

Functional inferences on the long bones of
Ischyrictis zibethoides (Blainville, 1841)
(Carnivora, Mustelidae) from
the middle Miocene locality
of Sansan (Gers, France)



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ABSTRACT

In the present paper, we carry out a deep analysis of the functional anatomy of the long bones of the fossil, wolverine-sized mustelid *Ischyriectis zibethoides* (Blainville, 1841) in comparison with that of several extant related species. The study reveals that this animal lacked specific adaptations for either climbing or running, probably being a terrestrial predator that foraged mostly on the ground. Thus, some features of the anatomy of its long bones suggests that *I. zibethoides* required a strong control of those articulations involved in terrestrial locomotion, such as the elbow or the coxofemoral joint. Besides this, the gentle caudal inclination of the ulna resembles the morphology exhibited by typical cursorial carnivorans, whereas the absence of lateral torsion in the olecranon suggests flexion-extension movements of the elbow in a parasagittal plane. Other small details, such as the small attachment area for the *m. biceps brachii*, points towards a general adaptation to terrestrial locomotion. Besides this, another set of features, shared with extant small arboreal mustelids, probably indicates a primitive, retained morphology from arboreal ancestors, rather than climbing abilities, although is very likely that *I. zibethoides* would be able to climb trees with some skill looking for food or shelter.

KEY WORDS

Functional anatomy,
Carnivora,
Mustelidae,
Miocene,
Europe.

RÉSUMÉ

Inférences fonctionnelles sur les os longs d'Ischyriactis zibethoides (Blainville, 1841) (Carnivora, Mustelidae) de la localité du Miocène moyen de Sansan (Gers, France).

Dans ce papier, nous étudions l'anatomie fonctionnelle des os longs de *Ischyriactis zibethoides* (Blainville, 1841), une espèce éteinte de Mustelidae de la taille d'un glouton et la comparons avec celle de nombreuses espèces actuelles phylogénétiquement proches. Cette étude met en évidence que cet animal présentait peu d'adaptations pour grimper ou courir et était probablement un prédateur terrestre qui cherchait sa nourriture au sol. En effet, *Ischyriactis zibethoides* présente des caractéristiques anatomiques des os longs suggérant un fort contrôle de ses articulations, associé à une locomotion terrestre, en particulier au niveau des articulations du coude et coxo-fémorale. En outre, la légère inclinaison caudale de l'ulna est typique des carnivores coureurs, alors que l'absence de torsion latérale de l'olécrane suggère des mouvements de flexion-extension du coude dans un plan parasagittal. D'autres détails, comme l'aire d'attachement réduit du *muscle biceps brachii*, semble indiquer une adaptation générale à une locomotion terrestre. À côté de cela, d'autres caractéristiques morphologiques sont partagées avec des petits mustélidés arboricoles. Ceci pourrait indiquer une morphologie primitive héritée de leurs ancêtres arboricoles plutôt que des capacités à grimper. Cependant, il est fort probable que *I. zibethoides* ait été capable de grimper aux arbres afin de chercher de la nourriture ou un abri.

MOTS CLÉS

Anatomie fonctionnelle,
Carnivora,
Mustelidae,
Miocène,
Europe.

INTRODUCTION

The genus *Ischyriactis* was created by Helbing (1930) for the fossil mustelid *Viverra zibethoides* Blainville, 1841, described for the first time in the French locality of Sansan (MN 6, middle Miocene). The genus is also present in several middle to late Miocene European localities (ranging from MN 4 to MN 12, that is from 18.5 to 8.0 Ma) such as La Retama and Hostalets de Pierola (Spain) (Roth 1989; Morales *et al.* 1993; Fraile *et al.* 1997), Quinta do Pombeiro, Quinta da Farinheira and Olival da Susana (Portugal) (Ginsburg & Antunes 1995), Bézian, Pellicaus, Baigneaux-en-Beauce, Auvergne, Noyant-sous-le-Lude, Channay-sur-Lathan, La Grive-Saint-Alban, Vieux-Collonges and Sansan (France) (Mein 1958; Ginsburg & Bulot 1982; Ginsburg 2001; Peigné 2012), and Sandelzhausen and Steinheim (Germany) (Nagel *et al.* 2009). Up to three species of *Ischyriactis* are recognised: *I. bezianensis* Ginsburg & Bulot, 1982, the most primitive and earliest species, *I. zibethoides* (Blainville, 1841), and *I. mustelinus* (Viret, 1933). Some of them are known on the basis of very scarce dental material, such as *I. bezianensis*, described from an isolated M1 from the middle Miocene locality of Bézian (France). The genus *Ischyriactis*, together with the closely related *Hoplistictis* (known from MN4 to MN8, that is around 17–11 Ma) belong to a lineage of Miocene large mustelids that developed a hypercarnivorous dentition, with reduction of both talonid and metaconid on m1, although retaining a complete set of more or less sharp premolars (Tseng *et al.* 2009). This lineage also includes the late Miocene genera *Mellalictis*, *Ekorus* and *Eomellivora* (Ginsburg & Morales 1992; Ginsburg 1977, 1999; Werdelin 2003; Tseng *et al.* 2009). Some of these genera are mostly known on the basis of cranial and dental remains, their postcranial skeleton being very poorly known; others are much better known, such as *Ekorus ekakeran*, which was described on the basis

of an almost complete skeleton from the Late Miocene of the lower member of the Nawata formation (Lothagam) (Werdelin 2003). Concerning *Ischyriactis*, only some appendicular bones of *I. zibethoides* have been briefly described (Ginsburg 1961; Peigné 2012), and thus their locomotor adaptations and ecological role remain basically unknown.

MATERIAL AND METHODS

The fossils of *Ischyriactis zibethoides* studied in this paper belong to the extensive sample from the fossil site of Sansan (France, Middle Miocene, MN 6), housed in the collections of Paleontology of the Muséum national d'Histoire naturelle (Paris, France; MNHN.F). They have been previously described in brief by Ginsburg (1961) and Peigné (2012), but here we provide detailed descriptions and comparisons with other mustelids, as well as functional explanations of the observed morphology. Nevertheless, a list of measurements of the studied fossils can be consulted in these latter works. The list of studied material is: proximal fragment of right humerus (MNHN.F.Sa418), proximal fragment of left humerus (MNHN.F.Sa419), distal fragment of right humeri (MNHN.F.Sa420 and Sa421), right radius (MNHN.F.Sa422), proximal fragment of left radius (MNHN.F.Sa15571), proximal fragment of left ulna (MNHN.F.Sa423), proximal fragment of right ulna (MNHN.F.Sa424), and left femur (MNHN.F.Sa431), representing at least three individuals. Comparisons with five extant mustelids showing various locomotor styles were made using the collections of the Museo Anatómico de la Universidad de Valladolid (Spain), which provided complete skeletons of *Gulo gulo* (Linnaeus, 1758) (catalogue number MAV469) and *Taxidea taxus* (Linnaeus, 1758) (MAV4938); the collections of the Muséum national d'Histoire naturelle (Paris, France), which provided a complete skeleton of

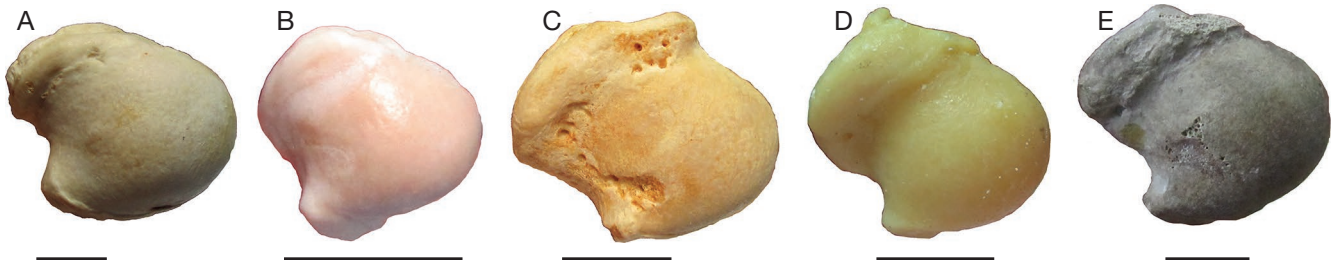


FIG. 1. — Proximal view of the head of the right humerus of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

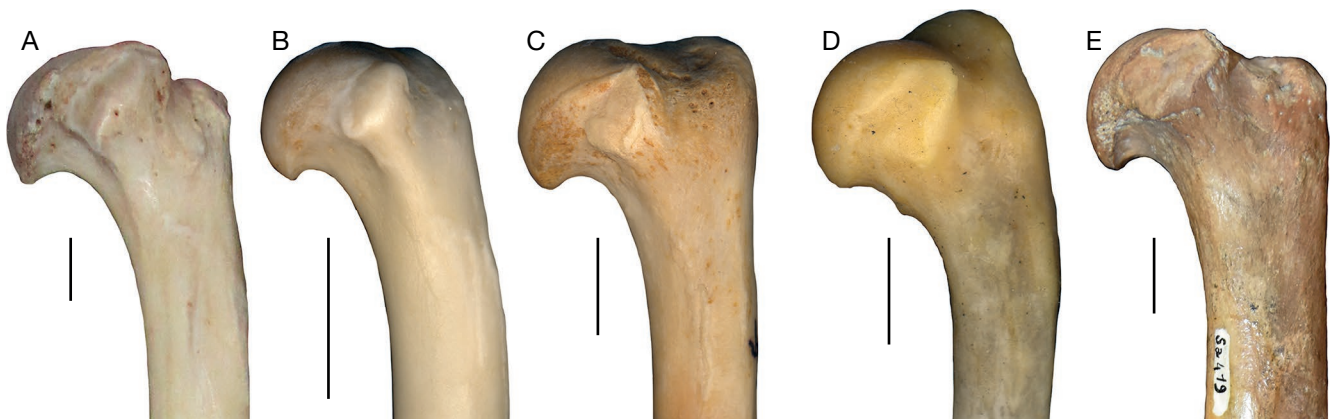


FIG. 2. — Medial view of the proximal epiphysis of the left humerus of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

the mustelid *Mellivora capensis* (Schreber, 1776), which was studied *in situ* in the exhibition of Anatomie Comparée, where it is mounted (MNHN.F.A3413); and the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain), which provided complete skeletons of the mustelids *Martes foina* (Erxleben, 1777) (MNCN 3731) and *Meles meles* (Schreber, 1778) (MNCN 80). For anatomical descriptions, we followed the terminology used by Barone (2010), Evans (1993), and the *Nomina Anatomica Veterinaria* (WAVA 2017).

