

Pads morphology in the Viverridae (Carnivora)

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A survey of the morphology of pads within the Viverridae has been related to locomotion, ecology, ethology and to other morphological features. Species with digitigrade hind foot are lacking metatarsal pads, have an elongated pes, a short tail, and non retractile claws. They are terrestrial and their fur is spotted. Species with plantigrade hind foot, have broad and long metatarsal pads, which form a bare sole. They have retractile claws, a long tail, and fur with few markings or are one-coloured. They are arboreal and most of them are omnivorous or fruit-eaters. The genets and *Poiana* are intermediate forms because they have digitigrade feet, but possess long metatarsal pads, retractile claws, a long tail and spotted coat. However, some of them are close to the plantigrade state and have a plantigrade manus. The form of the pes of the genets is an adaptation for jumping. *Prionodon* is arboreal but have no metatarsal pads and is digitigrade. The ancestral condition is assumed to be plantigrade and arboreality and the presence of all the pads, which could be approach by some genets or *Poiana*, while the morphology of the foot of the Paradoxurinae, *Nandinia* and *Cryptoprocta* seems to be a secondary condition.

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Introduction

The Viverridae form a heterogeneous taxon, which is probably not monophyletic (Hunt 1987, 1989, Hunt and Tedford 1993, Veron and Catzeflis 1993, Flynn and Nedbal 1998) and with uncertain intra-family relationships (Veron 1994, 1995). The systematic position of some species remains uncertain, and the relationships between the genera are still difficult to establish. The structure of the feet is variable in the Viverridae and associated with different forms of locomotion (Taylor 1988, 1989). The assumption is that the primitive forms have plantar pads (= interdigital pads 1 to 4 = tarsal pads; four lobes in plesiomorphic condition) including a hallucal / pollical plantar pad (= interdigital pad 1) and two metapodial pads (= proximal pads = metatarsal / metacarpal pads) (Brown and Yalden 1973, Ewer 1973). The evolution of the arrangement of the pads is difficult to establish in the absence of a complete fossil record.

The aim of this study was to discuss the link between the morphology of the pes and the ecology and locomotion of the Viverridae. For this purpose, I studied the

pads morphology of the hind foot in the viverrid species and added quantitative data that could be compared with locomotion of the viverrids and with other morphological features.

Methods

The morphology of viverrid pads was studied on 24 species (125 museum specimens; see Appendix) and from descriptions and figures in Pocock (1915a, 1915b, 1915c, 1915d, 1916, 1933) and in Wemmer *et al.* (1983) for *Macrogalidia*. The designation of the foot pads used in this study was that of Ewer (1973) and Brown and Yalden (1973) (see Fig. 1A). In order to support the description of the pads, I added quantitative data and obtained measures (taken with callipers) on the hind foot of 8 species. These measures were: greatest length of the metatarsal pads, greatest length of the plantar +

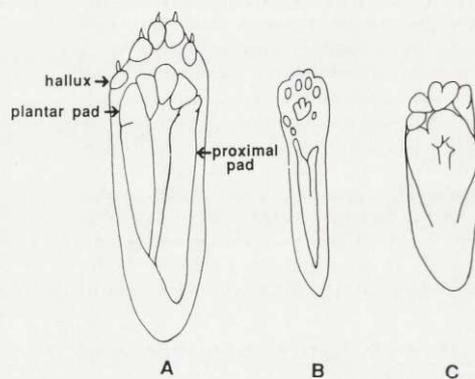


Fig. 1. Structure of the left pes of some Viverridae. A, *Cryptoprocta ferox*; B, *Genetta thierryi*; C, *Paradoxurus hermaphroditus*. Designation of foot pads from Ewer (1973) and Brown and Yalden (1973): plantar pad = interdigital pads = tarsal pads; proximal pads = metapodial pads = metatarsal pads for the hind foot.

metatarsal pads, greatest width of the metatarsal pads, surface area of the pads (product of length of the fused plantar + metatarsal pads with width of the fused pads). Measurements of the pads and also of tail length were compared to head and body length to correct for body size differences.

The morphological observations and the measurements were compared to the ratio of Taylor (1988): length of the third metapodial (metacarpal III; metatarsal III) divided by the sum of the length of the limb (sum of the humerus, radius and metacarpal III length; sum of the femur, tibia and metacarpal III length). Ecological characteristics and locomotion data have been compared to the measurements and to morphology.

