ORIGINAL PAPER

# Comparative Anatomy of the Shoulder Region in the Late Miocene Amphicyonid *Magericyon anceps* (Carnivora): Functional and Paleoecological Inferences

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**Abstract** We describe and discuss several aspects of the functional anatomy of the shoulder of the Miocene amphicyonid *Magericyon anceps*, focusing on the scapula and proximal half of the humerus. This species, only known from the late Miocene (Vallesian, MN 10) site of Batallones-1 (Madrid, Spain), is the last amphicyonid known in the fossil record of Western Europe. *Magericyon anceps* combines a more hypercarnivorous dentition than previous amphicyonids (including relatively more flattened canines) with primitive features on its shoulder region: its scapulo-humeral region shows a reduced caudoventral projection of the acromion, the postscapular fossa, and the teres major process, suggesting some differentiation from the two morphotypes exhibited by other derived amphicyonids, and showing similarities with primitive, generalized, medium-sized species of this family. This unique combination of a derived dentition and a relatively generalized shoulder region points towards *M. anceps* being a different ecological morphotype from that showed by other amphicyonids such as the larger, bear-like amphicyonines from the European middle Miocene and the markedly cursorial North American temnocyonines and daphoenines.

**Keywords** Anatomy · Amphicyonidae · Carnivora · Miocene · Shoulder · Locomotion · *Magericyon anceps*

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## Introduction

The Amphicyonidae is a very diverse and geographically widespread family of Arctoid carnivorans known from the late Eocene to the late Miocene of North America and Eurasia, which attained its greatest diversification during the Oligocene and early-middle Miocene. Its diversity was reduced in the late Miocene, with only a few taxa surviving in the Vallesian or earliest Turolian, around 8 Ma (Hunt 1998). The dentition of this group is relatively homogeneous, and a diet varying from omnivorous to hyper-carnivorous has been inferred depending on the species (Viranta 1996; Hunt 1998; Peigné et al. 2008). On the contrary, the overall morphology of the postcranial skeleton of amphicyonids shows a mosaic of features not seen together in any other group of extant carnivorans, although some of these traits are observed separately in ursids, canids, or even in felids (Olsen 1960; Ginsburg 1961; Bergounioux and Crouzel 1973; Viranta 1996; Hunt 1998, 2009; Argot 2010). In general, amphicyonids show a more generalized postcranial skeleton than that of extant large carnivorans, although some taxa (e.g., *Borocyon*) have features indicative of a cursorial specialization, similar to that of extant canids, and they were probably pursuit predators (Hunt 1998, 2009, 2011). Most other amphicyonids show less specialization for running, and they probably possessed an ambulatory locomotion with certain climbing abilities, resembling in some ways modern ursids (Hunt 1998, 2001, 2002, 2003; Sorkin 2006; Argot 2010).

Four subfamilies are traditionally recognized within Amphicyonidae: Amphicyoninae, Haplocyoninae, Daphoeninae, and Temnocyoninae, the two later restricted to North America, whereas Haplocyoninae is only present in the European faunas and Amphicyoninae is found in Eurasia, North America, and Africa (Hunt 1998). This last subfamily includes the late Miocene *Magericyon anceps,* the last amphicyonid of the Western European record. The most common genera of

European amphicyonines (*Amphicyon*, *Cynelos*, *Ysengrinia*) appear abruptly at various moments in the Miocene of North America and these appearances are interpreted as migration events (Hunt 1998, 2002, 2003). Thus, those North American middle and upper Miocene amphicyonids would derive from immigrant Eurasian species (Hunt 1998). The estimated body size of amphicyonids ranges from a few kilograms for the smallest species up to 550 kg for *Amphicyon ingens* (Viranta 1996; Hunt 2001, 2003; Sorkin 2006; Figueirido et al. 2011). Given this wide size range, Figueirido et al. (2011) proposed the existence of three different size categories within Amphicyonidae that these authors relate to different ecomorphs of extant carnivorans: small daphoenines would fit within the ecomorph of living foxes, jackals, and coyotes; mid-sized daphoenines would be similar to pack-hunting canids (*Canis lupus* or *Lycaon pictus*), and the largest amphicyonines would be the ecological equivalent to extant large bears.

The Cerro de los Batallones is a low hill located 30 km south of the city of Madrid (Spain) that has been exploited as an opencast mine of sepiolite since 1974. In July 1991, during mining works, the mechanical diggers discovered a rich accumulation of fossils of Carnivora within a lens of greenish marls intercalated between the levels of sepiolite. The site was named Batallones-1 and it was the first of a series of nine fossil sites discovered in the hill over the following years. The sites were formed during the late Miocene due to a geological process of piping, which consisted in the erosion of the sepiolite levels by water flowing along fractures, causing collapses and the development of a karst-like ('pseudokarst') topography (Pozo et al. 2004; Calvo et al. 2013). This process finally led to the formation of irregular cavities within the sepiolite levels, up to 15 m deep, later filled with greenish clay. These cavities acted as a natural trap for many animals inhabiting the area, probably due to the fact that when the sepiolite is wet, its surface becomes slippery, which would make escape from the trap almost impossible. Concerning Batallones-1, a remarkable 98 % of all the macro-mammal bones recovered from the site corresponds to members of the order Carnivora, which were probably trapped while attempting to scavenge (Antón and Morales 2000). This carnivoran assemblage includes the ailurid *Simocyon batalleri*, two species of mustelids (*Sabadellictis* sp. and *Proputorius* sp.), the primitive hyaenid *Protictitherium crassum*, the machairodont felids *Machairodus aphanistus* and *Promegantereon ogygia*, two species of felines, *Styriofelis vallesiensis* and an undetermined, larger species, and the amphicyonid *Magericyon anceps*. This impressive sample has allowed several systematic, paleoecological and functional studies on the carnivoran fauna (Morales et al. 2000, 2004; Antón and Morales 2000; Antón et al. 2004; Peigné et al. 2005, 2008; Salesa et al. 2005, 2006a, b, 2008, 2010a, b, 2012). The fossils of *M. anceps* from Batallones-1 represent one of the best samples of Amphicyonidae in Eurasia, with at least 12 individuals represented, including juveniles, young adults, and adults, in a fair state of preservation (Peigné et al. 2008).

The study of the cranial remains of *M. anceps* revealed a set of hypercarnivorous features that pointed towards a more specialized hunting technique than that of other amphicyonids (Peigné et al. 2008), with moderately flattened upper canines with weakly serrated margins, and absence or strong reduction of some teeth; these features suggest a reduced importance of the crushing function in the dentition, and a greater proportion of meat in its diet compared with other amphicyonines (Peigné et al. 2008), placing the genus *Magericyon* in a separate clade from other, less derived amphicyonids (Fig. 1). Although the derived dental morphology of *M. anceps* suggests that it was a hypercarnivorous predator, its postcranial skeleton has remained unstudied, and the present work is the first functional analysis on the locomotor adaptations of this species. Among large carnivorans, hypercarnivorous dentitions are in some cases associated with a cursorial or sub-cursorial postcranial skeleton, as is the case in some canids, hyaenids, or felids, which use sprint or sustained pursuit to catch their prey. In other cases, hypercarnivorous dentitions occur in taxa (such as some large extant felids and many extinct saber-toothed carnivorans) that have robust postcranial skeletons more fitting with patient stalking and subduing prey through muscular force (Taylor 1989; Andersson and Werdelin 2003; Argot 2004; Salesa et al. 2010a; Meachen-Samuels 2012). Although only a detailed study of the whole skeleton of
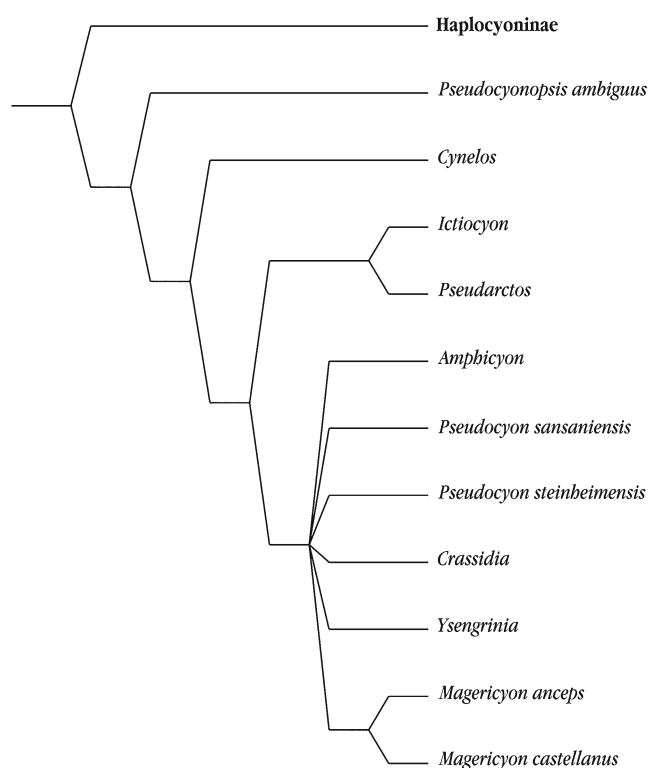


**Fig. 1** Phylogeny of *Magericyon* after Peigné et al. (2008)

*M. anceps* will reveal if this amphicyonid fitted any or none of these models, the present work provides the first detailed description of the shoulder anatomy of this species, the last of all the Western European fossil record. Although the shoulder could be seen as a small part of the whole appendicular skeleton, its study is imperative when analyzing the locomotion and behavior of amphicyonids due to its peculiar morphology, with a more or less developed postscapular fossa and teres major process, two structures whose functional significance remains an open question.