ANATOMY OF THE LONG BONES OF *ISCHYRICTIS ZIBETHOIDES*

The fossils of *Ischyrictis zibethoides* studied here have been already described by Ginsburg (1961) and Peigné (2012), although these authors did not deeply discuss the functional implications of the observed morphology. Ginsburg (1961) pointed out that the skeleton of *I. zibethoides* was lighter and more gracile than that of *G. gulo*, suggesting less massive body proportions. Thus, we complete here those previous studies, providing a full description of the available long bones of *I. zibethoides* from Sansan, as well as a functional discussion and comparison with those of several species of extant mustelids.

HUMERUS

The diaphysis of the humerus of *I. zibethoides* is quite straight in cranial view, whereas in both lateral and medial views, it shows a gentle curvature. In proximal view, the articular head is round, with a moderately rough greater tubercle developed along the craniolateral margin, and a smooth lesser tubercle located on the medial margin. The greater tubercles of *I. zibethoides* and *T. taxus* are relatively larger and more cranially projected than those of *G. gulo* and *Ma. foina*, but smaller and less projected than that of *Me. meles* (Fig. 1). The intertubercular groove in *I. zibethoides* and *T. taxus* is slightly wider than that of *G. gulo* and *Ma. foina*, but less open than that of *Me. meles*. In the latter, the groove is very shallow, whereas in *T. taxus*, *G. gulo* and *Ma. foina*, it is only slightly deeper than that of *Me. meles*.

In lateral or medial views, the greater tubercle of *I. zibethoides* does not surpass the level of the articular head, although it is slightly more proximally projected than in *G. gulo* and *Ma. foina*, and similar to those of *M. capensis* and *Me. meles*. On the other hand, *T. taxus* shows the most projected greater tubercle, which widely surpasses the level of the articular head (Fig. 2). On the middle of the lateral surface of the greater tubercle there is a marked and deep circular scar for the attachment of the *m. infraspinitus*. The crest of the greater tubercle is distally elongated along the cranial face of the proximal epiphysis, showing a similar development in all the compared species,

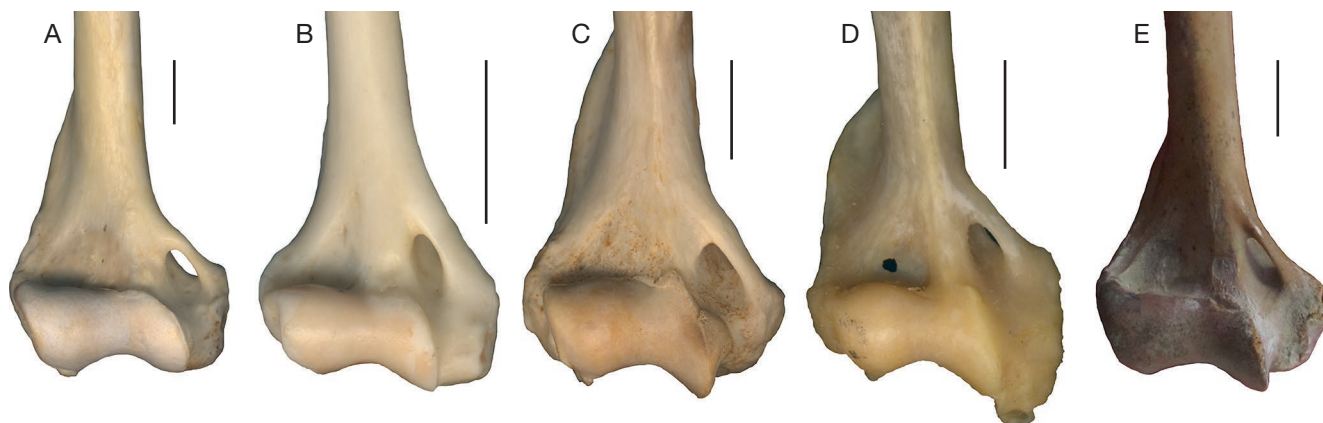


FIG. 3. — Cranial view of the distal epiphysis of the right humerus of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

although it is slightly more distally extended in *Me. meles* and *T. taxus* than in *G. gulo*, *Ma. foina* and *I. zibethoides*. The lesser tubercle of *I. zibethoides* is developed as in *G. gulo*, *M. capensis*, *T. taxus* and *Ma. foina*, that is, medially projected, cranially located to a deep intertubercular groove (which is shallower in *Me. meles*), and showing a marked facet for the *m. subscapularis*. In *I. zibethoides* the articular head is projected caudally, and the neck is marked, clearly distinguished from the head by means of a distal notch; the neck has a very rough lateral facet for the attachment of the *m. teres minor*, located just distally to that for the *m. infraspinatus*; this facet shows strongly ridged cranial and distal margins, which delimitate a strongly excavated area for the accessory branch of the *m. triceps brachii*. This pattern is similar to those of *Me. meles* and *M. capensis*, whereas in *G. gulo* and *T. taxus* the facet for the *m. teres minor* is well developed, but the cranial ridge is less marked and the area for the accessory branch of the *m. triceps brachii* is shallower; finally, in *Ma. foina* these structures are smoother. In *I. zibethoides* the ridged margin extends distally along the lateral face of the diaphysis, producing a very smooth tricipital line (for the attachment of the lateral branch of the *m. triceps brachii*), similar to that of *Ma. foina*, and much less marked than those of *G. gulo*, *T. taxus*, *Me. meles* and *M. capensis*. In medial view, just distally to the lesser tubercle the humerus of *I. zibethoides* shows a marked crest that extends distally onto the diaphysis, curving slightly cranially before its end; the proximal portion of this crest is located caudally to the proximal portion of the large attachment area for the medial branch of the *m. triceps brachii*, whereas the distal half, rougher than the proximal, corresponds to the attachment area of the *m. teres major* (Barone 2010; Ercoli *et al.* 2015); the crest is also well marked, although less distally extended in *Me. meles*, whereas in *G. gulo*, *T. taxus* and *M. capensis* it is smoother and shorter, and in *Ma. foina* it is practically absent.

In the distal epiphysis, the medial epicondyle of *I. zibethoides* is much more developed than the lateral one, being strongly medially projected. Nevertheless, the distal portion of the medial epicondyle of *I. zibethoides*, *Me. meles* and *Ma. foina* lacks the strong medial projection observed in *G. gulo*, *T. taxus*

and *M. capensis* (Fig. 3). In all the compared species there is a well-developed supracondylar foramen. In *I. zibethoides*, *M. capensis* and *Me. meles* the trochlea is projected distally, clearly surpassing the level of the medial epicondyle; in *G. gulo* both structures reach the same level distally, whereas in *Ma. foina* the trochlea just slightly surpasses the level of the medial epicondyle. In *T. taxus* the medial epicondyle is so distally projected that the trochlea does not surpass its distal margin, even when the trochlea is markedly distally projected relative to the capitulum (Fig. 3). In cranial view, the capitulum of *I. zibethoides* shows a proximal expansion on its latero-proximal margin, a feature which is missing in the rest of the compared species. In *I. zibethoides*, *M. capensis*, *T. taxus*, *Ma. foina* and *Me. meles* the trochlea is more distally projected than the capitulum, whereas in *G. gulo* both structures show a similar development. In medial view the cranial margin of the trochlea of *I. zibethoides*, *T. taxus*, *G. gulo*, *M. capensis* and *Ma. foina* is much less distally projected than that of *Me. meles*. The plane of the attachment facet of the *m. pronator teres* is medially oriented in *G. gulo*, *M. capensis* and *Ma. foina*, almost caudally oriented in *T. taxus* and *Me. meles*, and craniomedially oriented in *I. zibethoides*. Just distally to the attachment scar for the *m. pronator teres* there is another, smaller facet for the attachment of the *m. flexor carpi radialis*. Ercoli *et al.* (2015) stated that the Guloninae (which includes among others the genera *Gulo* and *Martes*) are characterised by the fusion in origin of the *m. pronator teres* and *m. flexor carpi radialis*, but this is difficult to infer in *I. zibethoides* from the disposition of the attachment areas of these muscles. In the caudal face of the distal epiphysis (Fig. 4) there is a deep olecranon fossa with a markedly ridged lateral border; this border is slightly laterally inclined in *G. gulo* and *Me. meles*, whereas in *I. zibethoides* and *Ma. foina* it is slightly inclined in medial direction, and thus the capitulum is wider than those of the former species; on the other hand, in *T. taxus* and *M. capensis* this ridge is strongly inclined in lateral direction, producing a relatively narrower capitulum (Fig. 4). The caudal surface of the medial epicondyle shows a rough surface for the medial branch of the *m. triceps brachii*, very similarly developed in

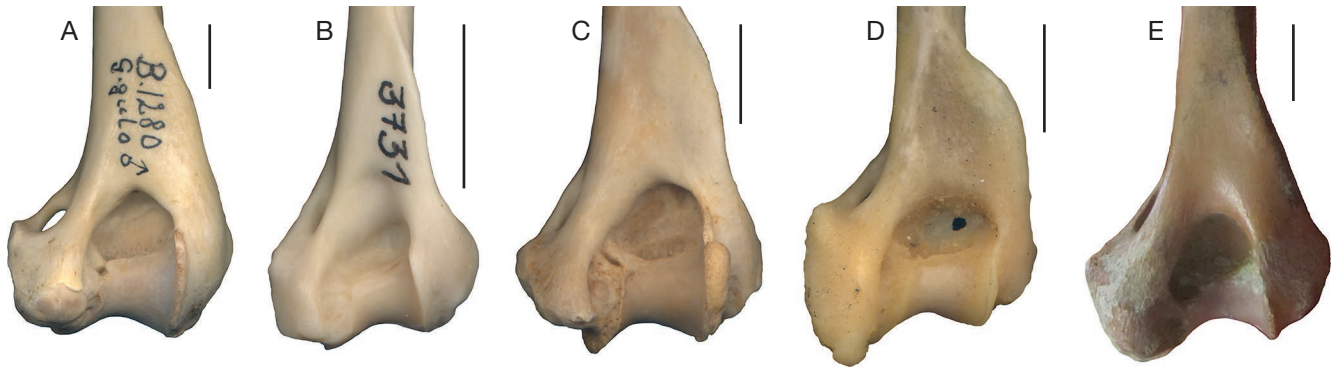


FIG. 4. — Caudal view of the distal epiphysis of the right humerus of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

all the compared species. The medial epicondyle of *I. zibethoides* is more distally projected than the lateral one, as in *T. taxus*, *M. capensis* and *Ma. foina*, whereas in *G. gulo* and *Me. meles*, both epicondyles show a similar distal projection. In the distal tip of the medial epicondyle there is an elliptical and rough surface for the attachment of the *m. flexor carpi ulnaris* (humeral head) and *m. palmaris longus*, more or less distally oriented, as in *T. taxus*, *M. capensis*, *Ma. foina* and *Me. meles*, although relatively much more developed than in these species; on the other hand, this facet is larger in *G. gulo*, in which it is disto-caudally oriented and developed as an inflated surface. Proximally to this surface, on the medial margin, there is an irregular, rough surface for the attachment of the *m. flexor digitorum superficialis* and *m. flexor digitorum profundus* (humeral head), very similarly developed in the rest of compared species. The lateral supracondylar crest shows a very rough lateral margin for the attachment of the *m. extensor carpi radialis*; the crest is as laterally projected as in *G. gulo*, *M. capensis* and *Ma. foina*, whereas in *Me. meles*, and especially in *T. taxus*, the crest is relatively more laterally developed. On the caudal surface of the crest there is a flat and smooth surface for the attachment of the *m. anconeus*, very similar to that seen in *G. gulo*, *M. capensis* and *Ma. foina*, and much less developed than the wide surface present in *T. taxus* and *Me. meles*.

