 11) but this is not the case of other arboreal quadrupedal carnivorans (*Nandinia*, *Paradoxurus*). In contrast, *Canis* possesses a reduced facet located more dorsally (Fig. 11). The navicular bone of *Eira* is similar to that of arboreal carnivoro-

Table 4
Factor loadings of the between-groups principal components analysis for each ratio.

Index	PC 1	PC 2
SCH/SCW	0.946	0.044
HW/HL	0.112	0.479
OL/UL	-0.051	0.405
BT/RL	-0.654	0.424
ISC/PEL	0.121	0.230
FW/FL	-0.085	-0.023
TPAP/TPML	0.773	0.171
RL/HL	0.366	-0.744
TL/FL	0.343	-0.926
RL/TL	-0.264	0.312
HL + RL/FL + TL	-0.477	0.469

rans and scansorial procyonids in possessing a particularly high and proximally projecting dorsal wall, surrounding the distal aspect of the metatarsals vary from short and equally developed (e.g. fossorial plantigrade or semidigitigrade species, such as *Conepatus* and *Meles*) to relatively long central elements and gracile peripheral ones (e.g. generalized as *Galictis*), or the loss of digit I (e.g. cursorial *Canis*). Howell's (1965) ratio of metatarsal III length/femoral length scored a mean of 33% for *Eira*, similar to those of other hind foot plantigrade carnivorans (Howell, 1965; Taylor, 1976).

All the metatarsals of *Eira* are relatively robust, but not medio-laterally waisted, as those of many arboreal carnivorans (Fig. 6). The metatarsals are long in relation to the rest of the hind foot, and the peripheral metatarsals (first and fifth) are not reduced compared to the central ones, a condition similar to other scansorial and arboreal species. In terrestrial species, the robustness and relative length of the metatarsals vary from short and equally developed (e.g. fossorial plantigrade or semidigitigrade species, such as *Conepatus* and *Meles*) to relatively long central elements and gracile peripheral ones (e.g. generalized as *Galictis*), or the loss of digit I (e.g. cursorial *Canis*). Howell's (1965) ratio of metatarsal III length/femoral length scored a mean of 33% for *Eira*, similar to those of other hind foot plantigrade carnivorans (Howell, 1965; Taylor, 1976).

Principal component analysis

In the bgPCA, the first two principal components explained 100% of the total variation among groups (PC1: 73.24%; PC2: 26.76%). Towards the positive side of PC1 are located those forms with high values for SCH/SCW, HW/HL, ISC/PEL, TPAP/TPML, RL/HL, and TL/FL; and low values for OL/UL, BT/RL, FW/FL, RL/TL, and HL + RL/FL + TL. In this way, from the negative to the positive side of the axis, the analyzed species tend to possess elongated long bones, especially the distal and posterior elements, long ischia and tibial condylar plateaus, short moment arms of the principal elbow flexor/extensor, robust humeri and slender femora (Table 4; Fig. 12). Towards the positive side of PC2 are located the forms with high values for SCH/SCW, HW/HL, OL/UL, BT/RL, ISC/PEL, TPAP/TPML, RL/TL, and HL + RL/FL + TL, and low values for FW/FL, RL/HL, and TL/FL. In this way, from the negative to the positive side of the axis, the analyzed species tend to display high scapulae, robust humeri, slender femora, long moment arms of the principal elbow flexor/extensor, long ischia and tibial condylar plateaus, short distal elements of the limbs, and anterior limbs longer than the posterior ones (Table 4; Fig. 12).

The arboreal forms are located on the negative side of PC1. Terrestrial species tend to cluster on the central or positive side of PC1 and PC2, whereas scansorial ones tend to locate on the central or negative sides of PC1 and PC2. Considering the two main axes, there is no superposition in the distribution of each locomotor group, but *Nasua nasua*, is positioned in the central part of both PC1 and PC2, at the transitional region of the morphospace between the three locomotor groups. The specimens of *Eira barbara* are located between the terrestrial and scansorial groups, near the scansorial procyonid *N. nasua* and the terrestrial mustelids *Galictis cuja* and *Meles meles*, but quite away from *Martes foina* (Fig. 12).

Table 5
Probabilities of reclassification of each carnivoran species and classification of *Eira* specimens resulting from the discriminant analysis with cross-validation (CV) procedure.