Results

Observations concerning the morphology of the hind foot pads are summarised in Table 1. Foot structure of adult and juvenile were compared in most of the species and there was no difference in the disposition of the pads. The plantar pad is formed by the plantar or interdigital pads 1 to 4. The metatarsal pads are absent in *Viverra*, *Viverricula*, *Prionodon*, and *Fossa*. There is one tiny metatarsal pad in *Eupleres* and in *Civettictis*, with two lobes in the latter. *Poiana* has a foot with two metatarsal pads, one is minuscule and round and the other is long and narrow. The foot of *Genetta* bears two long and narrow metatarsal pads. The outer one

(hypothernar) is longer than the inner one (thenar). In *G. victoriae* (Wemmer 1977), the two metatarsal pads are shorter than those of *G. tigrina*. In *G. thierryi* (Fig. 1B), the inner metatarsal pad (thenar) reaches the interdigital pad 1. The outer interdigital pad is elongated and reaches the outer metatarsal pad (hypothernar) in some specimens.

The sole is completely bare with two broad and long metatarsal pads, reaching the plantar pads, in *Cryptoprocta* (Fig. 1A), *Paradoxurus* (Fig. 1C), *Paguma*, *Arctictis*, *Arctogalidia*, *Macrogalidia*, *Cynogale* and *Nandinia*. In *Hemigale* and *Chrotogale*, the broad metatarsal pads cover half of the length of the foot.

In species with broad pads, there is a median depression between the metatarsal pads. The pads of *Macrogalidia* resemble those of *Cryptoprocta* and, in these two species, the median metatarsal depression is widest distally. In *Paradoxurus* and *Paguma*, it is the opposite. The depression is covered with coarse horny tubercles in *Paguma*, *Paradoxurus* and *Arctictis*. In *Cryptoprocta*, the depression is covered with lines which correspond to fold lines of the foot. In *Nandinia*, the proximal parts of the pads are fused and the heel is covered with numerous transverse folds. In *Macrogalidia*, *Arctogalidia* and *Cryptoprocta*, the skin of the pads is smooth rather than granular in *Paguma*, *Paradoxurus* and *Arctictis*. It is not granular (or less than in the last three species) in *Nandinia*. The third and fourth digit of the hind foot are fused at their proximal end in *Paguma*, *Paradoxurus* and *Arctictis*, but not in the related species *Arctogalidia*.

The measures are summarised in Table 1. The relative longest tail is obtained for *Nandinia*, *Poiana* and *Genetta servalina*. For Haltenorth and Diller (1980), Nowak (1991), Taylor (1970) and Wemmer (1977), the longest tail was also obtained for *Nandinia* and *Poiana* and for an additional species *Arctogalidia*. The shortest tails are those of *Viverra tangalunga*, *Viverra zibetha*, *Fossa* and *Eupleres*.

The broadest metatarsal pads are those of *Arctogalidia*. Those of *Nandinia*, *Paradoxurus* and *Paguma* are narrower. The narrowest are those of the genets.

The metatarsal pads length relative to head and body size was obtained for the genets. The shortest are those of *Genetta thierryi*. The length of metatarsal + plantar pads was compared between the different species (relative to head and body length). The shortest metatarsal + plantar pads were those of *Paguma* and the longest were those of *Nandinia*. The only genet for which this index was calculated (*G. thierryi*) has the pads length similar to those of *Paguma*.

The area of the pads was calculated in several species. Pads surfaces relative to head and body size are: 1.8% in *Paradoxurus hermaphroditus* and *Paguma*, 2.2% in *Nandinia* and 2.4% in *Arctogalidia*.

The measures and morphological observations were compared with the relative length of the third metapodial (= MtIII) from Taylor (1988) (Table 1). Species which have no metatarsal pads have MtIII of 16.2% (*Viverra megaspila*) to 19% (*Fossa*). *Eupleres* bears a tiny metatarsal pad and has MtIII of 16.8%. *Poiana* has a little round pad and a long and narrow pad and MtIII of 15.9%. The genets have long and narrow pads and MtIII of 15.3% to 17.5%. The species with two broad

Table 1. Results of the morphological observations and measurements and comparison with data from Taylor (1988). Legends: m.w/h&b - mean metatarsal pads width/head and body length, m.pl/h&b - mean metatarsal pads length/head and body length, m.pml/h&b - mean plantar + metatarsal pads length/head and body length, m.tail/h&b - mean tail length/head and body length. P 1915b and P 1915d - Pocock 1915b, 1915d; H&D 1980 - Haltenorth and Diller 1980; W 1977 - Wemmer 1977; W 1983 - Wemmer *et al.* 1983. *n* - the sample size is indicated.