RADIUS

The overall morphology of the radius of *I. zibethoides* resembles that of *G. gulo*, although it is relatively shorter. The diaphysis is craniocaudally compressed, and almost straight in cranial and lateral views. The concave proximal epiphysis is medially inclined and markedly elliptic, with a central notch on its cranial margin. In cranial view, the medial margin of the proximal epiphysis is markedly medially projected, whereas the lateral margin barely surpasses the level of the diaphyseal border. On the lateral border of the caudal face, just distally to the proximal epiphysis, the radial tuberosity of *I. zibethoides* shows an elongated ridge for the attachment of the *m. biceps brachii*. This facet is relatively smaller than those of *G. gulo*, *M. capensis*, *Ma. foina*, *Me. meles* and *T. taxus*

(Fig. 5). Medially to this ridge there is a large and rough surface for the *bursa bicipitoradialis*, similarly developed in *I. zibethoides*, *G. gulo* and *Ma. foina*, and much less marked in *M. capensis*, *Me. meles* and *T. taxus*. In *I. zibethoides* there is a smaller facet, located medioproximally to this surface, absent in *G. gulo*, *Ma. foina*, *Me. meles*, *T. taxus* and *M. capensis*, which probably is the attachment area of the cranial crus of the medial collateral ligament (*lig. collaterale mediale*) (Davis 1964; Evans 1993; Julik *et al.* 2012: fig. 7). On the caudolateral margin of the diaphysis, distally to the facet for the *m. biceps brachii* there is a proximodistally elongated rough scar for the attachment of the interosseous ligament, similarly developed as in *G. gulo* and *M. capensis*; in *Me. meles* this scar is smoother but marked, whereas in *T. taxus* and *Ma. foina* it is practically absent.

The distal epiphysis of *I. zibethoides* is medio-laterally expanded, in a similar way to that of the compared species (Fig. 5). In distal view the distal epiphysis is elliptic, with its lateral half craniocaudally longer than the medial one, as in *G. gulo*, *T. taxus* and *M. capensis*; in *Me. meles* the middle part is craniocaudally longer, whereas in *Ma. foina* the epiphysis is mediolaterally very elongated, with both medial and lateral parts of similar size. The distal articular facet for the scapholunar is mediolaterally elongated in *G. gulo*, *T. taxus*, *M. capensis* and *Ma. foina*, occupying almost the whole distal surface, whereas in *I. zibethoides* the facet is slightly less expanded laterally, the distal epiphysis showing a thick lateral border lacking any facet; in *Me. meles* the facet is almost round and relatively smaller than those of the former species. On the medial margin of the distal epiphysis of *I. zibethoides*, *G. gulo*, *T. taxus* and *M. capensis* there is a proximodistally elongated bony sheet, low but ridged, for the attachment of the *m. brachioradialis*; in *Me. meles* and *Ma. foina* this crest is restricted to the distal epiphysis. In *I. zibethoides* the cranio-lateral half of the distal epiphysis shows a rough tubercle delimitating a deep lateral groove that gives passage to the tendon of the *m. extensor digitorum communis*; this tubercle is similarly developed in *G. gulo* and *Ma. foina*, whereas in *M. capensis* and *M. meles* it is located in the middle of this cranial face and is much less developed than in the former species; finally, in



FIG. 5. — Caudal view of the right radius of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyriictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison.. Scale bar: 1 cm.

T. taxus this tubercle is very smooth. Medially to this tubercle there is a smooth surface where the tendons of the *m. extensor carpi radialis* are accommodated. On the craniomedial margin there is a deep groove for the passage of the tendon of the *m. abductor digiti I longus*, similarly developed in all the compared taxa. This groove is located medially to the styloid

process of the distal epiphysis, and does not show notable differences among the compared mustelids. On the lateral margin of the distal epiphysis of *I. zibethoides*, *Me. meles*, *T. taxus*, *M. capensis* and *Ma. foina* there is a round, markedly projected articular facet for the ulna; in *G. gulo* the facet is elliptical and craniocaudally elongated.



FIG. 6. — Medial view of the left ulna of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

ULNA

The available ulnae of *I. zibethoides* from Sansan are distally broken, so the actual proportions of this bone are difficult to

assess. The diaphysis shows a strong mediolateral flattening, and, based on specimen Sa.423, a slight caudal curvature on the distal part can be inferred, such as that seen in *G. gulo*, and, to a lesser

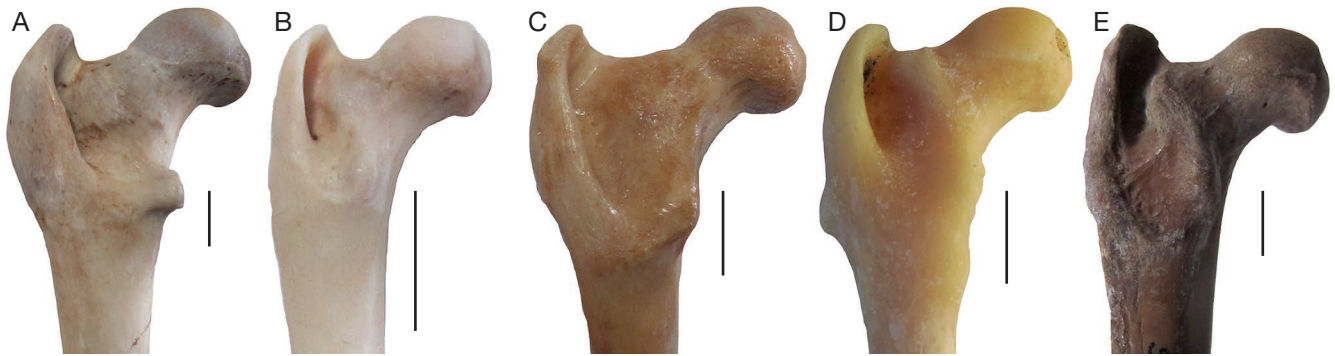


FIG. 7. — Caudal view of the proximal epiphysis of the left femur of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyriictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

extent, in *Ma. foina* and *Me. meles* (Fig. 6). The olecranon of *I. zibethoides* is well developed, very similar in length to that of *Me. meles*, and thus longer than those of *G. gulo* and *Ma. foina*; on the other hand, the olecranon of *M. capensis* and *T. taxus* are the longest among the compared sample (Fig. 6). The proximal border of the olecranon of *I. zibethoides* is slightly inclined cranially, as in *G. gulo*, *Me. meles*, *T. taxus* and *M. capensis*, whereas in *Ma. foina* this border is inclined caudally. The orientation of the olecranon in *I. zibethoides* shows a gentle caudal inclination, whereas in *G. gulo*, *M. capensis* and *Me. meles* it is almost vertical, being cranially inclined in *Ma. foina* and *T. taxus*. In cranial view, the olecranon of *I. zibethoides* shows a medial inclination, slightly less marked than in *G. gulo* and *M. capensis*, and similar to those of *Me. meles*, *T. taxus* and *Ma. foina*. The tuber olecrani of *I. zibethoides* show a similar morphology to that of *Ma. foina*, that is, the medial tubercle is markedly projected proximally, surpassing the level of the lateral tubercle, which is barely projected. In *G. gulo*, *Me. meles*, *T. taxus* and *M. capensis* the medial tubercle is also much more proximally projected than the lateral one, but the latter is very reduced in *G. gulo* and absent in *Me. meles*, *T. taxus* and *M. capensis*. The radial notch is located laterocranially, in a very similar way to that of *Ma. foina*, and thus more cranially than in *G. gulo*, *Me. meles*, *T. taxus* and *M. capensis*, in which the radial notch is almost completely laterally oriented.

The diaphysis is strongly lateromedially flattened in all the compared species. Its lateral surface is mostly smooth, although there is a rough, proximodistally elongated scar for the attachment of the interosseous ligament, also observed in *G. gulo* and *M. capensis*. In *I. zibethoides* there is a soft ridge on the caudolateral margin delimiting a proximodistally elongated groove for the attachment of the *m. abductor digiti I longus*, which extends proximally to the middle of the trochlear notch in all the compared mustelids. Caudally to this groove, and developed along the caudal margin, there is a slightly rough distally elongated surface for the attachment of the *m. extensor digiti I et II*. On the medial face of the proximal epiphysis, just distally to the trochlear notch there is an elliptical, proximodistally elongated groove for the attachment of the *m. brachialis*; this facet is relatively larger in *I. zibethoides* and *Ma. foina* than in *G. gulo*, *T. taxus*, *Me. meles* and *M. capensis*.