Species	Original classification	Reclassification using CV		
		Arboreal	Scansorial	Terrestrial
<i>Arctictis binturong</i>	Arboreal	98.6%	1.4%	0.0%
<i>Nandinia binotata</i>	Arboreal	0.3%	99.7%	0.0%
<i>Potos flavus</i>	Arboreal	99.4%	0.6%	0.0%
<i>Martes foina</i>	Scansorial	44.6%	55.3%	0.1%
<i>Nasua nasua</i>	Scansorial	17.3%	9.2%	73.5%
<i>Procyon lotor</i>	Scansorial	0.1%	97.4%	2.5%
<i>Conepatus chinga</i>	Terrestrial	0.0%	29.5%	70.5%
<i>Galictis cuja</i>	Terrestrial	0.0%	1.2%	98.8%
<i>Meles meles</i>	Terrestrial	0.1%	2.0%	98.0%
<i>Eira barbara</i>		classification		
MLP 1013	-	0.2%	8.0%	91.9%
MNHN 1985-157	-	1.5%	28.7%	69.8%
MNHN 1973-148	-	0.6%	15.7%	83.7%

The discriminant function analysis performed well, reclassifying in a correct manner 78% of the specimens (Table 5). Two exceptions were marked: the arboreal *Nandinia binotata*, classified as scansorial at 99% of probabilities, and the scansorial *Nasua nasua*, classified as terrestrial at 73% of probabilities (Table 5). The three specimens of *Eira barbara* were primarily classified as terrestrial (ranging from 70 to 92% of probabilities of correct assignment), and secondly as scansorial (ranging from 8 to 18%; Table 5).

Discussion

Locomotor and postural behavior of *Eira barbara*

The current study focused on arboreal behavior of tayras, which is related to foraging and traveling activities and characterises an important part of tayra biology (Kaufmann and Kaufmann, 1965; Brosset, 1968; Konecny, 1989; Presley, 2000). The present data, although they derive from a limited sample of observations, represent the first quantitative report on the arboreal locomotion and postures and substrate use of free-ranging tayras. Thus, they provide valuable information on frequent and critical modes and their associated limb and joint movements on specific substrates. In this way, they may be ultimately linked to the function of specific morphological complexes and help elucidate their adaptive significance.

Our observations showed that wild tayras use almost equally medium and small branches of mainly oblique orientation, where they stand, walk and clamber quadrupedally, as well as use their claws to negotiate up and down large vertical substrates. It is very likely that substrate availability in the site may have influenced these behaviors, but our preliminary data substantiate the ability of tayras to adequately exploit these substrates. Our observations seem to accord with similar quantitative data from captive animals, where walking and climbing/clambering were the dominant locomotor modes (Pereira and De Oliveira, 2010). Quadrupedal walk is the main mode of progressing along branches during traveling and foraging (Kaufmann and Kaufmann, 1965; Brosset, 1968; Delgado-V et al., 2011), which shifts to running and bounding and/or clambering during prey chasing (Kaufmann and Kaufmann, 1965; Galef et al., 1976; Bezerra et al., 2009; Delgado-V et al., 2011). Access to trees, vertical ranging, or escape behavior to the ground are assured by efficient upwards and downwards claw climbing, which is common to the species (Kaufmann and Kaufmann, 1965; Delgado-V et al., 2011). Although a primarily terrestrial mustelid, the flexible locomotor and postural behavior of tayras, as well as the

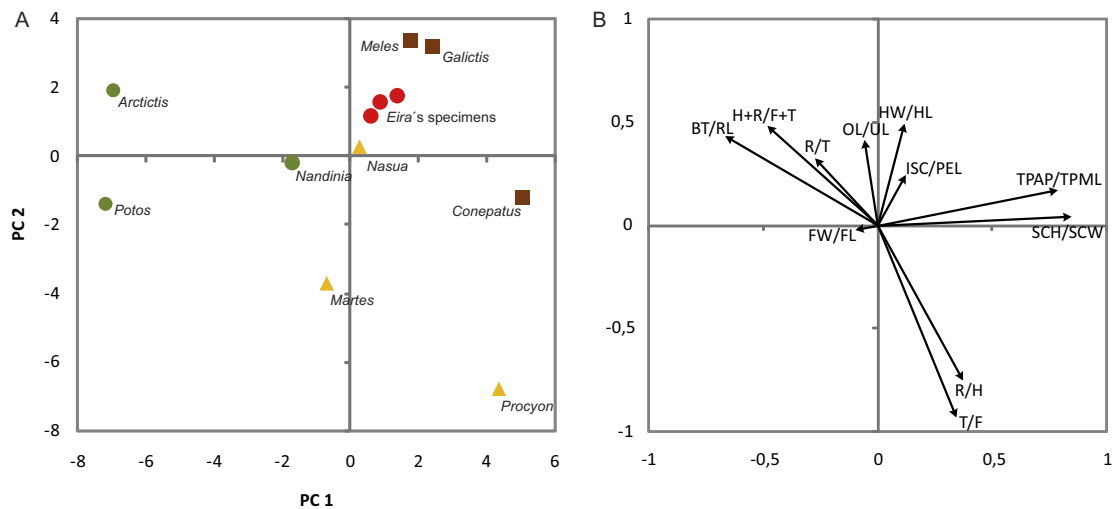


Fig. 12. Plot of the two first axes of the between-group PCA performed from the ratios listed in Table 3, showing the carnivoran species distribution and *Eira* specimens (a), and factor loadings (b).

use of different substrate categories supports the arboreal abilities of the species (Presley, 2000).