## Material and Methods

### Material

The fossils of *Magericyon anceps* analyzed in this study belong to the extensive sample from the late Miocene locality of Batallones-1 (Late Vallesian, MN 10, Madrid, Spain), housed in the paleontological collections of the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). We focus our study on the shoulder because this region plays an important role in the biomechanics of the forelimb, and also due to the presence of a postscapular fossa, a structure observed in other carnivorans, but with no clear functional explanation. The list of material is as follows: scapulae: six specimens: four right, B-713 (2), B-5255, B-5255 (1), and B-2703 (1), and two left, B-2215 and B-1903 (1); humeri: five specimens: three right, B-1440, B-1506-1 and BAT-1′05 E4-59, and two left, B-565 (1) and BAT-1′07 F3-35. Comparisons with extant carnivorans were made using the collections of the Museo Anatómico de la Universidad de Valladolid (Spain) (labeled with the acronym MAV) and Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain) (labeled with the acronym MNCN), which provided complete skeletons of the ursids *Ursus americanus* (MAV-259), *Ursus arctos* (MNCN-16821), *Tremarctos ornatus* (MAV-1661), and *Ailuropoda melanoleuca* (MNCN-12831), the mustelids *Gulo gulo* (MAV-469), *Aonyx cinerus* (MAV-2909, MAV-4616 and MAV-6038), *Lutra lutra* (MAV-6066), and *Lontra canadensis* (MAV-3784), the feline *Panthera leo* (MAV-2313, MAV-3046 and MAV-276), and the canid *Canis lupus* (MNCN-16118 and MNCN-16150). We performed dissections of two adults specimens of *T. ornatus*, one male and one female, at the departamento de Anatomía, Universidad de Valladolid (Spain) in order to complete the observations made by previous authors on the anatomy of some of the discussed muscles. We choose this species for dissection because it shows a relatively poorly developed teres major process within Ursidae, similar to that of *M. anceps*.

We compared the studied fossils with specimens belonging to three of the four subfamilies included in the Family Amphicyonidae: *Cynelos lemanensis*, *Ysengrinia americana*, and some species of the genus *Amphicyon* (Subfamily Amphicyoninae); *Daphoenodon (Daphoenodon) superbus* and *Daphoenodon (Borocyon) niobrarensis* (Subfamily Daphoeninae); and *Delotrochanter oryktes* (Subfamily Temnocyoninae). We did not include members of the subfamily Haplocyoninae in our comparisons due to the scarcity of available postcranial material. The material of *Cynelos lemanensis* from the locality of Saint Gerand-le-Puy (France) and *Amphicyon major* from the locality of Sansan was studied in the collections of the Museum national d'Histoire naturelle (Paris, France) and that of *Amphicyon ingens* in the collections of the American Museum of Natural History (New York, USA); for the two former species we also used published data (Ginsburg 1961, 1977; Bergounioux and Crouzel 1973; Argot 2010). Comparisons with other fossil Amphicyonidae (such as *Amphicyon longiramus*, *Amphicyon galushai*, *Daphoenodon superbus*, *Delotrochanter oryktes*, *Borocyon niobrarensis*, or *Ysengrinia americana*) were made using published data (Peterson 1910; Olsen 1960; Hunt 2002, 2003, 2009, 2011). Although the genera *Daphoenodon* and *Borocyon* were considered by Hunt (2009) as subgenera within the genus *Daphoenodon*, we have preferred to follow the traditional classification, and thus they are cited throughout the text as different genera.

### Methods

The anatomical descriptions follow the terminology used by Barone (2010), Evans (1993), and the Nomina Anatomica Veterinaria (2005). Here we describe and compare the principal structures of both scapula and humerus of *M. anceps* and other species of arctoid Carnivora, focusing on those features with remarkable relevance for the biomechanics of the shoulder. Thus, some muscles are only described, but not included in the discussion. The aim of our study is the comparative analysis of the shoulder biomechanics in *M. anceps* and other amphicyonids, but in the context of other large carnivorans. In consequence, we use for comparison several groups of carnivorans that are not closely related to Amphicyonidae.

In several parts of the manuscript we use the term "cursorial," following the definition of Hunt (2009: 72): "to refer to carnivorans with morphological specialization of their postcranial skeleton favoring parasagital alignment of the limbs and demonstrated ability for fore-aft movement of the limb segments and feet, indicating increased stride length and locomotor efficiency. There is the tacit assumption that physiological endurance and an economy of gait in some form are the likely accompaniments to this morphology."

## Body Mass Estimation in *Magericyon anceps*

We estimated the body mass of *M. anceps* using the formula of Figueirido et al. (2011) for Amphicyonidae, based on the

medio-lateral diameter of the femur at the middle of the diaphysis, a measure that shows a better correlation to body mass than other measurements taken on both long bones and skull (Figueirido et al. 2011). We had three complete adult femora of *M. anceps* (BAT-1′06 E3-91, BAT-1′06 D3-41, and B-5255), which provided a body mass estimation between 172–199 kg. We also obtained an estimated body mass of 152 kg from a right femur (B-2651) belonging to a sub-adult individual (the distal epiphysis is not totally fused and it is slightly displaced from the diaphysis). Besides this, we also calculated the body mass of *M. anceps* using the regression of Van Valkenburgh (1990) for Carnivora based on the total length of the skull, obtaining a range of 172–205 kg, very similar to the estimation provided by the femoral measurement. Thus, the variability in the estimated body mass of *M. anceps* is relatively low, and would imply that this species exhibited a low index of sexual dimorphism, which is not typical within Amphicyonidae (Ginsburg 1961; Viranta 1996; Hunt 1998, 2002, 2003, 2009; Peigné and Heizmann 2003). Nevertheless, the available sample of *M. anceps* from Batallones-1 (with a minimum number of 12 individuals) is dominated by juveniles and young adults (Peigné et al. 2008), and it could correspond to a biased sample lacking the larger male individuals. This is also supported by the fact that, although all the bones of *M. anceps* are represented at Batallones-1 (ribs, tarsals, carpals, even tibial sesamoids) not a single baculum has been found, suggesting the absence of males.

Other authors have estimated the body mass of most of the amphicyonids included in the present paper. Most of them are amphicyonines, such as *Amphicyon major,* with an estimated body mass of 140–183 kg (Argot 2010; Figueirido et al. 2011); the gigantic *Amphicyon ingens*: 547–706 kg (Sorkin 2006; Figueirido et al. 2011); *Ysengrinia americana*: 173–231 kg (Figueirido et al. 2011); *Amphicyon galushai*: 191–204 kg (Figueirido et al. 2011); and *Cynelos lemanensis*: 46–91 kg (Peigné and Heizmann 2003). There is no direct estimation of the body mass of the temnocyonines and daphoenines compared in this work: *Delotrochanter oryktes*, *Daphoenodon superbus,* and *Borocyon niobrarensis*. However, *De. oryktes* is considered as one of the largest Temnocyoninae, for which a body mass of 65–80 kg has been estimated (Hunt 2011). Regarding the daphoenines included in our study, a relatively good approach can be made considering the available data on the body mass of closely related forms, such as *B. robustum* (100–150 kg) (Hunt 2009) and *B. neomexicanum* (135 kg) (Figueirido et al. 2011). Taking into account that *B. niobrarensis* has an intermediate size between both *B. robustum* and *B. neomexicanum* (Hunt 2009), it probably did not weigh more than 150 kg. On the other hand, *Da. superbus* was smaller than all these taxa (Hunt 2009), and thus this species probably had a maximum weight of around 100 kg.

