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## The earliest modern mongoose (*Carnivora, Herpestidae*) from Africa (late Miocene of Chad)

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**Abstract** We report on the earliest modern mongooses of Africa, from the late Miocene (ca. 7 Ma) of the hominid locality TM 266, Toros-Menalla, Chad. The material is based on fragmentary dentitions of three individuals. The main diagnostic feature of the Chadian species is the great development of the shear in the carnassials, which distinguishes the Chadian specimens from all extant herpestids except *Herpestes* and *Galerella*. In comparison with most extinct and extant *Herpestes*, the species from Toros-Menalla differs by a markedly smaller size and, depending on the species, relatively more elongated carnassials, more transversely elongated M1 and more reduced p4. On the basis of a great morphological similarity and the absence of significant differences, we assign our material to *Galerella sanguinea*; the Chadian finding therefore represents the earliest appearance of an extant species of Herpestidae. This record ties the first appearance of the genus to a minimum age of ca. 7 Ma, which is consistent with the estimated divergence date of 11.4 Ma known from the literature for the species of *Galerella*.

### Introduction

The fossil record of the family Herpestidae (*Carnivora Feliformia*), which includes small terrestrial and mainly African species, is poor and/or fragmentary, with the best record from the Plio-Pleistocene of east Africa (Hunt 1996). The genus *Leptoplesictis* from the early-middle Miocene of Europe (Roth 1988) and the middle Miocene of Africa (Schmidt-Kittler 1987) would be the earliest true

Herpestidae (Hunt 1996) though no basicranial evidence is available. The earliest unequivocal evidence of the modern Herpestidae comes from the late Miocene of Pakistan with some fragmentary dental remains of 9.5 to 7 myr old of three indeterminate species of *Herpestes* (Barry 1983), *Atilax* n. sp. (Hill et al. 1985), *Herpestes* sp. and *Ichneumia* sp. (Morales et al. 2004) from the Lukeino Formation, Kenya (6.0–5.7 Ma; Sawada et al. 2002) are the earliest records of the modern mongooses in Africa to date. No description of this material has been published.

Here we describe the oldest modern mongoose of Africa, which is biochronologically much older than the records from Lukeino. The fossils were discovered in early 2003 by the Mission paléoanthropologique franco-tchadienne (MPFT) in the hominid-bearing site of TM 266, Toros-Menalla, Chad. The TM-266 fauna (Vignaud et al. 2002), which includes the earliest hominid *Sahelanthropus tchadensis* (Brunet et al. 2002), is more archaic than the fauna from Lukeino but similar to that from the lower Nawata Formation, Lothagam (7.4–6.5; McDougall and Feibel 2003). The TM-266 fauna is ca. 7 myr old (Brunet et al. 2004).

### Systematic paleontology

Mammalia Linnaeus, 1758  
Carnivora Bowdich, 1821  
Herpestidae Bonaparte, 1845  
Genus *Galerella* Gray, 1865

### Taxonomic remarks

We use the genus name *Galerella* following the taxonomy of Wozencraft (1993), which includes *G. sanguinea*, *G. pulverulenta*, *G. flaviscens* and *G. swalius*. The status of the two latter species is still disputed; in several recent papers, they are not mentioned and/or regarded as invalid species or synonyms of *G. sanguinea* (e.g. Taylor 1975; Wozencraft 1989; Cavallini 1992). Our comparison only

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includes the two most common species of *Galerella*, *G. sanguinea* and *G. pulverulenta*. Morphologically, these two species differ from the species of *Herpestes* by a smaller size (condylobasal length of skull shorter than 80 mm), the absence of p1 in most individuals (in ca. 83% in our comparative sample;  $N=29$ ) and an anterior chamber of the auditory bulla similar in size to the posterior portion (see Cavallini 1992). The diagnostic value of these features is still debated and some authors synonymize this genus with *Herpestes* (see Veron et al. 2004).

*Galerella sanguinea* (Rüppell, 1836)

See Wozencraft (1993) for taxonomic information.