Traits of *Eira barbara* morpho-functionally related to terrestrial half-bounder habits

The typical short-legged, long and flexible body of the mustelids has been proposed as the ancestral condition for most of mustelid lineages, mainly as an adaptation linked to run after and pursue rodents in their own burrows, a confined space inaccessible to other predators (Gambaryan, 1974; King, 1989). The radiation of most of the living mustelid subfamilies (including gulonines) has been related to an aridity turnover of the global climate, during the middle-late Miocene (Koepfli et al., 2008). At that moment, forests retracted and open environments began to dominate, accompanied by a consequent proliferation of fossorial prey. Bounding locomotion, a style of sinuous gallop, in which the synchronized extension of the axial region and limb movements generate a sequence of jumps with an extended suspended phase, was a suitable solution to reach relative high-speeds during running for these long and short-legged mammals (Gambaryan, 1974; Moritz et al., 2007; Schutz and Guralnick, 2007; Horner and Biknevicius, 2010). In relation to this evolutionary scenario, it has been suggested that the ability of perform bounding gaits (e.g. high speed runs of *Gulo gulo*) or undulating movements (swimming of lutrines) has been retained in many mustelid taxa with various ecomorphs, along with the associated functional morphological traits (e.g. *Gulo*, Melinae, Lutrinae; Tarasoff, 1972; Gambaryan, 1974; Williams, 1983; Fish, 1994; Ercoli, 2015; Ercoli et al., 2015).

In this context, the appendicular morphology of *Eira barbara* shows a striking combination of features linked to the use of terrestrial or arboreal substrates and half-bounder or ambulatorial gaits. In effect, many morphological characteristics of the proximal elements of the fore- and hind limbs evidence a number of traits that fit more with a mainly terrestrial half-bounder ecomorph than carnivoran climbers. Among these traits are the shape of the humeral distal articulation, the proximodistally extended contact between the humeral trochlea and the anconeal process of the ulna, the absence of a cranially tilted olecranon, and, to a lesser degree, the not fully rounded shape of the femoral head. All these traits indicate that *Eira*, and secondarily other gulonines such as *Martes*, demonstrate a relative reduced range of non-parasagittal movements of the elbow and hip, and an unusually hyper-flexed elbow

posture (Taylor, 1974; Jenkins and Camazine, 1977; Leach, 1977; Van Valkenburgh, 1987; Iwaniuk et al., 1999; Argot 2003; Fabre et al., 2013). The multivariate analysis of the ratios, performed in this study, further support this assertion, as *Eira* was located closer to terrestrial, and more specifically to terrestrial mustelids, than to most of the climber species. More precisely, the relatively long ischium (high ISC/PEL value), the cranially projecting tibial tuberosity (high TPAP/TPML value), the robust humerus (high HW/HL value), and, secondarily, the short zeugopodial elements (low RL/HL and TL/FL, and high OL/UL values) are more similar to the values of terrestrial mustelids than to those of climbing species, even to the closely related, but more derived gulonine, *Martes*.

In addition, some specific anatomical traits, such as the wide supraspinal scapular fossa and the relatively narrow scapula, the overall shape and the relatively acute angle between the ilium and the ischium, the long and wide ischium, and the posteriorly oriented lesser trochanter of the femur are also shared by other mustelids (beyond locomotor habits), as well as by *Nandinia*, a non-mustelid half-bounder. During bounding gaits (but also in isolated jumps and vertical looping progression), a well developed m. supraspinatus, originating from an equally wide supraspinous fossa, in association with the restricted mobility of the shoulder and elbow at the parasagittal plane, absorb the effects of the reactive forces of the ground and prevent the collapse of the articulations during the forelimb landing phase (Gambaryan, 1974; Leach, 1977; Seckel and Janis, 2008). Additionally, the relatively parasagittal orientation of the ilium and the long ischium favor the growth and increase the moment arms of the principal extensors of the lumbar region (i.e. m. iliocostalis lumborum) and hip (i.e. hamstrings), which act on the sagittal plane for an effective propulsive phase of each bound (Gambaryan, 1974; Roberts, 1974; Williams, 1983; Álvarez et al., 2013; Ercoli et al., 2013, 2015). Moreover, the posterior (in terrestrial half-bounders) or posteromedial (in climbing half-bounders) orientation of the lesser trochanter, where flexor muscles of the lumbar region and hip are inserted (i.e. m. iliopsoas), further guide hip movements mainly to the parasagittal plane, in contrast to the more abducted actions of other climbers (Davis, 1964; Taylor, 1976; Jenkins and Camazine, 1977; Ercoli, 2015). These mainly unidirectional sagittal movements of the limbs in *Eira* were also substantiated by the behavioral observations. In effect, during postural behavior and in most gaits, the shoulder and hip did not exhibit marked abduction, while the elbow and knee avoided significant rotational movements. Relatively increased abduction