In summary, the estimated body mass of *M. anceps* places this species within the third size group of Figueirido et al. (2011), which includes the largest known amphicyonines (*Amphicyon*, *Ischyrocyon*, *Ysengrinia,* and *Pseudocyon*), all weighing more than 150 kg.

## Anatomical Descriptions

### Scapula

The scapula of *M. anceps* has a quadrangular overall shape (Fig. 2), with a piriform, medio-laterally flattened, and slightly concave glenoid cavity. Dorsal to this, on the cranial border of the scapula, there is a well-developed supraglenoid tubercle for the attachment of the muscle biceps brachii. The coracoid process (attachment area for the muscle coracobrachialis), located on the dorsomedial margin of the supraglenoid tubercle, is developed as a very small bulge, lacking any projection, very similar to that of some ursids such as *U. americanus* or *T. ornatus*. The infraglenoid tubercle is developed as a small tuberosity, more or less similar to that seen in ursids. On this tubercle both the muscles teres minor and the long branch of the triceps brachii are attached, this latter extending its attachment area onto the caudal border of the infraspinous fossa, which is slightly caudally protruded (Davis 1949; Barone 2010). The scapular spine of *M. anceps* is well developed, and divides the lateral surface of the scapula into two similarly sized infraspinous and supraspinous fossae (attachment areas for the muscles infraspinatus and supraspinatus, respectively), the former having a slightly protruding and sinuous caudal border. The spine extends from near the dorsal border of the scapula, to the level of the glenoid cavity; it is not different from that of ursids, canids, or large felids. The spine has a rough surface for the attachment of the muscles trapezius and deltoideus pars scapularis. The cranioventral part of the spine has a broad and rough acromion (where the muscle deltoideus pars acromialis is attached) with a very small suprahamatus process, only developed as a small rugosity where the muscle omotransversarius attaches. The acromion is cranioventrally projected and strongly cranially curved over the border of the glenoid cavity, but it does not surpass the ventral border of the glenoid cavity (Fig. 2). This morphology is similar to that of ursids, although in this group the acromion widely surpasses the ventral level of the glenoid cavity (Davis 1949) (Fig. 3f). In some amphicyonids such as *Amphicyon longiramus* and *A. major* the acromion surpasses, to a greater or lesser extent, the level of the glenoid cavity (Olsen 1960; Argot 2010) (Fig. 3). In other species, such as the daphoenine *Da. superbus,* the acromion development resembles the morphology observed in *M. anceps* (Peterson 1910). The North American large amphicyonid *A. ingens* shows an acromion

that does not surpass that level of the glenoid cavity, although it is straighter than that of *M. anceps*, without cranial curvature.

The dorsal border of the scapula shows a rough surface for the attachment of the muscle rhomboideus; the shape and curvature of this border is similar to that of *Ursus arctos* and *U. americanus*, and different to that of *Ailuropoda melanoleuca,* which has a more craniocaudally elongated dorsal border (Davis 1964). On the craniodorsal angle of the medial surface of the scapula there is a rough and sub-rectangular facies serrata, where the muscle serratus ventralis would attach (Davis 1949; Barone 2010). The neck of the scapula of *M. anceps* is not so wide as that of ursids (Figs. 2 and 3f), although among this group, the ursines *U. arctos* and *U. americanus* show wider scapular necks than other bears such as *T. ornatus* or *A. melanoleuca*. Among the compared amphicyonids, *A. major* shows the relatively widest scapular neck, similar to that of extant ursids (Argot 2010).

Apart from the typical small foramina seen close to the ventral surface of the scapular spine of several species of carnivorans, the scapula of *M. anceps* also shows a much larger nutrient foramen on the ventral part of the infraspinous

fossa, just on the base of the acromion (Fig. 2); among the Carnivora, this character is only observed in other amphicyonids such as *A. longiramus*, *A. major*, and *Ysengrinia americana* (Olsen 1960; Hunt 2002; Argot 2010). The presence of this foramen in *Y. americana* was interpreted by Hunt (2002) as being the passage for both the suprascapular artery and nerve, which in other carnivorans lacking this foramen, such as felids or ursids, lie ventrally to the scapular spine (Hunt 2002). We agree with this interpretation, confirmed by means of a CT scan of the scapula of *M. anceps* that there is a canal going through the base of the acromion (in cranio-caudal direction) connected with another foramen in the supraspinous fossa (Fig. 4).

Nevertheless, one of the most interesting features of the scapula of *M. anceps* is the presence of postscapular fossa and teres major process (Fig. 2), two structures that are also developed in ursids and other amphicyonids. The postscapular fossa of *M. anceps* is developed as an excavation along the caudal border of the scapula, extending from the caudomedial margin, next to the glenoid fossa, to the lateral surface of the teres major process, on the caudal vertex. It is separated from the infraspinous fossa by the caudal border of the latter. This caudal border is caudally expanded along its ventral half, whereas the dorsal half shows a slight ridge that finishes before it reaches the dorsal border of the scapula. Given its similarity with that of ursids, we can assume that the postscapular fossa of amphicyonids was also completely occupied by the muscle subscapularis minor, as it has been described in bears (Davis 1949). In addition, the teres major process of *M. anceps,* as well as that of ursids and other amphicyonids, is developed as a thin bone expansion of the caudal angle of the scapula (Fig. 2a), with a smooth surface lacking any scar for the attachment of the muscle teres major, and separated from the infraspinous fossa by the caudal border of the scapula. It should be noted that, despite its name, the teres major process of ursids is not the attachment area for the muscle teres major, as this muscle exclusively attaches on a rough surface on the caudal margin of the process (Davis 1949, 1964; personal observation). In fact, most of the surface of the teres major process is occupied by the prolongation of the attachment area of the muscle subscapularis minor, as a continuation of the caudal excavation of the postscapular fossa (Fig. 2c). Given the similarities in morphology between ursids and amphicyonids, a similar muscular pattern can be inferred for the second group.

Within Ursidae, both the postscapular fossa and the teres major process show some minor differences, with *Ursus* and *Melursus* having the relatively largest postscapular fossae (Davis 1949), mainly due to the large size of the teres major process, whereas they are reduced in *Tremarctos* and *Ailuropoda*. The differences in the development of these two structures could seem related to body size, although this is not so clear when considering the maximum body mass of the compared species (*U. arctos*, 550 kg; *U. americanus*, 225 kg;
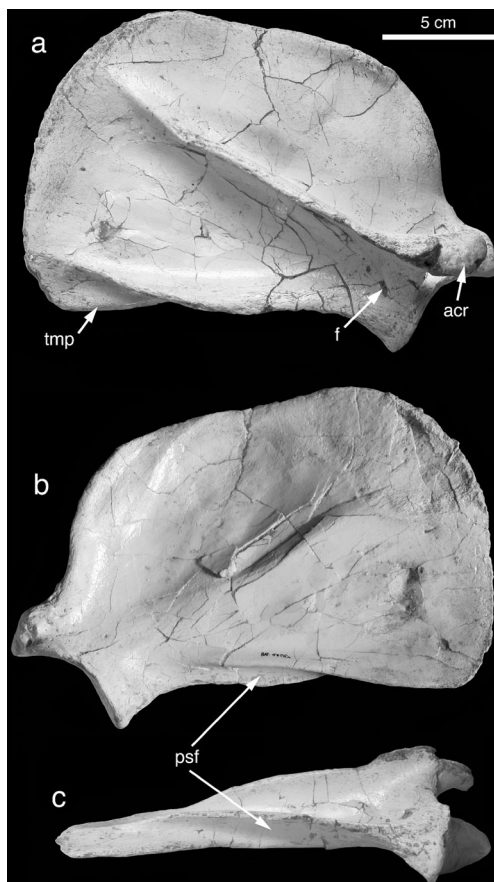


**Fig. 2** Right scapula (B-5255a) of *Magericyon anceps* from Batallones-1 in lateral (**a**), medial (**b**), and caudal (**c**) views, showing the development of the acromion (acr), the teres major process (tmp), the foramen of the base of the acromion (f), and the postscapular fossa (psf)