### Referred material

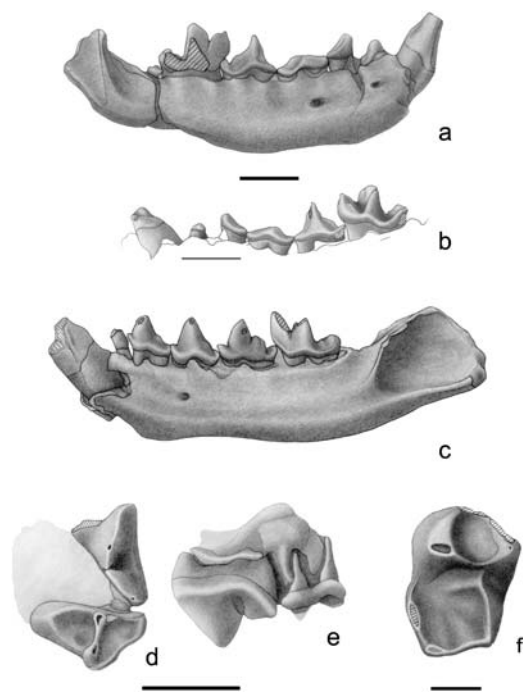
TM 266-03-291, closely associated right hemimandible and maxilla with c1-m2 and C1-M2, left hemimandible with p3-m1; TM 266-03-309, closely associated fragmentary left and right hemimandibles with c-m1 (Fig. 1a and b), fragment of left maxilla with partial P4, M1 (Fig. 1c and d), and fragment of right maxilla with poorly preserved partial P3, P4-M1, partial M2, isolated subcomplete right m2 (Fig. 1e); TM 266-03-292, fragment of left hemimandible with erupting m1. After the study at the University of Poitiers the material will be stored in the Département de Conservation des Collections, Centre National d'Appui à la Recherche (CNAR), N'Djamena, Chad.

### Origin and age

Locality TM 266, Toros-Menalla, Chad; late Miocene age (ca. 7 Ma) based on the evolutionary grade of the fauna (Vignaud et al. 2002; Brunet et al. 2004).

### Description

Due to sand blasting, the fossils are poorly preserved, the teeth in particular. On the fragmentary maxilla, the infraorbital foramen opens above the middle of P3. P1 is a very small single-rooted tooth, with a tall and simple crown. P2 is slightly smaller than P3. On the latter, the lingual root, which is highly visible on the specimens, is not cuspidated. The paracone and the metacone of P4 (Fig. 1c and d) are trenchant and narrow cusps; the carnassial notch is deep. The protocone is well developed and much larger than the parastyle; it is located approximately at the level of the parastyle. M1 is well preserved on TM-266-03-309 (Fig. 1c and d) and cannot be distinguished from that of the extant *Galerella* spp. In occlusal view, it is triangular and transversely elongated. The paracone and metacone are both small, similar in size and well separated. The metacone is slightly prominent backwards. The parastylar



**Fig. 1** *Galerella sanguinea* from Toros-Menalla (Chad, late Miocene). TM 266-03-309: right hemimandible in a, labial view and b, lingual view; c, left hemimandible in labial view; partial left maxilla in d, occlusal and e, labial view; f, right m2 in occlusal view. Scales for a–e = 5 mm; scale for f = 1 mm

wing is less developed than in most studied specimens of *G. sanguinea*. The protocone is much more developed than the labial cusps. It is triangular in shape and its lingual basis is relatively rounded. The trigone crests are dissymmetrical. The mesial one is more developed and taller lingually than the distal one. The trigone basin is deep and transversely elongated. M2 is preserved on TM-266-03-291 but only the labial cusps and the protocone are visible due to the close association of the maxillae and mandible. The tooth is much smaller than M1 and slightly more reduced than in the extant *Galerella* spp. The paracone and metacone are highly distinct though they are much more reduced than the protocone.

