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*

Christine ARGOT
Muséum national d'Histoire naturelle, Département Histoire de la Terre,
USM 0203 - UMR 7207 du CNRS, CR2P,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
argot@mnhn.fr

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.

ABSTRACT

The postcranial skeleton of the amphicyonid *Amphicyon major* from the middle Helvetian of Sansan (Gers, France) is described and compared to extant taxa belonging to the families Ursidae (*Ursus arctos*), Felidae (*Panthera leo*), and Canidae (*Canis lupus*). From the perspective of the forelimb, the scapula is very similar to that of a bear, as well as the elbow joint suggesting habitually abducted postures of the arm and the ability to supinate the forefoot. The mobile shoulder joint and massive triceps are features shared by both extant ursids and felids. A powerful hand musculature, short and divergent metacarpals, and an important range of dorsiflexion of the wrist recall the forefoot of an ursid and indicate good grasping ability. On the axial skeleton, the complex atlas/axis, the shape of the lumbar vertebrae, and a long, heavy tail are more similar to the same anatomical regions in felids than to any other extant carnivore. The pelvis and femur, as well as the knee and tibio-astragalar joints, are also more similar to those of a felid than an ursid, although the ischium and femur of *Amphicyon* allowed more abducted and erected postures. The size and shape of the tibia, calcaneum, and metatarsals are more similar to those of a bear. The short metatarsals, with a divergent Mt I and a powerful hind foot musculature also suggest potential grasping ability. Therefore, the skeleton of *Amphicyon major* that displays a series of bear-like and cat-like morphological similarities would deserve the term of "bear-lion" instead of "bear-dog".

KEY WORDS
Mammalia,
Carnivora,
Amphicyonidae,
Miocene,
functional adaptations,
Western Europe.

RÉSUMÉ

*Analyse morphofonctionnelle du squelette postcrânien d'*Amphicyon major *(Mammalia, Carnivora, Amphicyonidae) du Miocène de Sansan (Gers, France) comparé à trois carnivores actuels :* Ursus arctos*,* Panthera leo *et* Canis lupus.

Le squelette postcrânien de l'amphicyonidé *Amphicyon major* de l'Helvétien moyen de Sansan (Gers, France) est décrit et comparé à des taxons actuels appartenant aux familles Ursidae (*Ursus arctos*), Felidae (*Panthera leo*) et Canidae (*Canis lupus*). Au membre antérieur, la scapula est très semblable à celle d'un ours, tout comme le coude suggérant des positions abductées de l'avant-bras et la capacité à supiner la main. L'épaule mobile et le triceps massif sont des traits partagés à la fois par les ursidés et les félidés. Une musculature puissante de la main, des métacarpiens courts et divergents, et une grande amplitude de flexion dorsale au poignet rappellent l'extrémité antérieure d'un ours et assurent une capacité de préhension. Au niveau du squelette axial, le complexe atlas/axis, la forme des vertèbres lombaires et une longue et lourde queue sont plus semblables à ce qui est observé chez les félidés qu'à n'importe quel autre carnivore actuel. Le bassin et le fémur, ainsi que le genou et l'articulation tibio-astragalienne sont aussi plus semblables à ce qui est observé chez un félidé que chez un ursidé, bien que l'ischion et le fémur d'*Amphicyon* permettent des positions plus abductées et plus dressées. La taille et la forme du tibia, du calcanéum et des métatarsiens sont plus semblables à celles d'un ours. Les métatarsiens courts, avec un Mt I divergent et une puissante musculature du pied, suggèrent également une capacité de préhension. Le squelette d'*Amphicyon major*, qui présente donc une série de similitudes morphologiques avec les ours et les félins actuels, mériterait le nom d'« ours-lion » plutôt que son nom actuel d'« ours-chien ».

MOTS CLÉS
Mammalia,
Carnivora,
Amphicyonidae,
Miocène,
adaptations
fonctionnelles,
Europe Occidentale.

INTRODUCTION

The site of Sansan (south-western of France) of Miocene age was found in 1834 by Lartet (Ginsburg 1961). Blainville published the first illustrations of some fossils found there, especially some bones of a large specimen, which he called *Amphicyon major* (see the plates XIV and XV in the atlas of his "Ostéographie", 1839-1864), a taxon grouped with other "subursi antiquii", a name given by Blainville to the carnivores showing a massive body, five-clawed feet and a supposedly plantigrade locomotion. Although numerous elements of several specimens of *A. major* have been found in Sansan, a single near-complete skeleton is known, found in 1965 (Bergounioux & Crouzel 1966). Pressure forces damaged some parts of the skeleton, especially the skull, the left scapula, the right radius and humerus, the distal part of the left femur, the right part of the innominate, and many vertebrae; moreover, a few bones have been lost (some thoracics and the last caudal vertebrae, a few carpal and tarsal bones, and several ungual phalanges, see below). However, this specimen is remarkably complete, being by far the most complete specimen of *Amphicyon major* found in Western Europe. The genus *Amphicyon* Lartet, 1836 first appears in the Oligocene of Western Europe, and evolved there until the late Miocene; the genus is also known from Africa and North America from the early Miocene (see e.g., Hunt 2003). *Amphicyon major* belongs to one of the four sub-families of Amphicyonidae Haeckel, 1866, the Amphicyoninae Haeckel, 1866, the only subfamily being Holarctic in distribution – two others, the Daphoeninae Hough, 1948 and the Temnocyoninae Hunt, 1998, being American, and one, the Haplocyoninae Hunt, 1998, being Eurasian. During the early and mid-Miocene, amphicyonids were the first carnivorans to respond the extinction of large creodonts, rapidly deploying a variety of lineages to exploit the newly open ecological niches (Hunt 2003). The species of *Amphicyon* in North America increase in size from their first arrival (early Hemingfordian) to their last appearance (mid-Barstovian). However, in Europe, a smaller species, *A. major* (mid-Helvetian), succeeds *A. giganteus* Schinz, 1825 (Burdigalian-early Helvetian), the largest species of the genus to evolve in the Old World but that does not show significant morphological differences in comparison to smaller amphicyonid species (Ginsburg & Telles Antunes 1968). Although the Sansan subcomplete specimen of *A. major* has been described by Bergounioux & Crouzel (1973), it has never been the subject of a careful functional analysis focused on the articulations and muscular attachments, which is the subject of the present paper.

MATERIAL AND METHODS

The description and interpretation of the postcranial skeleton of *Amphicyon major* deals primarily with the near-complete specimen Sa844 attributed to a young female because of its small size relative to the other specimens of the same species from Sansan. Because the bones have been found in association and obviously belong to a single individual, functional interpretations are likely to be relevant for this specimen. Some other fragmentary and/or isolated bones of *A. major* from the same place, described by Ginsburg (1961), have been used as comparative material in order to complete the analysis.

The specimen Sa844 comprises the following elements:

Skull and two hemimandibles; 11 ribs more or less complete and several fragments; one element of the sternum; atlas, axis, four cervicals (C4-7 or C3-4 and C6-7), eight thoracic vertebrae, five lumbars, sacrum (= three fused vertebrae), 15 caudals and several damaged vertebral bodies not significant functionally; two scapulae, the left one being extremely damaged; two humeri, the right one being extremely damaged; two ulnae; two radii, the right one damaged; six right carpal bones (all except the pisiform) and four left carpal bones (scapholunar, unciform, pyramidal and trapezium); five right metacarpals and three complete left ones (Mc II, III and V) plus a fragment of Mc IV; 15 proximal phalanges all extremities included; 13 intermediate phalanges; 14 fragmentary ungual phalanges; left part of the pelvis (only a fragment of the right part); two femurs; two tibias; the right fibula; one patella; four right tarsal bones (all except the astragalus and the two inner cuneiforms) and the seven left tarsals (astragalus damaged); all the metatarsals (left Mt II and V are incomplete)

Listed below are the elements from other specimens of *A. major* found in the same site location, that have been used to complement the analysis.

From specimen Sa52: right and left ulnae; left complete radius and proximal part of the right one; right tibia. From other specimens: glenoid cavity Sa83; right humeri Sa87 (without distal extremity) and Sa89 (belonging maybe to the specimen Sa52 according to Ginsburg 1961); distal parts of humeri Sa84, Sa86, and Sa88; left ulnas Sa101, Sa103, and Sa105 (the last two without distal extremity); right ulna Sa102 (maybe from the same specimen as Sa101); right radii Sa94, 95, and 98 (the last one without distal extremity); left radius Sa96; fragmentary pelvis Sa145; right femur Sa147 (maybe from the same specimen as Sa145) and distal part of right femur Sa151; left tibia Sa155 + a few vertebrae, scapholunates, unciforms, pisiforms, calcanei, astragali, and metapods. The basic description of these bones exists in Ginsburg (1961).

The skeletal comparisons will consider joint structure, myological and eco-ethological data available for three living carnivores that have adult body sizes approaching or exceeding that inferred for the extinct *A. major*: the lion (*Panthera leo* Linnaeus, 1758), the wolf (*Canis lupus* Linnaeus, 1758), and the brown bear (*Ursus arctos* Linnaeus, 1758). All the material used is stored in the collections of paleontology and comparative anatomy of the Muséum national d'Histoire naturelle, Paris (MNHN).

DESCRIPTION

AXIAL SKELETON

Cervical vertebrae

In *Amphicyon*, the atlas, axis and four cervical vertebrae are known. The dorsal arch of the atlas is anteroposteriorly wider than the ventral one, with concave anterior and posterior edges (Fig. 1). When articulated, the anterior facets tightly wrap the occipital condyles and the anterior part of the dorsal arch is robust above these facets. The skull is crushed, transversely compressed, and the position of the head relative to the anterior cervicals cannot be ascertained. The ventral arch of the atlas is fused with the rest of the vertebra; it does not exhibit a ventral crest. An atlantal foramen can be seen on the dorsal arch, located in between the anterior part of the lateral wings and the occipital articular facets. Posteriorly, the facets articulating with the axis are flat and triangular in outline. On the axis, the corresponding facets are ovoid in outline, higher dorsoventrally than wide, broader than the atlantal facets. This suggests a very mobile articulation atlas-axis, and especially rotational capacities of the head. The lateral wings (transverse processes) of the atlas are anteroposteriorly well extended. Anteriorly they reach the level of the anterior articular facets and posteriorly, they protrude beyond the body of the vertebra. The neural process of the axis is also anteroposteriorly well developed: its anterior tip reaches the posterior edge of the atlantal dorsal arch when articulated, and the process extends posteriorly above the third cervical vertebra. The ventral side of the vertebral body exhibits a prominent crest at its posterior extremity. The four posterior cervicals are all more or less damaged. The neural process is broken in each of them. The dorsal arch is short anteroposteriorly. The anterior articular facets protrude anteriorly beyond the ventral vertebral body and are oriented dorso-medially. The posterior articular facets protrude posteriorly beyond the vertebral body and are oriented ventrolaterally. The ventral sagittal crest of the vertebral bodies where the long extensors of the neck originate is more robust posteriorly than anteriorly but it is never as much developed as that of the axis. The transverse processes are also broken, thus their extent cannot be ascertained.

Thoraco-lumbar vertebrae

Eight thoracic vertebrae (supposedly T1-T7 and a postdiaphragmatic vertebra, T12 or 13) and five lumbars are known (only seven thoracics but seven lumbars are reported – not illustrated – by Bergounioux & Crouzel 1973; they might have confused a lumbar with the most posterior thoracic, and another lumbar seems to be lost). The neural process of the anterior thoracic vertebrae is long and robust, prominent dorsally and wide anteroposteriorly at its base (Fig. 1). It may present lateral scars at its base, and also along the anterior edge, for the insertion of deep muscles of the neck and back (Mm. multifidus et spinalis cervicis and dorsi). The three most anterior neural processes are not inclined posteriorly. Their size is related to the large, heavy skull. No clavicle has been found but the first pair of ribs is extremely robust. On the most posterior thoracic vertebra preserved, the neural process, although broken, is inclined anteriorly; it is then a post-anticlinal and postdiaphragmatic vertebra, with a radial articular mode. It is not described by Bergounioux & Crouzel (1973), nor confused with a lumbar vertebra although it shows broad, concave articular facets with a pair of ribs. This vertebra also exhibits very well-developed anapophyses, almost as high as the postzygapophyses, which allow the prezygapophyses to bind tightly the following vertebra, a morphology that stabilises the vertebral column anterior to the lumbar region, preventing it from lateral flexions. These anapophyses are reduced or do not exist on the lumbars, except on one of them (a small pit can be seen on two others). The neural process of the lumbar vertebrae is fully preserved in only two of them. It is relatively short dorsoventrally (hardly more prominent dorsally than the mammillary processes on the most anterior lumbar), inclined anteriorly, and robust, with a broad apex. The mammillary processes are prominent on the most anterior vertebrae, but less developed posteriorly. The transverse processes of the lumbar vertebrae are not preserved. The anteroposterior lengthening of the lumbar vertebrae when going backwards is moderate.

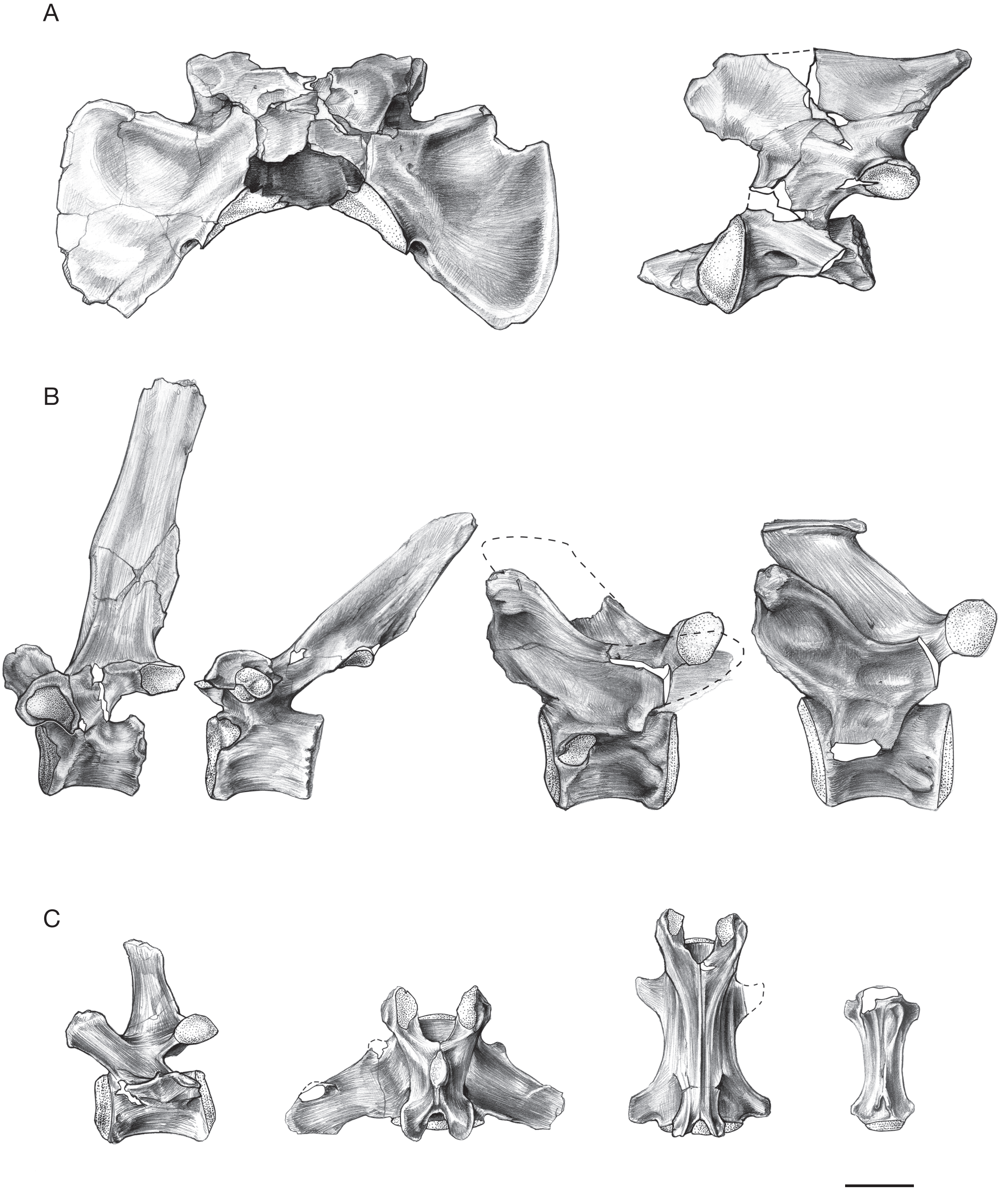

Fig. 1. — Vertebrae of *Amphicyon major* Blainville, 1841 MNHN Sa844: **A**, atlas in dorsal view and axis in lateral view; **B**, thoracic and lumbar vertebrae in lateral view: from left to right, T1, T7, T12 or 13 and L1; note the development of the neural processes and anapophyses on the posterior thoracic and anterior lumbar; **C**, caudal vertebrae: Ca1 in lateral and dorsal view and Ca7 and 15 in dorsal view, note the development of the neural and transverse processes suggesting a heavy, muscular basal tail. Scale bar: 1 cm.

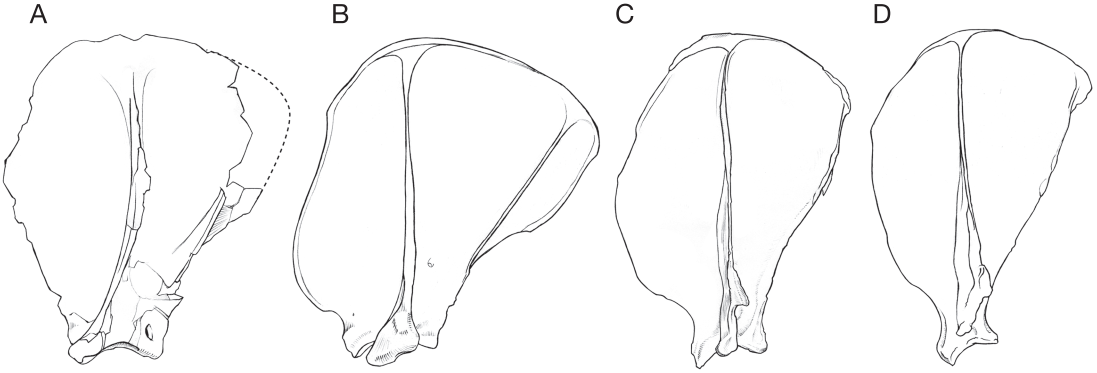

FIG. 2. — Left scapula in lateral view: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844 (right scapula reversed); **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279; note the development of the postscapular fossa on the scapula of *A. major* and *U. arctos*. Not to scale.