**Fig. 3** Comparison between right scapulae in lateral view of *Magericyon anceps* from Batallones-1, other Amphicyonidae, and extant Felidae and Ursidae (shown at the same size; scale bar represents 5 cm). *Daphoenodon superbus* (taken from Peterson 1910) (**a**), *Borocyon niobrarensis,* ACM-3452 (taken from Hunt 2009) (**b**), *Magericyon anceps* from Batallones-1 (**c**), *Amphicyon major* from Sansan (France) (**d**), *Panthera leo* (**e**), and *Ursus arctos* (**f**)
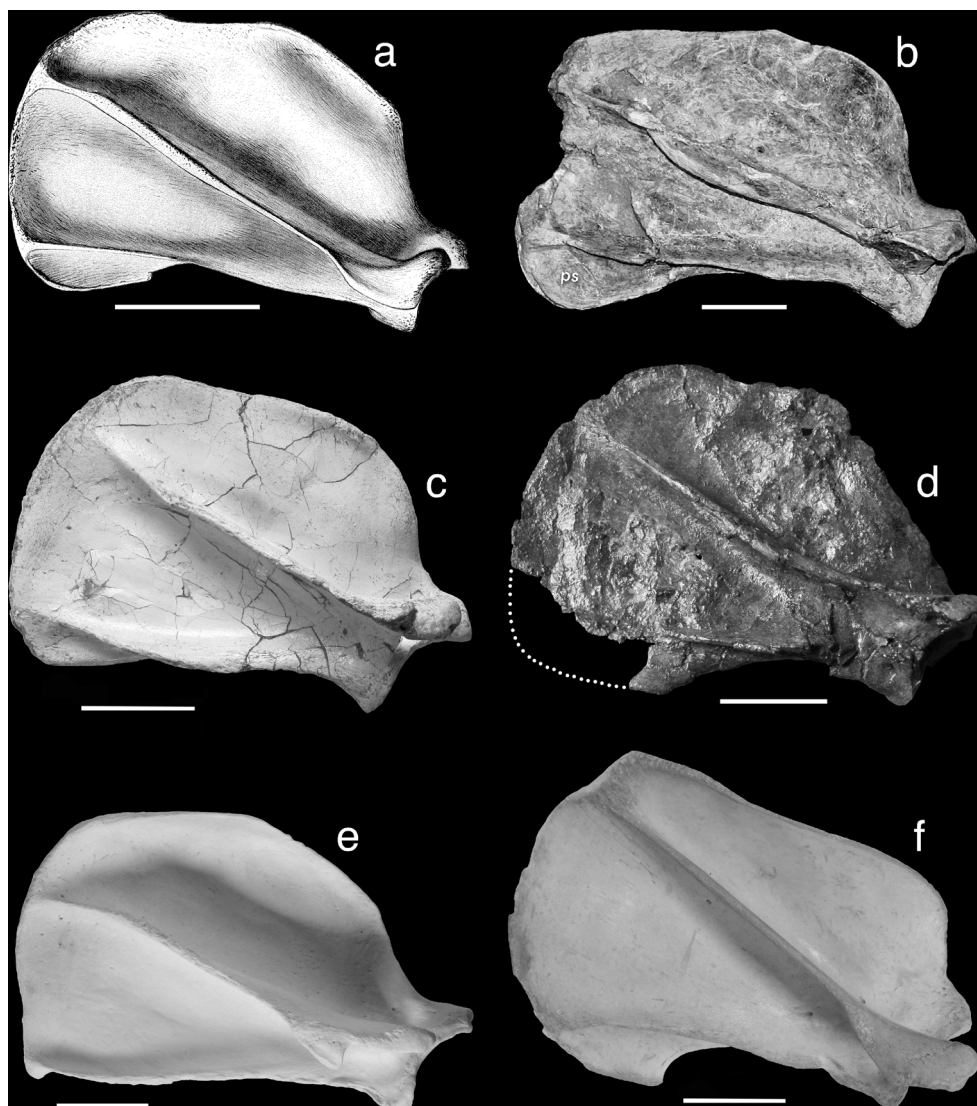
*T. ornatus*, 175 kg; *M. ursinus*, 145 kg; and *A. melanoleuca*, 125 kg) (Garshelis 2009). For example, in spite of the remarkable difference in body size between *U. arctos* and



**Fig. 4** 3D reconstruction of the ventrolateral region of a right scapula (B-5255a) of *Magericyon anceps* from Batallones-1, showing (white arrow) the passage for the suprascapular artery and nerve

*U. americanus*, their postscapular fossae show very similar proportions. On the other hand, although *T. ornatus* is larger than *M. ursinus,* this latter species has a more developed postscapular fossa than the former (Davis 1949).

The development of the postscapular fossa and the teres major process in *M. anceps* resembles that of *A. melanoleuca* and *T.ornatus*, although in this former species the teres major process is even slightly more reduced, and the caudal margin of the process is straight, lacking the marked notch typical of ursids (Fig. 3 c, f). Also, it is remarkable that in *M. anceps* the caudal margin of the teres major process does not show the rough area for the attachment of muscle teres major observed in ursids. In this group, the muscle teres major originates almost exclusively on the surface of the muscle subscapularis minor, although some fibers also attach on a rough area of the caudal border of the teres major process (Davis 1949). Given the absence of this area in *M. anceps*, it is probable that the muscle teres major was reduced in relation to that of bears.
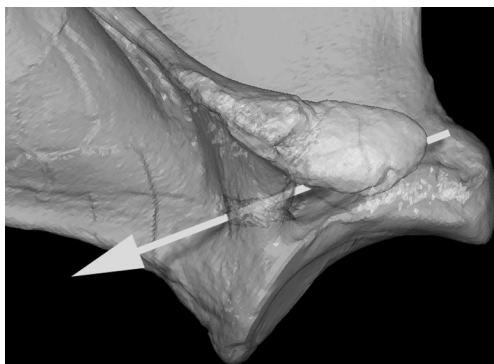
The development of both the teres major process and the postscapular fossa in some amphicyonids shows also differences with those of *M. anceps* (Fig. 3). Thus, in *A. major*, *A. longiramus*, *Y. americana*, and *B. niobrarensis* the development of these structures is similar to that observed in the ursids *U. arctos* or *U. americanus* (Olsen 1960; Hunt 2002, 2009; Argot 2010), mainly in relation to the size of the teres major process (Fig. 3). These amphicyonids have a much larger teres major process than *M. anceps*, although they also lack the ventral notch of the teres major process observed in ursids, it showing the continuous border seen in *M. anceps*. Nevertheless, the scapulae of some of these amphicyonids (*A. longiramus* and *A. major*) also resemble the morphology of the *Ursus* species in having a wide scapular neck and an acromion surpassing the glenoid cavity (Fig. 3d) (Olsen 1960; Argot 2010). On the other hand, other amphicyonids such as *Da. superbus* (Fig. 3a) and *De. oryktes* (Hunt 2011:fig. 57a) show a teres major process very similar to that of *M. anceps*. As described for Ursidae (see above) the development of these structures in Amphicyonidae is apparently independent from body mass. For example, although *M. anceps* and *A. major* show a similar estimated body weight, the former species shows a markedly reduced process (Fig. 3c, d). Furthermore, with *B. niobrarensis* being probably smaller than both *A. major* and *M. anceps*, it also shows a more developed teres major process than the latter, although smaller than that of *A. major*.

The teres major process is also present in extant procyonids: it is well developed in *Potos flavus*, whereas it is almost vestigial in *Procyon lotor* and *Nasua nasua* (Salesa et al. 2008). In the primitive late Miocene ailurid *Simocyon batalleri*, the process is large, but it is mostly occupied by the enlarged attachment area for the muscle teres major, that for the muscle subscapularis minor being relatively small (Salesa et al. 2008). This process is also present, although very reduced, in borophagine canids (Munthe 1989), probably indicating the presence of a relatively larger muscle teres major in relation to other canids, which lack this structure. The teres major process is also developed in the otters (Lutrinae), such as *Aonyx cinereus*, *Lutra lutra*, and especially *Lontra canadensis*, although there is no trace of a postscapular fossa; other mustelids, such as the wolverine (*Gulo gulo*) and the fisher (*Martes pennanti*) have medially expanded areas for the attachment of the muscle teres major (Leach 1977) but without forming the mentioned process. Finally, other groups such as most pinnipeds or xenarthran anteaters (*Myrmecophaga*, *Tamandua*) have a well-developed caudal accessory fossa of the scapula, which probably correspond to the postscapular fossa, although it is larger than that seen in the carnivorans mentioned above (Davis 1949; English 1977; Taylor 1978; Hildebrand 1988). Nevertheless, most pinnipeds (basically Phocidae and Otariidae) have wide scapulae showing other modifications such as an expanded supraspinous fossa, a low

spine with a very reduced acromion, and a great development of the postscapular fossa (English 1977). This implies a reorganization of the muscles attaching on the scapula, not only the teres major and the caudal portion of the muscle subscapularis, but also others such as the muscle deltoideus, which attaches on the postscapular fossa (English 1977: Fig. 1 and p. 329). On the other hand, in anteaters, the dorsal area of the postscapular fossa (teres major process in other groups) is principally occupied by the muscle teres major (Taylor 1978; Hildebrand 1988). Thus, in phocids, otariids, and anteaters, the attachment area for the caudal portion of the muscle subscapularis (which probably correspond to the subscapularis minor of Davis 1949), occupies only a caudoventral area of the postscapular fossa (English 1977; Taylor 1978: Fig. 1) it being relatively smaller than that of ursids or amphicyonids, and less caudo-dorsally extended (as it does not reach the dorsal margin of the fossa).