and rotation were rather infrequent and basically observed in crouched postures and during claw climbing and clambering.

Thus, the fact that the appendicular skeleton of *Eira barbara* shares many features with other mustelids and, in some cases, with non-mustelid half-bounder carnivorans, suggest a stronger, than expected, association with terrestrial and bounding gaits, despite the allegedly strong arboreal tendencies of the species. This is further supported by the anatomy of its axial skeleton, which is characterised by a long (in relation to limb length) and flexible thoraco-lumbar column (e.g., ample muscular attachments in detriment to ligament attachments in the spinous process of the thoracic region, slender and cranioventrally elongated transverse processes of the lumbar region), and a long and stocky neck (more similar to hypercarnivore musteloids rather than omnivore ones), indicating an ancestral link to a half-bounder weasel-like plan (Ercoli, 2015), as also indicated by our results. Contrary to the slower and controlled movements employed by many specialized stealthy predator or non-active predator climbers (Taylor, 1970, 1989; Argot, 2003), the bounding gaits employed by many active predator climbers can be considered as a versatile style of progression, because it is suitable for both terrestrial and arboreal substrates, allowing relatively agile and fast locomotion (Williams, 1983; Taylor, 1989). Bounding gaits are performed by ample flexion-extension movements of the axial region, reducing the stance phase and covering long distances quickly (Gambaryan, 1974; Williams, 1983; Taylor, 1989). This locomotor strategy is also used during vertical looping, which corresponds to vertical claw climbing (see Taylor, 1970, 1989), a vital behavior for entering or leaving the arboreal niche in *Eira*.

Interestingly, bounding carnivorans present many common features related to this gait, beyond the primary substrate used (Gambaryan, 1974; Williams, 1983). However, among those analyzed here, the arboreal predator *Nandinia binotata*, shares with other arboreal carnivorans some remarkable features, not present in half-bounder mustelid species, either terrestrial or scansorial. The cranially oriented olecranon at the elbow and wide and flattened tibial tuberosity at the knee suggest habitual fully flexed postures, that are more marked than those observed in fast half-bounder climbers (Taylor, 1974, 1989), and similar to the infrequent crouched postures of *Eira* (Table 2). Additionally, the relatively wide scapula, the supinator crest, and the medial epicondyle suggest a more marked development of joint stabilization muscles (e.g. rotator cuff of shoulder and m. anconeus, respectively), and powerful grasping (digital flexors), reflecting increase in strength, required to maintain the body close to the substrate, in order to assure safe navigation in the trees (Van Valkenburgh, 1987; Taylor, 1989; Argot, 2003). Our analyses revealed that these differences, related to the degree of flexion and stabilization of these joints, are more evident in the long bones between arboreal and non-arboreal half-bounder carnivorans.

Traits of Eira barbara morpho-functionally related to arboreal climber habits

In contrast to limb proportions and many qualitative traits of the proximal limb elements linked to terrestrial or half-bounder habits, many other traits in *Eira*, especially those of the fore- and hind foot, evidence clear arboreal adaptations. These traits differentiate *Eira* from terrestrial half-bounder mustelids, and in some cases are more marked than those encountered in other scansorial gulonines (e.g. *Martes*). Proximally, these arboreally related traits are the forward location of the acromion and the distally located and reduced metacromion, the relatively more rounded shape and transitional limits of the femoral head, the proximal position of the lesser trochanter, the slightly relatively wide femoral trochlea, and the more marked attachment of the medial collat-

eral ligament of the knee. The shape of the acromion of the scapula and the proximal femoral region indicate a relatively wider range of movements at the shoulder (extension and abduction) and hip (abduction and rotation) compared to those displayed by terrestrial half-bounder mustelids (Taylor, 1974, 1989; Jenkins and Camazine, 1977; Argot, 2003; Ercoli, 2015). On the other hand, the reduced and distally located metacromion is counter-indicative of a well developed and proximally located m. omotransversarius, a crucial shock-absorbing protractor of the forelimb during bounds (Seckel and Janis, 2008; Ercoli et al., 2015). These traits very likely represent clear deviations from the half-bounder specializations of the proximal limb elements of *Eira*, and are in agreement with the infrequent use of bounding gaits on arboreal substrates, and their limited use at high speed during terrestrial running (Kaufmann and Kaufmann, 1965; Brosset, 1968).