FEMUR

The two available fragments of femur of *I. zibethoides* from Sansan, one proximal and one distal, do not allow inferring the actual length and proportions of a complete femur, as they do not form a complete bone. The femoral head is projected proximomedially by means of a well-developed neck, but it does not surpass the level of the greater trochanter. In *Me. meles*, *G. gulo* and *Ma. foina* the head slightly surpasses the level of the greater trochanter, whereas in *T. taxus* and *M. capensis* the head is strongly proximomedially projected, greatly surpassing the level of the greater trochanter (Fig. 7). In lateral view, the greater trochanter of *I. zibethoides*, *G. gulo*, *T. taxus* and *Me. meles* has a rough gluteal tuberosity with a strongly ridged cranial margin and a smoother distal margin, whereas in *M. capensis* this latter margin is as strongly ridged as the cranial one; on the other hand, *Ma. foina* shows very smooth margins. On the proximal tip of the greater trochanter, the attachment areas for the *m. gluteus accessorius* and *m. gluteus medius* show a similar pattern in *I. zibethoides*, *Me. meles*, *T. taxus*, *Ma. foina* and *M. capensis* in so far as the attachment area for the *m. gluteus medius* is located proximally to that of the *m. gluteus accessorius*, with both restricted to the proximal surface of the greater trochanter, whereas in *G. gulo* both areas extend on the lateral face of the greater trochanter. In *I. zibethoides* the caudal face of the proximal epiphysis shows a deep trochanteric fossa and a rough intertrochanteric crest, which delimits a large attachment area for the *m. quadratus femoris* and *m. obturator externus*. This area is relatively larger than those of *G. gulo*, *M. capensis*, *T. taxus* and *Ma. foina*, and similar to that of *Me. meles* (Fig. 7). The lateral border of the trochanteric fossa is medially inclined, as in *Ma. foina*, *T. taxus* and *M. capensis*, whereas in *G. gulo* and *Me. meles* it is clearly laterally inclined and seems inflated in caudal view. In *I. zibethoides*, *Me. meles*, *T. taxus*, *M. capensis* and *Ma. foina* the lesser trochanter is developed as a low and rough tuberosity, slightly proximodistally elongated, whereas in *G. gulo* it is a large and round tubercle that is strongly caudomedially projected. In *I. zibethoides* and *M. capensis* the lesser trochanter continues distally, form-

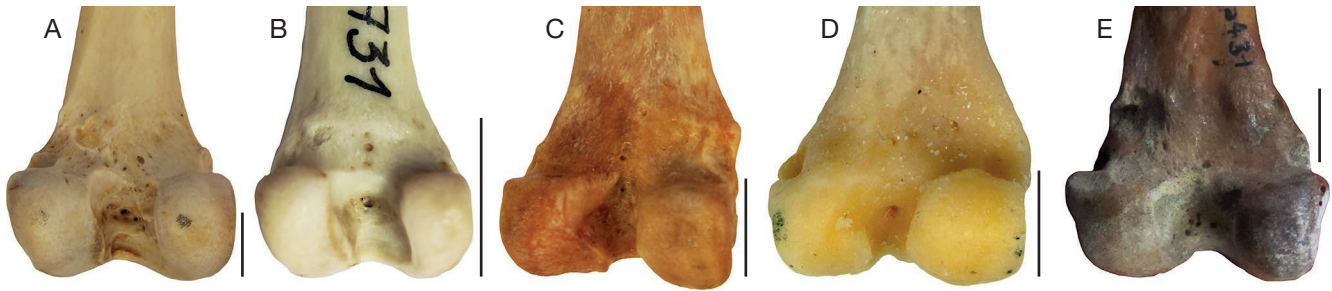


FIG. 8. — Caudal view of the distal epiphysis of the left femur of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

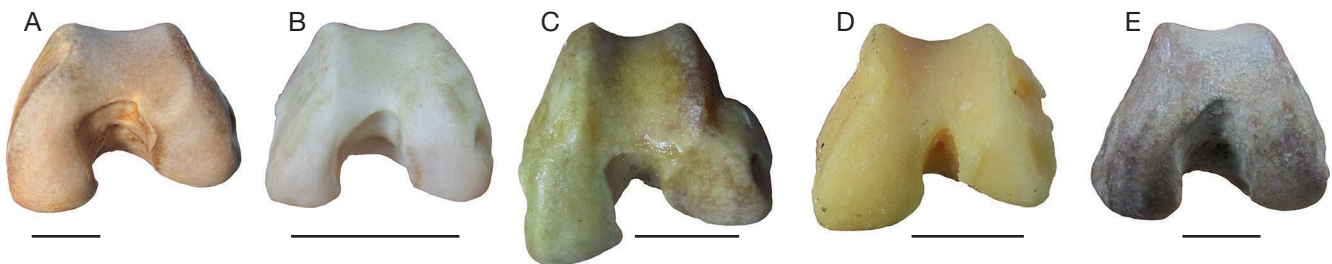


FIG. 9. — Distal view of the distal epiphysis of the left femur of several species of Mustelidae: *Gulo gulo* (Linnaeus, 1758) (A), *Martes foina* (Erxleben, 1777) (B), *Meles meles* (Schreber, 1778) (C), *Taxidea taxus* (Linnaeus, 1758) (D), and *Ischyrictis zibethoides* (Blainville, 1841) from Sansan (E), shown at the same size for a better comparison. Scale bar: 1 cm.

ing the rough and ridged medial lip of the facies aspera, where the *m. vastus medialis* and *m. adductor longus* are attached; in *G. gulo* this line is as distally developed as in these two former species, although it is less marked, lacking any ridge; in *Me. meles*, *T. taxus* and *Ma. foina* the line is very smooth and shorter than in *G. gulo*, as it barely surpasses the level of the distal margin of the lesser trochanter.

In the distal epiphysis of *I. zibethoides*, the lateral condyle is medio-laterally wider than the medial one. In caudal view it is evident that whereas the medial condyle is inclined medially, the lateral one shows the opposite orientation, being clearly laterally inclined. This morphology is different from that of *G. gulo*, *M. capensis* and *Ma. foina*, in which both condyles show a lateral inclination in caudal view, and from that of *Me. meles*, in which the medial condyle is more or less proximodistally oriented; on the other hand, *T. taxus* shows the same morphology as *I. zibethoides* (Fig. 8). As a consequence of this morphology, the intercondyloid fossa of *I. zibethoides* is proximally wider than those of the other compared taxa (including *T. taxus*). In distal view all the compared taxa show a medial condyle that is more caudally projected than the lateral one, although to different degrees, with *I. zibethoides* and *Ma. foina* showing a less projected medial condyle (Fig. 9). In both lateral and medial views, the cranio-caudal length of the distal epiphysis and the curvature of the femoral trochlea are very similar to those of *G. gulo*, *M. capensis* and *Ma. foina*. In *Me. meles* and *T. taxus* the distal epiphysis is cranio-caudally shorter.

FUNCTIONAL IMPLICATIONS

HUMERUS

In proximal view, the development and cranial projection of the greater tubercle of *I. zibethoides* show more similarities with the morphology observed in *Me. meles* and *T. taxus*. This tubercle is the attachment area for the *m. supraspinatus*, which abducts and extends the gleno-humeral articulation (Barone 2010), and besides the *m. infraspinatus*, it stabilizes this articulation, restricting both the cranial displacement of the humeral head, and the transverse movement of the scapula (Evans 1993; Barone 2010). A strong cranial projection of the greater tubercle increases the distance between the origin and the attachment areas of the *m. supraspinatus*, and thus the range of extension of the gleno-humeral articulation in the parasagittal plane (Feeney 1999; Siliceo *et al.* 2015), also improving its mechanical stabilization. Strongly cranially projected greater tubercles are usually found among cursorial and digging carnivores (Taylor 1978; Spoor & Badoux 1986), whereas arboreal species tend to exhibit greater tubercles lacking this cranial projection (Taylor 1974). Thus, in both *Me. meles* and *T. taxus* the cranially projected greater tubercle can be related to their digging adaptations, which require strong flexion and extension movements of the forelimb, as well as an adequate joint stabilization. *Ischyrictis zibethoides*, also showing a markedly cranially projected greater tubercle, probably required a strong stabilization of the glenohumeral articulation, and although this cannot be directly associated to a specific locomotor type, at least it is an indication of strong biomechanical tensions affecting the shoulder joint

during locomotion. In any case, since other features of the appendicular skeleton of *I. zibethoides* indicate terrestrial locomotion, the presence of a cranially projected greater tubercle would fit this interpretation.

The distally more elongated crest of the greater tubercle of both *Me. meles* and *T. taxus* in relation to those of *G. gulo*, *Ma. foina* and *I. zibethoides*, is also a clear indication of the digging adaptations of the former species (Hildebrand 1985). This crest is the attachment area for the *mm. pectorales* (*superficialis* and *profundus*) and *m. deltoideus*, the latter attaching on the deltoid tuberosity in the distal part of the crest (Davis 1964; Barone 2010; Ercoli *et al.* 2015). Thus, an elongated crest provides a long area for the *mm. pectorales*, but also determines that the insertion area for the *m. deltoideus* is located farther from the proximal articulation (the shoulder), which increases the strength of the muscle, which is typical of diggers such as badgers (Hildebrand 1985; Ercoli *et al.* 2015). Considering this, the morphology of this crest in *I. zibethoides* suggests that this species had not developed the specialized digging capabilities of other mustelids.

The intertubercular groove for the passage of the tendon of the *m. biceps brachii* is slightly more excavated in *I. zibethoides*, *G. gulo* and *T. taxus* than in *Ma. foina* and *Me. meles*, probably indicating the presence of a relatively stronger muscle (Taylor 1974). Indeed, among Mustelidae, *G. gulo* and *T. taxus* show a relatively larger *m. biceps brachii*, with the development of extra muscle bellies (Ercoli *et al.* 2015). In extant viverrids, this groove is much more excavated in arboreal than in terrestrial species, probably due to the need for stronger flexor and extensor muscles in the former (Taylor 1974). Among the compared sample the arboreal *Ma. foina* exhibits a slightly shallower intertubercular groove than the more terrestrial and much larger *G. gulo*, more probably due to their differences in body size rather than to a contradiction with the observations by Taylor (1974).