Proximal Half of the Humerus

The proximal epiphysis of the humerus of *M. anceps* (Fig. 5) shows a round, slightly distally inclined articular head, and a marked humeral neck, mostly developed on the caudal side of the humerus. This neck is more marked in *M. anceps* than in the ursines and *T. ornatus*, and similar to that of *A. melanoleuca* and large felids such as *Panthera leo*. These latter species also show a distally inclined and projected articular head. Most of the compared ursids, except *A. melanoleuca*, have more circular and convex articular heads, lacking any distal projection, and they have a relatively less marked humeral neck (Fig. 6a, d, e). The morphology of both the articular head and the neck in *M. anceps* is also different from that of other amphicyonids such as *A. major* (Fig. 6b) and *A. longiramus*, which show less marked necks and a shorter caudal projection, in a similar way to that of ursids (Olsen 1960; Argot 2010).

The lesser tubercle of *M. anceps* (the attachment area for the muscle subscapularis in ursids) (Davis 1964) does not significantly differ from the morphology observed in ursids and other amphicyonids. It is located on the craniomedial margin of the articular head, slightly proximally prominent. In turn, the greater tubercle is located on the craniolateral margin of the articular head, more cranially and proximally projected than that of ursids. The proximal and caudal faces of this tubercle are the attachment areas for the muscle supraspinatus, whereas the muscle infraspinatus attaches on a marked and deep round scar located on the lateral face. The greater tubercle of *M. anceps* slightly surpasses proximally the level of the humeral head, just a little more than in ursids and *A. major*, it being more similar to that of other amphicyonids such as *C. lemanensis* and *Da. superbus* (Fig. 6 a–c). The distance between the cranial border of the greater tubercle and the articular head of the humerus is longer in *M. anceps* than in

**Fig. 5** Left humerus (BAT-1′ 07 F3-35) of *Magericyon anceps* from Batallones-1 in cranial (**a**), medial (**b**), and lateral (**c**) views, showing the principal structures: lesser tubercle (lt), greater tubercle (gt), tricipital crest (tc), and greater tubercle crest (gtc)



the ursids, a morphology that is more similar to that of large felids and canids than to that of ursids (Fig. 6a, d, e). The greater tubercle continues distally in a marked crest for the attachment of the muscles pectorales (superficialis and profundus) (Davis 1964). This crest extends along the two-thirds of the cranial margin of the diaphysis. Both the morphology and development of this crest in *M. anceps* is similar to that of ursids and other amphicyonids such as *A. major*, *A. longiramus*, *C. lemanensis,* or *Da. superbus,* whilst in the temnocyonine amphicyonid *De. oryktes* the crest is restricted to the proximal part of the humerus (Hunt 2011).

The intertubercular groove of *M. anceps*, developed between both lesser and greater tubercles, is L-shaped in proximal view (Fig. 6a), due to the cranially projected greater tubercle, much more open than in ursids, and similar to that of other compared amphicyonids such as *A. major* and *C. lemanensis* (Fig. 6b, c). Extant felids and canids also show a cranially projected, similarly L-shaped intertubercular groove, whereas in all the compared ursids both the greater and the lesser tubercles are similarly cranially projected, with the former being located closely to the articular head, and with a more enclosed intertubercular groove, developed as a shallow canal separating both tubercles (Fig. 6d).

On the lateral face of the diaphysis, the tricipital line (for the attachment of the lateral head of the muscle triceps brachii) extends from the neck to the distal end of the greater tubercle crest, where it joins this crest (Fig. 5c). On the cranial margin, adjacent to the proximal extreme of the tricipital line, there is a smooth bulge for the attachment of the muscle teres minor, whereas on the distal third of the line, a marked deltoid tuberosity is present. The length of the greater tubercle crest and the tricipital line in *M. anceps* is similar to those of ursids (Fig. 6) but the latter structure is less ridged and its surface is smoother in the former. The distal joining of both crests is markedly rough and slightly cranially projected, this area being the attachment surface of the muscles cleidobrachialis and pectoralis superficialis (Davis 1964). There is no humeral crest, as in some ursids such as *A. melanoleuca* and large felids.

## Functional Implications of the Shoulder Anatomy of *Magericyon anceps*

The overall shoulder morphology of amphicyonids (including *M. anceps*) resembles that of ursids in several features, such as the general shape of the scapula and proximal humerus, and the presence of postscapular fossa and teres major process (Ginsburg 1961; Olsen 1960; Hunt 2002, 2009; Sorkin 2006; Argot 2010; Figueirido et al. 2011). But it also shows interesting differences with ursids, such as the presence of a large nutrient foramen on the ventral surface of the infraspinous fossa (Olsen 1960; Hunt 2002; Argot 2010), the absence of a caudal notch in the teres major process, the lesser
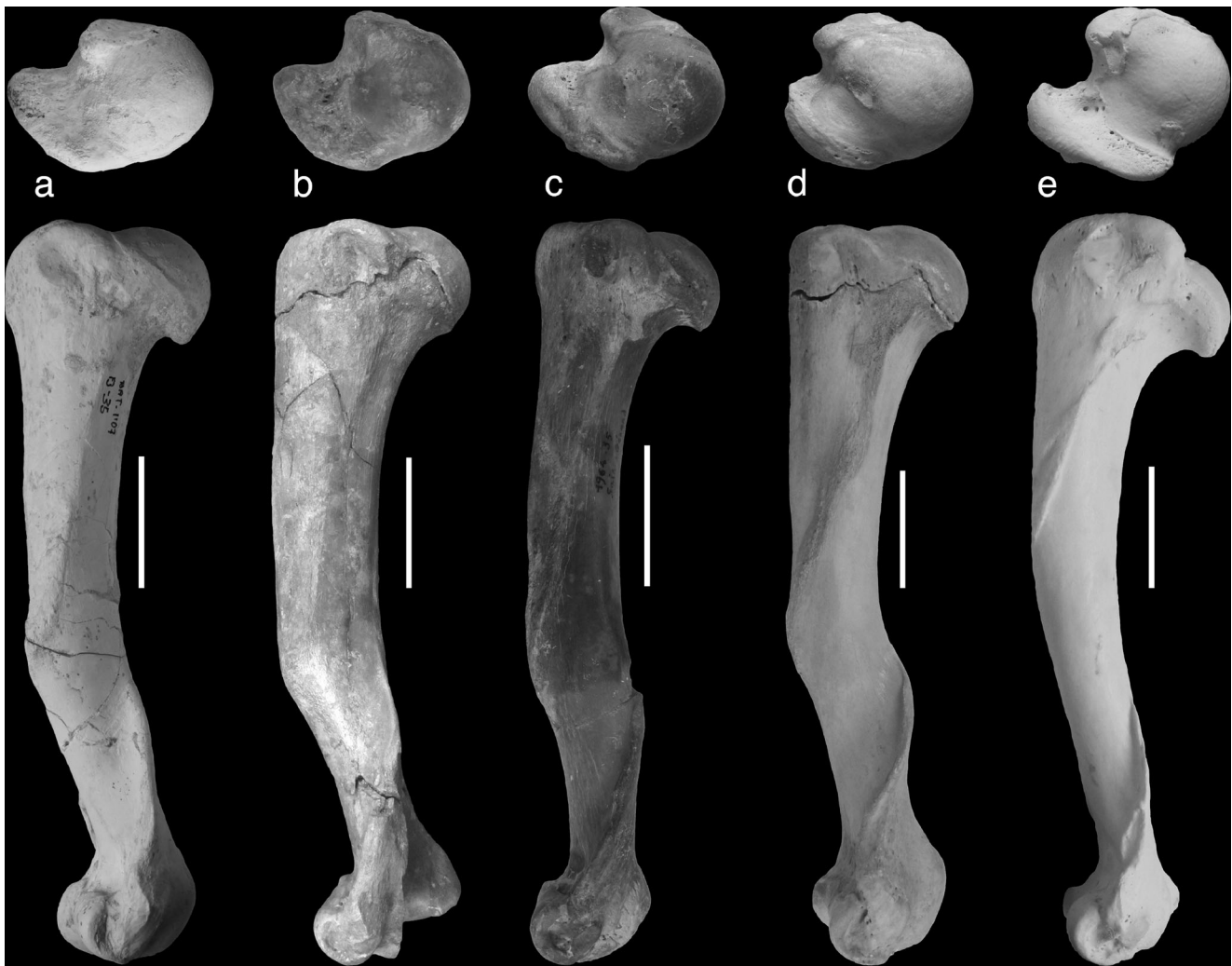
**Fig. 6** Comparison between humeri in proximal and lateral views of *Magericyon anceps* from Batallones-1, other Amphicyonidae, extant Felidae, and Ursidae (shown at the same size; scale bar represents 5 cm). *Magericyon anceps* from Batallones-1 (**a**), *Amphicyon major* from Sansan (France) (**b**), *Cynelos lemanensis* from Saint Gerand-le-Puy (France) (**c**), *Ursus arctos* (**d**), and *Panthera leo* (**e**)