Sub-families/species	Description of metatarsal pads	m.w/h&b (%)	m.pl/h&b (%)	m.pml/h&b (%)	m.tail/h&b (%)	Mt III (%) (Taylor 1988)
1	2	3	4	5	6	7
Viverrinae						
<i>Civettictis civetta</i>	one tiny pad, two lobes				45.3 (n=3)	16.2 (n=1)
<i>Viverra megaspila</i>	absent					16.9 (n=8)
<i>Viverra tangalunga</i>	absent				37.6 (n=2)	16.6 (n=5)
<i>Viverra zibetha</i>	absent				43.0 (n=2)	18.5 (n=11)
<i>Viverricula indica</i>	absent				57.1 (n=12)	17.5 (n=1) (Pr.sp)
<i>Prionodon linsang</i>	absent				72.6 (n=1)	
<i>Prionodon pardicolor</i>	absent				86.8 (n=4)	15.9 (n=1)
<i>Poiana richardsoni</i>	two pads (one long) (P 1915b)					
<i>Osbornictis piscivora</i>	bare sole (H&D 1980)					
<i>Genetta abyssinica</i>						
<i>Genetta angolensis</i>						
<i>Genetta genetta</i>	two pads, long and narrow	0.9 (n=2)	5.4 (n=2)		83.8 (n=7)	17.5 (n=7)
<i>Genetta johnstoni</i>	two pads, long and narrow	0.9 (n=1)	5.1 (n=1)		84.9 (n=1)	
<i>Genetta maculata</i> (incl. <i>pardina</i>)	two pads, long and narrow				72.7 (n=5)	
<i>Genetta servalina</i>	two pads, long and narrow				85.5 (n=7)	17.5 (n=1)
<i>Genetta thierryi</i> (= <i>villiersi</i>)	two pads, long and narrow	0.7 (n=5)	4.3 (n=5)	7.5 (n=5)	74.8 (n=5)	
<i>Genetta tigrina</i>	two pads, long and narrow	0.8 (n=3)	5.4 (n=3)		76.7 (n=11)	16.8 (n=16)
<i>Genetta victorinae</i>	two narrow pads (W 1977)					15.3 (n=1)
Cryptoproctinae						
<i>Cryptoprocta ferox</i>	two broad pads, bare sole				70.9 (n=1)	14.2 (n=2)

Table 1 - concluded.

	1	2	3	4	5	6	7
Paradoxurinae							
<i>Paradoxurus hermaphroditus</i>		two broad pads, bare sole	4.1 (n=5)		8.4 (n=5)	80.4 (n=5)	13.7 (n=17)
<i>Paradoxurus jerdoni</i>		two broad pads, bare sole					
<i>Paradoxurus zeylonensis</i>		two broad pads, bare sole	3.3 (n=1)		7.4 (n=2)	79.4 (n=1)	13.3 (n=6)
<i>Paguma larvata</i>		two broad pads, bare sole					
<i>Arctictis binturong</i>		two broad pads, bare sole (P 1915d)					12.6 (n=11)
<i>Arctogalidia trivirgata</i>		two broad pads, bare sole	5.1 (n=1)		9.3 (n=1)		
<i>Macrogalidia musschenbroekii</i>		two broad pads, bare sole (W 1983)					
Hemigalinae							
<i>Hemigalus derbyanus</i>		two broad pads, half sole naked					14.1 (n=6)
<i>Hemigalus hosi</i>		two broad pads, half sole naked					
<i>Cynogale bennetti</i>		two broad pads, bare sole					15.7 (n=1)
<i>Chrotogale oustoni</i>		two broad pads, half sole naked				72.4 (n=3)	
Euplerinae							
<i>Eupleres goudoti</i>		one tiny pad				43.3 (n=5)	16.8 (n=2)
<i>Fossa fossana</i>		absent				47.1 (n=11)	19.0 (n=1)
Nandiinae							
<i>Nandinia binotata</i>		two broad pads, bare sole	4.2 (n=5)		9.9 (n=5)	95.1 (n=13)	14.3 (n=7)
Terrestrial viverrids						49.4	16.9
Arboreal viverrids			4.2		8.8	80.8	14.5
Semi-arboreal viverrids			0.8		7.5	79.7	16.8