The smooth tricipital line of *I. zibethoides*, more similar to that of the much smaller *Ma. foina* than to those of *G. gulo*, *Me. meles*, *T. taxus* and *M. capensis* would indicate the presence of a relatively small lateral branch of the *m. triceps brachii*. This branch of the *m. triceps brachii* originates along the tricipital line by means of an aponeurosis (Barone 2010), and thus a smoother line implies the presence of a smaller muscle. The lateral branch of the *m. triceps brachii* assists the long branch in the extension of the forearm (Evans 1993; Barone 2010), and given the fact that in dogs it contains about 75% fast fibres, it probably stores elastic energy during locomotion, which suggests a dynamic role in this activity (Armstrong *et al.* 1982; Evans 1993). In consequence, we would expect to find relatively more developed lateral branches of the *m. triceps brachii* in those species moving mainly on open terrain, such as *G. gulo*, *Me. meles*, *T. taxus* and *M. capensis* (Pasitschniak-Arts & Larivière 1995; Vanderhaar & Hwang 2003; Nowak 2005) in comparison to arboreal forms such as *Ma. foina* (Nowak 2005). In this respect, it is remarkable that both *G. gulo* and *M. capensis* have relatively large lateral branches of the *m. triceps brachii*, whereas that of *Ma. foina* shows a smaller size (Gambaryan 1974). Thus, from the

development of the tricipital line, *I. zibethoides* probably had a relatively small lateral branch of the *m. triceps brachii*, which could reflect a primitive pattern, shared with arboreal mustelids, but also less cursorial abilities than large extant mustelids such as *G. gulo* and *M. capensis*. In contrast with the limited development of the lateral branch of the *m. triceps brachii*, the medial branch of *I. zibethoides* seems to have been as well developed as that of other large mustelids, as the morphology of its attachment surface suggests. It is remarkable that this medial branch in dogs contains only 4% fast fibres (Armstrong *et al.* 1982), that is, around 96% of its fibres are slow-twitch fibres. This implies a slow contraction, but also a muscle that fatigues less rapidly than a muscle with a predominance of fast fibres (Ranvier 1880; Jones *et al.* 2004).

The distal epiphysis of the humerus of *I. zibethoides* shows some differences with the compared mustelids, such as the less medial projection of the medial epicondyle, the more distally projected trochlea, and the more cranially located medio-distal surface of the supracondylar bar. Among these anatomical differences, the less projected medial epicondyle has interesting consequences for the configuration of the pronator and flexor muscles of the forearm, basically the *m. pronator teres*, *m. flexor carpi radialis*, and *m. flexor digitorum profundus*, which attach onto this structure (Davis 1964; Evans 1993; Barone 2010; Ercoli *et al.* 2015). Among mammals, a marked medial projection of the medial epicondyle is associated to a strong development of these forearm muscles, indicative of high pronatory-supinatory abilities, typical of arboreal and forest-dweller species, but also of aquatic and semi-fossorial species, whereas a reduction in this epicondyle is observed in cursorial species (Taylor 1974; Argot 2001; Andersson 2004; Milne *et al.* 2008; Fabre 2013; Samuels *et al.* 2013; Fabre *et al.* 2015). Concerning the attachment surface of the *m. pronator teres* on the humerus, in *I. zibethoides* and *Me. meles* it is more cranially located than in *G. gulo*, *T. taxus* and *M. capensis*, and medially oriented (as in *G. gulo*, *M. capensis* and *Ma. foina*). This muscle is an important pronator of the forearm (Evans 1993; Barone 2010), and the more caudal location of its attachment area on the humerus means an increase in the length of the muscle, which produces an increase in the pronation range. This attachment area is located in a similar position in *I. zibethoides* and *Ma. foina*, suggesting a similar relative length of the *m. pronator teres*, whereas it would be relatively longer in *G. gulo*, *T. taxus*, *M. capensis* and *Me. meles*, although by means of slightly different anatomical changes. The attachment surfaces for the *m. flexor carpi ulnaris* (humeral head) and *m. palmaris longus*, located on the distal tip of the medial epicondyle, are larger in *I. zibethoides* than in the rest of the compared taxa except *G. gulo*, in which it is even larger, distocaudally oriented, and developed as an inflated surface. In the latter species, the relative weights of the *m. flexor carpi ulnaris* and *m. palmaris longus* are, respectively, 1.7% and 1.1% of the total mass of the muscles of the fore and hind limb, whereas in the other compared species these relative masses range from 0.5 to 0.9% (for the *m. flexor carpi ulnaris*) and from 0.6 to 0.8% (for the *m. palmaris longus*) (Gambaryan 1974). These relatively larger muscles in *G. gulo* could explain the size of their attachment facets. Similarly, and given the

size of this facet in *I. zibethoides*, this species would have possessed relatively large *m. flexor carpi ulnaris* and *m. palmaris longus*, although probably smaller than those of *G. gulo*. The *m. flexor carpi ulnaris* flexes and abducts the forepaw (Evans 1993), and contains significantly more slow fibres in dogs and cats than any other forearm muscle (Gonyea *et al.* 1981; Armstrong *et al.* 1982), which suggests that this muscle is probably important in performing an antigravity role during stance and locomotion (Glenn & Whitney 1987; Evans 1993). Thus, it is to be expected that terrestrial, relatively large animals have a well-developed *m. flexor carpi ulnaris*. It is remarkable that, despite other similarities with *G. gulo*, the distally projected trochlea of *I. zibethoides* shows a very different morphology to that observed in the former. In fact, this is one of the main differences in the long bones of these two large mustelids. A distally projected medial margin of the trochlea, surpassing the level of the capitulum, is also observed in the rest of the compared species, and it has been described as a mechanism for stabilizing the articulation during terrestrial locomotion (Andersson 2004; Taylor 1974). In this respect, *I. zibethoides* would exhibit an elbow better suited for cursorial locomotion than that of *G. gulo*, although in this latter, an elbow capable of a wider range of mediolateral movement could be a specialization for moving on the snow during winters.

The proximal projection in the lateral margin of the capitulum observed in *I. zibethoides*, and absent in the rest of the compared species, has been also reported in the extant bare-tailed woolly opossum (*Caluromys philander*), in relation to elbow stabilization during the flexion movements produced when climbing (Argot 2001). Nevertheless, this extant didelphid is an arboreal, much smaller animal than *I. zibethoides*, with adults reaching 300–400 g body mass (Atramentowicz 1995), whereas *I. zibethoides* is a *Gulo*-sized species whose body weight would be around 10.9–32 kg (Hall 1981; Nowak 2005), with no traits for arboreality. Thus, the presence of this proximal expansion of the capitulum in *I. zibethoides* would probably improve elbow stabilization during flexion, but in the context of terrestrial locomotion. Another feature, the orientation of the lateral border of the olecranon fossa and capitulum, also can be associated with elbow stabilization. This border is slightly medially inclined in *I. zibethoides* and *Ma. foina*, slightly laterally inclined in *G. gulo* and *Me. meles*, and strongly laterally inclined in *T. taxus* and *M. capensis*. This produces evident differences in the relative width of the capitulum, which is relatively wider in *I. zibethoides* and *Ma. foina*, whereas *T. taxus* and *M. capensis* have the proportionally narrowest capitula, at least in caudal view. These differences in the capitulum width and the orientation of the lateral margin of the olecranon fossa have implications for elbow biomechanics, as they determine the relative position of humerus, ulna and radius during flexion and extension of the forearm (Gonyea 1978). Thus, in those terrestrial mammals with no special adaptations to cursoriality, the lateral border of the olecranon fossa is laterally inclined, which makes the proximodistal axes of both ulna and radius form an angle to the proximodistal axis of the humerus when the elbow flexes and extends during locomotion (Jenkins 1971; Gonyea 1978). On the other hand, in cursorial mammals, such

as canids or the cheetah, the ridges of the olecranon fossa are almost parallel to the proximodistal axis of the humerus, and thus during flexion and extension of the elbow, both the ulna and the radius are located in a quite straight position in relation to the humerus (Gonyea 1978). In this respect, the morphology of the olecranon fossa of *T. taxus* and *M. capensis* would fit with that expected for non-cursorial mammals, whereas that of *G. gulo*, and *Me. meles* would reflect more cursorial capacities, or at least a more parasagittal posture. The morphology shown by the olecranon fossa of *I. zibethoides* and *Ma. foina*, with its lateral ridge slightly medially inclined, is also observed in ursids, and it has been interpreted as a mechanism for increasing the lateral stability of the elbow during locomotion (Argot 2010). In any case, Fabre *et al.* (2015) found a remarkable convergence between aquatic and arboreal/semi-arboreal species of musteloid carnivorans, with both groups displaying a broad capitulum, as a consequence of the necessity for augmenting the degree of pronation/supination in these groups (Fabre *et al.* 2015). Thus, the morphology of the capitulum of *I. zibethoides* suggests a good capacity for pronation/supination, and the necessity of a strong control of elbow lateral movements; nevertheless, both requirements have no clear implications for the locomotor capacities of this carnivoran, and they also could be related to hunting strategies. Besides this, the distally projected trochlea of *I. zibethoides*, similar to that of the rest of compared mustelids except *G. gulo*, is a feature that provides additional stability against forces acting in a non-parasagittal plane during locomotion, that is, when flexion and extension movements are not developed in a strict parasagittal plane (Gonyea 1978; Andersson 2004; Argot 2004); on the other hand, the trochlea of those carnivorans whose forelimbs are used primarily for locomotion is moderately distally projected (Andersson 2004). In summary, the distal morphology of the humerus of *I. zibethoides* suggests a generalised locomotor behaviour, and in any case, it is not indicative of well-developed cursorial capacities.

RADIUS

The radial tuberosity, the attachment area for the *m. biceps brachii*, is relatively smaller in *I. zibethoides* than in *Me. meles*, *M. capensis*, *Ma. foina*, *T. taxus* and *G. gulo*, with the two latter species showing the relatively largest and most distally expanded radial tuberosities. This would suggest a relatively smaller muscle in *I. zibethoides*, and a larger, well-developed one in *G. gulo* and *T. taxus*. Interestingly, as pointed out above, several authors have found that the *m. biceps brachii* is relatively large, even showing extra bellies, in *G. gulo* and *T. taxus* (as well as in ursids, felids, ailurids and some procyonids), that is, those carnivorans exhibiting climbing or digging abilities (Davis 1949, 1964; Gambaryan 1974; Quaipe 1978; Fisher *et al.* 2009; Julik *et al.* 2012; Ercoli *et al.* 2015). This muscle is one of the main flexors of the elbow (Barone 2010; Ercoli *et al.* 2015), and it is usually reduced in terrestrial and cursorial species (Taylor 1974; Feeney 1999). The existence of a relatively small *m. biceps brachii* in *I. zibethoides* would indicate a mostly terrestrial lifestyle, which fits with our observations on other bones of its skeleton.