The coronoid and angular processes are not preserved. The mandibular corpus (Fig. 1a and b) does not show any morphological differences compared to that of *G. sanguinea*. The masseteric fossa is deep and extends forwards below the m2 alveolus (Fig. 1b). Two mental foramina are present, one below p1, and another slightly smaller one below the mesial root of p3.

A small portion of the lower canine is preserved and shows a mesiolingual crest at the basis of the crown. The cheekteeth are all set closely together with an extremely short postcanine diastema (less than 1 mm long) (Fig. 1a and b). p1 is very reduced and single-rooted. p2 is much larger and has an asymmetrical crown with a small but distinct mesial accessory cuspid and a poorly developed distal one; the distal cingulid is short and narrow. p3 has a very small mesial accessory cuspid and a relatively symmetric crown compared to that of p2. p4 is longer but not distinctly

**Table 1** Comparative measurements (mm) of mandible and dentition of *Galerella*

	<i>G. sanguinea</i> from TM		Extant <i>G. sanguinea</i>	N	mean	range	CV	<i>Herpestes debilis</i> <sup>a</sup>	<i>Herpestes mesotes</i> <sup>b</sup>	<i>Herpestes abdelatii</i> <sup>c</sup>	<i>Herpestes palaeose</i> <sup>d</sup>	<i>Herpestes transvaal</i> <sup>d</sup>	
	TM 266-03-309	TM 266-03-291											
C	L	-	-	15	2.94	2.55-3.20	7.24	-	5.50	-	-	3.60	-
	w	-	-	15	1.98	1.70-2.20	7.29	-	4.20	-	-	3.00	-
P1	L	1.40	-	5	1.61	1.45-1.85	12.92	-	2.40	-	-	3.20	-
	w	-	-	5	1.23	1.20-1.30	3.82	-	2.10	-	-	2.00	-
P2	L	3.70	-	17	3.50	3.20-3.80	5.42	-	5.80	-	-	4.60	-
	w	-	-	17	1.74	1.40-2.00	9.20	-	3.45	-	-	2.40	-
P3	L	4.00	-	16	4.00	3.50-4.35	6.73	-	6.40	5.53 (3)	-	5.10	-
	w	2.10	-	16	2.63	2.10-3.40	11.89	-	4.70	4.05 (3)	-	3.70	-
P4	L	6.10	-	22	6.15	5.20-6.70	5.88	-	9.30	7.42 (3)	-	7.20	-
	w	3.80	-	17	3.99	3.60-4.50	5.16	-	7.00	5.45 (3)	-	5.20	-
M1	L	2.60	3.00	17	2.88	2.30-3.30	8.06	-	5.70	-	-	4.80	-
	labL	2.90	3.90	20	3.54	3.00-4.00	7.84	-	-	-	-	-	-
M2	w	5.20	6.00	20	5.83	5.20-6.60	5.95	-	9.35	-	-	7.40	-
	L	-	-	26	1.41	1.10-1.80	12.82	-	3.70	-	-	2.60	-
alv. L (C-M2)	labL	2.30	-	22	1.77	1.20-2.30	12.91	-	-	-	-	-	-
	w	3.50	-	26	3.14	2.70-4.05	10.39	-	6.10	-	-	4.80	-
c	23.10	-	12	22.45	21.60-24.30	3.46	-	-	-	-	-	-	-
	L	-	3.80	16	3.15	2.75-3.50	7.04	-	6.00	-	-	-	-
p1	w	-	2.45	14	2.20	1.90-2.50	9.25	-	4.60	-	-	-	-
	L	-	1.30	1	1.30	-	-	-	-	-	-	1.80	-
p2	w	-	1.00	1	1.00	-	-	-	-	-	-	-	-
	L	3.10	3.60	16	3.20	2.80-3.50	6.50	-	4.95	4.77 (3)	-	4.70	3.70
p3	w	-	(1.60)	16	1.56	1.40-1.80	7.83	-	3.20	2.50 (3)	-	3.10	-
	L	3.90	4.00	16	3.83	3.45-4.10	5.96	-	6.30	5.38 (4)	-	5.20	5.60
p4	w	-	-	16	1.82	1.60-2.10	7.48	-	3.45	2.92 (4)	-	2.40	-
	L	5.00	5.00	16	4.56	4.20-4.90	5.85	-	7.35	6.41 (9)	-	5.70	5.80
m1	w	>2.00	-	16	2.19	1.80-2.60	8.91	-	4.00	3.22 (9)	-	2.70	-
	L	-	6.00	17	5.44	5.00-6.00	5.41	4.00	8.75	7.08 (5)	-	7.50 (3)	7.50
m2	w	-	>3.00	17	3.04	2.60-3.40	6.63	-	5.40	3.95 (5)	-	4.05 (2)	-
	trdL	-	3.95	17	3.66	3.40-3.90	5.40	-	-	-	-	-	-
m2	L	3.00	>3.10	17	2.80	2.20-3.25	10.17	-	5.15	-	-	-	-
	w	-	2.10	17	2.00	1.70-2.30	8.45	-	3.80	-	-	-	-