metatarsal pads have MtIII of 12.6% (*Arctictis*) to 14.3% (*Nandinia*). *Cynogale* has a bare sole and broad metatarsal pads and MtIII is bigger (15.7%) than other species with broad pads.

I performed an analysis of variance to test the hypothesis that arboreal, semi-arboreal and terrestrial viverrids differ significantly from one another in the indices shown in Table 1. Semi-arboreal and arboreal viverrids differ significantly in pads width (p -value $< 5 \cdot 10^{-4}$, F -ratio = 81.37). Arboreal, semi-arboreal and terrestrial viverrids differ significantly in tail length (p -value $< 5 \cdot 10^{-4}$, F -ratio = 24.22) and it is also significant when I compare semi-arboreal + arboreal species with terrestrial viverrids (p -value $< 5 \cdot 10^{-4}$, F -ratio = 51.29). Semi-arboreal, arboreal and terrestrial viverrids also differ significantly in MtIII (Taylor 1988) (p -value < 0.02 , F -ratio = 4.95) but when arboreal and semi-arboreal species are grouped together and compared with terrestrial species, the difference is not significant (p -value = 0.09, F -ratio = 3.36).

Discussion

The relative length of third metapodial (= MtIII) of Taylor (1988) compared with pads morphology indicates that the elongation of the pes is associated with the reduction or disappearance of the metatarsal pads. The assumption is that MtIII is an index of digitigrady or plantigrady and Taylor (1988) stated that the foot was plantigrade if the MtIII is lower than 15%. The results of the present study show that the species with the larger indices are lacking the metatarsal pads (digitigrade terrestrial species) and those with the smaller indices have broad and long metatarsal pads which reach the plantar pads to form a completely bare sole (plantigrade arboreal species). But with the data of Taylor, *Genetta victoriae* would approach plantigrady (MtIII = 15.3%) and then this species has smaller metatarsal pads than the genets which have larger indices. This species lives in primary forest while most of the other genets live in more arid habitats (Taylor 1970, Wemmer and Wilson 1983, Nowak 1991). The metatarsal pads are missing in *Prionodon* which has a long MtIII; *G. genetta* has the same index but bears two metatarsal pads. In species with plantigrade foot, the size of the pads could be assumed to be correlated with the index of plantigrady (pads size increasing with decreasing MtIII). But when I compare *Nandinia*, *Paguma* and *Paradoxurus*, I obtained the opposite result. The bigger pads are those of *Nandinia*, but this species has a bigger MtIII than the other species.

Comparison of the morphological observations (summarised in Table 1) with the data from literature about morphology, locomotion and ecology of the viverrids (Taylor 1970, Albignac 1973, Ewer 1973, Lekagul and McNeely 1977, Haltenorth and Diller 1980, Wemmer *et al.* 1983, Payne *et al.* 1985, Wemmer and Watling 1986, Nowak 1991, and G. Veron, pers. obs., summarised in Table 2) shows that the reduction of the metatarsal pads is correlated with a terrestrial habitat, big relative MtIII length (digitigrady), reduction of the hallux, a relatively short tail and not