Many of the remaining features linked to arboreal locomotion are mostly concentrated on or directly affect the movements of the fore- and hind feet. These traits include the lateral location of the radius, the protruding diarthrodial articulation of the ulna, the configuration of the articular surfaces of the wrist, the subtalar and transverse tarsal joints, and the dorsodistally directed calcaneocuboid facet of the calcaneum. The arrangement of the wrist elements allows for a wide flexion-extension and ulno-radial deviations of the forefoot, while the subtalar and transverse tarsal joints of the hind foot show a wide range of rotational movements on the transverse and longitudinal planes, allowing inversion of the foot (Trapp, 1972; Taylor, 1976, 1989; Yalden, 1970; Jenkins and McClearn, 1984; Heinrich and Rose, 1997; Sargis, 2002; Candela and Picasso, 2008; Polly, 2010). Along with these ample non-sagittal movements, some other traits, such as the more prominent interlocking contact between carpal IV (=unciform) and the proximal carpal elements, and the wide contact between tarsal elements assured by the proximal protrusion of the cranial wall of the navicular, and the wide development of the carpus, with the robust radial sesamoid and ulnarly deviated accessory bone, and that of the tarsus, as well as the development of the peripheral digits, seem to enhance intercarpal and intertarsal contact and mobility, while increasing the contact surface with the substrate (Yalden, 1970; Antón et al., 2006; Salesa et al., 2006; Salton and Sargis, 2008). The fact that most arboreally related traits are concentrated on the distal elements is apparently linked to their direct contact with the arboreal substrates. This agrees with patterns of differential selection pressures in different anatomical regions, in which the physical properties of the substrate could be interpreted as a primary selective factor driving the evolution of autopodial configuration. In this way, the autopodial morphology of *Eira*, definitely highly specialized within the mustelids, allows the effective placement of the fore- and hind feet upon the arboreal substrates during the various postures and locomotor gaits, and more particularly during standing or clambering over randomly oriented branches [see also Taylor (1974) for viverrids], which is practically unachievable by terrestrial mustelids.

Conclusions

Links between morphology and behavior constitute an essential tool for understanding the biological roles and adaptive significance of morphological complexes that can ultimately contribute to the elucidation of evolutionary processes. In the present report, we attempted to associate a morphometric and qualitative functional anatomical analysis with a preliminary quantitative description of the locomotion and postures and limb movements of a scansorial mustelid carnivoran, the tayra *Eira barbara*. Although tayras basically travel terrestrially by walking or galloping, they also display a quite diversified positional repertoire in the trees. In

effect, our preliminary quantitative field observations of wild tayras revealed frequent quadrupedal standing, clambering, and walking, and critical vertical clawed climbing. These modes comprise limb movements that are slightly different in the degree of arm and thigh abduction, elbow and knee flexion, but differ largely in the degree of intrinsic mobility of the plantigrade fore- and hind feet.

The morphological and behavioral analysis of *Eira barbara* revealed traits that can be interpreted as a mixture of both phylogenetic inertia and functional/ecological signals. The species is considered to have derived from a terrestrial, half-bounder, weasel-like ancestral lineage (Gambaryan, 1974; Wayne et al., 1989) and it mainly travels terrestrially over long daily ranges (Kaufmann and Kaufmann, 1965; Brosset, 1968; Presley, 2000). In this way, many behavioral and morphological traits related to the girdles and long bones seem to be functionally linked to these modes related to terrestriality, and are less modified for arboreal climbing than other non-mustelid climbers. However, major modifications, from a hypothetical ancestral weasel-like body plan, associated with ample range of movements and related osteo-muscular morphology seem to have occurred on the distal appendicular elements, as adaptations to the direct interaction with the multidirectional and complex arboreal substrates. These combinations of traits, although partially opposing to an arboreal specialized carnivoran model, related to controlled and slow movements (typically present in many herbivore and omnivore climbing carnivorans), seem to provide the necessary agility for rapid explorations, chases and escapes among terrestrial and a wide range of arboreal substrates. This generalized outline provides tayras with the necessary morpho-behavioral versatility for an efficient and effective exploitation of diverse habitats and multiple resources that have very likely contributed to the wide range of the species across Central and South American forests.