The presence of a marked facet for the cranial crus of the medial collateral ligament (*lig. collaterale mediale*), observed in *I. zibethoides*, and absent in *G. gulo*, *Ma. foina*, *Me. meles*, *T. taxus* and *M. capensis*, probably indicates a strong ligament, although the functional implications of this difference are difficult to assess. In canids, the medial collateral ligament originates on the medial epicondyle of the humerus, crosses the annular ligament of the radius, and then it divides into two crura, one cranial, weaker, and attaching on the radius, and another one, caudal, much more thicker, and attaching mainly on the ulna and partially on the radius (Evans 1993; Barone 2010). The presence in *I. zibethoides* of a relatively thick cranial crus of the *lig. collaterale mediale* probably indicates the necessity for strong control of the mediolateral movements of the elbow, which can be associated to both locomotion and the use of the forelimb in other activities, such as hunting or intraspecific interactions.

ULNA

Although several features of the ulna of *I. zibethoides* are also seen in other carnivorans, the olecranon shows a distinctive morphology among the compared Mustelidae. It is relatively long, similar to those of *Me. meles* and *M. capensis*, although it is caudally inclined as in *Ma. foina*. An elongated olecranon, besides a non-curved diaphysis, is typical of terrestrial forms, and indicates a probably well-developed *m. triceps brachii*, associated to a powerful extension (Taylor 1974; Argot 2001), although the former feature has been also associated with semiaquatic and semi-fossorial species (Fabre 2013; Samuels *et al.* 2013). Thus, the olecranon length by itself does not provide with an indication of locomotor type, and it should be taken in combination with other ulnar features, such as the proportions of this bone or the orientation of the radial notch. Aquatic and fossorial species, although showing an elongated olecranon, also have relatively robust radii and ulnae (Fabre 2013).

In lateral and medial views, the orientation of the olecranon and its proximal border affects the function of the long branch of the *m. triceps brachii*, which attaches onto the caudal border of the olecranon. Thus, a cranially inclined olecranon indicates that the long branch of the *m. triceps brachii* acts from a more flexed elbow than in those species with a caudally inclined olecranon, whose triceps group will be predominantly associated with the later part of protraction and the beginning of retraction of the limb (Ondrias 1961; Taylor 1970, 1974). These two morphologies have been thus associated to locomotor types, with those species having a caudally inclined olecranon being cursorial forms, whereas those with cranially inclined olecrani show arboreal adaptations (Taylor 1974; Argot 2001, 2004). In *I. zibethoides* the olecranon morphology would be typical of a large, relatively terrestrial species, even more cursorial than *G. gulo*.

The tuberosities of the olecranon of *I. zibethoides* show a similar pattern to those of the other compared species, with the medial one being markedly proximally projected, much more so than the lateral tuberosity; the only difference is the strong reduction or absence of the lateral tuberosity in

G. gulo, *Me. meles* and *M. capensis*, whereas in *I. zibethoides* and *Ma. foina* this tuberosity is well developed. The lateral and medial tuberosities of the ulna are the attachment areas, respectively, of the *m. triceps brachii caput laterale* and *m. triceps brachii caput mediale* (Davis 1964; Fisher *et al.* 2009; Barone 2010; Julik *et al.* 2012; Ercoli *et al.* 2015). Thus, the reduction in the size of the lateral tuberosity in *G. gulo*, *Me. meles* and *M. capensis* would suggest a relatively smaller *m. triceps brachii caput laterale*, as has been described in other carnivorans (Gonyea 1978). The *m. triceps brachii* is one of the main extensors of the elbow (Evans 1993; Barone 2010; Ercoli *et al.* 2015); in Mustelidae in general it is composed of seven well-separated bellies (Ercoli *et al.* 2015). Among them, the *m. triceps brachii caput laterale* is the second heaviest of the seven bellies, with the *m. triceps brachii caput longum* being the heaviest (Ercoli *et al.* 2015). This gives an idea of the importance of the *m. triceps brachii caput laterale* in the biomechanics of the elbow, and why the development of the ulnar tuberosities is so important for locomotion. Terrestrial, and especially digging mustelids, which need strong extension of the forearm, are characterized by the dominance in the elbow of the extensor muscles over the flexor ones (Ercoli *et al.* 2015), and thus the presence of a well-developed *m. triceps brachii*. Gonyea (1978: 116) associated the morphology of the ulnar tuberosities in Felidae with “degree of deviation of the anterior limb from the parasagittal plane during locomotion; those felids with a relatively large lateral tuberosity probably have the greatest parasagittal deviation of the elbow during locomotion, and those with a relatively large medial tuberosity probably exhibit little deviation of the forelimb from a ‘pendulum-like’ motion”. Also, this author observed that a well-developed lateral tuberosity, associated with a large *m. triceps brachii caput laterale*, was typical of felids inhabiting forested habitats, whereas those species with reduced or absent lateral tuberosities were capable cursors, preferring more open habitats (Gonyea 1978). At this respect, the compared extant species of Mustelidae fit well within this classification, with *Ma. foina* being a woodland-dweller, and *G. gulo*, *Me. meles* and *M. capensis* occupying less structured habitats (Nowak 2005; Larivière & Jennings 2009). In the case of *I. zibethoides*, which has a well-developed lateral ulnar tuberosity, it would be linked to well vegetated areas.

The overall morphology of the ulnar diaphysis also provides interesting data on the biomechanics of this fossil mustelid; for example, the absence of lateral torsion in the olecranon of *I. zibethoides* suggests that the movements of flexion-extension of the elbow took place in a more or less parasagittal plane (Argot 2004), unlike in the rest of the compared mustelids. Also, the slight caudal inclination of both the proximal epiphysis and the diaphysis resembles the morphology exhibited by typical cursorial carnivorans, in contrast to the cranial curvature observed in digging, climbing and scansorial carnivorans (Taylor 1974; Argot 2004; Heinrich & Houde 2006; Rose *et al.* 2014; Ercoli & Youlatos 2016; Henderson *et al.* 2016). On the other hand, the relatively large facet for the *m. brachialis* of *I. zibethoides* and *Ma. foina* suggests the presence of a well-developed muscle, which is typical of climbing and

digging carnivorans (Davis 1949, 1964; Gambaryan 1974; Quaife 1978; Fisher *et al.* 2009; Julik *et al.* 2012; Ercoli *et al.* 2015). These species need powerful elbow flexion in order to maintain the body close to the substrate, which increases the stability and the control of the movements (Davis 1964; Taylor 1974; Leach 1977; Van Valkenburgh 1987; Hildebrand 1988; Argot 2001; Ercoli *et al.* 2015). This is something expected in *Ma. foina*, which is a forest-dweller and thus a capable climber (Leach 1977; Hall 1981), but does not fit with the presence, in *I. zibethoides*, of a relatively reduced *m. biceps brachii*, another important flexor of the elbow. In any case, and given other features in the postcranial skeleton of *I. zibethoides* pointing towards terrestrial locomotion, this trait could be a primitive retained morphology.

FEMUR

A proximal projection of the greater trochanter, surpassing the level of the femoral head, is typical of cursorial terrestrial carnivorans (Ercoli & Youlatos 2016). Only *I. zibethoides* shows this feature among the sample of studied mustelids, although in a moderate state. The different proximal projection of the femoral head has also a direct relationship with the action of both the *m. piriformis* and the *m. gluteus medius*, two muscles attaching on the greater trochanter of the femur (Davis 1964; Barone 2010; Ercoli *et al.* 2013), which can show different degrees of fusion among Musteloidea (Lucae 1875; Mackintosh 1875; Alix 1876; Hall 1927; Fisher *et al.* 2008; Ercoli *et al.* 2013). In non-cursorial mustelids, those muscles that extend the coxofemoral articulation (the gluteus group) are relatively less developed than in cursorial species when compared to total hind limb musculature (Maynard Smith & Savage 1956; Gambaryan 1974; Ercoli *et al.* 2013). Thus, in a number of species of the genera *Mustela* and *Martes*, Gambaryan (1974) indicates a weight for the *m. gluteus medius* of 1.9–2.1% of the total fore and hind limb muscles, whereas in the more robust *G. gulo* this relative weight is 3.1%, it reaching a percentage of 3.3% in *M. capensis*. This difference in the relative weight of this muscle can be associated with the size of its attachment area on the greater trochanter, which is relatively smaller (mediolaterally shorter) in *Ma. foina* than in *G. gulo*; in *I. zibethoides* this area is very similar to that of *Ma. foina*, suggesting a less developed muscle. Interestingly, other muscles, such as the *m. quadratus femoris* and *m. obturator externus*, seem to have been very well developed in *I. zibethoides*, as suggested by their attachment surfaces on the trochanteric fossa. This structure is relatively much larger than in *G. gulo*, *M. capensis*, *T. taxus* and *Ma. foina*, and similarly sized to that of *Me. meles*. The *m. quadratus femoris* is a thick and short muscle, developed from the lateral surface of the ischium to the caudodistal region of the greater trochanter and the trochanteric fossa (Barone 2010; Ercoli *et al.* 2013); its functions are extending and rotating the coxofemoral articulation, as well as preventing its medial rotation during weight bearing (Evans 1993; Barone 2010). In any case, the relative weight of this muscle in Mustelidae is really low, as it does not surpass 0.4% of the total weight of the fore and hind limb muscles (Gambaryan 1974); thus, the presence of

a relatively larger *m. quadratus femoris* in both *I. zibethoides* and *Me. meles* in comparison to other species would have a low impact on the overall hind limb musculature. On the other hand, the *m. obturator externus* does show remarkable differences in relative weight among extant Mustelidae: in *G. gulo* is 1.5% of the total weight of the fore and hind limb muscles, whereas in *Ma. foina* it is 1.1%, in *M. capensis* it is 0.9%, and in the *Mustela* species it does not surpass 0.7% (Gambaryan 1974). This muscle is thin, but much larger than the *m. quadratus femoris*, and its functions are the lateral rotation of the coxofemoral articulation, and the prevention of its medial rotation during weight bearing (Evans 1993; Barone 2010; Ercoli *et al.* 2013). Houghton (1867) found remarkable differences in the relative weight of the *m. obturator externus* among different dog breeds, with the Greyhound having a muscle almost twice the size of that of less cursorial breeds. In consequence, if a relatively large *m. obturator externus* is typical of terrestrial mustelids such as *G. gulo*, and *I. zibethoides* shows a large attachment area for this muscle, that would be another feature pointing towards the importance of terrestrial locomotion in this fossil mustelid.

Finally, a caudally projected medial condyle has been associated to slight rotation capabilities of the tibia relative to the femur, that is, the latter rotates medially when flexing the knee, which provides stability to this articulation (Grohé *et al.* 2012; Argot 2013) something important in digging animals such as *Me. meles*. At this respect, *I. zibethoides* would be showing a generalised condition observed in other mustelids.