retractile claws (eg *Civettictis*, *Eupleres* and *Fossa*) or semi-retractile claws (eg *Viverra*, *Viverricula*). On the other hand, the presence of pads which cover the entire sole is correlated with an arboreal habitat, the presence of retractile or semi-retractile claws, a small MtIII (plantigrady), a relative long tail and the presence of a uniformly coloured fur or with few spots or stripes. This is true in *Cryptoprocta*, *Paradoxurus*, *Paguma*, *Arctictis*, *Arctogalidia*, *Macrogalidia* and *Nandinia*. These species present other arboreal features: they can descend a vertical trunk head first (Taylor 1970, Laborde 1986, Wemmer and Watling, 1986, and G. Veron, pers. obs.); they can «vertical looping» (Taylor 1970, and G. Veron, pers. obs.), which is a progression using alternatively the two fore pes and the two hind pes; moreover their hind foot can be rotated to allow head first descent (Albignac 1973, Wemmer *et al.* 1983, and G. Veron, pers. obs.); and the copulation can be arboreal (*Arctictis*: Wemmer and Murtaugh 1981; *Cryptoprocta*: Albignac 1975). The genets (*Genetta*) have long MtIII and long metatarsal pads, except *G. victoriae* which have a shorter MtIII. The genets have long tails, spotted fur and live in various habitats, including forests, savannahs and grasslands (Nowak 1991). *Prionodon* is arboreal, has a long tail like other arboreal species, but has a digitigrade foot and lacks metatarsal pads. *G. servalina* is considered as one of the most arboreal genet by Taylor (1989) and it has the relative longest tail of the genets studied. *Poiana* has a shorter MtIII than the genets (except *G. victoriae*) and *Prionodon*, and is said to be arboreal and to move more in trees than on the ground (Payne *et al.* 1985).

A significant association has been found by Ortolani and Caro (1996) between having a spotted fur and being «mainly arboreal». In fact, the genets (*Genetta*) and *Poiana* have spotted fur and are arboreal or semi-arboreal. But we can see here (Table 1 and 2) that some species which are mainly arboreal (*Cryptoprocta*, the Paradoxurinae and *Nandinia*) have uniformly coloured fur (or with few spots) and on the other hand that the civets (*Civettictis*, *Viverra*, *Viverricula*) which are terrestrial have spotted coat.

The ancestral Aeluroidea may be arboreal and carnivorous, and have a plantigrade foot (Ginsburg 1961), with four plantar pads and two metatarsal pads (Ewer 1973). Several categories can be seen in living arboreal species (Hildebrand 1982, Taylor 1989) and they can be related to different morphological features. Some forms evolved to more arboreal habits, moving rarely on the ground, and their pads fused to form a broad and long bare sole, but distinctive characters can be seen in their hind foot morphology. In *Paguma*, *Paradoxurus* and *Arctictis*, the bare sole is covered with coarse horny tubercles and the digits 3 and 4 of the hind foot are united; these digits are located in the axis of the foot. These two features could be related to their habit of walking on branches instead of hopping as many arboreal forms do (Davis 1962, Nowak 1991). In the other species with broad pads (*Nandinia*, *Cryptoprocta*), the sole is covered with transverse folds showing that the foot is more flexible than in the first species. The pes of *Macrogalidia* is also remarkably flexible and that could be related to its acrobatic climbing skill

Table 2. Biological, ecological and locomotion data from the literature. Legends: A 1973 - Albignac 1973, H&D 1980 - Haltenorth and Diller 1980, L&M 1977 - Lekagul and McNeely 1977, N 1991 - Nowak 1991, P 1985 - Payne *et al.* 1985, T 1970 - Taylor 1970, W 1983 - Wemmer *et al.* 1983, W&W 1983 - Wemmer and Wilson 1983, W&W 1986 - Wemmer and Watling 1986.

Species	Habits (N 1991, P 1985)	Vertical looping (T 1970)	Claws (N 1991)	Fur (on the back) (N 1991, G. Veron, pers. obs.)	Habitat
1	2	3	4	5	6
<i>Civettictis civetta</i>	terrestrial		not retractile (H&D 1980)	spotted	forests, bush & tree savannahs (W&W 1983)
<i>Viverra megaspila</i>	terrestrial, climb well		semi-retractile (L&M 1977)	spotted	forests, brush, grassland (N 1991)
<i>Viverra tangalunga</i>	terrestrial		semi-retractile (L&M 1977)	spotted	forests, brush, grassland (N 1991)
<i>Viverra zibetha</i>	terrestrial		semi-retractile (L&M 1977)	spotted	forests, brush, grassland (N 1991)
<i>Viverricula indica</i>	terrestrial, climb well		semi-retractile (L&M 1977)	spotted	forests, grassland (N 1991)
<i>Prionodon linsang</i>	arboreal, sleep in ground or in tree		retractile	broad transverse bands	forests (N 1991)
<i>Prionodon pardicolor</i>	arboreal		retractile	broad transverse bands	forests (N 1991)
<i>Poiana richardsoni</i>	arboreal, rarely on the ground		semi-retractile (H&D 1980)	spotted	primary forests (W&W 1983)
<i>Osbornictis piscivora</i>	semiaquatic			no spots, no bands	primary forests (W&W 1983)
<i>Genetta abyssinica</i>	semiarboreal		retractile	spotted (big spots)	forests, savannahs, grasslands (N 1991)
<i>Genetta angolensis</i>	semiarboreal		retractile	spotted (big spots)	desert, grass & bush savannahs (W&W 1983)
<i>Genetta genetta</i>	semiarboreal		retractile	spotted (big spots)	desert, grass & bush savannahs (W&W 1983) < 67mm rain/an (T 1970)