CAUDAL VERTEBRAE

Fifteen complete caudal vertebrae are known as well as two fragmentary ones. According to the size of the last one identified in the series, it can be hypothesised that approximately between six and ten vertebrae are lacking, which gives a long tail to the specimen, approximately as long as the rest of the vertebral column. Olsen (1960) estimates the tail of *A. longiramus* White, 1942 to 28 caudal vertebrae in total. The first two caudal vertebrae exhibit laterally prominent transverse processes, and one of them a dorsally prominent, very well-developed neural process (Fig. 1; the neural process of the other as well as those of the sacral vertebrae are broken). The vertebral foramen of those vertebrae is oval in outline, much wider than high. Like in the cervical vertebrae, the vertebral body is oblique in lateral view. On the three following vertebrae (Ca3-5), the transverse processes protrude less laterally but more posteriorly. These vertebrae show no neural process but an overall anteroposterior lengthening. On Ca6-7, the posterior transverse processes reduce, whereas anterior ones appear; the zygapophyses are still prominent and functional. From Ca9, which can then be called the transitional caudal vertebra, the zygapophyses lose their functionality, and from Ca12 the anteroposterior length of vertebrae decreases. The vertebral canal can also be observed until Ca12. No hemal arch has been found.

PECTORAL GIRDLE AND FORELIMB

Scapula and proximal humerus: shoulder joint

Only the right scapula is preserved enough to be described, although partly damaged (especially the cranial border and caudal angle). The scapula of *Amphicyon* shows relatively large, subequal supra- and infraspinous fossae (Fig. 2). On the posterolateral side of the larger tubercle of the humerus, the insertion of the M. infraspinatus is a broad, circular, deep fossa. This tubercle protrudes anteriorly (Fig. 3), giving rise to a thick, long deltopectoral crest that extends along almost the proximal two-thirds of the humeral shaft (see measurements in the Appendices). Along the distal third of this crest, the insertions of the Mm. pectoralis, deltoideus pars acromialis, and possibly cephalohumeralis (a muscle resulting from the fusion of the clavicular parts of the Mm. deltoid and trapezius, and that is powerfully developed in extant bears according to Davis 1964) are well defined. The smaller tubercle of the humerus is tightly pressed against the humeral head; only the anterior part is slightly prominent. The latissimus dorsi insertion is located in the bicipital groove, more proximal than at the midshaft level. The teres major insertion cannot be observed (attachment area possibly shared by the two muscles?).

The scapular spine forms a subperpendicular angle with the vertebral border; the spine is not very high and not inclined posteriorly. Although damaged,

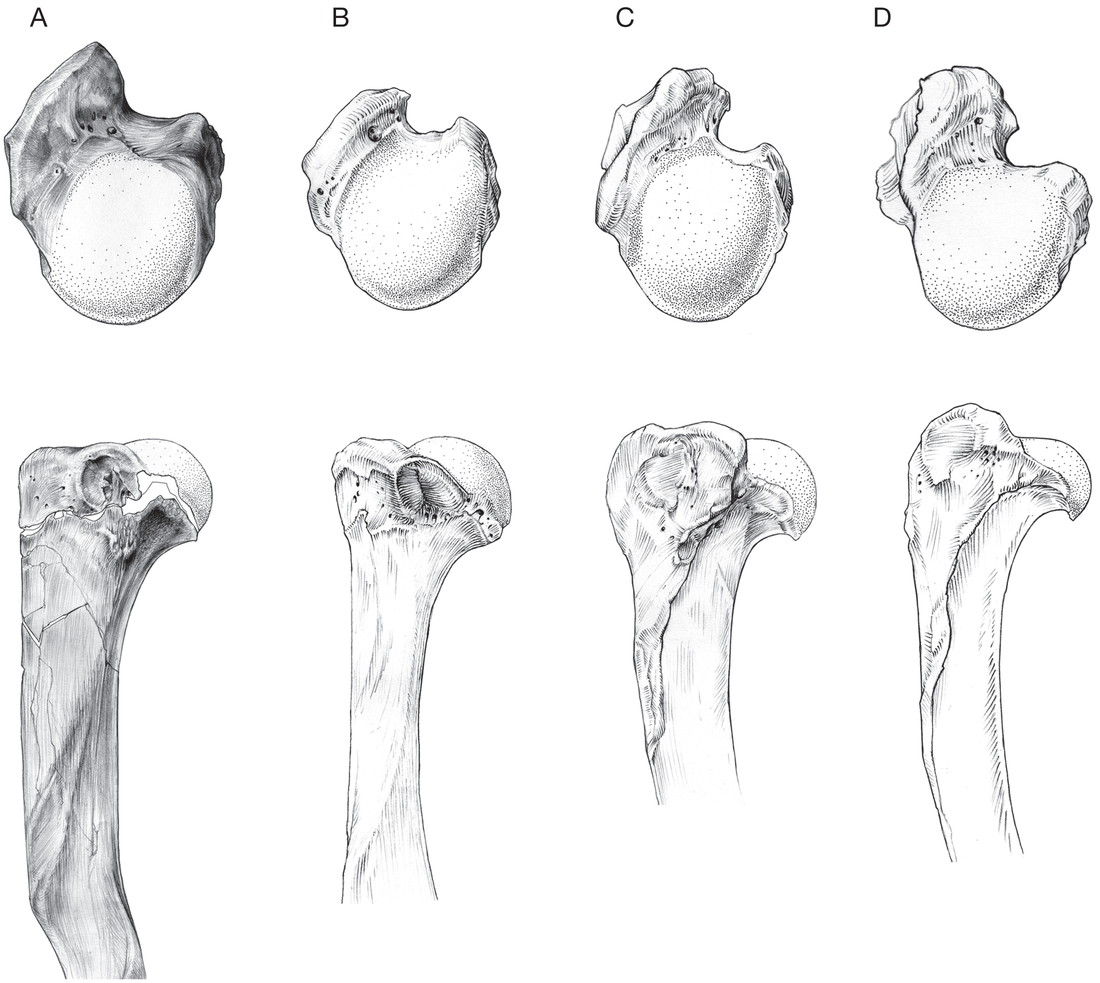

Fig. 3. — Proximal part of the left humerus in proximal and lateral view: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279. Not to scale.

a secondary scapular spine, prominent toward the glenoid fossa, can be observed. It delimits an accessory fossa that is preserved only partially in the specimen observed; thus the development of the caudal angle cannot be observed. The origin of the M. triceps caput longum (anterior part only? see Discussion) is subtriangular and located on the caudal border, next to the glenoid fossa.

The scapular neck is wide, giving a massive aspect to the distal part of the scapula. As described in *A. longiramus* (Olsen 1960) the scapula of *A. major* shows a large nutrient foramen at the base of the acromion process, directed at right angle to the long axis of the blade. This foramen does not exist in extant carnivores. The glenoid cavity has a pear-shaped outline, smoothly concave, with regularly convex ventral and caudal borders, and a more sinuous dorsal border. In lateral view, the humeral head that articulates with this cavity is fully convex and higher than both tubercles. It is slightly asymmetrical in posterior view, its apex being continuous with the smaller tubercle, whereas a groove separates it from the greater tubercle. In proximal view the articular facet is subcircular. The proximal epiphysis of the humerus is not completely fused with the shaft of the body, highlighting the young age of the individual at death.

The acromion is relatively small and tuberous; its posterior part (metacromion) is broken (but it was not developed in *A. longiramus*: see Olsen 1960). The damaged scapular spine prevents from knowing its exact position. It probably overhung the glenoid fossa, and its small size suggests a restricted wrapping of the shoulder joint by the M. deltoideus pars acromialis; this could have been partly compensated by the development of the cephalohumeralis, which unfortunately lacks specific scars on bones. No clavicle has been found and nothing on the acromion suggests an articulation with such a bone. The coracoid is a small protuberance, that is hardly prominent medially.

Distal humerus and proximal ulna and radius: elbow joint

In *Amphicyon* the lateral epicondylar crest is long and thick, but not very prominent laterally; similarly, the ectepicondyle is massive but not prominent. Medially, the entepicondylar crest is thin and delimitates a wide entepicondylar foramen. The entepicondyle is massive and protrudes posteriorly.

The anterior part of the humeral trochlea is slightly concave because of an anteriorly prominent medial lip. Moreover, it is much narrower transversely than the capitulum (Fig. 4). On the ulna, the coronoid process is anteriorly prominent and deflected medially. On the posterior side of the humerus, the olecranon fossa is extremely deep (although the bone is not perforated), especially laterally, but it is not wider than the articular facet located below it. The posterior part of the trochlea is asymmetrical. Although partly broken, it appears that the lateral crest was sharp, posteriorly prominent, and long proximo-distally. In contrast, the medial lip is smooth, not prominent. Similarly, the anconeal process (i.e. upper margin of the ulnar trochlear notch) is asymmetrical and narrow, prominent anteriorly and with an extremely well-developed lateral lip covering a part of the lateral surface of the olecranon, whereas the medial lip is reduced and not prominent. The trochlear notch forms almost a perfect semi-circle in profile, limited by prominent upper and lower processes, and the longer axis of flexion-extension is: proximo-lateral/disto-medial, giving a slightly abducted position (elbow pointing outward) to the articulated forelimb.

On the anterior part of the humerus the capitulum is cylindrical and flat, much wider transversely than the trochlea and slightly more extended proximally. The lateral border is not distinct from the body, and not prominent. The capitulum is separated from the trochlea by a smooth, thick crest. The articular facet does not extend far distally, thus preventing full extension. On the ulna the radial notch covers a wide arc of curvature, the medial and posterior borders forming an angle of about 130°. In anterodistal view, the coronoid process and medial part of the radial notch form a sharp angle. The radial head is oval in outline, with a thick anterolateral border, and a capitular eminence is elevated on its anteromedial margin. On the posterolateral part of the circumference, the articular facet with the ulna is long and regularly convex. The radius of *Amphicyon major* is also twisted, the transverse axes of the proximal and distal epiphyses forming an angle of approximately 45-50° (Fig. 5). This means that the radius is located more laterally than anteriorly when the bones of the forearm are in articulation. In proximal view, with the radius and ulna in articulation, the area of the radial head is slightly larger than that of the coronoid process; this suggests a slightly reduced loading on the medial part of the elbow joint.

Morphology of the ulna and radius

In *Amphicyon* the ulna and radius are robust and separated by a wide space, especially distally. The ulna is anteroposteriorly wide in its proximal part and more slender distally. Its posterior border is straight proximally and slightly concave distally but overall, straighter than in *A. galushai* (Hunt 2003: fig. 4.10). The olecranon is short, robust, and massive posteriorly; the posterior part protrudes medially (area of attachment of Mm. triceps caput mediale, epitrochlearis, and flexor carpi ulnaris), and the anterior tip protrudes proximally. The apex of the olecranon forms a right angle with the posterior border of the ulna.

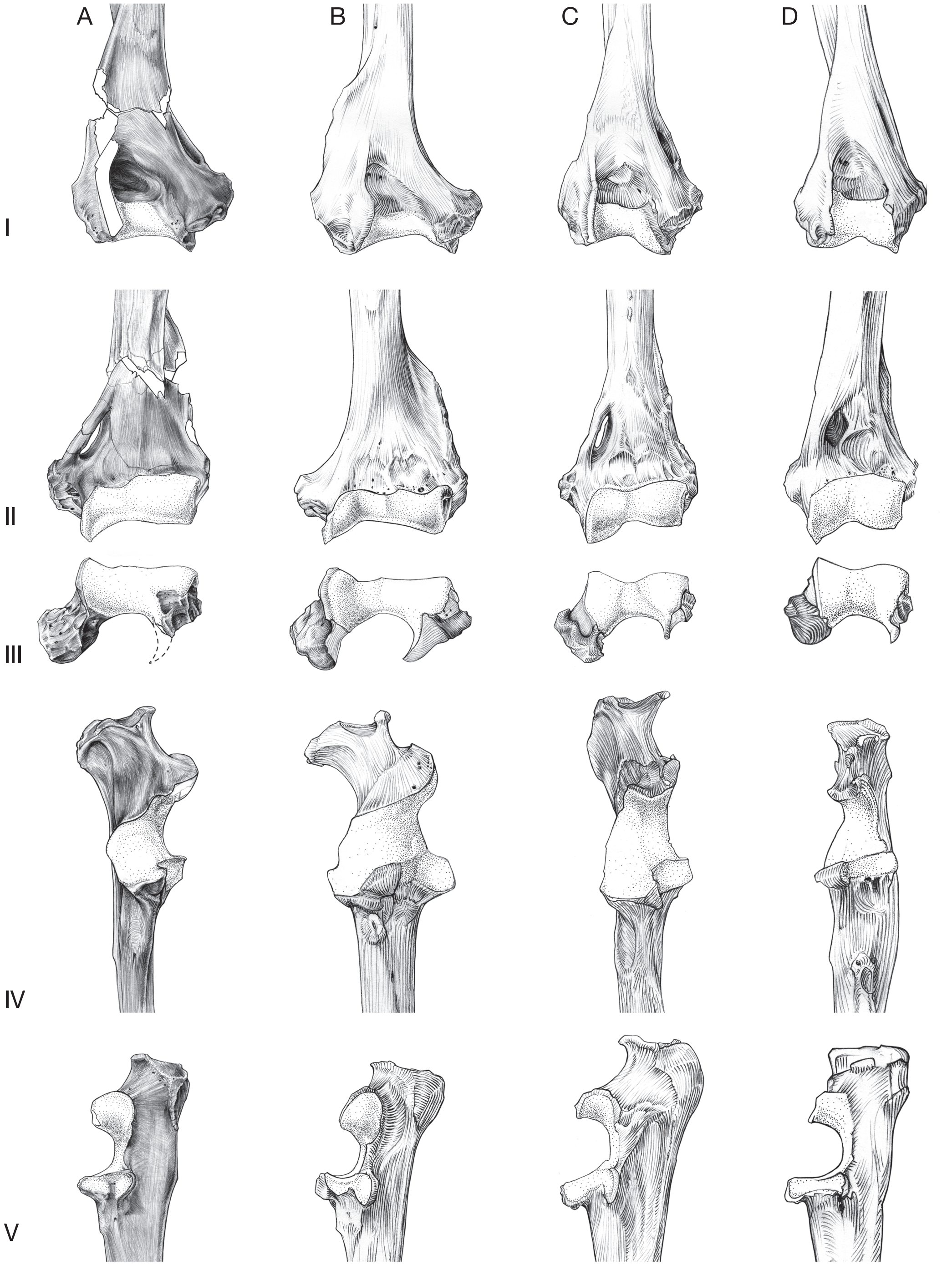

Fig. 4. — Elbow joint: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279; **I-III**, distal extremity of the left humerus; **I**, anterior view; **II**, posterior view; **III**, distal view; **IV**, **V**, trochlear notch of the left ulna; **IV**, anterior view; **V**, lateral view. Not to scale.

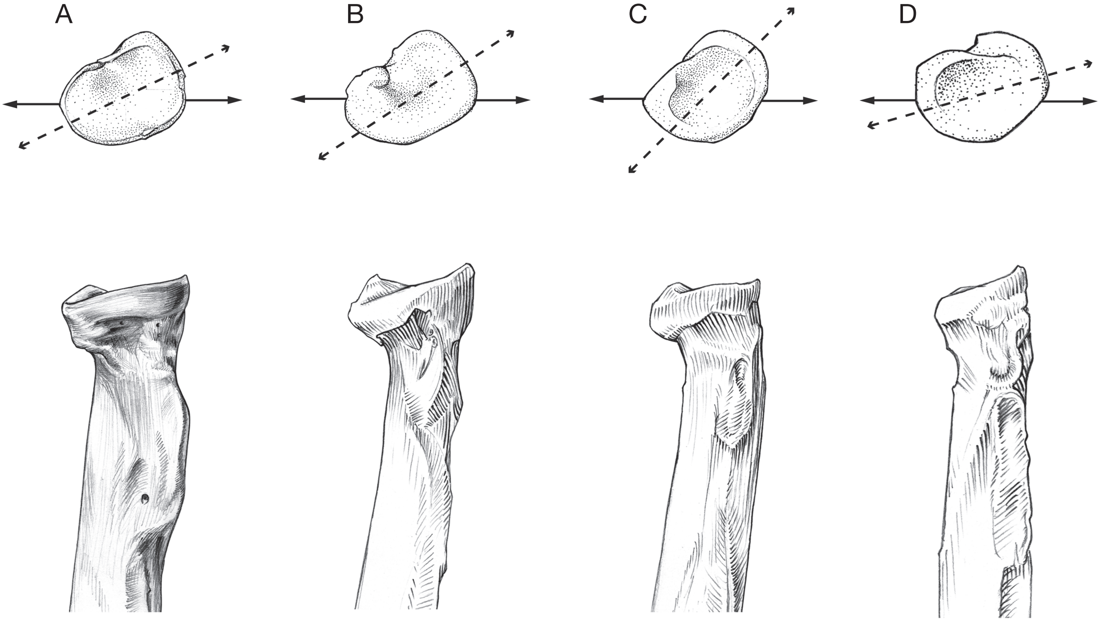

Fig. 5. — Proximal part of the left radius in proximal (top) and posterior (bottom) views: note the difference in the orientation of the long axis of the proximal (dashed line) and distal (full line) epiphyses, as well as the development of the bicipital tuberosity on the radius of *A. major*; **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279. Not to scale.

Although the coracoid process was reduced to a small protuberance on the scapula, the bicipital tuberosity on the radius is very well developed, long, and massive (Fig. 5), filling in the proximal space between the two bones of the forearm. On the ulna, the scar for biceps and brachialis is well marked just distal to the coronoid process, although less extended proximodistally than the bicipital tuberosity. On the radius, lateral to the bicipital tuberosity, a small scar probably served as an attachment for a stabilising ligament joining the radius to the ulna (no known muscular insertion corresponds to that scar).

The posterior prominence of the humeral entepicondyle moves the flexor digitorum profundus humeral head and pronator teres away from the transverse axis of the humero-ulnar joint. There is no deep lateral or medial fossa on the ulna, but a rugose scar, along the anterior border, for the interosseous ligament.

The radial diaphysis shows a similar rugose scar. It is convex along its anterior border, increasing the space between the two bones and then the capacities of rotation. Proximally, the insertion for the M. supinator brevis cannot be seen, but the insertion for M. pronator teres forms a long arc of curvature that extends along the distal half of the diaphysis. The distal facet of articulation with the ulna is wider than its equivalent on the ulna, also providing for rotational capacities, while the strong interosseous ligament limits the risk of dislocation of the wrist.