development of the acromion, and the different configuration of the intertubercular groove. This combination indicates that, although both groups share a generally similar shoulder architecture, they should not be considered as mere ecological homologues; moreover if we consider the presence of different morphotypes within Amphicyonidae (Hunt 1998; Figueirido et al. 2011), including the medium-sized, relatively generalized *C. lemanensis*, the giant, bear-like *A. major*, or the more cursorial species *Da. superbus* and *B. niobrarensis* (the former species being medium-sized, whereas the latter is larger) (Peigné and Heizmann 2003; Hunt 2009; Argot 2010; Figueirido et al. 2011). Given this scenario, it seems clear that, although some amphicyonids could have been biomechanically roughly similar to ursids, other species probably exhibited a wider range of locomotor behaviors, which were independent from body size.

Focusing on the scapula of *M. anceps*, the presence of a postscapular fossa and a teres major process allows interpreting a similar muscular disposition in this area as that of ursids, with the muscle subscapularis minor occupying most of the surfaces of these two structures (Fig. 7), whereas the muscle teres major would be relatively reduced and attached almost exclusively onto the muscle subscapularis minor, as strongly suggested by the absence of an attachment area on the caudal border of the scapula. It is remarkable that although the teres major process is also well developed in other carnivorans, such as ailurids, procyonids (especially in *P. flavus*), and otters, in all these taxa the process is almost completely occupied by the enlarged attachment area for the muscle teres major (Howard 1973; Salesa et al. 2008; Fisher et al. 2009). In phocids and otariids, the process also provides the attachment area for other muscles, such as the deltoideus (English 1977). In all these carnivorans the attachment area for the muscle subscapularis minor is relatively reduced in comparison to the condition seen in ursids. Even in non-carnivorans such as the Myrmecophagidae (anteaters), the

attachment area for the muscle subscapularis minor occupies only the ventral part of the very large postscapular fossa, whereas its dorsal part serves as the attachment surface for the muscle teres major (Davis 1949; Taylor 1978). In some of these groups the peculiar morphology of their scapulae has been associated to a special locomotion type: aquatic locomotion in phocids, otariids, and otters (Howard 1973); English 1977), climbing abilities in fossil ailurids (Salesa et al. 2008) and the arboreal anteater *Tamandua* (Taylor 1978), or digging capacities in the anteater *Myrmecophaga* (Hildebrand 1988). Also, in anteaters the scapular morphology has been associated to their special feeding behavior, which includes strong tearing movements with their forelimbs (Davis 1949; Taylor 1978; Hildebrand 1988).

It should be noted that in all these groups of mammals having well-developed teres major process and postscapular fossa the relative importance of the muscles subscapularis minor and teres major is different, with ailurids, procyonids, otters, phocids, otariids, and anteaters having a proportionally large muscle teres major, whereas this is relatively small in ursids, which have a proportionally large muscle subscapularis minor (Davis 1949). Nevertheless, the implications for shoulder biomechanics of the presence of a large muscle subscapularis minor are not clear. According to Davis (1949) the fibers of the muscle subscapularis minor are separated from the main mass of the much larger muscle subscapularis by a fascial septum, it being innervated by a separate subscapular branch of the axillary nerve. However, Hunt (2009), in a dissection of the shoulder of a specimen of sun bear (*Helarctos malayanus*), observed that the subscapularis minor is "a fusiform ventral derivative of the muscle subscapularis" and "its fibers merge with the ventral part of the subscapularis." In a dissection of an adult male specimen of *T. ornatus* we observed a similar morphology for these muscles as that described by Hunt (2009) for *H. malayanus*, with the muscle subscapularis occupying the whole medial part of the scapula, and being composed of several fusiform fascicles that can be easily delimited but remain part of the same muscular mass (Fig. 7b). One of these fascicles, the most caudally located, fits into the postscapular fossa, with some of its fibers attaching on the lateral portion of the teres major process (Fig. 7a). This caudal portion of the muscle subscapularis in *T. ornatus* is not separated from the rest of the fascicles forming the muscle, and it joins them before attaching onto the same area of the humerus (Fig. 7b). The only difference of the muscle subscapularis minor with respect to the rest of the fibers of the subscapularis is that some fibers of the former attach on a small lateral area of the teres major process.

Given this, the function of the muscle subscapularis minor should not be markedly different from that of the muscle subscapularis. Hunt (2009) suggested that the presence of both teres major process and postscapular fossa in ursids and amphicyonids would be a retention of an ancestral, common pattern shared by these families, with no clear functional significance. This idea is also supported by the presence of similar structures in other arctoid carnivorans, as discussed above, such as ailurids, otters, procyonids, some canids, and some pinnipeds (Davis 1964; Howard 1973; English 1977; Munthe 1989; Salesa et al. 2008; Fisher et al. 2009). It is easy to assume that, since both muscles (subscapularis and subscapularis minor) share the same attachment area on the humerus (Fig. 7b), and they originate on adjacent areas of the scapula, their functions have to be very similar. But there is a difference in the conformation of these muscles that could determine some degree of functional separation: whereas the muscle subscapularis occupies most of the medial surface of the scapula, the subscapularis minor attaches along its caudal margin occupying both the lateral and medial surfaces of the postscapular fossa. This change from the lateral to the medial surface along its length, probably affects the function of the muscle subscapularis minor, and even that of the muscle subscapularis due to the fact that both muscular masses are not independent (see above). However, at least in *T. ornatus* the muscle subscapularis minor can be considered as the last caudal fascicle of the muscle subscapularis, and only a few fibers of the former attach onto the teres major process. The muscle subscapularis is essentially an adductor of the shoulder, its tendon also acting as a medial collateral ligament that restricts the abduction range of the shoulder (Barone 2010). Other muscles, such as the infraspinatus and supraspinatus (the former abducts the gleno-humeral articulation, whereas the latter abducts and extends it) also stabilize this articulation, restricting both the cranial displacement of the humeral head, and the transversal movement of the scapula (Evans 1993; Barone 2010). Several studies on electromyography of the muscles subscapularis, infraspinatus, and supraspinatus in dogs and cats reveal that they are electrically active throughout most of the stance phase of the locomotion, which is consistent with the importance of these muscles in the shoulder joint stabilization (Tokuriki 1973a, b; English 1978; Goslow et al. 1981). Thus, an important function of these muscles is stabilizing the gleno-humeral articulation during the movement of the humerus, restricting its range of abduction-adduction. Also, the function of the muscles subscapularis, infraspinatus, and supraspinatus has been related to the necessity for a strong control of rotatory movements of the shoulder in pinnipeds during swimming, in which the large muscle subscapularis would have an important role due to the complex orientation of their fascicles (English 1977). It is possible that in ursids and amphicyonids, due to their wide range of movements in the shoulder articulation (Davis 1949; Argot 2010), the muscle subscapularis minor, as a caudoventral projection of the muscle subscapularis, actually improves this shoulder stabilization. Also, the prolongation of the attachment area of the subscapularis minor onto the lateral