Table 2 – concluded.

1	2	3	4	5	6
<i>Genetta johnstoni</i>	semiarboreal		retractile	spotted (big spots)	forests, savannahs, grasslands (N 1991)
<i>Genetta maculata</i> (incl. <i>pardina</i>)	semiarboreal		retractile	spotted (big spots)	forests, savannahs (W&W 1983)
<i>Genetta servalina</i>	semiarboreal		retractile	spotted (big spots)	forest and thick wood, > 160 mm rain/yr (T 1970)
<i>Genetta thierryi</i> (= <i>villiersi</i>)	semiarboreal		retractile	spotted (big spots)	forests, savannahs, grasslands (N 1991)
<i>Genetta tigrina</i>	semiarboreal	yes	retractile	spotted (big spots)	secondary forests, bush & tree savannahs (W&W 1983)
<i>Genetta victoriae</i>	semiarboreal		retractile	spotted (big spots)	primary forests (W&W 1983)
<i>Cryptoprocta ferox</i>	arboreal	yes	retractile	no spots, no bands	forests, woodland savannahs (N 1991)
<i>Paradoxurus</i> <i>hermaphroditus</i>	arboreal, sleep in tree		retractile (Ewer 1973)	few stripes and spots	forests (N 1991)
<i>Paradoxurus jerdoni</i>	arboreal		retractile (Ewer 1973)	few stripes and spots	forests (N 1991)
<i>Paradoxurus</i> <i>zeylonensis</i>	arboreal		retractile (Ewer 1973)	few stripes and spots	forests (N 1991)
<i>Paguma larvata</i>	arboreal, sleep in tree		semi-retractile	no spots, no bands	forests, brush (N 1991)
<i>Arcictis binturong</i>	arboreal		(L&M 1977)	no spots, no bands	dense forests (N 1991)
<i>Arctogalidia</i> <i>trivirgata</i>	arboreal, rarely on the ground			three longitudinal stripes	dense forests (N 1991)
<i>Macrogalidia</i> <i>musschenbroekii</i>	semiarboreal	yes (W&W 1986)	semi-retractile (W 1983)	no spots, no bands	forests (N 1991)
<i>Hemigalus</i> <i>derbyanus</i>	terrestrial		retractile	broad transverse stripes	tall forests (N 1991)
<i>Hemigalus hosei</i>	terrestrial		retractile	no spots, no bands	mountain forests (N 1991)
<i>Cynogale bennetti</i>	aquatic and terrestrial		semi-retractile (Ewer 1977)	no spots, no bands	near streams and swampy areas (N 1991)
<i>Chrotogale oustoni</i>	terrestrial			broad transverse bands	near rivers in forests (N 1991)
<i>Eupleres goudoti</i>	terrestrial		not retractile	no spots, no bands	humid, lowland forests (N 1991)
<i>Fossa fossana</i>	terrestrial (A 1973)		not retractile	spots	forests (N 1991)
<i>Nandinia binotata</i>	arboreal	yes	retractile	two spots	forests (N 1991)

(Wemmer *et al.* 1983), observed also in *Cryptoprocta* (Albignac 1970) and *Nandinia* (Taylor 1970). Moreover, the median depression between the metatarsal pads is widest distally in these species while it is widest in proximal end in *Paguma*, *Paradoxurus* and *Arctictis*. These two groups of species can be referred to the grasping category of arboreal species (Hildebrand 1982) but this study shows that their morphology and so their habits are somewhat different.