Carpal bones and manus

All the carpal bones of the right manus are preserved except the pisiform (although described by Bergounioux & Crouzel 1973: 55, 56). The scapholunar is by far the largest bone of the carpus, quadrangular in shape, with a massive but not very salient palmar process that protrudes more medially than ventrally (Fig. 6). The proximal articular facet is regularly convex, without prominent borders. It extends far anteriorly, emphasising the potential

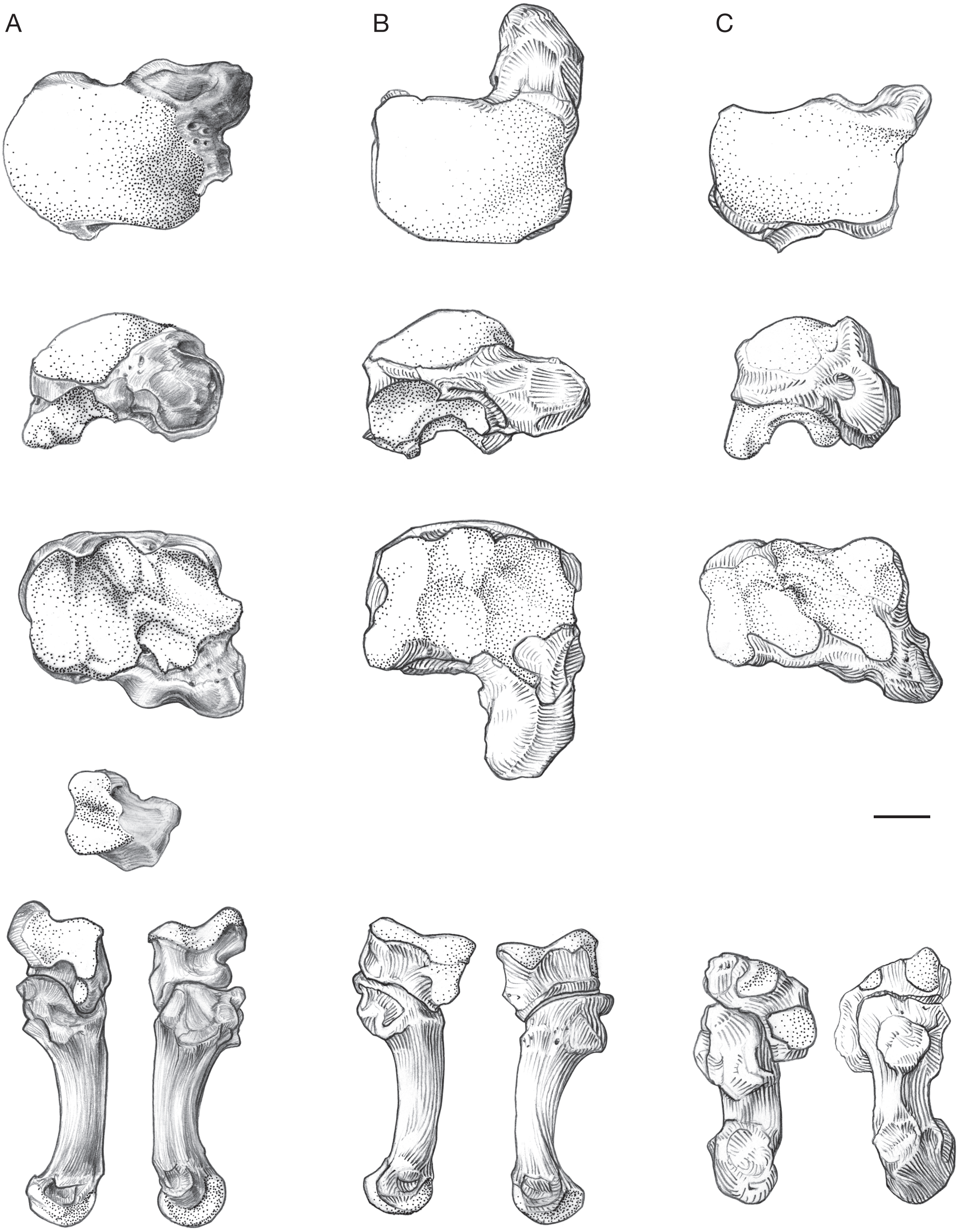

Fig. 6. — Focus on of the scapholunar, trapezium and McI: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; right scapholunar, from top to bottom, in proximal, lateral and distal views; right trapezium articulated to McI, from left to right, in lateral and medial (inner) views, and focus on the trapezium of *Amphicyon* in proximal view. Scale bar: 1 cm.

degree of dorsi-flexion. Distally, four articular facets can be observed. The facets for the unciform and magnum are both rectangular, parallel one to the other, and well extended dorso-ventrally. The dorsal end of the articular facet with the magnum is concavo-convex and forms a ventrally prominent process. The trapezoid, a small bone flattened proximo-distally, articulates mainly with the medial side of that process. The articular facet with the trapezium is concavo-convex, its long axis being oriented obliquely (anterolaterally-posteromedially, parallel to the palmar process). This facet is longer than necessitated by the size of the trapezium, which allows some gliding movements. In medial view, the concave part of the facet with the trapezium is confluent with the proximal facet articulating with the radius (Fig. 6). Laterally, there is no facet on the scapholunar articulating with the pyramidal, which articulates fully with the unciform. The pyramidal also exhibits two proximolateral articular facets, both concave and subequal in size. The anterior one articulates with the styloid process of the ulna, and the posterior one with the pisiform. The lateral end of the latter forms a small process that protrudes distally and could have been used for the attachment of an external ligament joining the pyramidal to the fifth metacarpal. The pisiform, known in other specimens of *A. major* (Sa52, 114, 115, and 333) is massive, with a globular extremity.

The unciform is the largest carpal bone of the distal row. The anterior side is triangular in outline. The lateral facet that articulates with the pyramidal is regularly convex and bears distally a small process that forms an antero-lateral stop to stabilise the mid-carpal joint in dorsal flexion. Distally, the articular facet with Mc V and IV is slightly concave antero-posteriorly, broad and trapezoid in outline. A palmar tuberosity can be observed, but it is not very salient. Medially, the articular facet with the magnum is slightly concave and arched anteroposteriorly. The two bones reach the same level distally; the distal articular facet of the magnum with Mc III is rectangular in outline and anteroposteriorly concave. The magnum is as high as the unciform, but much narrower transversely. Its anterior side is extremely reduced because of the articulation with the prominent process of the scapholunar, which also stabilises the mid-carpal joint. The palmar tuberosity of the magnum is more developed than that of the unciform. Medially, it exhibits two small articular facets with the proximal epiphysis of Mc II. As mentioned previously, the trapezoid is a small bone, smaller than the proximal articular facet of Mc II. The trapezium is bigger and higher. The facet of the trapezium that articulates with the scapholunar is formed by two convex processes separated by a small groove (Fig. 6). The articular facet with Mc I is concave and ovoid, longer anteroposteriorly than wide, and faces distomedially. Laterally, the trapezium articulates with the trapezoid and Mc II. Neither the trapezoid nor the trapezium exhibits a palmar process, the former because it is covered palmarly by the trapezium and the trapezium because it is located dorsally to the prominent palmar process of the scapholunar.

The five metacarpals are known (Fig. 7). When articulated, Mc III reaches the same level distally as Mc IV and Mc II the same level as Mc V. The pollex was not reduced, although Mc I is the shortest metacarpal and when articulated it hardly reaches the Mc II midshaft (also because the level of articulation with the trapezium is the most proximal one, and its distomedial orientation abducts and shortens the final length of the most internal digit). Mc I did not articulate to Mc II, which allowed relatively free movements of the pollex, whereas the four most lateral digits articulate one to the other. Mc V even exhibits a medially prominent process interlocked to Mc IV. A prominent scar occurs on the posterolateral surface of the diaphysis of Mc IV, extending slightly below the midpoint of the diaphysis. It could represent an attachment for a ligament of the carpus, consistent with the interpretation of Hunt (2002) for the amphicyonid *Ysengrinia*. The metacarpals are short and robust, with broad distal epiphyses and wide gaps in between them, suggesting a powerful hand musculature. The proximal epiphyses present rugose palmar tuberosities, especially Mc III, consistent with the developed palmar process of the magnum and suggesting that the maximal loading passed through the middle of the hand. Mc V is massive. It exhibits lateral tuberosities at the proximal and distal ends,

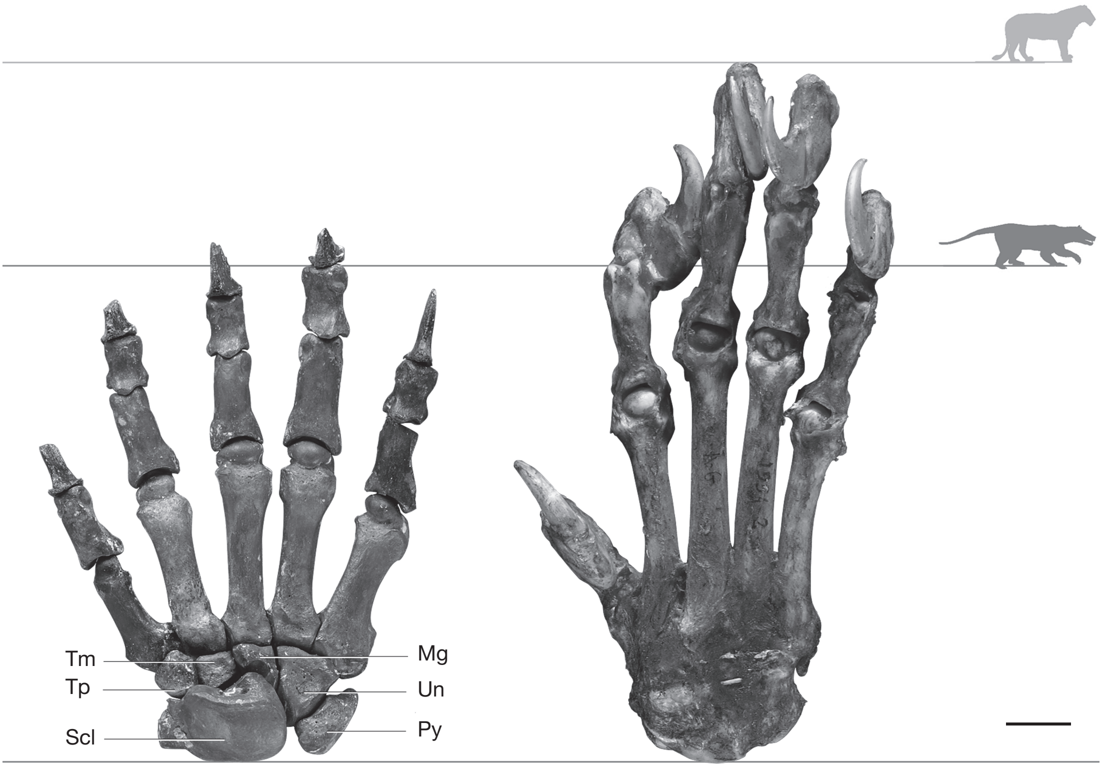

Fig. 7. — General morphology of the right manus of *Amphicyon major* Blainville, 1841 MNHN Sa844 in dorsal view in comparison to that of *Panthera leo* Linnaeus, 1758: the association of phalanges is conjectural in the fossil species; note the development of the pollex and width of the palm. Abbreviations: **Mg**, magnum; **Py**, pyramidal; **Scl**, scapholunar; **Tm**, trapezium; **Tp**, trapezoid; **Un**, unciform. Scale bar: 2 cm.

and a dorso-proximal scar for the attachment of M. extensor carpi ulnaris. On its dorsal side, Mc II exhibits proximomedially a rugose scar, probably for the insertion of the tendon of a long extensor of the digit (M. extensor carpi radialis longus, coming from the ectepicondylar humeral crest). Mc I exhibits a medio-proximally prominent process for the insertion of the M. abductor pollicis longus. The distal articular facets are particularly asymmetrical in Mc I and V (in both cases the condyle facing the rest of the hand is the more developed, increasing the grasping power of the hand).

The proximal phalanges are robust and are half as long as the metacarpals. Their length (in Sa844) varies between 25 and 37 mm. Their attribution to a specific digit cannot be ascertained. Ventrally, they exhibit rugose scars for the attachment of tendinous sheaths, suggesting powerful deep flexors of the digits. Their broad proximal articular facets, together with the bulbous distal ends of metacarpals, emphasise the range of flexion-extension that was possible at that joint. The intermediate phalanges show the usual shape and are slightly longer than wide. Their length (in Sa844) varies between 17.8 and 24 mm. The ungual phalanges are very often badly preserved. They are dorso-ventrally broad, not arched except the distal tip, and sharp transversely. They were obviously not retractile. They present the usual ventral bulbous process for the insertion of the deep flexors of the digits and the proximal articular facet is higher than wide. The length of the ungual phalanges preserved in Sa844 varies between 25 and 32 mm, and the proximal dorso-ventral depth between 15.7 and 18.8 mm.

PELVIC GIRDLE AND HINDLIMB

Innominate and hip joint

In *Amphicyon major* the left part of the pelvis is preserved, except the most anterior part of the ilium and a part of the pubis. The ilium is slightly longer than the ischium, and makes an angle of approximately 140° with it (Fig. 8), a feature not observed in *Ysengrinia americana* (Hunt 2002). The gluteal fossa is broad and deep and faces laterally. The fossa for the M. iliacus is reduced to a ventral slender strip. Although not complete, the anterior part of the ilium does not seem to be particularly prominent laterally. Anterior to the acetabulum, the tuberosity for the M. rectus femoris (a head of the quadriceps) is long and prominent. Ventrally, a small tuberosity for the psoas minor may be observed but is not very developed. The ramus of the ischium is robust, as well as the posterior ischial tuberosity, which is not deflected outward (Fig. 9). On the proximal side of the ramus, posterior to the acetabulum, a well-developed tuberosity for the Mm. ischio-caudalis (abductor of the tail) and gemellus superior (external rotator and abductor of the femur) is present. The acetabular facet covers approximately 320° of the circumference and is regular in width although slightly larger anteriorly (at the level of the rectus femoris tuberosity) than posteriorly. The acetabulum lies below the level of the sacrum, but because of the angle between the ischium and ilium, the ischial tuberosity lies at the same level as the first caudals.

On the femur the neck is relatively long and the head protrudes proximo-medially, higher than the greater trochanter (Fig. 8). It is regularly convex and the articular surface does not extend towards the greater trochanter, nor is it twisted in relation to the distal epiphysis. The fovea capitis (ligamentum teres insertion) is broad and deep. The greater trochanter is not particularly prominent proximally or anteriorly. Posteriorly, the trochanteric fossa is deep. The lesser trochanter, where the M. iliacus inserts, protrudes posteromedially and is visible in anterior view. There is no well-defined third trochanter, but a lateral scar for the insertion of the M. gluteus superficialis. Anteriorly, there is no trace for the origin of the various heads of the quadriceps but posteriorly, the insertion of adductors is rugose along three main lines and the longest and most lateral one extends along almost the whole diaphysis.

Knee joint

The distal epiphysis of the femur seen in distal view is slightly higher than wide (Fig. 10). The groove of the femoral trochlea is well defined but not very deep between symmetrical ridges. An ossified patella is known. The anterior tuberosity of the tibia is prominent and located much more distally than the level of the tibial condyles. The length of the trochlea and condyles is similar seen in lateral view. The intercondyloid space is deep and broad.

In distal view the femoral condyles appear to be approximately equal in width but asymmetrical, the medial condyle being more prominent posteriorly than the lateral one. Moreover, its separation from the trochlea is more emphasised, and the articular facet faces laterally (i.e. towards the intercondylar fossa). In posterior view, this asymmetry is still more emphasised, the medial condyle being more prominent distally than the lateral one. Moreover, the lateral condyle exhibits proximally a small lateral extension that does not exist medially. On the tibia, the shape of the tibial articular facets reflects the asymmetry of the femoral condyles: the medial articular facet is flat to slightly concave, whereas the lateral one is slightly convex, the most posterior part of the facet facing posteriorly and not proximally, and this suggests some rotational capabilities.

Morphology of the leg: tibia and fibula

Two complete tibiae and one complete fibula are known. The tibia represents approximately three quarters of the femoral length (Fig. 11 and Appendices). The tibia and fibula are straight in lateral and anterior views, although the thick anterior tibial crest is slightly convex medially. On the lateral side of the tibia, the fossa where M. tibialis anterior originates is broad and deep. On the anterior crest, the insertions of the Mm. gracilis and semitendinosus caput ventrale extend until the middle of the shaft. The medial side of the tibia bears proximally a shallow scar for the insertion of the medial collateral ligament. Posteriorly, a crest for the M. popliteus is well marked, long and sharp.