CONCLUSIONS

The present study on the long bones of the fossil mustelid *Ischyriictis zibethoides* suggests that this extinct carnivoran had a mostly terrestrial way of life, foraging mainly on the ground and being capable of developing an efficient terrestrial locomotion, although lacking the specialised cursorial adaptations observed in other carnivorans such as canids or hyaenids. At this respect, it is interesting that *I. zibethoides* shows marked differences with the closely related Plio-Pleistocene mustelid *Ekorus ekakeran*, from the Mio-Pliocene of Lothagam, Kenya, which has several postcranial features indicating highly cursorial abilities (Werdelin 2003). For example, the inferred presence of a relatively thick cranial crus of the *lig. collaterale mediale* on the elbow, or the great development of some muscles of the coxofemoral articulation suggest that *I. zibethoides* required a strong control of some articulations involved in an efficient terrestrial locomotion. Besides this, the gentle caudal inclination of the ulna of *I. zibethoides* resembles the morphology exhibited by typical cursorial carnivorans, lacking the cranial curvature observed in digging, climbing and scansorial carnivorans (Taylor 1974; Argot 2004; Heinrich & Houde 2006; Rose *et al.* 2014; Ercoli & Youlatos 2016; Henderson *et al.* 2016). The absence of lateral torsion in the olecranon, unlike the rest of the compared mustelids, suggests that the movements of flexion-extension of the elbow of *I. zibethoides* took place in a more or less parasagittal plane, something typical of cursorial species (Argot 2004); this relates

to the reduced attachment area for the *m. biceps brachii*, one of the main flexors of the elbow joint (Barone 2010; Ercoli *et al.* 2015), which suggests a relatively small muscle, such as that of extant terrestrial carnivorans (Taylor 1974; Feeney 1999). Other traits, shared with extant small arboreal mustelids probably indicate a primitive, retained morphology from arboreal ancestors, rather than especially developed climbing abilities, although is very likely that *I. zibethoides* would be able to climb with some skill, at least to the lowest part of the trees crown, looking for food or escaping from other, larger predators. Nevertheless, our study is only focused on the long bones, and more information on other elements would be necessary to assess the whole locomotor adaptations of *I. zibethoides*. Ginsburg (1961) and Peigné (2012) already pointed out the overall similarities between the talus and calcaneum of *I. zibethoides* and *G. gulo*, but other elements, such as the vertebral column, the pelvis, or the scapula, whose morphology remains unknown for *I. zibethoides*, would be necessary to fully understand the role of this predator in the Middle Miocene faunas of Europe.

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REFERENCES

- ALIX M. E. 1876. — Mémoire sur la myologie du putois (*Putorius communis*, Cuv.). *Journal de Zoologie* 5: 152-188. <https://biodiversitylibrary.org/page/13356543>
- ANDERSSON K. 2004. — Elbow-joint morphology as a guide to fore-arm function and foraging behaviour in mammalian carnivores. *Zoological Journal of the Linnean Society* 142: 91-104. <https://doi.org/10.1111/j.1096-3642.2004.00129.x>
- ARGOT C. 2001. — Functional-Adaptive Anatomy of the Forelimb in the Didelphidae, and the Paleobiology of the Paleocene Marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* 247: 51-79. [https://doi.org/10.1002/1097-4687\(200101\)247:1<51::AID-JMOR1003>3.0.CO;2-%23](https://doi.org/10.1002/1097-4687(200101)247:1<51::AID-JMOR1003>3.0.CO;2-%23)
- ARGOT C. 2004. — Functional-adaptive analysis of the postcranial skeleton of a Laventan borhyaenoid, *Lycopsis longirostris* (Marsupialia, Mammalia). *Journal of Vertebrate Paleontology* 24: 689-708. [https://doi.org/10.1671/0272-4634\(2004\)024\[0689:FAOTPS\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2004)024[0689:FAOTPS]2.0.CO;2)
- ARGOT C. 2010. — Morphofunctional analysis of the postcranium of *Amphicyon major* (Mammalia, Carnivora, Amphicyonidae) from the Miocene of Sansan (Gers, France) compared to three extant carnivores: *Ursus arctos*, *Panthera leo*, and *Canis lupus*. *Geodiversitas* 32 (1): 65-106. <https://doi.org/10.5252/g2010n1a2>
- ARGOT C. 2013. — Postcranial Analysis of a Carnivoran-Like Archaic Ungulate: The Case of *Arctocyon primaevus* (Arctocyonidae, Mammalia) from the Late Paleocene of France. *Journal of Mammalian Evolution* 20: 83-114. <https://doi.org/10.1007/s10914-012-9198-x>
- ARMSTRONG R. B., SAUBERT C. W., SEEHERMAN H. J. & TAYLOR C. R. 1982. — Distribution of fiber types in locomotory muscles of dogs. *American Journal of Anatomy* 163: 87-98. <https://doi.org/10.1002/aja.1001630107>
- ATRAMENTOWICZ M. 1995. — Growth of pouch young in the bare-tailed woolly opossum, *Caluromys philander*. *Journal of Mammalogy* 76: 1213-1219. <https://doi.org/10.2307/1382614>
- BARONE R. 2010. — *Anatomie comparée des Mammifères domestiques, tome second, Arthrologie et Myologie*. Quatrième édition. Éditions Vigot Frères, Paris, 1021 p.
- BLAINVILLE H. M. D. DE 1841. — *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles pour servir de base à la zoologie et à la géologie*. Fascicule 9. Petits Ours. G. Subursus. J. B. Baillière, Paris, 62 p.
- DAVIS D. D. 1949. — The shoulder architecture of bears and other carnivores. *Fieldiana: Zoology Memoirs* 31: 285-305. <https://doi.org/10.5962/bhl.title.1291>
- DAVIS D. D. 1964. — The giant panda: a morphological study of evolutionary mechanisms. *Fieldiana: Zoology Memoirs* 3: 1-339. <https://doi.org/10.5962/bhl.title.5133>
- 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*). *Journal of Mammalian Evolution* 20: 309-336. <https://doi.org/10.1007/s10914-012-9219-9>
- 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. *Journal of Mammalian Evolution* 22: 57-91. <https://doi.org/10.1007/s10914-014-9257-6>
- ERCOLI M. D. & YOULATOS D. 2016. — Integrating locomotion, postures and morphology: The case of the tayra, *Eira barbara* (Carnivora, Mustelidae). *Mammalian Biology* 81: 464-476. <https://doi.org/10.1016/j.mambio.2016.06.002>
- EVANS H. E. 1993. — *Miller's Anatomy of the Dog*. 3rd edition. Saunders, Philadelphia, 1113 p.
- FABRE A. C. 2013. — *How can the Interplay between form and Function Enlighten the Evolution of Organisms in their Ecological Context?* PhD dissertation, Université Paris Diderot, Paris, 249 p. (unpublished).
- FABRE A. C., CORNETTE R., GOSWAMI A. & PEIGNÉ S. 2015. — Do constraints associated with the locomotor habitat drive the evolution of forelimb shape? A case study in musteloid carnivorans. *Journal of Anatomy* 226: 596-610. <https://doi.org/10.1111/joa.12315>
- FRAILE S., PÉREZ B., DE MIGUEL I. & MORALES J. 1997. — Revisión de los Carnívoros presentes en los yacimientos del Neógeno español, in CALVO J. P. & MORALES J. (eds), *Avances en el conocimiento del Terciario ibérico, III congreso del Grupo Español del Terciario*. Cuenca: Museo Nacional de Ciencias Naturales-CSIC, Universidad Complutense de Madrid: 77-80.
- FEENEY S. 1999. — *Comparative Osteology, Myology, and Locomotor Specializations of the Fore and Hind Limbs of the North American Foxes Vulpes vulpes and Urocyon cinereoargenteus*. PhD dissertation, University of Massachusetts, Massachusetts, 534 p. (unpublished).
- FISHER R. E., ADRIAN B., ELROD C. & HICKS M. 2008. — The phylogeny of the red panda (*Ailurus fulgens*): evidence from the hindlimb. *Journal of Anatomy* 213: 607-628. <https://doi.org/10.1111/j.1469-7580.2008.00987.x>
- FISHER R. E., ADRIAN B., ELROD C. & HICKS M. 2009. — The phylogeny of the red panda (*Ailurus fulgens*): evidence from the forelimb. *Journal of Anatomy* 215: 611-635. <https://doi.org/10.1111/j.1469-7580.2009.01156.x>