The ancestral structure of the foot could be close to that observed in the foot of the genets, and this can be supported by the fact that, in the genets, all the pads are present, which could be regarded as a plesiomorphic trait (Ewer 1973). However, in the genets, MtIII is long and this is probably related to their jumping ability. The relative length of metacarpal III (Taylor 1988) is always smaller than the relative length of metatarsal III (= MtIII), but in the genets this difference is larger and some of them have a more plantigrade hand than those of *Nandinia*, *Cryptoprocta* and the Paradoxurinae (Taylor 1988), showing that the elongation of the foot of the genets is a secondary jumping adaptation, therefore the genets can be referred to the jumping and lumping category of arboreal species (Hildebrand 1982). The long metatarsal pads are used in locomotion and also in bipedal stance while face grooming with the fore limbs (Wemmer 1977). *Prionodon* is lacking metatarsal pads, showing that different morphological traits can be referred to the jumping category of arboreal species. The foot of *Poiana* is less elongated than those of genets and may be less adapted for jumping. The most plantigrade genets or *Poiana* may better approximate the ancestral viverrine condition than the other species. *Poiana* builds arboreal nests (Walker 1968) which can be interpreted as a primitive feature (Wemmer 1977).

Conclusions

The morphological diversity observed within arboreal species can be related to their locomotor behaviour and to the relationships between locomotion and strategies for obtaining food (Taylor 1989, McClearn 1992), but also to their historical evolution. Like skeletal characteristics (Van Valkenburgh 1987), pads morphology and tail length could be related to locomotor behaviour.

The assumption that climbing ability is proportional to the extent of foot pad development in the viverrids (Wemmer 1977) is confirmed by this study on the hind foot. The terrestrial forms have no metatarsal pads or only a small tiny metatarsal pad. The arboreal and semi-arboreal species have long metatarsal pads and these pads are widest in arboreal than in semi-arboreal species. The arboreal *Prionodon* could be compared to felids, having digitigrade foot, a long tail and no metatarsal pads.

The tail is used in arboreal locomotion as a balancing organ (Taylor 1989) and in fact, this study confirms that arboreal viverrids have a longer tail than terrestrial ones.

The relative MtIII length (Taylor 1988) indicates whether a foot is plantigrade or not and this is correlated with the presence or absence of the metatarsal pads,

but this study shows that sometimes the size of the pads is not correlated with the size of MtIII. Some secondary modifications may have occurred; for instance, the elongation of MtIII (related to jumping ability) with little modification of the pads size, and also the contrary, the absence of metatarsal pads without modification of MtIII. The present study shows that arboreal viverrids have a shorter MtIII than the terrestrial species.

The plantigrade forms with broad and fused pads like those seen in the Paradoxurinae may not represent the primitive plantigrade condition for the foot structure which could be seen in the genets or *Poiana*. The genets have a hand more plantigrade than the foot, and this shows that their hind foot is secondary adapted to jumping. This adaptation does not occurred in *Poiana*.

The viverrids can be referred to several major grouping regarding to their morphology and habits:

- terrestrial species with digitigrade foot, MtIII length > 16% (Taylor 1988), no metatarsal pads (or one very tiny pad), short tail, spotted fur (spots sometimes running in to stripes);

- arboreal or semi-arboreal species with digitigrade foot, MtIII length > 15% (Taylor 1988), metatarsal pads long and narrow (or absent), long tail, spotted fur; species of this group can be referred to jumping and leaping category of arboreal species (Hildebrand 1982); the elongation of the foot is related to their jumping ability.

- arboreal species with plantigrade foot, MtIII < 15% (Taylor 1988), large metatarsal pads, bare sole, long tail, uniformly coloured coat or with few spots or stripes. These species can be referred to grasping category of arboreal species (Hildebrand 1982), but some of them are used to move slowly on horizontal support while the other progress more quickly and nimbly even on vertical support (Davis 1962, Taylor 1989). The large and fleshy pads are of use in grasping branches (Taylor 1989).

Some particular forms must be added: the semi-aquatic species (*Osbornictis* and *Cynogale*) with bare sole, and the species belonging to the Hemigalinae which are terrestrial viverrids with broad pads covering half of the sole, long tail, one-coloured coat or with broad transverse bands, and plantigrade foot.