Table 1 Continued.

	<i>G. sanguinea</i> from TM		Extant <i>G. sanguinea</i>	CV	<i>Herpestes debilis</i> <sup>a</sup>	<i>Herpestes mesotes</i> <sup>b</sup>	<i>Herpestes abdelatii</i> <sup>c</sup>	<i>Herpestes palaeose</i> <sup>d</sup>	<i>Herpestes transvaal</i> <sup>d</sup>
	TM 266-03-309	TM 266-03-291							
alv. <i>L</i> (p2-m2)	20.30	5	19,21	—	—	—	—	—	—
md	—	3.60	16	17.50–19.80	—	—	—	—	—
Tp3	—	3.60	16	3.24	—	—	—	—	—
Tm1	—	3.50	16	3.18	—	—	—	—	—
Dp2-3	—	—	16	5.77	—	—	—	—	—
Dp3-4	—	6.10	16	5.63	—	—	—	—	—
Dp4-m1	—	7.20	16	6.30	—	—	—	—	—
Dm1-2	—	7.30	16	6.14	—	—	—	—	—
Ddistm2	—	7.00	16	6.07	—	—	—	—	—

Note. *L*: Length; *w*: width; *labL*: labial length, distance between the mesiolabial corner (parastylar wing) and the distal face of the metacone; alv. *L*: alveolar length; trd*L*: trigonid length; md: mandible; Tp3: thickness across p3; Dp2-3: depth below p2-3; N = sample size; CV = coefficient of variation; *palaeose*: *palaeoserengeretensis*; *transvaal*: *transvaalensis*. If mean, the sample size is in parentheses

<sup>a</sup> Petter (1973)

<sup>b</sup> Ewer (1956)

<sup>c</sup> Geraads (1997)

<sup>d</sup> Petter (1987)

taller than p3. It has much larger mesial and distal accessory cuspids than do p2 and p3 and a longer distal cingulid that is particularly developed distolingually. The lower carnassial is a trenchant tooth, with a tall opened trigonid and a deep carnassial notch. The paraconid is long but lower than the protoconid. The metaconid is a sharp cuspid that is well detached from other cuspids, in particular from the paraconid. The metaconid is slightly lower than the protoconid and placed lingually to the latter; both cuspids have a vertical distal face. The talonid is low and markedly narrower than the trigonid. It consists of a sharp labial crest with a prominent hypoconid; a shallow distinct notch separates the distal rim and the hypoconid. The lingual rim is prominent only distally; the talonid is mesiolingually opened. m2 (Fig. 1e) is much more reduced than m1 and single-rooted. Although incompletely preserved, the trigonid resembles that of *Galerella* spp., with a large metaconid and protoconid, and a probable small mesial paraconid. The small trigonid basin is closed distally by a low ridge that links the metaconid and protoconid. The talonid is low and relatively wider than on m1. The labial crest is low; there are poorly developed hypoconid and, distally, hypoconulid. There is no evidence of an entoconid.