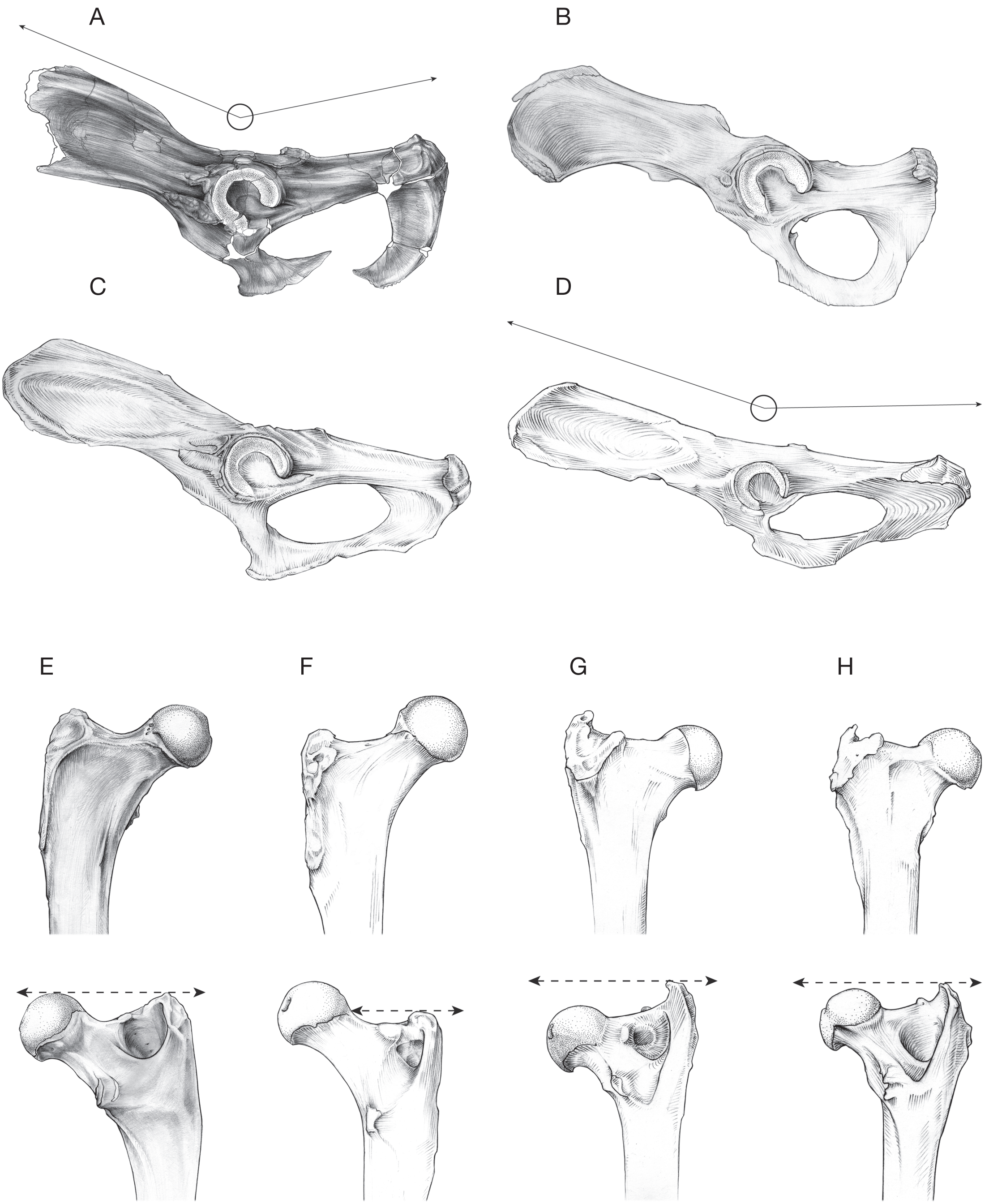

Fig. 8. — Hip joint: **A**, **E**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, **F**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, **G**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, **H**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279; **A**-**D**, innominate in lateral view; **E**-**H**, proximal part of the right femur in anterior and posterior views. Not to scale.

The fibular shaft is triangular in cross-section, due to the development of a sharp lateral crest. The fibular head is narrow, with a medial, inner facet articulating with the tibia, and a lateral posterior one that could have been in contact with a well-developed parafibula or a sesamoid in the tendon of the lateral gastrocnemius. The distal epiphysis is as wide as the head, with a prominent anterolateral malleolus, that shows laterally a well-defined groove for the tendon of the M. peroneus longus. Medially, a broad facet oriented medioanteriorly articulates partly with the tibia and especially with the astragalus. The corresponding facet on the tibia is small and oriented laterodistally. The fibula does not articulate proximally with the femur, and there is no rotational possibility between the tibia and fibula.

Tarsal bones and pes

All the tarsal bones of the specimen Sa844 are known except a complete astragalus, but several astragali and calcanei of other specimens of *A. major* are known from Sansan. The calcaneum is massive and exhibits a robust tuber calcanei whose medial tip protrudes postero-medially. The ectal and sustentacular facets are fully separated. The ectal facet is elongated anteroposteriorly, regularly convex, and faces dorsomedially. The sustentacular facet protrudes medially; it is flat and circular in outline except for a distal narrow strip that extends until the calcaneocuboid facet. The sustentaculum is slightly grooved on its plantar surface. The calcaneocuboid facet is slightly concave and triangular in outline, better developed laterally than medially. Plantarly, the crest running from the apex of the tuber to the calcaneocuboid facet is thick, and ends distally in a robust tuberosity. There is no lateral peroneal process (only a small lateral flange), and no lateral articulation with the fibula.

On the astragalus, the trochlea shows a deep groove between prominent ridges, the lateral one being more prominent dorsally and wider transversely than the medial one (Fig. 12). On the tibia, the corresponding grooves are asymmetrical, the medial one being deeper than the lateral one that is shallower but wider transversely. The main axis of these grooves is oriented anterolaterally-posteromedially. The medial malleolus of the tibia is prominent distally whereas laterally, the astragalo-fibular contact is broad, restricting the movements of the upper ankle joint to parasagittal flexion-extension. In order to further increase this stability, the distal epiphysis of the tibia also exhibits prominent anterior and posterior processes. The astragalus overhangs the calcaneum dorsally, and the navicular head is located proximomedially to the calcaneocuboid facet. The navicular articular facet is transversely convex and much wider than high. The small articular area connecting the navicular facet to the sustentacular astragalar one articulates with the narrow strip existing on the calcaneum between the sustentacular and the calcaneocuboid facets.

The navicular has the shape of a cupule, proximodistally flat (between the astragalar and cuneiforms articulations), with a wide and concave astragalar facet. Posteriorly, it bears a small tuberosity, like the calcaneum, cuboid, and cuneiforms. Distally, the facet that articulates with the cuneifoms is divided in two parts, a lateral one, flat to slightly concave, that articulates with the ectocuneiform, and a medial one, convex, that articulates loosely with the two most internal cuneiforms.

The cuboid is a massive quadrangular bone, which bears a quadrangular proximal articular facet oriented proximo-laterally. Medially, two articular facets with the ectocuneiform can be observed. Posteriorly, a strong tuber overhangs a groove for the tendon of the peroneus longus. Distally, the articular facet with Mt V and IV is triangular in outline.

The ectocuneiform is the second largest bone of that distal row. It is quadrangular in shape in anterior view but does not reach proximally the level of the calcaneocuboid articulation. Laterally it bears two articular facets with the cuboid and medially, three facets that articulate with the mesocuneiform and Mt II. Posteriorly, similarly to the cuboid, it shows a strong tuberosity.

The mesocuneiform is a small bone, with a quadrangular anterior side, and concave, trapezoidal proximal and distal articular facets. The proximal facet that articulates with the navicular is at the same level as the proximal facet of the ectocuneiform. Mt II articulates proximally both

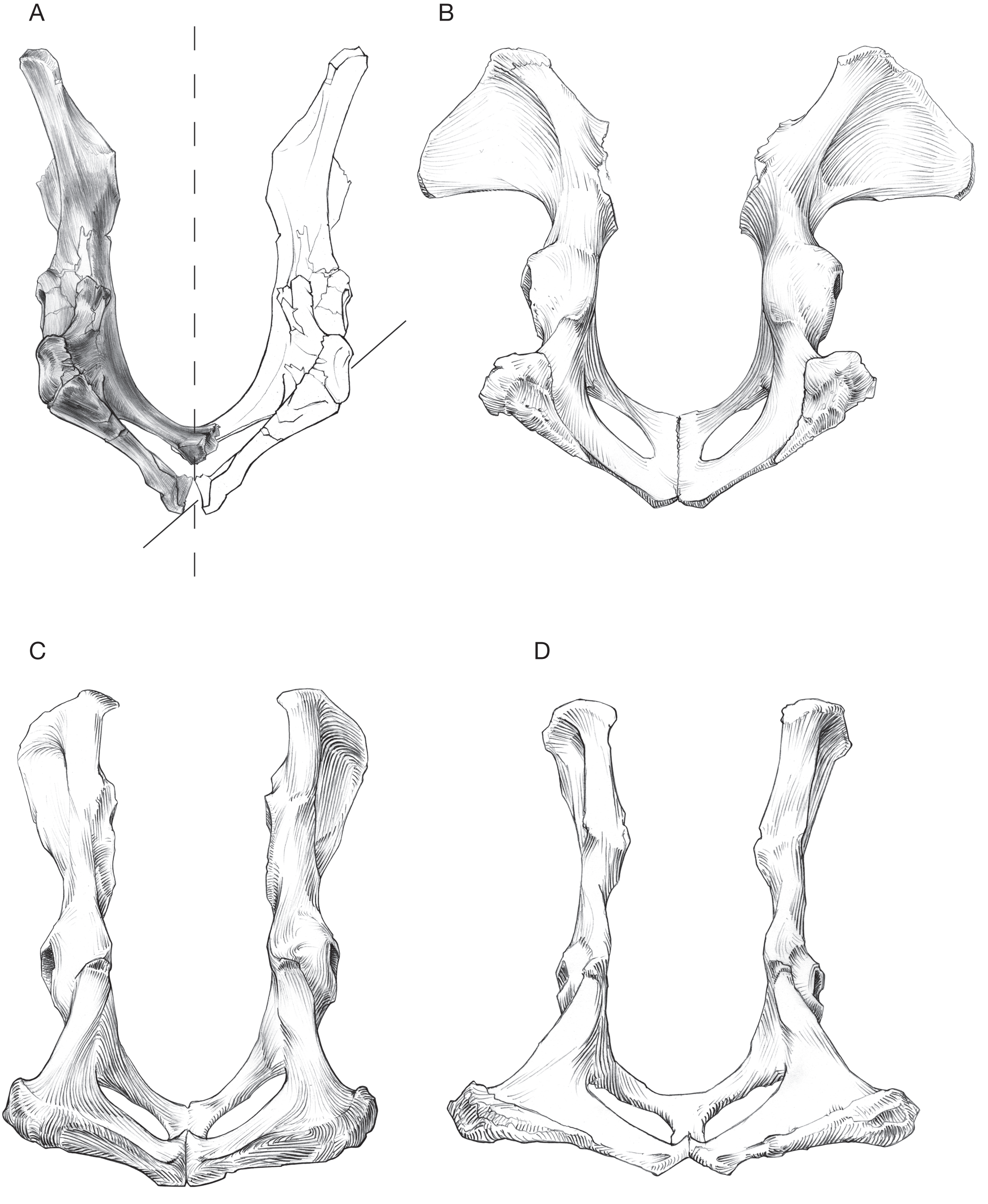

Fig. 9. — Innominate in postero-dorsal view: note the relative length and orientation of the ilium and ischium; **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279. Not to scale.

with the mesocuneiform (proximally) and ectocuneiform (laterally); therefore, its apex stands much more proximally than the apex of the most lateral metatarsals and than Mt I.

The entocuneiform is transversely compressed and proximodistally higher than the mesocuneiform; both cuneiforms articulate through a small facet. The distal facet of the entocuneifom that articulates with Mt I is anteroposteriorly long, and transversely wider at mid-level. It allows mainly anteroposterior gliding movements, the proximal part of Mt I bearing lateroposteriorly a process that protrudes proximally and prevents further plantar flexion. When articulated, the Mt I is slightly divergent relative to the other metatarsals. It is also much shorter, representing hardly more than half the length of Mt IV.

The five metatarsals are known and barely longer than the metacarpals (Fig. 13). When articulated, Mt IV is slightly longer than Mt III, which reaches the same level as Mt V. Mt II is a bit shorter, especially in relation to the proximal position of its apex. Mt I is the shortest and most divergent metatarsal but it is not reduced; it articulates with a well-developed phalanx, and ends with a strong claw. Like in the hand, the most internal metapod does not articulate to Mc II/Mt II, which allowed relatively free movements of the hallux and pollex, whereas the four most lateral metapods articulate one to the other (especially Mt III-IV-V, Mt V and IV exhibiting a medially prominent process interlocked respectively to Mt IV and III). The proximal articular facet of Mt V is reduced, the cuboid articulating mainly with Mt IV. A prominent lateroplantar process also characterises Mt V proximally. The metatarsals are short and robust, with broad distal epiphyses and wide gaps in between them, suggesting a powerful foot musculature as in the hand. The proximal epiphyses present rugose plantar tuberosities, consistent with the developed plantar processes of the lateral cuneiforms, cuboid, navicular and calcaneum, suggesting a usual contact with the ground. The distal epiphyses are the most asymmetrical in Mt I and V, like in the hand. The phalanges, described in the forelimb part, will not be discussed here again.

DISCUSSION

The comparisons will refer to "*Amphicyon*" in general. It is always *A. major* but because no significant differences have been noted between the material compared, no number of specimen will be given.

AXIAL SKELETON

Cervical vertebrae

The articulations occipital condyles-atlas and atlas-axis are similar enough in the extant lion and bear and in *Amphicyon* to suggest a similar range of head movements. The atlas of the lion and *Amphicyon* look more massive than that of the brown bear because of a dorsal arch that is relatively wider anteroposteriorly; moreover, in the former two taxa the anterior articular facets are more independent from the anterior part of the transverse processes. The extension of the lateral transverse processes is also similar in the lion and *Amphicyon*. The morphology of the axis is extremely similar in *A. major*, *P. leo* and *U. arctos*, whereas in *C. lupus* the neural process of the axis protrudes more anteriorly, reaching the level of the tip of the den, but less posteriorly, as it hardly reaches the level of the postzygapophyses. The axis of *A. major* and *P. leo* also look more massive than that of the bear because of the anteroposterior width of the lateral walls of the dorsal arch. The anteroposterior width of the dorsal arch of the following cervical vertebrae is restricted in *Amphicyon* that exhibits prominent zygapophyses, whereas the dorsal arch is extremely broad in the lion, while the bear is intermediate. The development of the neural and transverse processes of the posterior cervicals cannot be compared between *Amphicyon* and the extant taxa because of their poor preservation. Therefore, the atlantal-axial complex of *Amphicyon* suggests rotational capabilities of the head similar to those of a lion.

Thoraco-lumbar vertebrae

Panthera leo has got 13 thoracic vertebrae and 6 lumbars. The diaphragmatic (i.e. change of the articular mode) and anticlinal (i.e. change of orientation of the neural process) vertebra is T11. The neural processes of the anterior vertebrae are inclined posteriorly (except for the most anterior

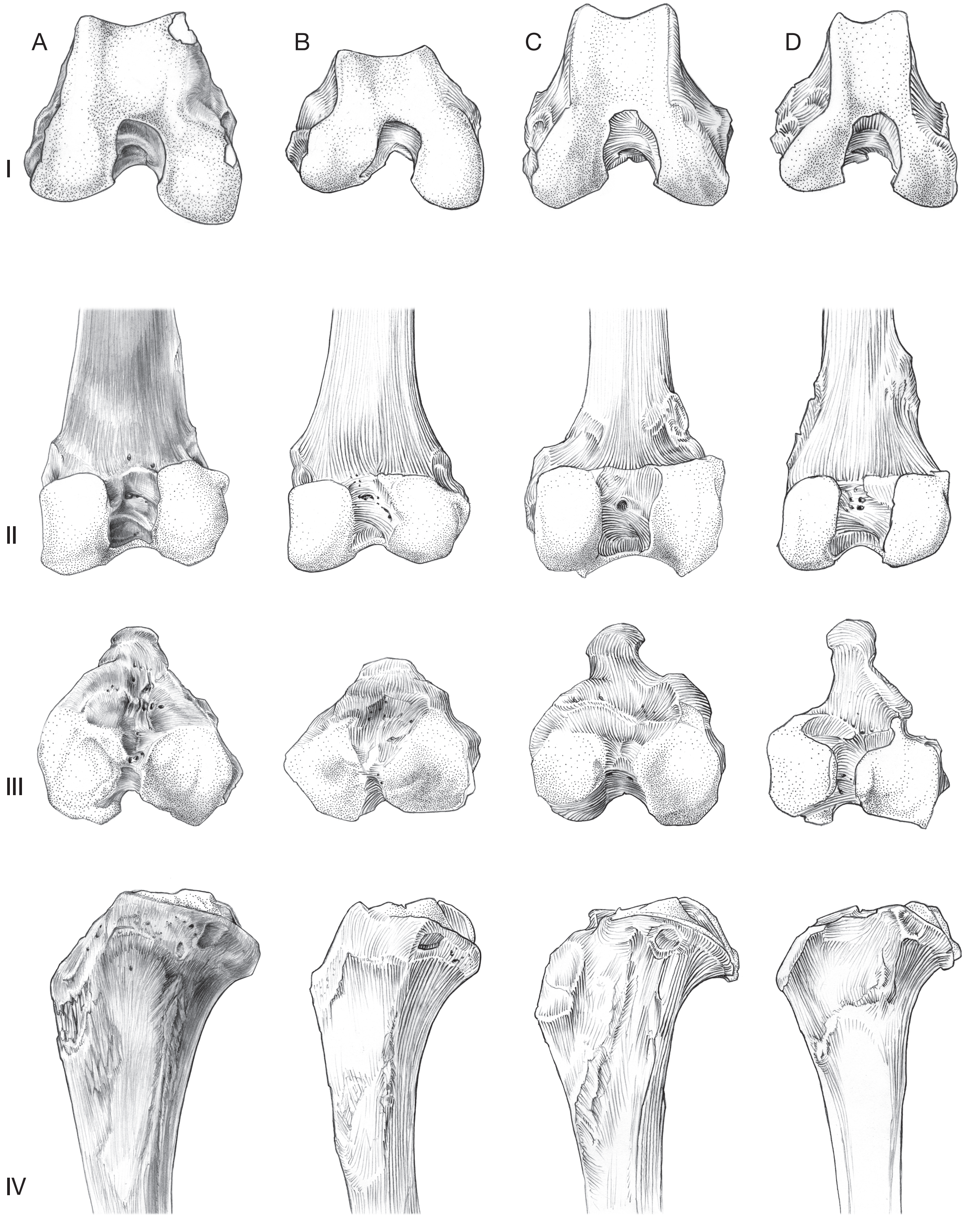

Fig. 10. — Knee joint: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279; **I**, **II**, distal extremity of the right femur in distal (**I**) and posterior (**II**) views; **III**, **IV**, proximal extremity of the right tibia in proximal (**III**) and medial (**IV**) views. Not to scale.

ones where the neck musculature attaches), whereas those of the posterior vertebrae are inclined anteriorly. The height of the thoracic neural processes decreases regularly when going posteriorly towards the anticlinal vertebra, whereas the height of the post-anticlinal thoraco-lumbar vertebrae increases until L3-L4 and then decreases towards the sacrum. These processes are robust, with a broad apex on the post-anticlinal vertebrae, and they are relatively taller than in *Amphicyon*, taller than the mammillary processes. Anapophyses exist on T11-L5 and are particularly developed on T12-L1, thus laterally stabilising this area of the vertebral column. In *C. lupus* the diaphragmatic vertebra is T10 and the anticlinal is T11. The morphology of the thoraco-lumbar neural processes is similar to that of *P. leo*.

Ursus arctos exhibits 14 to 15 thoracic vertebrae, and 5 lumbars, i.e. a long anterior area stabilised by the rib cage and a short area free of ribs, the whole suggesting a rigid vertebral column. This stability is increased by the anapophyses that are present on T12-L2 and particularly developed on T13-15. The diaphragmatic vertebra is T12 but there is no anticlinal vertebra. The neural processes of T3-13 show a basal part that is inclined posteriorly whereas the apical part stands vertical. Their height decreases regularly towards the diaphragmatic vertebra. By contrast, the neural processes of all the post-diaphragmatic vertebrae are vertical, of similar height, and anteroposteriorly wide, which increases the robustness and massive aspect of the vertebral column.