**Fig. 7** Reconstruction of the shoulder joint of *Magericyon anceps* showing the disposition of some of the muscles discussed in the text. Lateral view showing the muscles supraspinatus, infraspinatus, and subscapularis minor (occupying the postcapular fossa) (**a**); and medial view showing the muscle subscapularis minor and the different fascicles composing the muscle subscapularis (**b**). Artwork by M. Antón
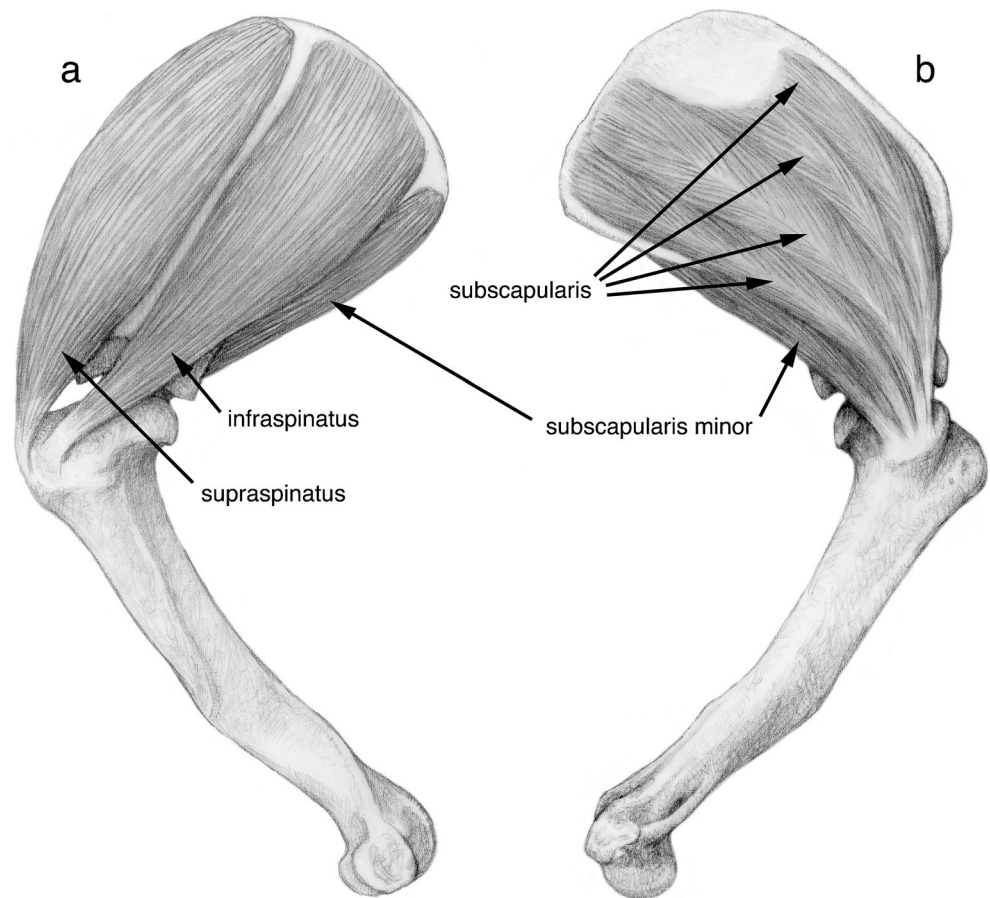


surface of the teres major process could add an inwards rotatory component to the adduction of the humerus (Salesa et al. 2008) or at least increase the shoulder stabilization during lateral rotation of the humerus. Thus, the combined contraction of the muscles subscapularis and subscapularis minor would improve the shoulder joint stability during the grasping and pulling actions in ursids and amphicyonids (Hunt 2009), as it has been also proposed for *P. flavus* and *S. batalleri* (Salesa et al. 2008). In ursids, the development of both the postscapular fossa and the teres major process besides the mobile shoulder articulation and the overall powerful shoulder musculature have been related to the ability of this group for climbing trees, an activity that implies that part of the body weight is supported by the forelimbs (Davis 1949; Argot 2003, 2010), but also to other types of behavior, such as overturning stones and digging (Gambaryan 1974).

Some of the mentioned activities (climbing, digging) could have been also accomplished by the primitive species of amphicyonids, most of them considered as having a non-cursorial, generalized postcranial skeleton (Hunt 1998, 2001, 2009; Peigné and Heizmann 2003). Following this, it would be expected that in more cursorial amphicyonids such as *De. oryktes* and *B. niobrarensis,* the increased importance of shoulder stabilization during running should have provoked a certain

degree of differentiation from the scapular morphology seen in more typical amphicyonids, producing scapulae more similar to those of cursorial carnivorans, which are elongated and slender, and lack both the postscapular fossa and the teres major process (Smith and Savage 1956; Gambaryan 1974; Seckel and Janis 2008). In this respect, Hunt (2009) suggested that the necessity for digging would have been a strong reason for retaining these structures on the scapula of the most cursorial amphicyonids, moreover when specimens of at least two species (*De. oryktes* and *Da. superbus*) have been found in fossil burrows (Hunt et al. 1983; Hunt 2011). In amphicyonids, improving the shoulder stabilization would have been also useful during prey capture, an activity in which the forelimbs exert a great strength to subdue prey (Sorkin 2006), especially since most of the larger amphicyonids are considered ambush predators and more active hunters than extant ursids (Hunt 2002, 2003; Sorkin 2006; Argot 2010). Also, as Gambaryan (1974) suggested for ursids, the strong shoulder musculature of amphicyonids, which would be primarily used for digging and climbing in primitive species, would have been secondarily used during the support period of the gallop in more cursorial forms, basically providing strength and stabilization. In this regard, it is remarkable that the scapula of *M. anceps* shows the relatively smallest teres major process of all the compared

amphicyonids, including both ursid-like and cursorial forms (*A. major* and *B. niobrarensis*, for example, showing both the larger teres major processes). This suggests that the presence of this structure cannot be associated to a specific locomotor adaptation in Amphicyonidae, and its reduction in *M. anceps* should be considered in the context of the whole scapular morphology. In fact, Argot (2010) already pointed out the difficulty in providing a completely satisfactory hypothesis explaining the origin and functional significance of the postscapular fossa. Within Ursidae, the species with less cursorial adaptations such as *T. ornatus* and *A. melanoleuca*, show reduced teres major processes in comparison to ursine ursids such as *U. arctos*. But the former species are also much smaller than the latter, and a strong allometric relationship could be determining part of the variation in the size of this process. In our opinion, and considering the morphology observed in ailurids, procyonids, ursids, and amphicyonids, the presence of a muscle subscapularis minor and its attachment areas (postscapular fossa and teres major process) in terrestrial carnivorans could be interpreted as indicative of the development of a secondary function for this muscle, from primarily stabilizing the shoulder when climbing (Davis 1949; Argot 2010), to improving that stabilization during running, digging, and even prey immobilization.

The relatively narrower scapular neck of *M. anceps* when compared to that of ursids and *A. major* would be pointing towards relatively less-developed climbing abilities, as the presence of a robust scapular necks in ursids and other scansorial mammals has been related by Argot (2003, 2010) with an increase of resistance against tensile forces during climbing. Considering that *M. anceps* and *A. major* had similar body sizes, and the suggestion of Argot (2010) that the latter was only an occasional climber, it would be expected that *M. anceps* was a very rare climber, with only young individuals being able of an effective development of this activity.

The presence of the teres major process and postscapular fossa in the scapulae of ursids and amphicyonids also produces a slight increase in the length of the attachment surfaces of the muscles rhomboideus and serratus ventralis (the former attaching on the dorsal margin of the scapula, and the latter on the dorsomedial margin). The functions of these two muscles are related to rotation of the scapula, the suspension of the limb from the trunk, and the load transmission from trunk to limb (Davis 1949; Taylor 1978; Barone 2010). In anteaters, phocids, and otariids these muscles are relatively large when compared to those of other groups, and this has been related to the rotation movements of the scapula during climbing, tearing, or swimming (English 1977; Taylor 1978). Also, an expanded caudodorsal border of the scapula has been related to an increase in the mechanical advantage of the muscle teres major due to the increased moment arm in fossorial and aquatic mammals (Smith and Savage 1956). However, in

amphicyonids and ursids this caudal angle is not as elongated as in those groups, and the attachment surface for the muscle teres major just occupies a small portion of this area (as commented above). Furthermore, the quadrangular overall shape of the scapula in amphicyonids and ursids is very similar to that of other arctoid carnivorans, very far from the fan-shaped scapulae of phocids, otariids, and anteaters, which markedly expand their dorsal margin (English 1977; Taylor 1978). Besides this, the expansion of the caudal angle in *M. anceps* is small when compared to other amphicyonids, with *A. major* showing the largest caudal angle, which would point towards the relatively enhanced climbing abilities suggested by Argot (2010).