Acknowledgements

The authors would like to thank the staff of the Laboratoire d'Anatomie Comparée and Mammifères et Oiseaux, MNHN, Paris, F. Renoult and J. Cuisin, the staff of the Mammalogy Division of the MACN, Dr. D. Flores, Dr. P. Teta, Dr. G. Cassini, and Mr. S. Lucero, staff of the Mammalogy Section of the MLP, Dr. D. Verzi and I. Olivares, and staff of the Mammalogy Division of The Field Museum of Natural History FMNH, Dr. B. Patterson, for granting access to osteological material. Fieldwork in French Guiana by D.Y. was made feasible through funds provided by the CNRS UMR 1137, and facilitated by Prof. J.-P. Gasc and Prof. P. Charles-Dominique. Special thanks go to Dr. Anne-Claire Fabre for her kind help during manuscript preparation. M. D. E. want to thanks Alicia Álvarez and Jeremías E. Tabora for their kind contribution during manuscript preparation, and to IOM for facilitating a trip to USA for visiting the FMNH collections. Finally, we wish to thank the two anonymous reviewers, as well as the editors for their valuable and constructive suggestions that greatly improved this manuscript.

References

- Álvarez, A., Ercoli, M.D., Prevosti, F.J., 2013. Locomotion in some small to medium-sized mammals: a geometric morphometric analysis of the penultimate lumbar vertebra, pelvis and hindlimbs. *Zoology* 116, 356–371.
- Andersson, K., 2004. Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zool. J. Linn. Soc.* 142, 91–104.
- Antón, M., Salesa, M.J., Pastor, J.F., Peigné, S., Morales, J., 2006. Implications of the functional anatomy of the hand and forearm of *Ailurus fulgens* (Carnivora, Ailuridae) for the evolution of the 'false-thumb' in pandas. *J. Anat.* 209, 757–764.
- Argot, C., 2003. Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mammalia, Metatheria), *Borhyaena* and *Prothylacinus*, from South America. *Palaeontology* 46, 1213–1267.
- Bezerra, B.M., Barnett, A.A., Souto, A., Jones, G., 2009. Predation by the tayra on the common marmoset and the pale-throated three-toed sloth. *J. Ethol.* 27, 91–96.
- Bisbal, E.F.J., 1986. Food habits of some neotropical carnivorans in Venezuela (Mammalia, carnivora). *Mammalia* 50, 329–339.
- Bongers, F., Charles-Dominique, P., Forget, P.-M., Thery, M., 2001. *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Forest*. Kluwer Academic Publishers, Dordrecht.
- Brosset, A., 1968. Observations sur l'éthologie du tayra *Eira barbara* (Carnivoran). *Terre Vie* 115, 29–50.
- Candela, A.M., Picasso, M.B.J., 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in Miocene porcupines. *J. Morphol.* 593, 552–593.
- Cant, J.G.H., Youlatos, D., Rose, M.D., 2003. Suspensory locomotion of *Lagotrix lagotricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador. *J. Hum. Evol.* 44, 685–699.
- Cartelle, C., 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In: Eisenberg, J., Redford, K.H. (Eds.), *Mammals of the Neotropics*, vol. 3. The University of Chicago Press, Chicago, pp. 27–46.
- Dagg, A.I., 1973. Gaits in mammals. *Mamm. Rev.* 3, 135–154.
- Davis, D.D., 1964. *The Giant Panda: A Morphological Study of Evolutionary Mechanisms*. Chicago Natural History Museum, Chicago.
- Delgado-V, C.A., Arias-Alzate, A., Botero, S., Sánchez-Londoño, J.D., 2011. Behaviour of the Tayra *Eira barbara* near Medellín, Colombia: preliminary data from a video-capturing survey. *Small Carniv. Conserv.* 44, 19–21.
- Eizirik, E., 2012. A molecular view on the evolutionary history and biogeography of neotropical carnivorans (Mammalia: Carnivora). In: Patterson, B.D., Costa, L.P. (Eds.), *Bones, Clones, and Biomes: An Extended History of Recent Neotropical Mammals*. The University of Chicago Press, Chicago, pp. 123–142.