The morphology of the transverse processes of the lumbars also differs strongly between the lion and wolf on one hand and the brown bear on the other hand. They are much longer, anteroventrally prominent in the active predators, whereas they are horizontally placed and protrude laterally in the brown bear, which does not provide for a great mechanical advantage of the M. quadratus lumborum, the main flexor of the lumbar area. Although they are not preserved in the specimen of Sansan, Olsen (1960) mentioned that in *Amphicyon longiramus*, "the transverse processes have a strong forward deflection almost identical to that seen in *Felis* and are proportionately longer than those of *Canis*" (p. 6). The general morphology of the neural and transverse processes therefore emphasises the flexibility of the vertebral column in the lion and wolf, vs a lesser mobility in the massive brown bear, with reduced sagittal flexion-extension. It is noteworthy that, although exhibiting distinct morphologies, the cervical vertebrae of the lion and brown bear do not allow themselves to establish which one is the active predator. Concerning that particular point, the thoraco-lumbar vertebrae are thus much more informative. The general morphology of the neural thoracolumbar processes of *Amphicyon major* is more similar to that of active extant predators, and the anterior position of the diaphragmatic and anticlinal vertebra (T10 to T12 as in extant felids and canids) indicate the development of powerful back flexors and extensors, and a role of the lumbar area in the propulsion, through powerful flexion/extension.

Caudal vertebrae

The tail of the bear is extremely reduced, made of less than ten small vertebrae. In the wolf and lion, the tail is made of 20-25 caudal vertebrae. They exhibit transverse processes prominent posteriorly until Ca3, functional zygapophyses until Ca5 and a foramen vertebrale until Ca7. None exhibits a neural process. The vertebral body increases in length until Ca9 and then decreases in length and robustness. In comparison, the caudal vertebrae of *Amphicyon* are more robust than in the lion relative to the lumbar vertebrae, and the transition between the anterior and the posterior parts of the tail occurs further posteriorly than in extant carnivores. Its robustness is especially emphasised by the protrusion of the neural and transverse processes of the anterior vertebrae. Moreover, the zygapophyses that remain functional far posteriorly increase the strength of the inter-caudal articulations, and the foramen vertebrale existing until Ca12 also suggests an innervation that extends further posteriorly than the extant carnivores examined here.

PECTORAL GIRDLE AND FORELIMB

Scapula and proximal humerus: shoulder joint

The scapulae of the lion and wolf are similar in shape, with subequal supra- and infraspinous fossae, whereas in the bear the infraspinous fossa is definitely larger (Fig. 2). Moreover, bears and the

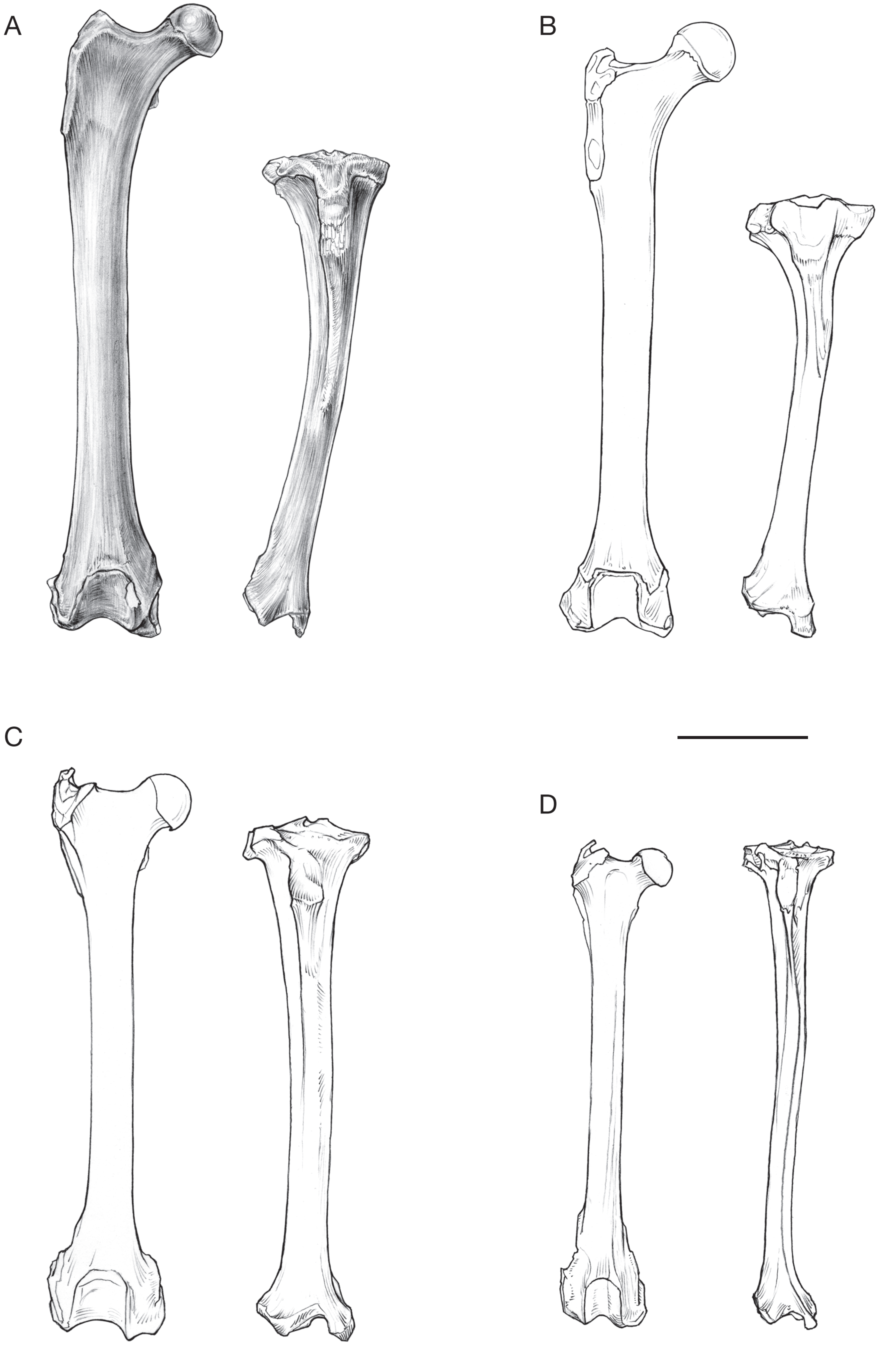

Fig. 11. — Femur and tibia in anterior view, emphasising the relative length of the two bones of the leg: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa844; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; **D**, *Canis lupus* Linnaeus, 1758 MNHN 2005-279. Scale bar: 5 cm.

procyonid kinkajou (*Potos flavus* Schreber, 1774) are the only extant carnivores showing a large accessory fossa lying caudad of the infraspinous fossa, between a secondary scapular spine and the caudal border. Although damaged in *A. major*, the distal extension of this fossa is similar to that observed in bears. A similar fossa also characterises the amphicyonid *Ysengrinia americana* (Hunt 2002) and the ailurid *Simocyon batalleri* Viret, 1929 (Salesa *et al.* 2008: fig. 4). The only myological study relating to that feature (Davis 1949) associates this fossa with the origin of a part of the subscapular muscle (M. subscapularis minor) and of the caput longum of the triceps (posterior part). The scapula of *A. major* exhibits such a fossa, as well as a wide scapular neck, much more similar to that of bears than to any other carnivore. Davis noted that among mammals, similar features can be found in armadillos and anteaters, not suspected to be phylogenetically closely related to bears, and where forelimbs are adapted to dig (i.e. retracting the forelimb against a resistance); because bears are not powerful diggers, Davis related the features observed (wide scapular neck, large postscapular fossa, heavy scapular musculature, large subscapularis minor, extensive origin of triceps caput longum) to their ability to climb trees by bracing trunks, the body weight being suspended from the forelimbs. However, this behaviour is also seen in the big cats but they do not present the same development of the postscapular fossa, although the caput longum of the triceps is also extremely developed in the lion (Barone 1967). Thus, the origin and functional meaning of the postscapular fossa is not yet fully understood, and the rest of the skeleton will help us to discard one of the hypotheses: climber or digger. The estimated body mass of the fossil specimen will be also compared to that of living bears and lions.

The greater tubercle of the humerus is anteriorly prominent in all three extant carnivores, but especially so in *P. leo* and *C. lupus* relative to *U. arctos* (Fig. 3). The fossa of insertion of the infraspinatus is broad in all three carnivore species. This tubercle is higher than the humeral head in lions and wolves, but as high as the head or lower in bears, like in *Amphicyon*. The smaller tubercle is tightly pressed against the head in the three extant taxa observed, with the cranial border slightly prominent anteriorly. The proximal part of the humeral head is much flatter transversely in the wolf than in the lion or bear. In the latter two taxa, the articular facet is regularly convex in lateral view and subcircular in proximal view, looking still more rounded in the bear because of the lower greater trochanter, and the less prominent posterior "beaking" of the head. Moreover, the glenoid cavity of bears is less rounded, more ovoid and shallower than in lions. The humeral shaft of bears is more slender than in *Amphicyon*, although bears exhibit the longest deltopectoral crest of the three carnivores observed, as long as in *Amphicyon*. This crest is usually long in taxa characterised by a manipulative behaviour, or that are able to climb by bracing or to dig, i.e. characteristic of taxa where the forelimb is not restricted to locomotion, with powerful pectoralis and deltoideus pars acromialis (Argot 2004). In *C. lupus* and *P. leo*, the deltopectoral crest is shorter than the half part of the shaft, and exhibits a rugose deltoidian area. In canids, the medial latissimus dorsi insertion is more proximally located than in the other carnivores. Therefore the proximal part of the humerus of *Amphicyon* is intermediate between felids (anterior protrusion of the greater tubercle) and bears (greater tubercle lower than the head, ball-shaped humeral head, very little "beaking" (overhang) of that head, and long deltopectoral crest). The shoulder joint suggests a greater mobility in bears and in *Amphicyon*.

Distal humerus and proximal ulna and radius: elbow joint

The distal part of the humerus is wider in *P. leo* and especially *U. arctos* than in *C. lupus*, relatively to the length of the humerus (25 to 28% in the lion and bear vs 17% in the wolf; 27% in *A. major*). The lateral epicondylar crest is also longer in the lion and bear, where it reaches the distal level of the pectoralis insertion, than in the wolf. This crest protrudes more laterally in the bear than in the felid, widening the area of origin of the brachioradialis and long extensors of the digits. *Ursus arctos* is the only carnivore observed to lack an entepicondylar crest and foramen (Fig. 4). The entepicondyle is more massive and prominent in the lion and bear than in the wolf, and is still more protruding posteriorly in the bear than in the lion. For that feature, *A. major* appears to be very similar to *U. arctos*.

In the three extant carnivores observed, the anterior part of the humeral trochlea is transversely narrower than the capitulum, and is characterised by a medial lip that protrudes anteriorly and distally. The trochlea is relatively wider transversely in *U. arctos* than in *P. leo*, relatively to the total width of the distal articular area. Consistently, on the ulna the coronoid process is wider in *U. arctos* than in *P. leo*. On the posterior side of the humerus, the olecranon fossa is deep but imperforate in the three extant carnivores. It is more symmetrical in the wolf and lion than in the bear, suggesting parasagittal flexion-extension in the two former taxa. The bear is characterised by a prominent lateral lip, which is slightly bent medially, which hides the most lateral part of the olecranon fossa (Fig. 4). This feature probably strongly increases the lateral stability of the joint; a similar stabilisation exists medially, thanks to the posterior protrusion of the entepicondyle. Although in the lion the lateral lip of the trochlea is also prominent, it does not reach the extension observed in the bear, and the entepicondyle is also less prominent posteriorly. The lateral lip of the trochlea is broken in most of humeri preserved of *Amphicyon* but considering the asymmetry of the trochlea and olecranon fossa, the morphology was probably intermediate between that of the lion and the bear, almost reaching the situation observed in *U. arctos*. By contrast, in the amphicyonid *Ysengrinia*, the elbow joint is less stabilised (Hunt 2002). It is noteworthy then that an increased specialisation of the elbow joint in amphicyonids evolved towards a typical ursid-like morphology.

On the ulna, the anconeal process is asymmetrical in the three extant carnivores observed, the lateral lip covering a part of the lateral side of the olecranon whereas the medial lip is reduced. This asymmetry is also more emphasised in *U. arctos*, and more similar to *Amphicyon* in that respect. The trochlear notch forms a semi-circle in all carnivores, but the asymmetry of this notch in anterior view (with the longest axis of flexion-extension oriented proximo-laterally/disto-medially) is much more emphasised in the bear than in the two other extant carnivores, consistent with the most parasagittal flexion-extension in felids and canids. In distal view, the distal humeral end is anteroposteriorly deeper in the lion and wolf than in the bear.

The articular facet of the capitulum is more convex in the lion and wolf than in the bear where it is flat, as in *Amphicyon*. It also extends further distally in the wolf and lion than in the bear and *Amphicyon*, suggesting a more flexed usual posture in the latter two species. The main difference between *U. arctos* and *A. major* is the presence of a lateral lip of the capitulum that is more developed in the bear, which probably stabilises the humeroradial joint laterally. On the ulna the radial notch covers approximately the same arc of circumference in the lion and in the wolf. It is more open in the bear, where the most posterior part is also much broader than the medial part. In anterodistal view, the coronoid process and medial part of the radial notch form a sharp to sub-perpendicular angle in all the species examined.

The radial head is ovoid in *P. leo* and *C. lupus*, and angular in *U. arctos*. It is deflected medially in the three taxa, and the capitular eminence is much more developed and prominent in the bear than in the lion or wolf, similar to that observed in *Amphicyon* (Fig. 5). It is twisted in relation to the distal extremity in both the lion and bear, but not in the wolf where the radius is located very anteriorly to the ulna. The result is a more abducted humerus and flexed position of the elbow in the lion and especially the bear, with a lateral position of the radius vs a more erect and parasagittal position of the forelimb in the wolf, with a more anterior position of the radius. This is consistent with the ability of the lion and bear to supinate their forefeet to some degree when catching or bracing prey or supports. The articular area of the radial head is sub-equal to the area of the coronoid process in the three extant taxa or may be slightly broader in the bear and lion. Therefore the distal part of the humerus and elbow joint of *Amphicyon* is more similar to that of an extant brown bear than any other extant carnivores and reflects an elbow joint that is well stabilised in extensions but asymmetrical, i.e. that the joint did not move in a strict parasagittal plane.

Morphology of the ulna and radius

The ulna is more massive in the lion and bear than in the wolf where it tapers gradually, becoming extremely thin distally. The radius and ulna lie close one to the other in *C. lupus*, but less in the lion and still less in the bear where the radius presents the greatest curvature, convex anteriorly from midshaft. The scar for the interosseous ligament is long and rugose in the three taxa. The posterior border of the ulna is straight proximally, more concave distally, especially in the wolf. In posterior view, the ulna exhibits a medial concavity in the three taxa. The olecranon is short and massive everywhere, looking still shorter in the bear because of the proximal extension of the lateral lip of the anconeal process. Moreover, the medial protrusion of the olecranon, noted in *Amphicyon*, is much more emphasised in the bear than in the two other extant taxa, but its relationship to the development of a specific muscle is not clear, as is noted by Davis (1964).

The bicipital tuberosity is well developed in *P. leo* and *U. arctos* but never reaches the extent observed in *Amphicyon* (Fig. 5). Laterally, the scar for a stabilising ligament is also better emphasised in the bear. On the ulna, the scar for the Mm. brachialis and biceps is better marked in the bear than in the lion. There is no specific lateral or medial fossa on the ulnar shaft.

Although the radial diaphysis is more convex anteriorly in the bear than in the lion, the insertion of the pronator teres is more visible in the lion. This muscle inserts only on the proximal third of the radius in the wolf. Distally, the facet articulating with the ulna is reduced in the wolf; it is broader in the two other taxa, especially in the lion, providing for better rotational ability of the distal extremity of the radius in the taxa retaining grasping ability.

Carpal bones and manus

In this section *A. major* will be compared only to the digitigrade *P. leo* and to the plantigrade *U. arctos* (Fig. 6). On the proximal carpal row, the main differences of the scapholunar between the bear and the lion lie: 1) in the protrusion of the palmar process, much more prominent palmarly in the bear than in the lion and *Amphicyon*; 2) in the shape of the proximal articular facet, more convex anteroposteriorly in lateral view in the lion, whereas it is flatter in the bear and in *Amphicyon*; moreover, the most medial part, articulating with the styloid process of the radius, is more concave in the lion, with a palmar border that protrudes proximally, stabilising the joint (the wrist forming a vertical column in digitigrade taxa); 3) in medial view, the distal facet that articulates with the trapezium is confluent with the proximal articular facet in the bear and in *Amphicyon*, in contrast to the lion. The distal facets also differ, but these differences will be examined with the morphology of the bones of the distal carpal row. On the proximal carpal row, the pyramidal is broader in the bear than in the lion relative to the other bones of the hand. The articular facets are smaller and flatter in the lion, especially that articulating with the styloid process of the ulna, which limits the lateral part of the wrist in weight transfer. Moreover, the lateral process of the pyramidal that protrudes distally towards the unciform and Mc V in the bear is almost non-existent in the lion. For those features the pyramidal of *A. major* is very similar to that of the brown bear. The pisiform of extant taxa cannot be compared to that of *Amphicyon*, but it is much more robust in the bear than in the lion, especially the bulbous palmar extremity, probably because of the usual contact of the palmar pad covering it with the ground. The development of this pad and contact with the ground is also consistent with the developed palmar process of the scapholunar.