Terms like semi-digitigrade or semi-plantigrade, as well as semi-arboreal, frequently used about the viverrids, yield some confusion and this study shows that they can be related to different mode of locomotion and to different morphological features. Studies on the locomotor behaviour in arboreal carnivores are needed (Taylor 1989) notably to better characterise different climbers categories (eg arboreal / scansorial, Van Valkenburgh 1987; leaping and jumping / grasping, Hildebrand 1982 and Taylor 1989), and to be correlated with morphological features and with other lifestyle attributes (eg feeding behaviour, McClearn 1992).

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Appendix. List of specimens (Muséum National d'Histoire Naturelle, Paris, France)

- Arctogalidia trivirgata*: C.G.1970-371.
Chrotogale owstoni: C.G.1929-407; C.G.1941-83.
Civettictis civetta: C.G.1912-847; C.G.1966-44; C.G.1995-430.
Cryptoprocta ferox: C.G.1880-2544; C.G.1960-3841; C.G.1965-403.
Cynogale bennetti: C.G.1962-170.
Chrotogale owstoni: C.G. 1929-407; C.G. 1929-408; C.G.1941-83.
Eupleres goudoti: C.G.1932-3540; C.G.1932-3541; C.G.1932-3542; C.G.1960-3683; C.G.1961-1029; C.G.1962-1121.
Fossa fossa: C.G.1882-1582; C.G.1882-1586; C.G.1882-1589; C.G.1882-1590; C.G. 1882-1592; C.G.1882-1594; C.G.1932-3555; C.G.1932-3556; C.G.1932-3557; C.G. 1932-3558; C.G.1932-3559.
Genetta genetta: C.G.1917-60; C.G.1963-1366; C.G.1967-955; C.G.1970-295; C.G.1985-117; C.G.1992-2000; C.G.1994-2446; C.G.1995-418.
Genetta johnstoni: C.G. 1986-246.
Genetta maculata: C.G. 1897-508; C.G. 1961-416; C.G. 1963-1365; C.G. 1959-938; C.G. 1995-1261.
Genetta servalina: C.G.1965-368; C.G.1966-52; C.G.1966-55; C.G.1966-57; C.G.1967-958; C.G.1970-389; C.G.1970-390.
Genetta thierryi: C.G.1977-678; C.G.1977-680; C.G.1977-687; C.G.1977-688; C.G.1995-421; C.G.1995-424.
Genetta tigrina: C.G.1901-1069; C.G.1904-2011; C.G.1933-2314; C.G.1960-3667; C.G.1962-1058; C.G.1965-338; C.G.1965-339; C.G.1965-350; C.G.1969-470; C.G.1972-395; C.G.1973-118; C.G.1989-34; C.G.1990-685.
Hemigalus derbyanus: C.G.1877-1957; C.G.1897-1319.
Nandinia binotata: C.G.1902-1409; C.G. 1909-127; C.G. 1914-690; C.G. 1936-994; C.G. 1939-180; C.G.1939-182; C.G.1947-840; C.G.1949-330; C.G.1960-3668; C.G.1964-238; C.G.1965-407; C.G.1966-50; C.G.1968-801; C.G.1970-384; C.G.1970-385; C.G.1970-386; C.G.1970-385; C.G.1971-688; C.G. 1974-105; C.G. 1995-463.
Paguma larvata: C.G. 1896-2064; C.G.1962-152.
Paradoxurus hermaphroditus: C.G.1875-1145; C.G.1973-19; C.G.1982-848; C.G.1982-850; C.G.1982-853; C.G.1982-855.
Poiana richardsoni: C.G.1947-18; C.G.1947-19; C.G.1958-777; C.G.1962-1190.
Prionodon linsang: C.G.1879-2132; C.G.1932-3543.
Prionodon pardicolor: C.G. 1860-389; C.G. 1929-424.
Viverra tangalunga: C.G.1884-1810; C.G.1886-22; C.G.1959-258.
Viverra zibetha: C.G.1929-394; C.G.1985-120.
Viverricula indica: C.G.1894-1433; C.G.1898-1595; C.G.1899-56; C.G.1907-840; C.G.1912-714; C.G.1929-397; C.G.1929-398; C.G.1929-399; C.G.1931-866; C.G.1976-335; C.G. 1982-845; C.G. 1982-846.

(C.G.: Collection Générale)