## Comparisons and discussion

Our comparisons are based on the study of about 50 specimens of extant herpestids of the genera *Atilax*, *Bdeogale*, *Crossarchus*, *Cynictis*, *Dologale*, *Galerella*, *Herpestes*, *Helogale*, *Ichneumia*, *Mungos*, *Rhynchogale* and *Suricata*, from the collections of mammalogy, Museum national d'Histoire naturelle, Paris. Previous studies also serve as a comparison (e.g. Petter 1969).

The great development of shear in the carnassials of the Chadian specimens provides the best support for a close relationship between this material and the *Herpestes/Galerella* group. In comparison with these genera, other herpestines display marked differences in the dental morphology and proportions, including: a more compressed m1 trigonid (e.g. *Cynictis*, *Ichneumia*, *Atilax*, *Mungos*, *Crossarchus*, *Bdeogale*, *Helogale*), which is due to a more oblique orientation of the paraconid and a closer relationship or partial fusion of the paraconid and metaconid; a much less reduced and longer m2 (e.g., *Cynictis*, *Ichneumia*, *Mungos*, *Bdeogale*, *Rhynchogale*, *Dologale*); and a much larger protocone on P4-M2 (e.g., *Suricata*, *Atilax*, *Mungos*, *Dologale*, *Helogale*).

Extinct species that have been previously assigned to *Herpestes* or *Galerella* are middle Pliocene to early Pleistocene in age and are now ascribed to *Herpestes*. Comparative measurements of these fossil *Herpestes* species and of the extant *G. sanguinea* are presented in Table 1. *Galerella* from TM-266 is much larger than *H. debilis* (Petter 1973) and markedly smaller than *H. mesotes* (Ewer 1956), *H. abdelalii* (Geraads 1997), *H. palaeoserengensis* (Dietrich 1942) and *H. transvaalensis* (Broom 1937). In addition, Chadian specimens differ from *H. palaeoserengensis* and

*H. transvaalensis* by a p3 distinctly more reduced relative to p4; from *H. mesotes* and *H. palaeoserengensis* by a much more elongated m1 and a more transversely elongated M1; and from *H. abdelalii* and *H. palaeoserengensis* by a more elongated P4.

The Chadian material is distinguished from most of the extant species of *Herpestes* by its very small size. Most of the measurements of the specimens from Chad are within the range of variation of the sample of the extant *G. sanguinea* (Table 1). The biggest difference is in the lower canine length, which is 3.80 mm in the fossil *G. sanguinea* while it reaches a maximum of 3.50 mm in the studied sample of extant *G. sanguinea* ( $N=16$ ). Except for this feature and the presence of p1, there is a great morphological similarity between our material and *Galerella sanguinea*. We did not regard the above-mentioned differences as diagnostic at a specific level and we therefore assign the Toros-Menalla material to *Galerella sanguinea*. In comparison, *G. pulverulenta* is larger than *G. sanguinea* (Cavallini 1992). The early appearance of *G. sanguinea* reveals a species longevity of ca. 7 Ma. Such a long duration for a species is not exceptional in the fossil record and there are many cases of species longevity exceeding 10 Ma (e.g. Flynn et al. 1995; Wang et al. 1999). This duration is not in conflict with the previous estimate of the divergence age of *Galerella* spp. (11.4 Ma; Bininda-Emonds et al. 1999) although the monophyly of the genus remains to be tested and needs to be further studied (see Veron et al. 2004). Given the poor fossil record for the Herpestidae, which is mainly due to the lack of Miocene localities in Africa. This record is also significant in providing an additional date for phylogenetical studies.

Within the extant mongooses, *Galerella sanguinea* is one of the best climbers and an efficient killer. Its diet is very broad although it chiefly includes small vertebrates and insects (Taylor 1975; Estes 1991). *G. sanguinea* from the late Miocene of Chad probably had a similar ecology and behaviour. In the reconstructed environment of TM-266 (Vignaud et al. 2002), this species may have occupied a wide variety of habitats, similar to its extant relative (i.e. from grassland to gallery forest).

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