On the distal carpal row, the difference in size between the pair trapezoid-trapezium vs unciform-magnum is more emphasised in the brown bear and *Amphicyon* (where the external pair is broader) than in the lion. The medial articular facet of the unciform with the magnum is more arched in *Amphicyon* than in the two extant taxa, and the lateral facet articulating with the pyramidal is more convex. Moreover, the unciform and magnum reach proximally the same level in *Amphicyon* (as in *P. leo*) whereas in the brown bear the unciform is higher proximally. Consistently, the lateral articular facets on the scapholunar are much deeper in *U. arctos* and limited by strong processes (dorsal for that articulating with the magnum, palmar for that articulating with the unciform), a feature that indicates a better-stabilized mid-carpal joint than in *A. major*. The morphology of the scapholunar of *P. leo* is intermediate between *A. major* and *U. arctos* for those features. Medially, this is the opposite, the relief of the articular facets with the trapezoid-trapezium being more emphasised in *Amphicyon* than in *U. arctos*, with the lion showing an intermediate morphology. The distal articular facet of the trapezium with Mc I is also wider transversely in *Amphicyon* than in the brown bear, increasing the potential range of movements of the pollex. The articulation trapezoid-Mc II also differs between the bear and *Amphicyon*, the proximal articular facet of Mc II being more trochlear-shaped in the bear. Therefore it appears that *Amphicyon* had a mid-carpal joint that was relatively less stabilised laterally but more medially than in the bear, and that the two most internal metacarpals had a greater range of movements (articulations trapezoid-Mc II and trapezium-Mc I more mobile, increasing the grasping ability of the hand).

The metacarpals are short and robust in the bear, much shorter than in the lion, relative to the forearm length. In both extant carnivores, when articulated, the metacarpals present the same relative length as in *Amphicyon* (i.e., Mc III = Mc IV and Mc II = Mc V). However, the lion differs by the length of the palm, with long, straight metacarpals (Fig. 7), closely interlocked proximally and with narrower gaps between diaphyses. Except for their robustness (a feature that depends on the individual specimen observed), the metacarpals of *U. arctos* are relatively similar in shape to those of *A. major*. The robustness of Mc V is emphasised in the bear, probably in relation to the palmigrade posture. In *P. leo*, this is the shortness of Mc I that is emphasised, the first metacarpal representing hardly more than a quarter of Mc II. In the brown bear, Mc I is longer than in *Amphicyon* relatively to the length of Mc II and, like in the fossil, does not articulate to Mc II. On its dorsal side, the Mc II of *U. arctos* also exhibits a rugose scar proximomedially, for the insertion of M. extensor carpi radialis longus. The proximal epiphyses of the three lateral metacarpals do not differ significantly between the bear and the fossil taxon, the palmar process being more developed on Mc III than in the other metacarpals in the brown bear as well as *Amphicyon*. On Mc II, the proximal articular facet is flatter in *Amphicyon* than in the bear, and extends farther on the dorsal side of the metacarpal, suggesting potential increased dorsiflexions. On the first metacarpal, the proximal articular facet is more oblique in *Amphicyon* than in the brown bear relative to the transverse axis of the distal epiphysis, suggesting possible more abducted flexion-extension.

The proximal phalanges are as robust as the metacarpals in the bear and as long as, or longer than, the half part of the diaphyses. Like in *Amphicyon* they bear palmarly rugose scars for a tendinous sheath holding the tendons of the M. flexor digitorum profundus. In the lion, they also bear these scars although they are relatively short in comparison to the metacarpal length; there is no particular feature at the proximal end relating to a usual digitigrade posture. In both extant carnivores the intermediate phalanges are relatively long, longer than the half part of the proximal phalanges; the distal end is modified in the lion because of the retractile claws. The ungual phalanges of the bear are longer than the proximal phalanges, slightly arched, with a sharp dorsal border, and a well-developed sheath at their proximal extremity. Comparatively, although the comparison digit by digit is impossible, the claws of *Amphicyon* were relatively shorter.

Pelvic girdle and hindlimb

Pelvis and hip joint

The pelvis of *Amphicyon* is much more similar to that of a lion or wolf than to that of a bear (Figs 8; 9). In both the lion and wolf, the iliac blades are mostly parallel one to the other except for the most anteroventral tip, slightly deflected outwards (more in the lion than in the wolf). They are oval in outline, longer than the ischium, and show deep gluteal fossae. The ventral fossa for the M. iliacus is better emphasised in *Amphicyon* than in these two extant taxa. *Amphicyon* is especially characterised by the angle formed between the ilium and ischium, an angle that does not exist in the lion nor in the wolf, and is difficult to interpret functionally (a similar angle has been noticed in a specimen of a leopard by Bergounioux & Crouzel 1973). Ventrally, the tuberosity for the M. psoas minor can be observed in all. The tuberosity for the M. rectus femoris is much better developed in the lion, which stalks its prey and performs only short runs, than in the wolf. Dorsoposteriorly to the acetabulum, the tuberosity for the origin of Mm. ischio-caudalis and gemellus superior is well developed both in the lion and the wolf, as in *Amphicyon*. Posteriorly, the ischial tuberosity (origin of Mm. biceps femoris and semitendinosus and attachment for ligamentum sacrotuberosum) is more prominent laterally in the lion, and especially in the wolf than it is in *Amphicyon* (Fig. 9). A consequence is that the descending ramus of the ischium faces more ventrally than laterally in the wolf (and, to a lesser extent, in the lion) whereas it faces more laterally in *Amphicyon*. According to Jenkins & Camazine (1977), the more ventral that surface is, the less abducted is the femur. This suggests that the range of abduction of the femur was more important in *Amphicyon*. Although the acetabulum does not show any significant difference between the three taxa, in the femur, the femoral neck is longer in *Amphicyon* and the femoral head protrudes more proximally than in the two extant taxa. It is actually higher than the greater trochanter (in contrast to what is observed in the lion and wolf) and the anterior part of the articular facet is more developed towards the greater trochanter in *A. major* than in *P. leo*. This seems to confirm the greater possible range of femoral abduction in *Amphicyon* than in both the lion and wolf.

Comparatively, the pelvis of the extant bear differs by the length of the ilium (relative to the total length of the pelvis) and by the outward deflection of its anteroventral tip (Fig. 9), possibly related to the short lumbar area and development of the epaxial musculature between the last ribs and the anterior tip of the ilium. By contrast, the length of the lumbar area of *Amphicyon* was comparable to that of an extant lion. The tuberosity of the rectus femoris is less developed in *U. arctos* than in *A. major*. The dorsal ramus of the ischium of *U. arctos* is short and the ischial tuberosity is massive and protrudes laterally. This robustness is certainly related to occasional sitting postures, what *Amphicyon* did not do because of its long and robust tail, probably rigid at the base. The iliac neck is also particularly short in *U. arctos*, the sacral articulation being located just in front of the acetabulum. The iliac neck is comparatively longer in *P. leo* and *A. major*, and still longer in *C. lupus*. On the femur, the femoral head of *U. arctos* is still more prominent proximally than in *A. major*, and the brown bear is also characterised by a long femoral neck and a low greater trochanter. The extent of the articular facet of the femoral head is comparable in *A. major* and *U. arctos*. The lesser trochanter is located more posteriorly and especially more distally (it is much lower than the distal end of the trochanteric fossa) in the bear than in *Amphicyon*, where it is comparable in shape and location to that of the lion and wolf.

Knee joint

The shape of the distal epiphysis of the femur of *P. leo* is relatively similar to that of *A. major*, being slightly higher than wide and with a groove of the trochlea that is well-defined between asymmetrical ridges. The groove of the trochlea is deeper and narrower in *C. lupus*, between sharper ridges, whereas it is much shallower in the bear, where the distal femoral epiphysis is wider than high in distal view (Fig. 10). This morphological gradient coincides with the behavioural gradient between slow-moving and agile, cursorial species, the latter ones being characterised by more parasagittal excursion of the leg relative to the thigh. An ossified patella is known in the three extant taxa and the anterior tibial crest is much sharper and prominent anteriorly in *C. lupus* than in both *U. arctos* and *P. leo* with *A. major* intermediate in shape.

Seen in distal view, the medial femoral condyle protrudes more posteriorly than the lateral one in the three extant taxa, and bears a convex articular facet whereas the facet of the lateral condyle is more flat and faces internally, towards the intercondylar fossa. The medial condyle also protrudes more distally than the lateral one. The intercondylar fossa is broad and the proximolateral extension of the lateral condyle is more developed in *C. lupus* than in *P. leo* and does not exist in *U. arctos*. The proximodistal extension of the femoral condyles (seen in posterior view) is more important in *C. lupus*, *P. leo* and *A. major* than in *U. arctos*.

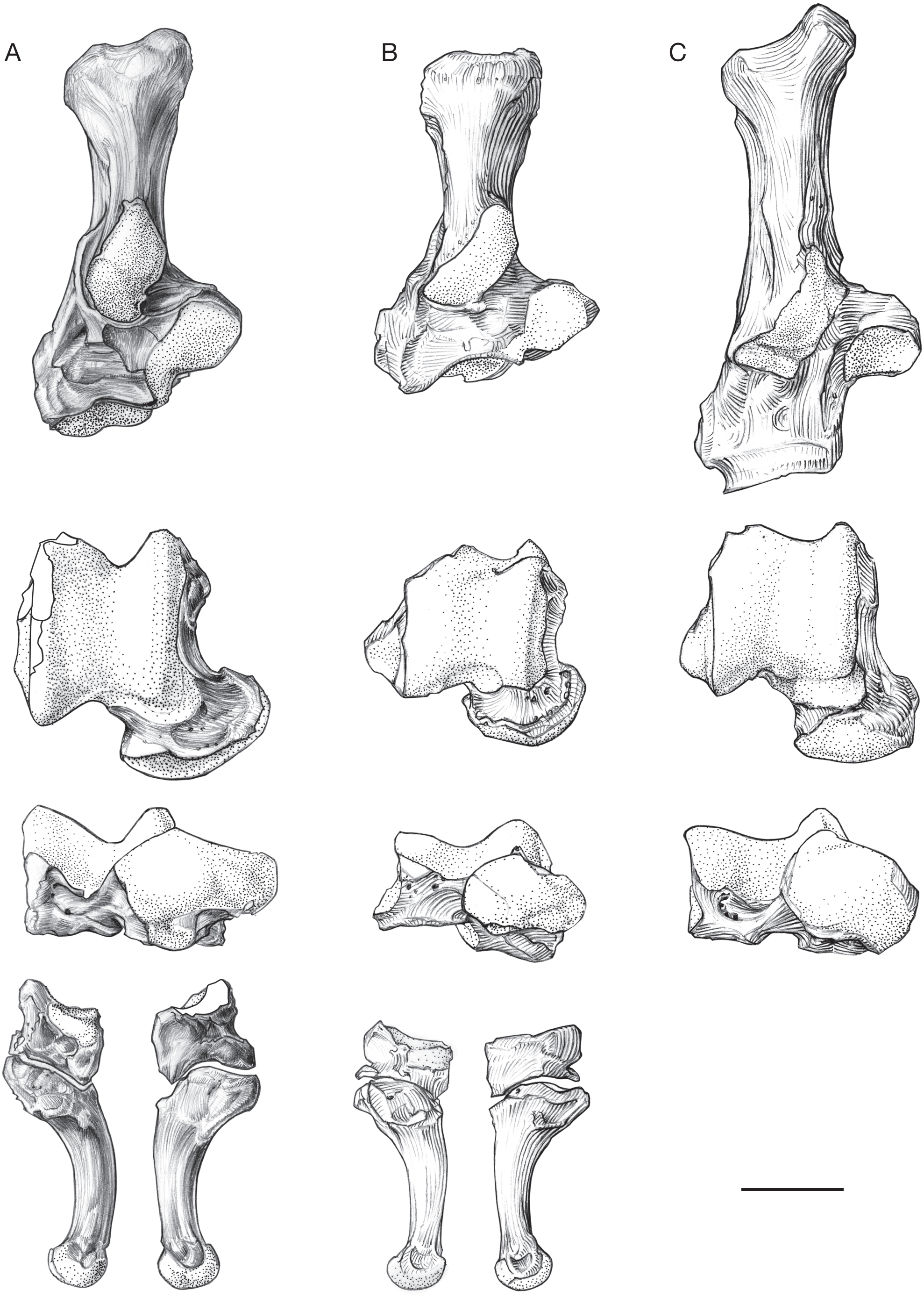

Fig. 12. — Focus on the calcaneum, astragalus, entocuneiform and Mt I: **A**, *Amphicyon major* Blainville, 1841 MNHN Sa166; **B**, *Ursus arctos* Linnaeus, 1758 MNHN 1974-25; **C**, *Panthera leo* Linnaeus, 1758 MNHN 1954-2; from top to bottom, right calcaneum in proximal view, right astragalus in proximal and anterior views, right entocuneiform and Mt I in lateral and medial views. Scale bar: 2 cm.

The corresponding facets on the tibia are more asymmetrical in *U. arctos*, the lateral tibial facet being flat to slightly convex whereas the medial one is concave. This difference is less emphasised in the two other extant carnivores and suggests a less restricted parasagittal excursion of the leg in the bear, and a potential reduced stability in this joint during support. Although rotational capacities have also been suggested for *A. major*, the distal end of its femur is more similar to that of *P. leo* than to that of *U. arctos*. However, the M. gastrocnemii originate very distally and laterally in the femur of *A. major*, like in *U. arctos* but distinct from *P. leo* and especially *C. lupus* where the muscle scars are located much more proximally.

Morphology of the leg: tibia and fibula

Whereas the tibia is as long as the femur (or even slightly longer) in *C. lupus*, it is shorter in *P. leo* and still shorter in *U. arctos* and *A. major* (Fig. 11). It is straight in anterior and lateral view in *P. leo* and *U. arctos* whereas the distal part of the tibia of *C. lupus* is slightly concave anteriorly. The proximal extremity is modified in relation to the sharpness of the anterior crest as discussed above. On the medial side of this crest, the insertions of the hamstring muscles (Mm. gracilis, semitendinosus, semimembranosus) are located at the same level in *P. leo*, *U. arctos* and *Amphicyon* whereas they are located very proximally in *C. lupus*. This, together with the laterally prominent ischiatic tuberosities in the wolf, provides for fast flexions at the beginning of the propulsive phase in this specialised runner, in contrast to the three other taxa observed.

The fibula is straight and thin in the three extant taxa; its size indicates that it obviously does not bear any significant body weight. It is similar in all these carnivores and *A. major*, with a small, tuberous head, slightly more extended anteroposteriorly in the lion and *Amphicyon* than in the bear, and more massive in *Amphicyon*. The articular facet with the tibia is oriented proximally in the lion and bear, and especially in the wolf, more medially in *Amphicyon*. On the lateral side of the head, the posterior facet that exists in *Amphicyon* (contact with a sesamoid?) cannot be observed in the lion or in the bear. Distally, the grooves for the tendons of the peronei are better marked in the lion and *Amphicyon* than in the bear. The extension of the distal articular facet is comparable in the lion and *Amphicyon*; it is more irregular in the wolf, precluding any movement between the two bones of the leg that act as a single unit. In contrast, the fibula of *Amphicyon* was more mobile relative to the tibia, similar to what is reported for felids and ursids (Barnett & Napier 1953), suggesting an adaptation to move on uneven substrates.

Tarsal bones and pes

The main differences in the calcaneum of the bear compared to digitigrade taxa lie (Fig. 12): 1) in the shortness and robustness of the tuber calcanei; 2) in the fact that the apex of the tuber does not present a deep groove with a prominent medial lip, in contrast to the lion and wolf; for that feature, *Amphicyon* is more similar to the lion and wolf although its proximal groove is shallower than in the extant taxa; 3) in the shape of the ectal facet, regularly convex in the bear, much more angular in the lion and wolf, which stabilises the lower ankle joint; 4) in the medial protrusion of the sustentacular facet, the calcaneum of the bear being much wider transversely than that of digitigrade taxa; for that feature, the calcaneum of *Amphicyon* is more similar to that of an extant bear and 5) in the development of the peroneal process, that is almost non-existent in the digitigrade taxa (nevertheless, a groove for the tendon of the peroneus longus can be observed in the lion). Moreover, the space between the calcaneoastragalar and calcaneocuboid facets is much broader in the digitigrades (especially the wolf) than in the bear, and for that feature *Amphicyon* is also more similar to an extant bear.

On the astragalus, the proximal groove is much deeper in the wolf than in the bear, while the lion is intermediate between the two. The asymmetry of the astragalar trochlea is the most accentuated in the lion, with a lateral lip that is transversely wider than the medial one. *Amphicyon* exhibits an astragalus whose morphology is relatively similar to that of a lion. The distal epiphysis of the tibia, which could rotate through the entire length of the astragalar trochlea, is also similar in *A. major*

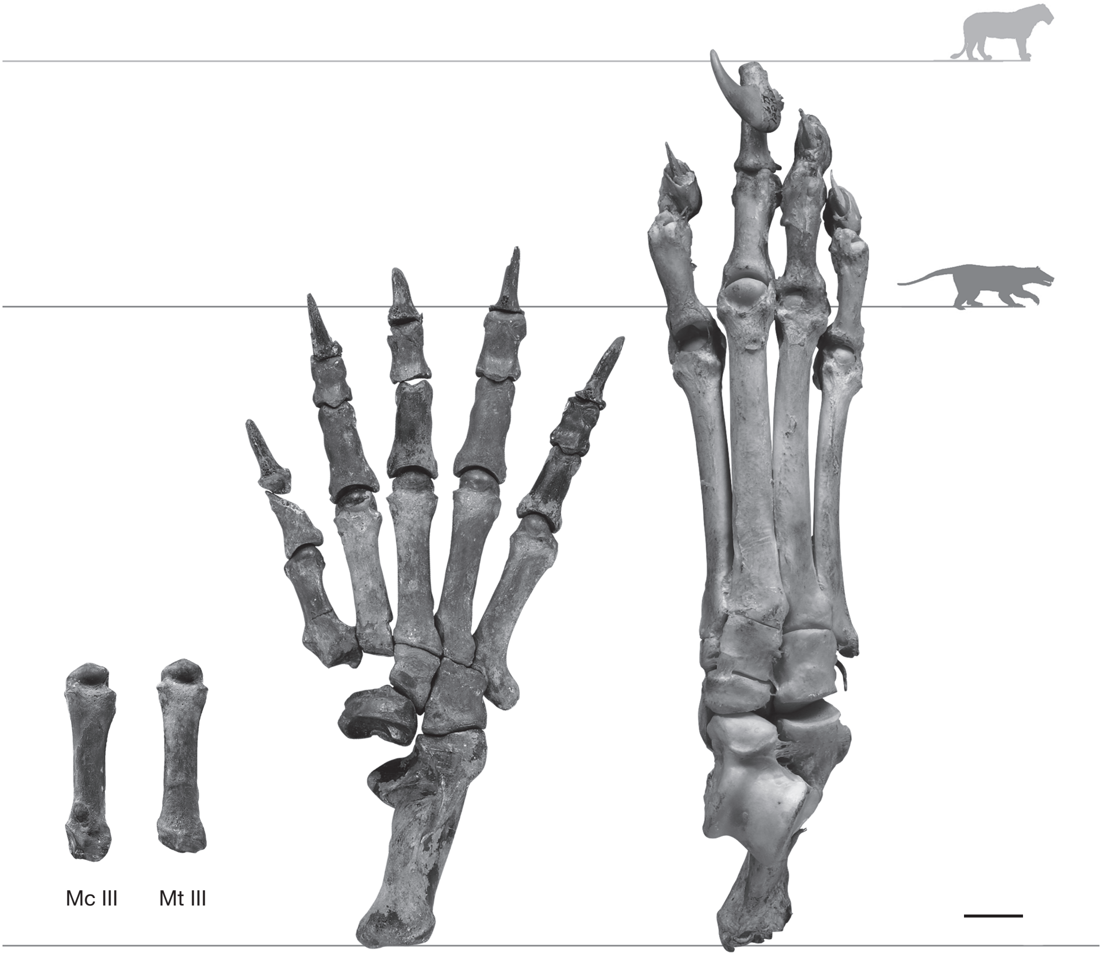

Fig. 13. — General morphology of the right pes of *Amphicyon major* Blainville, 1841 MNHN Sa844 in dorsal view in comparison to that of *Panthera leo* Linnaeus, 1758; on the left, comparison of Mc III and Mt III of *A. major* in dorsal view: note that they are sub-equal in length. Scale bar: 2 cm.

and *P. leo* with prominent anterior and posterior processes. The main axis of flexion-extension at the upper ankle joint is oriented anterolaterally-posteromedially. Although Wang (1993) states that the main difference between digitigrady and plantigrady relies on the degree of plantar extension between the tibia and astragalus, the difference between the specimens available of *U. arctos* and *P. leo* is not obvious, and it is still less when adding *A. major*, which shows an intermediate morphology for this feature.