- Emmons, L.H., 1990. *Neotropical Rainforest Mammals*. The University of Chicago Press, Chicago.
- Ercoli, M.D., Prevosti, F.J., Álvarez, A., 2012. Form and function within a phylogenetic framework: locomotory habits of extant predators and some Miocene Sparassodonta (Metatheria). *Zool. J. Linn. Soc.* 165, 224–251.
- Ercoli, M.D., Echarri, S., Busker, F., Álvarez, A., Morales, M.M., Turazzini, G.F., 2013. The functional and phylogenetic implications of the myology of the lumbar region, tail, and hind limbs of the lesser grison (*Galictis cuja*). *J. Mammal. Evol.* 20, 309–336.
- Ercoli, M.D., Álvarez, A., Stefanini, M.I., Busker, F., Morales, M.M., 2015. Muscular anatomy of the forelimbs of the lesser grison (*Galictis cuja*), and a functional and phylogenetic overview of Mustelidae and other Caniformia. *J. Mammal. Evol.* 22, 57–91.
- Ercoli, M.D., 2015. *Morfología del aparato músculo-esquelético del postcráneo de los mustélidos (Carnivora, Mammalia) fósiles y vivientes de América del Sur: implicancias funcionales en un contexto filogenético*. PhD Thesis. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata.
- Fabre, A.-C., Cornette, R., Slater, G., Argot, C., Peigné, S., Goswami, A., Puydebat, E., 2013. Getting a grip on the evolution of grasping in musteloid carnivorans: a three-dimensional analysis of forelimb shape. *J. Evol. Biol.* 26, 1521–1535.
- Fish, F.E., 1994. Association of propulsive swimming mode with behavior in river otters (*Lutra canadensis*). *J. Mammal.* 75, 989–997.
- Galef, B.G., Mittermeier, R.A., Bailey, R.C., 1976. Predation by the tayra (*Eira barbara*). *J. Mammal.* 57, 760–761.
- Gambaryan, P.P., 1974. *How Mammals Run*. John Wiley & Sons, New York.
- Ginsburg, L., 1961. Plantigradie et digitigradie chez les carnivorans fissipedes. *Mammalia* 25, 1–21.
- Heinrich, R.E., Rose, K.D., 1997. Postcranial morphology and locomotor behaviour of two early Eocene miacid carnivorans, *Vulpavus* and *Didymictis*. *Paleontology* 40, 279–305.
- Hildebrand, M., 1995. *Analysis of Vertebrate Structure*. John Wiley and Sons, New York.
- Holmes, T., 1980. Locomotor adaptations in the limb skeletons of North American mustelids. In: *Dissertation*. Humboldt State University, California.
- Horner, A.M., Biknevicius, A.R., 2010. A comparison of epegean and subterranean locomotion in the domestic ferret (*Mustela putorius furo*): Mustelidae: Carnivora). *Zoology* 113, 189–197.
- Howell, A.B., 1965. *Speed in Animals*. Hafner, New York.
- Iwaniuk, A.N., Pellis, S.M., Wishaw, I.Q., 1999. The relationship between the forelimb morphology and behaviour in North American carnivores (Carnivora). *Can. J. Zool.* 77, 1064–1074.
- Iwaniuk, A.N., Pellis, S.M., Wishaw, I.Q., 2001. Are long digits correlated with high forepaw dexterity? A comparative test in terrestrial carnivores (Carnivora). *Can. J. Zool.* 79, 900–906.
- Jenkins Jr., F.A., Camazine, S.M., 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. *J. Zool.* 181, 351–370.
- Jenkins Jr., F.A., McClearn, D., 1984. Mechanisms of hind foot reversal in climbing mammals. *J. Morphol.* 182, 197–219.
- Kaufmann, J.H., Kaufmann, A., 1965. Observations of the behavior of tayras and grisons. *Z. Säuget.* 30, 146–155.
- Kavanau, J.L., 1971. Locomotion and activity phasing of some medium-sized mammals. *J. Mammal.* 52, 386–403.
- King, C., 1989. The advantages and disadvantages of small size to weasels, *Mustela* species. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*, vol. 1. Cornell University Press, Nueva York, pp. 302–334.
- Koepfli, K.-P., Deere, K.A., Slater, G.J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G., Wayne, R.K., 2008. Multigene phylogeny of the Mustelidae:

- resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biol.* 6, 10.
- Konecny, M.J., 1989. Movement patterns and food habits of four sympatric carnivoran species in Belize, Central America. In: Redford, K.H., Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. The Sanhill Crane Press, Inc., Gainesville, pp. 243–264.
- Laborde, C., 1986. Description de la locomotion arboricole de *Cryptoprocta ferox* (Carnivoran viverridé malgache). *Mammalia* 50, 369–378.
- Leach, D., 1977. The forelimb musculature of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben). *Can. J. Zool.* 55, 31–41.
- Martin, P., Bateson, P., 1993. *Measuring Behaviour*, 2nd ed. Cambridge University Press, Cambridge, 222 pp.
- Maynard Smith, J., Savage, R.J.G., 1956. Some locomotory adaptations in mammals. *Zool. J. Linn. Soc.* 42, 603–622.
- McClean, D., 1992. Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. *J. Mammal.* 73, 245–261.
- Mitteroecker, P., Bookstein, F., 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evol. Biol.* 38, 100–114.
- Moritz, S., Fischer, M.S., Schilling, N., 2007. Three-dimensional fibre type distribution in the paravertebral muscles of the domestic ferret (*Mustela putorius f. furo*) with relation to functional demands during locomotion. *Zoology* 110, 197–211.
- Nowak, R.M., 1991. *Walker's Mammals of the World*, 5th ed. Johns Hopkins University Press, Baltimore.
- Pereira, R.L.A., De Oliveira, M.A.B., 2010. Etograma do *Eira barbara* (Carnivora: Mustelidae) em cativeiro. *Etologia* 9, 45–57.
- Polly, P.D., 2010. Tiptoeing through the trophics: geographic variation in carnivoran locomotor ecomorphology in relation to environment. In: Goswami, A., Friscia, A. (Eds.), *Carnivoran Evolution: New Views on Phylogeny, Form, and Function*. Cambridge University Press, Cambridge, pp. 374–410.
- Presley, S.J., 2000. *Eira barbara*. *Mammal. Species* 636, 1–6.
- R Development Core Team, 2013. *Foundation for statistical computing*. R: A Language and Environment for Statistical Computing. R Development Core Team, Vienna <http://www.R-project.org>.
- Roberts, D., 1974. Structure and Function of the Primate Scapula. In: Jenkins, F.A. (Ed.), *Academic Press, New York*, pp. 171–200.
- Rozhnov, V.V., Kuznetsov, G.V., Neklyudova, T.I., Fam Chong, A., Van Dyk, C., 1992. Ecological and ethological observations of arboreal species of true civets in Vietnam. In: Sokolov, V. (Ed.), *Zoological Investigations in Vietnam*, Nauka Moscow (In Russian), pp. 132–147.
- Salesa, M.J., Siliceo, G., Antón, M., Abella, J., Montoya, P., Morales, J., 2006. Anatomy of the false thumb of *Tremarctos ornatus* (Carnivora, Ursidae, Tremarctinae): phylogenetic and functional implications. *Estud. Geol.* 62, 389–394.
- Salton, J.A., Sargis, E.J., 2008. Evolutionary morphology of the Tenrecoidea (Mammalia) carpal complex. *Biol. J. Linn. Soc.* 93, 267–288.
- Sargis, E.J., 2002. Functional morphology of the hindlimb of Tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J. Morphol.* 254, 149–185.
- Savage, R.J.G., 1977. Evolution in carnivorous mammals. *Palaeontology* 20, 237–271.
- Schutz, H., Guralnick, R.P., 2007. Postcranial element shape and function: assessing locomotor mode in extant and extinct mustelid carnivores. *Zool. J. Linn. Soc.* 150, 895–914.
- Seckel, L., Janis, C., 2008. Convergences in scapula morphology among small cursorial mammals: an osteological correlate for locomotory specialization. *J. Mammal. Evol.* 15, 261–279.
- Soley, F.G., 2012. Notes on the flexibility of foraging behaviour in tayras *Eira barbara*. *Small Carniv. Conserv.* 46, 33–35.
- Tarasoff, F.J., 1972. *Anatomical Observations on the River Otter, Sea Otter and Harp Seal with Reference to Those Structures That Are of Known Significance in Thermal Regulation and Diving*. PhD Thesis. McGill University, Montreal.
- Taylor, M.E., 1970. Locomotion in some east African viverrids. *J. Mammal.* 51, 42–51.
- Taylor, M.E., 1974. The functional anatomy of the forelimb of some African Viverridae (Carnivora). *J. Morphol.* 143, 307–336.
- Taylor, M.E., 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). *J. Morphol.* 148, 307–336.
- Taylor, M.E., 1989. Locomotor adaptation by carnivorans. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Nueva York, pp. 383–409.
- Trapp, G.R., 1972. Some anatomical and behavioral adaptations of ringtails, *Bassariscus astutus*. *J. Mammal.* 53, 549–557.
- Van Valkenburgh, B., 1987. Skeletal indicators of locomotor behavior in living and extinct carnivorans. *J. Vertebr. Paleontol.* 7, 162–182.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, 4th ed. Springer, New York.
- Wayne, R.K., Benveniste, R.E., Janczewski, D.N., O'Brien, S.J., 1989. Molecular and biochemical evolution of the Carnivora. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, pp. 465–494.
- Williams, T.M., 1983. Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body on running energetics and gait patterns. *J. Exp. Biol.* 115, 283–295.
- Wilson, D.E., Mittermeier, R.A., 2009. *Handbook of the Mammals of the World*, vol. 1. Carnivorans. Lynx Edicions, Barcelona.
- Yalden, D.W., 1970. The functional morphology of the carpal bones in carnivorans. *Acta Anat.* 77, 481–500.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice Hall, London.