- GAMBARYAN P. P. 1974. — *How Mammals Run. Anatomical Adaptations*. John Wiley & Sons, New York, 367 p.
- GINSBURG L. 1961. — *La faune des carnivores miocènes de Sansan (Gers)*. Muséum national d'Histoire naturelle, Paris, 190 p. (Mémoires du Muséum national d'Histoire naturelle, Sér. C – Sciences de la Terre [1950-1992] ; 9). <https://biodiversitylibrary.org/page/58360916>
- GINSBURG L. 1977. — Les carnivores du Miocène de Beni Melal (Maroc). *Géologie Méditerranéenne* 4: 225-239. <https://doi.org/10.3406/geolm.1977.1005>
- GINSBURG L. 1999. — Order Carnivora, in RÖSSNER G. E. & HEISIG K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, München: 109-148.
- GINSBURG L. 2001. — Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lathan (France). *Geodiversitas* 23: 381-394.
- GINSBURG L. & ANTUNES M. T. 1995. — Les Carnivores du Miocène de Lisbonne (Portugal). *Annales de Paléontologie* 81: 125-165.
- GINSBURG L. & BULOT C. 1982. — Les carnivores du Miocène de Bézian près de la Romieu. *Proceedings of the koninklijke Nederlandse Akademie van Wetenschappen Series B* 85: 53-76.
- GINSBURG L. & MORALES J. 1992. — Contribution à la connaissance des Mustélidés (Carnivora, Mammalia) du Miocène d'Europe *Trochictis* et *Ischyrictis*, genres affines et genres nouveaux. *Comptes rendus de l'Académie des Sciences* 315: 111-116. <https://gallica.bnf.fr/ark:/12148/bpt6k5489535w/f115.item>
- GLENN L. L. & WHITNEY J. F. 1987. — Contraction properties and motor nucleus morphology of the two heads of the cat flexor carpi ulnaris muscle. *Journal of Morphology* 191: 17-23. <https://doi.org/10.1002/jmor.1051910103>
- GONYEA W. J. 1978. — Functional implications of felid forelimb anatomy. *Acta anatomica* 102: 111-121. <https://doi.org/10.1159/000145627>
- GONYEA W. J., MARUSHIA S. A. & DIXON J. A. 1981. — Morphological organization and contractile properties of the wrist flexor muscles in the cat. *The Anatomical Record* 199: 321-339. <https://doi.org/10.1002/ar.1091990303>
- GROHÉ C., MORLO M., CHAIMANEE A., BLONDEL C., COSTER P., VALENTIN X., SALEM M., BILAL A. A., JAEGER J.-J. & BRUNET M. 2012. — New Apterodontinae (Hyaenodontida) from the Eocene Locality of Dur At-Talah (Libya): Systematic, Paleocological and Phylogenetical Implications. *PLoS ONE* 7 (11): e49054. <https://doi.org/10.1371/journal.pone.0049054>
- HALL E. R. 1927. — The muscular anatomy of the American badger (*Taxidea taxus*). *University of California Publications in Zoology* 30: 205-219.
- HALL E. R. 1981. — *The Mammals of North America*. John Wiley & Sons, Inc., New York, 1300 p.
- HAUGHTON S. 1867. — Notes on animal mechanics: No. 12. On the muscular anatomy of the Irish terrier, as compared with that of the Australian dingo. *Proceedings of the Royal Irish Academy* 9: 504-507. <https://www.jstor.org/stable/20488933>
- HEINRICH R. E. & HOUDE P. 2006. — Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal Carnivora. *Journal of Vertebrate Paleontology* 26: 422-435. [https://doi.org/10.1671/0272-4634\(2006\)26\[422:PAOVMC\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2006)26[422:PAOVMC]2.0.CO;2)
- HELBING H. 1930. — Zur Kenntnis der miocänen, “*Mustela*” zibethoides Blainville. *Eclogae Geologicae Helveticae* 23: 637-644.
- HENDERSON K., PANTINOPLE J., MCCABE K., RICHARDS H. L. & MILNE N. 2016. — Forelimb bone curvature in terrestrial and arboreal mammals. *PeerJ* 5: e3229. <https://doi.org/10.7717/peerj.3229>
- HILDEBRAND M. 1985. — Digging of quadrupeds, in HILDEBRAND M., BRAMBLE D. M., LIEM K. F. & WAKE D. B. (eds.), *Functional Vertebrate Morphology*. Belknap Press of Harvard University Press, Cambridge: 89-109. <https://doi.org/10.4159/harvard.9780674184404>
- HILDEBRAND M. 1988. — *Analysis of Vertebrate Structure*. John Wiley & Sons, Inc., New York, 718 p.
- JENKINS F. A. 1971. — Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *Journal of Zoology* 165: 303-315. <https://doi.org/10.1111/j.1469-7998.1971.tb02189.x>
- JONES D., ROUND J. & HAAN A. 2004. — *Skeletal Muscle from Molecules to Movement. A Textbook of Muscle Physiology for Sport, Exercise, Physiotherapy and Medicine*. Churchill Livingstone, Elsevier Science Limited, London, 202 p. <https://doi.org/10.1016/B978-0-443-07427-1.X5001-8>
- JULIK E., ZACK S., ADRIAN B., MAREDA S., PARSA A., POOLE M., STARBUCK A. & FISHER R. E. 2012. — Functional Anatomy of the Forelimb Muscles of the Ocelot (*Leopardus pardalis*). *Journal of Mammalian Evolution* 19: 277-304. <https://doi.org/10.1007/s10914-012-9191-4>
- LARIVIÈRE S. & JENNINGS A. P. 2009. — Family Mustelidae, in WILSON D. E. & MITTERMEIER R. A. (eds), *Handbook of the Mammals of the World*. Vol. 1. Carnivores. Lynx Edicions, Barcelona: 564-656.
- LEACH D. 1977. — The forelimb musculature of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben). *Canadian Journal of Zoology* 55: 31-41. <https://doi.org/10.1139/z77-003>
- LUCAE J. C. G. 1875. — Die Robbe und die Otter in ihrem knochen und muskel-skelet. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 8: 277-378.
- MACKINTOSH H. W. 1875. — Notes on the myology of the coatimundi (*Nasua narica* and *N. fusca*) and common marten (*Martes foina*). *Proceedings of the Royal Irish Academy, Series II, Science* 2: 48-55. <https://biodiversitylibrary.org/page/34746989>
- MAYNARD SMITH J. & SAVAGE R. J. G. 1956. — Some locomotory adaptations in mammals. *Journal of the Linnean Society of London, Zoology* 42: 603-622. <https://doi.org/10.1111/j.1096-3642.1956.tb02220.x>
- MEIN P. 1958. — Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 5: 1-122.
- MILNE N., VIZCAÍNO S. F. & FERNICOLA J. C. 2008. — A 3D geometric morphometric analysis of digging ability in the extant and fossil cingulate humerus. *Journal of Zoology* 278: 48-56. <https://doi.org/10.1111/j.1469-7998.2008.00548.x>
- MORALES J., ALCALÁ L., HOYOS M., MONTOYA P., NIETO M., PÉREZ B. & SORIA D. 1993. — El yacimiento del Aragoniense medio de La Retama (Depresión Intermedia, Provincia de Cuenca, España): significado de las faunas con *Hispanotherium*. *Scripta Geologica* 103: 23-39.
- NAGEL D., STEFEN C. & MORLO M. 2009. — The carnivoran community from the Miocene of Sandelzhausen (Germany). *Paläontologische Zeitschrift* 83: 151-174. <https://doi.org/10.1007/s12542-009-0008-6>
- NOWAK R. M. 2005. — *Walker's Carnivores of the World*. The Johns Hopkins University Press, Baltimore and London, 328 p.
- ONDRIAS J. C. 1961. — Comparative osteological investigations on the front limbs of European Mustelidae. *Arkiv för Zoologie* 13: 311-320.
- PASITSCHNIK-ARTS M. & LARIVIÈRE S. 1995. — *Gulo gulo*. *Mammalian Species* 499: 1-10. <https://www.jstor.org/stable/3504124>
- PEIGNÉ S. 2012. — Les Carnivora de Sansan, in PEIGNÉ S. & SEN S. (eds.), *Mammifères de Sansan*. Mémoires du Muséum national d'Histoire naturelle, Paris: 559-660 (Mémoires du Muséum national d'Histoire naturelle ; 203).
- QUAIFE L. R. 1978. — *The Form and Function of the North American Badger (Taxidea taxus) in Relation to its Fossorial Way of Life*. M. Sc. Thesis, The University of Calgary, Calgary, 394 p. (unpublished).
- RANVIER L. 1880. — *Leçons d'anatomie générale sur le système musculaire*. V. A. Delahaye et Compagnie, Libraires-Éditeurs, Paris, 494 p. <https://gallica.bnf.fr/ark:/12148/bpt6k6209238m>

- ROSE J., MOORE A., RUSSELL A. & BUTCHER, M. 2014. — Functional osteology of the forelimb digging apparatus of badgers. *Journal of Mammalogy* 95: 543-558. <https://doi.org/10.1644/13-MAMM-A-174>
- ROTH C. H. 1989. — Die Raubtierfauna (Carnivora, Mamm.) der untermiozänen Spaltenfüllung von Erkertshofen 2 bei Eichstätt/Bayern. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 29: 163-205. <http://www.biodiversitylibrary.org/page/28727858>
- STALHEIM-SMITH A. 1989. — Comparison of the Muscle Mechanics of the Forelimb of Three Climbers. *Journal of Morphology* 202: 89-98. <https://doi.org/10.1002/jmor.1052020107>
- SAMUELS J. X., MEACHEN J. A. & SAKAI S. A. 2013. — Postcranial Morphology and the Locomotor Habits of Living and Extinct Carnivorans. *Journal of Morphology* 274: 121-146. <https://doi.org/10.1002/jmor.20077>
- SILICEO G., SALESA M. J., ANTÓN M., PASTOR J. F. & MORALES J. 2015. — Comparative Anatomy of the Shoulder Region in the Late Miocene Amphicyonid *Magericyon anceps* (Carnivora): Functional and Paleoecological Inferences. *Journal of Mammalian Evolution* 22: 243-258. <https://doi.org/10.1007/s10914-014-9270-9>
- SPOOR C. F. & BADOUX D. M. 1986. — Descriptive and Functional Myology of the Neck and Forelimb of the Striped Hyena (*Hyaena hyaena*, L. 1758). *Anatomischer Anzeiger* 161: 375-387.
- TAYLOR B. K. 1978. — The Anatomy of the Forelimb in the Anteater (*Tamandua*) and its Functional Implications. *Journal of Morphology* 157: 347-368. <https://doi.org/10.1002/jmor.1051570307>
- TAYLOR M. E. 1970. — Locomotion in some East African viverrids. *Journal of Mammalogy* 51: 42-51. <https://doi.org/10.2307/1378530>
- TAYLOR M. E. 1974. — The functional anatomy of the forelimb of some African Viverridae (Carnivora). *Journal of Morphology* 143: 307-336. <https://doi.org/10.1002/jmor.1051430305>
- TSENG Z. J., O'CONNOR J. K., WANG X. & PROTHERO D. R. 2009. — The first Old World occurrence of the North American mustelid *Sthenictis* (Mammalia, Carnivora). *Geodiversitas* 31 (4): 743-751. <https://doi.org/10.5252/g2009n4a743>
- VAN VALKENBURGH B. 1987. — Skeletal indicator of locomotor behavior in living and extant carnivores. *Journal of Vertebrate Paleontology* 7: 162-182. <https://doi.org/10.1080/02724634.1987.10011651>
- VANDERHAAR J. M. & HWANG Y. T. 2003. — *Mellivora capensis*. *Mammalian Species* 721: 1-8. <https://doi.org/10.1644/721>
- VIRET J. 1933. — Contribution à l'étude des Carnassiers miocènes de La Grive-Saint-Alban (Isère). *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 21: 1-31.
- WAVA – WORLD ASSOCIATION OF VETERINARY ANATOMISTS 2017. — *Nomina Anatomica Veterinaria*. 6th Edition. International Committee on Veterinary Anatomical Nomenclature, Hanover, Ghent, Columbia and Rio de Janeiro, 160 p.
- WERDELIN L. 2003. — Mio-Pliocene Carnivora from Lothagam, Kenya, in LEAKEY M. G. & HARRIS J. M. (eds), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York: 261-328. <https://www.jstor.org/stable/10.7312/leak11870.15>

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