In the brown bear the calcaneocuboid and astragalonavicular articular facets are both transversely wider than high, and the navicular head does not overhang the calcaneocuboid articulation. By contrast, in the wolf the navicular head slightly overhangs the calcaneocuboid facet. This facet is approximately circular in outline and the navicular head is slightly oblique, oriented proximolaterally/distomedially. Therefore, the mid-tarsal joint is much narrower transversely in the wolf than in the bear and the joint in *Amphicyon* is more similar to that of an extant bear, despite the absence of peroneal process and a calcaneocuboid facet that is narrower transversely. On the navicular, the main axis of the facet articulating with the astragalus is oriented dorso-plantarly and not transversely in *C. lupus*, in contrast to what is observed in *A. major* and *U. arctos*, in relation to the developed hallux in the two latter taxa. Distally, the navicular articulates mainly to the ectocuneiform in the lion and especially in the wolf, the medial facet for the two most internal cuneiforms being extremely reduced, consistent with the extreme reduction of these cuneiforms. In comparison, in *Amphicyon* the most medial part of the navicular facet is broader than that articulating with the ectocuneiform. In the bear the case is different: the distal articular facet of the navicular can also be divided in two parts but the most lateral one articulates with the cuboid whereas the medial part contacts the three cuneiforms without distinction. In fact, the three cuneiforms are extremely small, the ecto- and entocuneiforms having the same size (whereas the ectocuneiform is much larger than the entocuneiform in *Amphicyon*).

The first metatarsal is vestigial in digitigrade taxa, whereas it is as much developed in the brown bear as it is in *Amphicyon*. In the wolf and lion the metatarsals are elongated relatively to the metacarpals (especially in the wolf); they are slender, straight, deeply interlocked proximally and with narrow gaps between the distal diaphyses (Fig. 13). The digitigrady is also especially emphasised by the large size of the sesamoids standing plantarly at the metatarso-phalangeal articulation. As in the hand, the metatarsals are short and robust in the bear, much shorter than in the digitigrade taxa, relative to the leg length. When articulated, the lateral metatarsals (Mt III to V) are the longest in the bear. In the lion, Mt III is the longest metatarsal and the ectocuneiform is massive, suggesting that the maximal loading passes through that axis. The metatarsals of *U. arctos* are relatively similar in shape to those of *A. major*, including the prominent proximal process and asymmetrical distal epiphyses of Mt I and V. The feet of both *U. arctos* and *A. major* are then robust, short and with a powerful musculature. Whereas "the very nature of digitigrady relies on the metatarsals to support the force of the body through the limb" (Carrano 1997: 96), a reduced spread allowing them to function as columns and minimizing bending forces, it is clear that in both *Ursus* and *Amphicyon*, the widely spread metatarsals are the main elements of contact with the substrate. The differences between *A. major* and *U. arctos* for the ankle and pes lie therefore mainly: in the tibio-astragalar joint; in the apex of the tuber calcanei whose medial tip is more prominent in *Amphicyon*; in the robustness of the navicular and cuneiforms, and especially the size of the ectocuneiform relative to the two most medial ones.

BODY WEIGHT ESTIMATES AND PALEOBIOLOGY ELEMENTS

The body mass is estimated for *A. major* Sa844 using regression equations derived from long bone length and average midshaft diameters (Anyonge 1993). The equations of Egi (2001) refer to small animals only, and those of Van Valkenburgh (1990) that refer to cranial dimensions are not taken into account here, because of the relative great size of the skull of Miocene predators in comparison to extant ones, which usually overestimates the body mass of fossils.

All the measurements taken on *Amphicyon major* exceed those taken on the extant specimens except for the length of the humerus, which is longer in the brown bear. Consistently, whichever regressions are used, the body mass of *Amphicyon* is larger than that of the other specimens. When focusing on the results given by the humeral and femoral circumferences, which are considered as better predictors than bone lengths according to % SEE (a measure of the predictive strength of the regressions – the smaller value, the greater predictive power), this specimen of *A. major*, considered as a female, weighed approximately 150 kg (140-180 kg: Table 1), which exceeds the available weight estimates of the specimens of lion and brown bear examined in this study, but is still within the range of the weight known for those species. Using the least squares regression equations for head-body lengths given by Van Valkenburgh (1990), Viranta (1996) found that the predicted weight for *A. major* Sa844 is 67 kg, but she underlines that *A. major* has a greater skull length relative to head-body length than do canids, ursids,

TABLE 1. — Estimated body weight of *Amphicyon major* Blainville, 1841 compared to the specimens of extant taxa used in the study. In Anyonge (1993), the complete sample is calculated for 28 carnivoran species (4 families) with mean body masses between 5 and 500 kg. The felid sample is calculated for 14 felid species with mean body masses between 5 and 181 kg. The ursid sample is calculated for 4 ursid species with mean body masses between 102 and 500 kg. Abbreviations: **circ.**, circumference; **L.**, maximum length; **r**, correlation coefficient; **SE**, standard error of estimate; **%SEE**, percentage standard error of estimate.

Skeletal variable	***A. major* Sa844**	***U. arctos* 1974-25**	***P. leo* 1954-2**	***C. lupus* 2005-279**
Humeral L. (mm)	284.5	293	276	235.5
Humeral circ. (mm)	96.92	78.85	87.73	61
Femoral L. (mm)	335	321	303.5	258.5
Femoral circ. (mm)	87.80	75.16	78.30	57.02
Femoral distal condyles area (mm^2)	1433.2	1224.6	1326.85	558

Skeletal variable	**Slope**	**Intercept**	**r**	**SE**	**%SEE**	**Body mass (kg)**			
						A. major	*U. arctos*	*P. leo*	*C. lupus*
All sample									
Humeral L.	2.93	-5.11	0.94	0.214	51	120	131	110	69
Average humeral circ.	2.47	-2.72	0.98	0.116	29	153.5	92	120	49
Femoral L.	2.92	-5.27	0.95	0.201	46	127	112	95	59.5
Average femoral circ.	2.88	-3.40	0.98	0.131	30	157.5	100.5	113	45.5
Femoral condylar area	1.31	-2.12	0.99	0.047	24	103.5	84	93.5	30
Felids only									
Humeral L.	3.13	-5.53	0.95	0.294	42	141.5	–	129	–
Average humeral circ.	2.65	-3.00	0.97	0.187	30	183.5	–	141	–
Femoral L.	3.20	-5.90	0.96	0.282	39	151.5	–	110.5	–
Average femoral circ.	2.92	-3.46	0.96	0.251	38	164	–	117.5	–
Femoral condylar area	1.32	-2.16	0.98	0.072	24	126	–	91.5	–
Ursids only									
Humeral L.	4.38	-8.69	0.95	1.05	35	114.5	130	–	–
Average humeral circ.	3.04	-3.89	0.99	0.198	8	140.5	75	–	–
Femoral L.	3.85	-7.62	0.95	0.932	33	126.5	107	–	–
Average femoral circ.	3.96	-5.55	0.99	0.391	13	140	75.5	–	–
Femoral condylar area	1.55	-2.94	0.93	0.446	41	89.5	70	–	–

mustelids or felids. The weight estimates based on skull length are indeed higher, from 117 to 393 kg, whereas occiput to orbit length gives estimates from 78 to 133 kg. Finally, Viranta (1996) acknowledges that most of the measurements of *A. major* Sa844 are within the range of variation of the leopard and approach those of the female lion. The shoulder height of *A. major* Sa844 is approximately 65 cm, whereas that of *P. leo* MNHN 1954-2 was about 75 cm, a difference related to the plantigrade or the digitigrade stance of these animals (Fig. 14). Considering its body size and weight (*A. major* was the largest carnivore of the faunal assemblage, see below), it can be underlined that despite its capabilities to abduct and flex limbs, *A. major* was not a specialized climber, but it was able to use these capabilities and its muscular power for handling prey (Fig. 15) and, possibly, for pursuing them occasionally in trees, like some felids do.

In Sansan, the sediments were deposited in a lake or a marsh environment, near an open or semi-open hot, dry area (Salard-Cheboldaeff & Ollivier-Pierre 2000). The fauna is diversified, containing: a rich and diverse sample of amphibians (Rage & Hossini 2000) and squamates (Augé & Rage 2000), turtles (Lapparent de Broin 2000), crocodiles (Antunes 2000), and an abundant avifauna (Cheneval 2000). Although a revision of the mammalian fauna remains to be done (it is currently in progress), we can mention: insectivores, bats, primates, lagomorphs, rodents (castorids, sciurids, cricetodontids, glirids), carnivores (canids, ursids,

Table 2. — Proportions of the limbs. Abbreviations: **F**, femur length; **H**, humerus length; **McIII**, third metacarpal length; **MtIII**, third metatarsal length; **R**, radius length; **T**, tibia length. The lengths used are functional lengths, taken between proximal and distal articular facets.

Specimens **Indices**	***Amphicyon major*** **Sa844**	***Ursus arctos*** **MNHN 1974-25**	***Panthera leo*** **MNHN 1954-2**	***Canis lupus*** **MNHN 2005-279**
Brachial index (R/H)	0.84	0.79	0.93	0.99
Crural index (T/F)	0.76	0.70	0.90	1.01
Tibio-radial index (R/T)	0.91	0.99	0.90	0.84
Intermembral index (H+R+McIII/ F+T+MtIII)	0.87	0.94	0.88	0.84
McIII/H+R+McIII	0.12	0.10	0.17	0.16
McIII/MtIII	1.01	1.06	0.86	0.78
MtIII/F+T+MtIII	0.10	0.09	0.17	0.17
MtIII/F	0.20	0.16	0.41	0.43

amphicyonids, procyonids, mustelids, viverrids, barbourofelids and felids), proboscideans, perissodactyls (equids, chalicotheriids, rhinocerotids), and artiodactyls (suids, tragulids, cervids, bovids). The most abundant species of the site is a cervid, *Dicrocerus elegans* Lartet, 1837. The fauna of carnivores was abundant and diverse, many specimens being known by postcranial remains (see Ginsburg 1961): Amphicyonidae Haeckel, 1866 (*Amphicyon* Lartet, 1836, *Pseudocyon* Lartet, 1851*, Pseudarctos* Schlosser, 1899), Ursidae Fischer de Waldheim, 1817 (*Hemicyon* Lartet, 1851, *Plithocyon* Ginsburg, 1955), Procyonidae Gray, 1825 (*Schlossericyon* Crusafont, 1959), Mustelidae Fischer de Waldheim, 1817 (*Ischyrictis* Helbing, 1930, *Martes* Pinel, 1792, *Proputorius* Filhol, 1890, *Taxodon* Lartet, 1851, *Mionictis* Matthew, 1924), Viverridae Gray, 1821(*Semigenetta* Helbing, 1927, *Viverra* Linnaeus, 1758), Herpestidae Bonaparte, 1845 (*Herpestes* Illiger, 1811), Barbourofelidae Schultz, Schultz & Martin, 1970 (*Sansanosmilus* Kretzoi, 1929) and Felidae Fischer de Waldheim, 1817 (*Pseudaelurus* Gervais, 1850) are represented. *Amphicyon major* is the largest and the most powerful carnivore represented in the fossil assemblage. The other large carnivores were hemicyonids and felids, and artiodactyls and rodents could have represented the best prey for them. In the fauna, there was no hypercarnivorous predator with bone-cracking ability like extant hyaenas, although the analysis of the enamel structure of amphicyonids shows that *Amphicyon* was likely to supplement its diet with bones (Stefen 2001). Carbone *et al.* (1999) showed that among living carnivores, almost all species larger than 21.5-25 kg take prey as large or larger than themselves, whereas smaller species feed mostly on prey that is 45% or less of their body weight. However, the omnivorous bears are an obvious exception. From its dental microwear, *A. major* is considered to have been omnivorous, eating meat but including more vegetable matters in its diet than extant meat and bone eaters (Peigné pers. comm.). Sorkin (2006) produced a detailed study of the possible diet and hunting behaviour of *Amphicyon* and *Ischyrocyon*, and concluded that both had a primarily or exclusively carnivorous diet and that their cranial morphology suggests that they did not kill their prey with a carefully directed bite, although they were obviously able to use their forelimbs to immobilise a prey animal, much like the extant big cats. Sorkin thinks that the morphology of amphicyonids is consistent with pursuing prey for a long distance (> 200 m) at a relatively slow speed (< 50 km/h), this matching well with the locomotor performances of mediportal ungulates.

According to Christiansen (2002), the best variables to use for predicting speed in fossil mammals are the radius/humerus and metatarsus/femur ratios. The brachial index is 0.84 in *A. major* (Table 2), higher than in *U. arctos* but lower than in *P. leo* and *C. lupus* (in the specimens observed) but in the range of the values given for the leopard and tiger by Christiansen (2002). The metatarsus/femur ratio is 0.20, i.e. lower than in extant felids and canids, but in the range of the values given for *Ursus*

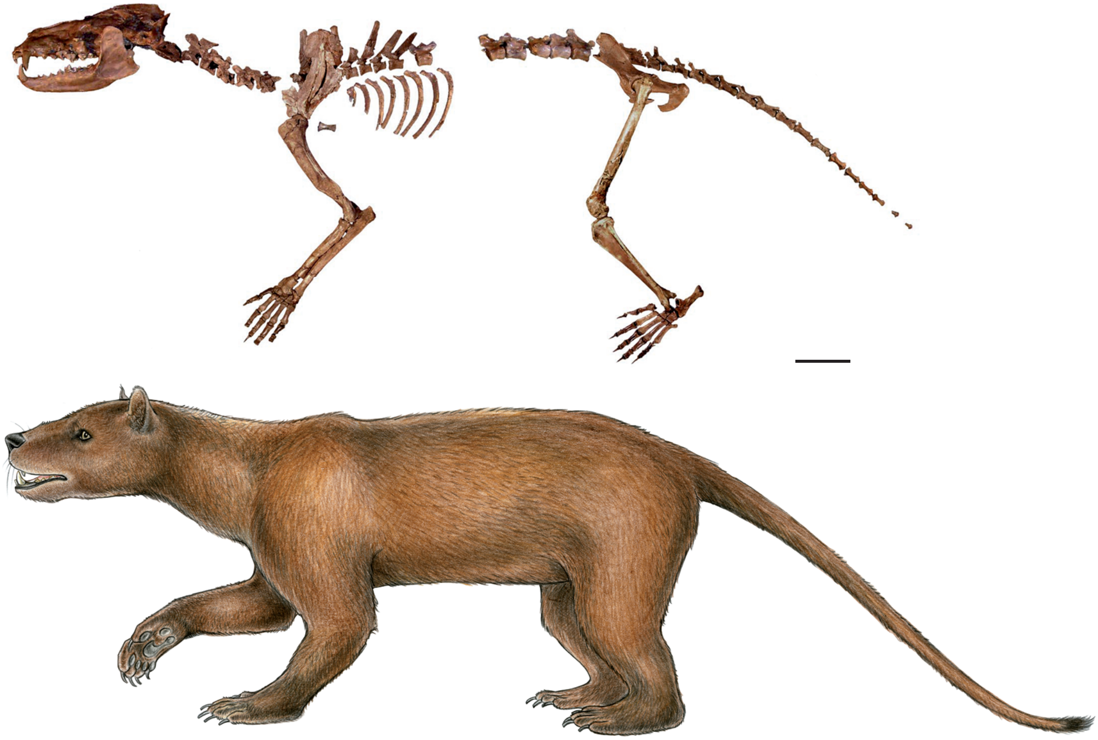

Fig. 14. — Skeletal remains and reconstitution of *Amphicyon major* Blainville, 1841 MNHN Sa844 from the Miocene (mid-Helvetian) of Sansan (Gers), France: the reconstruction does not aim at depicting one particular activity but at reflecting the conclusions reached in the text concerning the limbs and posture: powerful forelimbs, muscular and long thigh, tail long and stiff proximally, plantigrade feet; this specimen, supposedly a young female, weighed approximately 125 kg (in the range of extant female lions) and was 65 cm tall at shoulder height. Scale bar: 10 cm.

americanus by Christiansen (2002). Viranta (1996) proposed the living big cats (genus *Panthera*) but also the living brown bear, *Ursus arctos*, as models for the hunting behaviour of *Amphicyon*, considering that its hunting modes could have been: stalk and pounce, or laceration. The three North American species of *Amphicyon*, with powerful limbs, short autopods and short, divergent metapods with massive clawed feet, and heavily muscled jaws with a composite crushing/shearing dentition, are likely to have adopted ecological roles similar to the large living felids, stalking and ambushing prey from cover (Hunt 2003). Hunt (2002) also suggests a similar mode of life for *Ysengrinia americana*. The hindlimb morphology of *A. major* was obviously not optimised for running fast, in contrast to the ursids of the same age and locality, *Hemicyon* and *Plithocyon*, who were apparently built more lightly, with longer legs and especially longer metapods (except the relatively reduced lateral ones), implying longer stride lengths (Ginsburg 1961). The ursids of that time were then probably better runners than *Amphicyon* and especially than extant ursids. *Sansanosmilus* and *Pseudaelurus* were smaller; Ginsburg (1961) suggests that the postcranium of *Pseudaelurus* was morphologically quite similar to that of a living puma, and he compared *Sansanosmilus* to a jaguar: plantigrade and able to climb trees.

Although pursuit predation does not appear before the Plio-Pleistocene (Janis & Wilhelm 1993), it is not possible to conclude that until that epoch all the predators were necessarily ambush predators. Actually, a previous comparative study of two Miocene carnivorous metatherians showed a morphological diversification between contemporaneous predators (Argot 2004). Van Valkenburgh *et al.* (2003) also emphasized that some borophagines regularly ate preys larger than themselves and that many species hunted much of their preys, and did so in groups: "While limb morphology and skeletal proportions of most of all borophagines do not appear adapted for the kind of hunts observed today in the African wild dog *Lycaon pictus*, long-distance, high-speed pursuits over shorter distances would have been possible for borophagines" (p. 148). However, it is clear that the most specialised pursuit predators, the recent large canids, that lost all manual manipulation capacities, are poor ecological, morphological and behavioural analogues for large predatory fossils (Andersson 2003, 2004), especially amphicyonids.

CONCLUSIONS

The development of the lateral wings of the atlas and neural process of the axis of *Amphicyon*, suggesting a M. obliquus capitis caudalis (a muscle allowing rotations of the head) as developed as in an extant lion, is consistent with active predatory habits. The neural processes of the thoracolumbar vertebrae, much more similar to those of a lion or a wolf than to those of a bear are also consistent with active predatory habits. The caudal vertebrae are remarkable by their robustness. The tail of *Amphicyon* was long and powerful, muscular along at least its anterior half, and certainly more rigid at its base than in the wolf. Its weight was considerable, and thus the tail probably played a part in the equilibrium of the whole animal when running/jumping.

The morphology of the whole forelimb of *Amphicyon major* is very much like that of a bear. As in extant bears, an accessory fossa and a wide neck characterise the scapula of the fossil taxon. These two features as well as the broad spinati fossa suggest a heavy scapular musculature. In addition, abductors (deltopectoral muscles) and flexors (biceps + brachialis) were also powerfully developed. The ball-shaped humeral head, higher than both tubercles, indicates a mobile shoulder joint. The elbow joint is very similar to that of a bear, indicating an abducted humerus with usual flexed positions and a maximised humeroulnar stability in extensions. Flexion-extension did not occur in a strict parasagittal plane and extensions were stabilised by the posterior development of the lateral lip of the humeral trochlea and the posterior protrusion of the entepicondyle. In the wrist, the shape of the scapholunar, with confluent proximal radial and distal trapezial facets indicates a more plantigrade posture of the hand of *Amphicyon* than in extant felids, a position more similar to that of extant bears. The development of the lateral carpal bones, consistent with the lateral position of the radius, indicates a lateral loading in *Amphicyon*. According to the shape of the carpal facets, the mid-carpal joint is more stabilised medially than laterally, providing for a stabilised base for the pollex, that was probably slightly mobile relative to the other digits. Considering the palm of the hand, it appears that it was robust, short and with a powerful musculature both in *A. major* and *U. arctos*, but whereas in the bear the palm appears as a unit, the most internal digits of *Amphicyon* and especially the pollex seem to have been more mobile, and then more independent to the rest of the hand. Moreover, although the distal epiphyses of Mc I and Mc V are also asymmetrical in the bear, this asymmetry is more emphasised in *Amphicyon*, especially concerning Mc V, suggesting an increased potential grasping ability in the fossil taxon. The ungual phalanges of *Amphicyon* are shorter relative to the palm of the hand than in extant bears.

By contrast, the pelvic girdle and femur of *A. major* (as well as the lumbar area, playing a role in the propulsion) are more similar to that of an extant lion than to that of a brown bear. However, *A. major* shows a mix of features between those observed in the lion (general shape of the pelvis except for the ischiums, proximal position of the lesser trochanter, development of the rectus femoris tuberosity) and those observed in the bear (general morphology of the proximal part of the femur, although the femoral head of the bear is still more prominent proximally). *Amphicyon major* was certainly more

Fig. 15. — Artistic view of *Amphicyon major* Blainville, 1841 MNHN Sa844 in a plausible life pose.

active at hunting than are modern bears and able to perform short, powerful runs, although the range of abduction at hip joint, suggested by the proximally prominent femoral head and the lateral orientation of the descending ramus of the ischium indicate that a fully parasagittal course of the limb is not achieved in this species at that time. The general shape of the knee joint of *A. major* is nevertheless more similar to that of a felid than to that of an ursid, and its morphology suggests that the range of excursion of the leg relative to the thigh was certainly more parasagittal than that of the forearm relative to the arm. Moreover, the upper ankle joint, between the tibia and astragalus, is quite similar in a modern lion and *A. major*, also providing for efficient parasagittal flexion-extension of the foot relative to the leg, a feature consistent with the hypothesis that *A. major* was a more efficient runner than are modern bears. However, the tibia of *A. major* is still short in comparison to the femur (relatively shorter than in modern felids) and the metatarsals are also extremely short, as they are in bears, and in contrast to what is observed in modern fast runners. The distal tibio-fibular joint and calcaneoastragalar joints (general shape and orientation of the ectal facet, accessory facet between the ectal and the calcaneocuboid ones, medial protrusion of the sustentaculum) and mid-tarsal joints in *Amphicyon* are more similar to those of an extant plantigrade (modern bear) than to those of extant digitigrade taxa. The foot of *Amphicyon* was therefore certainly plantigrade and retained a functional, developed hallux providing for grasping capacities.

Acknowledgements

Special acknowledgements are due to Charlène Letenneur (École Estienne d'arts appliqués & MNHN, Paris) who realised the figures of this paper. Thanks are due to the two reviewers, Mauricio Antón and Stephen Wroe, as well as to Stéphane Peigné and Sally Reynolds for reading, commenting and improving the manuscript. Thanks also to Christine Lefèvre for providing access to the skeleton of extant specimens used.

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Submitted on 11 February 2008;
Accepted on 6 October 2008.

APPENDICES

Measurements of the material examined for the study. All measurements are in millimeters. Abbreviations: **e**, estimated measurements; **L**, left side; **R**, right side (left and right sides are indicated only when a single side was available; if not, the mean is given); **?**, measurement not available.

APPENDIX 1

Measurements of the scapula	***Amphicyon major*** **Sa844**	***Amphicyon major*** **Sa83**	***Ursus arctos*** **MNHN 1974-25**	***Panthera leo*** **MNHN 1954-2**	***Canis lupus*** **MNHN 2005-279**
Maximum length, parallel to the spine	218 R	?	176	218	178
Maximum width, perpendicular to the spine	166e R	?	182	150	120
Anteroposterior width of the neck	62 R	77 L	55	46	25
Anteroposterior length of the glenoid cavity	43 R	52 L	43	44	27
Dorsoventral height of the glenoid cavity	33 R	39e L	29	36.5	23.5

APPENDIX 2

Measurements of the humerus: **1**, humerus functional length, between articular surfaces; **2**, anteroposterior length of the humeral head; **3**, transverse width of the humeral head; **4**, maximum anteroposterior length of the proximal extremity; **5**, length of the deltopectoral crest; **6**, deltopectoral crest length expressed as a percentage of the humerus length; **7**, maximum transverse width of the distal extremity; **8**, transverse width of the distal articular surface in distal view; **9**, transverse width of the capitulum in anterior view; **10**, proximodistal height of the capitulum in anterior view; **11**, length of the lateral epicondylar ridge; **12**, lateral epicondylar ridge expressed as a percentage of the humerus length; **13**, distance between the medial lip of the trochlea and the apex of the medial epicondyle (T-E); **14**, T-E expressed as a percentage of the distal extremity width; **15**, mid-shaft anteroposterior diameter; **16**, mid-shaft transverse diameter.

	Amphicyon major							***Ursus arctos***	***Panthera leo***	***Canis lupus***
	Sa844	**Sa84**	**Sa86**	**Sa87**	**Sa88**	**Sa89**	**(no number)**	**MNHN 1974-25**	**MNHN 1954-2**	**MNHN 2005-279**
1	274 L	?	?	?	?	325 R	?	284	262	223
2	46 L	?	?	55 R	?	54 R	?	47	51	32
3	41 L	?	?	54 R	?	53 R	?	39	48	30
4	75 L	?	?	86e R	?	81 R	?	62	76	53
5	180 L	?	?	205e R	?	205 R	?	190	127	107
6	65% L	?	?	?	?	63% R	?	67%	48%	48%
7	79	110 L	98 L	?	92 L	80e R	91 R	80	68	39
8	54	72 L	67 L	?	67 L	66 R	65 R	60	49	29
9	29	38 L	34 L	?	35 L	33 R	36 R	29	23	16
10	23	32 L	28 L	?	28 L	28.5 R	28 R	20	24	18
11	100	120 L	107 L	?	100 L	110 R	?	90	90	55
12	36%	?	?	?	?	34%	?	31%	34%	24%
13	28	40 L	39 L	?	35 L	?	31 R	21	18	7.5
14	35%	36%	39%	?	38%	?	34%	26%	26%	19%
15	39 L	?	?	?	?	45 R	?	25	31	22
16	24 L	?	?	?	?	31 R	?	24.5	23	15

APPENDIX 3

Measurements of the ulna: **1**, total length; **2**, distance between the apex of the olecranon and the centre of rotation of the elbow joint (DO); **3**, DO expressed as a percentage of the ulna length; **4**, distance between the insertion of the Mm. biceps/brachialis and the centre of rotation of the elbow joint (DFU); **5**, DFU expressed as a percentage of the ulna length; **6**, maximum transverse width of the apex of the olecranon; **7**, anteroposterior depth of the apex of the olecranon; **8**, proximodistal length of the trochlear notch in medial view; **9**, anteroposterior depth of the ulnar diaphysis at the level of the coronoid process; **10**, mid-shaft transverse diameter; **11**, mid-shaft anteroposterior diameter.

	Amphicyon major						***Ursus arctos* MNHN 1974-25**	***Panthera leo* MNHN 1954-2**	***Canis lupus* MNHN 2005-279**
	Sa844	**Sa52**	**Sa101**	**Sa102**	**Sa103**	**Sa105**			
1	299.5	?	347 L	340e R	?	?	279.5	306	265
2	54.5	62	63 L	62e R	63 L	70 L	46	58	39
3	18%	?	18%	18%	?	?	16%	19%	14.5%
4	36	40	43 L	40 R	43 L	48 L	27	34	19
5	12%	?	12%	11.5%	?	?	9.5%	11%	7%
6	27.5	31	38 L	36 R	33 L	38 L	32	22	13.5
7	35.5	43	42 L	41 R	41 L	49 L	32	38	28
8	30	33	36 L	?	33 L	35.5 L	24	30	18
9	51.5	63	61 L	?	58 L	70 L	46	46.5	33
10	19	19	21 L	23 R	?	?	17	16	10
11	28	35	43 L	35 R	?	?	23	23	11.5

APPENDIX 4

Measurements of the radius: **1**, functional length; **2**, maximum diameter of the head; **3**, minimum diameter of the head; **4**, compression ratio of radial head (min. diameter/max. diameter × 100); **5**, mid-shaft anteroposterior diameter; **6**, mid-shaft transverse diameter; **7**, anteroposterior length of the distal extremity; **8**, transverse width of the distal extremity.

	Amphicyon major						***Ursus arctos* MNHN 1974-25**	***Panthera leo* MNHN 1954-2**	***Canis lupus* MNHN 2005-279**
	Sa844	**Sa52**	**Sa94**	**Sa95**	**Sa96**	**Sa98**			
1	247	256 L	273 R	265 R	263 L	?	224	245	221
2	35	43	47 R	40 R	40 L	42 R	35.5	32	20
3	26	32	33 R	30 R	31 L	32.5 R	27.5	24	15
4	74%	74%	70%	75%	77%	77%	77%	75%	75%
5	16.5	19 L	22 R	19 R	19 L	?	12	15	10
6	23	29 L	31 R	27 R	27 L	?	19	22	18
7	33.5	35.5 L	43 R	37 R	38 L	?	30	32	17
8	49	55.5 L	64 R	56 R	54 L	?	48	48	30

APPENDIX 5

Measurements of the metapods	***Amphicyon major* Sa844**	***Ursus arctos* MNHN 1974-25**	***Panthera leo* MNHN 1954-2**	***Canis lupus* MNHN 2005-279**
Mc I length	41.3 R	42	35	22
Mt I length	42.5 R	41	–	–
Mc II length	60.4	54.5	92.5	72
Mt II length	59 R	49	107	99
Mc III length	68	57	106	87
Mt III length	65.5 R	54.5	123	111
Mc IV length	68.3 R	60.5	105	85
Mt IV length	71 R	63	122	112
Mc V length	59 R	59	84.5	66.5
Mt V length	65 R	60.5	106	95

APPENDIX 6

Measurements of the innominate	***Amphicyon major* Sa844**	***Amphicyon major* Sa145**	***Ursus arctos* MNHN 1974-25**	***Panthera leo* MNHN 1954-2**	***Canis lupus* MNHN 2005-279**
Total anteroposterior length (anterior tip broken)	260e L	?	258	261	208
Length of the ilium, between the apex and the centre of the acetabulum	143e L	180e L	162	151	116
Ilium length expressed as a percentage of pelvic length	55% L	?	62.5%	58%	55.5%
Maximum dorsoventral breadth of iliac blade	55.5 L	60 L	81	53	36
Length of the origin of the rectus femoris	32.7 L	36 L	17	27	14
Length of the ischium, between the apex and centre of the acetabulum	117 L	?	96	110	92
Ischium length expressed as a percentage of pelvic length	45% L	?	37.5%	42%	44.5%
Anteroposterior diameter of the acetabulum	39.7 L	47e L	42	38	25
Dorsoventral diameter of the acetabulum	41 L	47 L	40	38	25

APPENDIX 7

Measurements of the femur	***Amphicyon major***			***Ursus arctos* MNHN 1974-25**	***Panthera leo* MNHN 1954-2**	***Canis lupus* MNHN 2005-279**
	Sa844	**Sa147**	**Sa151**			
Functional length, between articular surfaces	332 R	375 R	?	325	303	256
Anteroposterior depth of the head in medial view	35	41 R	?	35.5	34	24
Proximodistal height of the head in medial view	34	40 R	?	35	33	23
Distance between the apex of the greater trochanter and the fovea capitis	63	65 R	?	64	63	41
Distance between the lesser trochanter and the fovea capitis	50	55 R	?	60	33	25
Mid-shaft anteroposterior diameter	26 R	29 R	?	21	24	17
Mid-shaft transverse diameter	29 R	33 R	?	26.5	25	17
Compression ratio of femoral shaft (min. diameter/max. diameter × 100)	89.5%	88%	?	79%	96%	100%
Width of the lateral condyle in posterior view	24	25 R	30 R	20	23	17
Height of the lateral condyle in posterior view	37	38 R	38 R	29	35	27
Width of the medial condyle in posterior view	22.5	26 R	28 R	21	22	15
Height of the medial condyle in posterior view	36	40 R	43 R	31	35	27
Width of the distal epiphysis in distal view	63	71 R	75 R	57	61	46
Height of the distal epiphysis in distal view	59.5	70 R	74 R	54	61	46

APPENDIX 8

Measurements of the tibia	***Amphicyon major***			***Ursus arctos*** **MNHN 1974-25**	***Panthera leo*** **MNHN 1954-2**	***Canis lupus*** **MNHN 2005-279**
	Sa844	**Sa52**	**Sa155**			
Functional length	262.4	?	298 L	220	261	257
Maximum transverse width of the proximal epiphysis	68	71 R	82 L	65	65	48
Maximum anteroposterior length of the proximal epiphysis	68	73 R	83 L	55	71	64
Mid-shaft anteroposterior diameter	28	30 R	36 L	23	26	20
Mid-shaft transverse diameter	23	26 R	28 L	16	23	18
Transverse width of the distal epiphysis	44	48 R	56e L	45	52	33
Anteroposterior length of the distal epiphysis	40	38e R	47 L	26	35	22

APPENDIX 9

Measurements of the astragalus	***Amphicyon major***								***Ursus arctos*** **MNHN 1974-25**	***Panthera leo*** **MNHN 1954-2**	***Canis lupus*** **MNHN 2005-279**
	Sa52	**Sa159**	**Sa162**	**Sa164**	**Sa166**	**Sa168**	**Sa171**	**Sa172**			
Maximum anteroposterior length	49 R	57.4 L	56.5 R	51.5 R	53 L	49.5 L	57 L	48 R	40	47	35
Maximum transverse width	50 R	57 L	56.5 R	51 R	50 L	46e L	54 L	48 R	41	45	30
Length of the astragalotibial facet (proximal view)	36 R	43 L	42 R	39 R	37 L	38 L	43 L	34 R	30	34	24
Width of the astragalotibial facet (proximal view)	29 R	34 L	34 R	30 R	27 L	30 L	35 L	27 R	27	26	20
Height of the astragalonavicular facet (anterior view)	18 R	19 L	20 R	18 R	17 L	?	20 L	17 R	14	19	13
Width of the astragalonavicular facet (anterior view)	27 R	33 L	31 R	30 R	30 L	?	31 L	26 R	24	23	19

APPENDIX 10

	Amphicyon major								***Ursus arctos***	***Panthera leo***	***Canis lupus***
Measurements of the calcaneum	**Sa844**	**Sa52**	**Sa160**	**Sa161**	**Sa165**	**Sa167**	**Sa169**	**Sa175**	**MNHN 1974-25**	**MNHN 1954-2**	**MNHN 2005-279**
Total length	83	92 L	97 R	?	92 L	89 L	87 R	62 L	68	99	76
Length of the tuber calcanei (until the posterior end of ectal facet)	33	41 L	45 R	?	41 L	39 L	40 R	24 L	31	47	39
Proximodistal length of the ectal facet	25	31 L	33 R	30 L	30 L	31 L	30 R	22.5 L	22	27	16
Transverse width of the ectal facet	14	16 L	17 R	16 L	16 L	16 L	16 R	12 L	11	14	7
Proximodistal length of the sustentacular facet	15	?	17 R	16 L	18 L	16 L	?	12 L	13	13	11
Transverse width of the sustentacular facet	13	?	17 R	17 L	18 L	17 L	?	10 L	16	14	10
Maximum width at the level of calcaneoastragalar facets	34	?	47 R	47 L	40 L	40 L	?	29 L	41	37	23
Height of calcaneocuboid facet	20	20e L	25 R	21.5 L	22.5 L	22 L	23 R	14e L	13.5	21	14
Transverse width of calcaneocuboid facet	22	25 L	26 R	26.5 L	25.5 L	24 L	23e R	18e L	20	22	14