Another interesting feature observed in the scapula of *M. anceps* is the reduced acromion, which does not surpass the level of the glenoid cavity (Fig. 2a). This morphology is different from that of ursids, and it has been associated to a decreased abductor function of the acromial part of the muscle deltoideus in cursorial carnivorans (Taylor 1974), in which the humerus moves around the scapula mostly in the parasagittal plane. Other amphicyonids show different patterns, with *A. major* (Fig. 3d) or *A. longiramus* showing an acromion more similar to that of ursids, and *Da. superbus* (Fig. 3a) and *A. ingens* showing a reduced acromion in a similar way to that of *M. anceps*. Thus, this character would indicate that most of the amphicyonids had more cursorial abilities than ursids, with *A. major* probably being the most bear-like of all the compared amphicyonids.

The abduction of the humerus is also restricted by the size of its greater tubercle, because if this is large enough, it could contact the lateral surface of the glenoid cavity (Barone 2010), preventing any abduction movement of the humerus. Thus, with ursids and amphicyonids having relatively small greater tubercles, the importance of the subscapularis minor and the teres major process in the shoulder stabilization could be higher in relation to other carnivorans with relatively larger greater tubercles, which would a priori show lower ranges of humerus abduction. However, the morphology of the greater tubercle of *M. anceps* and most of the compared amphicyonids, (*Y. americana*, *C. lemanensis*, *A. galushai*, and *De. oryktes*) is slightly different from that observed in ursids and more bear-like amphicyonids such as *A. major*, which show a less proximally projected greater tubercle (Fig. 6b). Within the former group *De. oryktes* shows a strongly proximally projected greater tubercle, more than the other compared amphicyonids, once again indicating the presence of different locomotor types within Amphicyonidae. A more projecting greater tubercle is typical of cursorial carnivorans (Taylor 1974) and it would indicate that many amphicyonids, including *M. anceps,* were more capable runners than ursids and bear-like amphicyonids such as *A. major*. It is remarkable that this morphology is already present in the primitive form *C. lemanensis* (Fig. 6c), which would indicate

that the earliest amphicyonids, although being generalized forms, already exhibited certain cursorial capabilities (Viranta 1996; Peigné and Heizmann 2003), and a projected greater tubercle would be a plesiomorphy for Amphicyonidae, which later changed in ursid-like forms such as *A. major,* which shows a less projected greater tubercle.

*Magericyon anceps* also shows long greater tubercle crest and tricipital line, which imply the existence of a distally elongated attachment area for the muscles pectorales, deltoideus, and cleidobrachialis (Fig. 5a). These muscles control the shoulder rotation and thus are related to manipulative behavior, as well as to climbing or digging abilities (Argot 2003, 2010; Barone 2010). Both the greater tubercle crest and the tricipital line are long and rough in ursids, and shorter in felids and canids, implying relatively smaller muscles in the latter groups. In *M. anceps* these crests are as long as those of ursids (Fig. 6a,d), suggesting similarly powerful muscles pectorales and deltoideus. Most of the compared amphicyonids show this pattern, except the cursorial temnocyonine amphicyonids such as *De. oryktes*, which show a relatively reduced crest, restricted to the proximal part of the humerus (Hunt 2011).

Besides all these features of the scapula and the proximal half of the humerus indicating some degree of similarity between ursids and amphicyonids, there are other traits, observed in most of the species of amphicyonids except *A. major* that resemble the morphology present in large felids such as *Panthera leo*. These features are: 1) the greater tubercle is proximally projected, surpassing the level of the articular head of the humerus (although slightly less than in large felids); 2) the scapular neck is relatively narrow; 3) the articular head of the humerus is distally inclined, which produces a marked humeral neck; 4) the intertubercular groove of the humerus is open, L-shaped in proximal view (all the amphicyonids compared, including *A. major*); and 5) at least in *M. anceps* and *Da. superbus* the acromion does not surpass the level of the glenoid cavity. Among these traits, the intertubercular groove morphology has interesting functional implications: the tendon of the muscle biceps brachii runs into this groove, with the transversal humeral ligament (developed between both the greater and the lesser tubercles) keeping the tendon in place inside the groove (Evans 1993; Barone 2010). As described previously, the shape of the intertubercular groove is similar in canids, felids, and amphicyonids in general (thus including *M. anceps*), it being markedly different from that of ursids, which have a much more closed, canal-like groove (Fig. 6). Taylor (1974) associated this character with both the power of the muscle biceps brachii and the degree of usage: a clearly defined intertubercular groove, such as that of ursids, would allow a better control of movements, and probably a powerful muscle. According to Taylor (1974) the nandiniid *Nandinia binotata*, which shows an ursid-like groove, employs this muscle to a much greater degree than the viverrid *Civettictis civetta* (with a much more open groove) and this would be

related to the greater climbing ability of the former. In the case of ursids and amphicyonids, the different shape of the intertubercular groove, besides reflecting differences in muscle strength, would indicate its different usage. Thus, whereas in ursids the muscle biceps brachii probably participates in a higher range of activities, such as those related to food acquisition, and also climbing, manipulating stones, or digging, in amphicyonids the muscle biceps brachii would have had a more restricted role, mainly related to locomotor activities. In addition, the more cranially projected greater tubercle of amphicyonids compared to that of ursids, implies a longer distance between the gleno-humeral articulation and the attachment area of the muscle supraspinatus (Feeney 1999). As this muscle helps in the extension and stabilization of the gleno-humeral articulation, this longer distance increases the extension range of this joint in the parasagittal plane, as it has been described in canids (Feeney 1999), also improving its mechanical stabilization. In this respect it is remarkable that this cranial projection of the greater tubercle is also observed in larger felids such as *P. leo*, indicating similar degree of extension in the forelimb as that of most of the amphicyonids.

In summary, although the scapulo-humeral morphology of *M. anceps* is similar to that of other amphicyonids, it also shows interesting peculiarities. Among these, the relatively reduced acromion, postscapular fossa, and teres major process suggest some differentiation from the two ecological morphotypes shown by derived Amphicyonidae, and a similarity with primitive, generalized forms such as *C. lemanensis*. This would indicate that *M. anceps* occupied an intermediate ecological niche between that of the ursid-like amphicyonines and that of the highly cursorial North American daphoenines and temnocyonines.

## Conclusions

*Magericyon anceps* is an atypical amphicyonid for several reasons. Its dentition, although being roughly similar to that of other amphicyonids, also shows several derived features pointing towards a more hypercarnivorous diet than those of most of the species of this family (Peigné et al. 2008). Besides this, the presence of postcranial features suggesting more cursorial abilities than those of the middle Miocene amphicyonines (such as *A. major*), including reduced postscapular fossa and teres major process, and a more projected greater tubercle, would place *M. anceps* in a different ecological niche than that of these larger forms. In fact, its shoulder anatomy is similar to that of the primitive and relatively generalized species *Cynelos lemanensis* and *Daphoenodon superbus*, and thus intermediate between that of the ursid-like amphicyonines (*A. major*) and that of the markedly cursorial temnocyonines (*Delotrochanter oryktes*) and daphoenines (*Borocyon niobrarensis*). Thus, with *M. anceps* showing a relatively large body size and a non-

specialized shoulder, it is very likely that it inhabited moderately vegetated habitats, very different from those open environments probably occupied by the cursorial temnocyonines and daphoenines. This agrees with the habitat inferred for the Batallones environment, probably a mosaic of woodland areas besides more open, savannah-like patches (Salesa et al. 2006b); this landscape was derived from the progressive aridification process that started in the Vallesian, and finally led to the predominance of savannas over wooded habitats during the Turolian (Agustí et al. 1999; Fortelius et al. 2002). This habitat is very different from that inferred for *A. major*, a species that inhabited Europe during the middle Miocene, when climatic conditions were more humid and warm than during the Vallesian and Turolian (Zachos et al. 2001; Böhme 2003; Tong et al. 2009; Bruch et al. 2010; Böhme et al. 2011). Thus, it is not surprising that these two similarly sized amphicyonids show different models on their shoulder region: *A. major* has an ursid-like scapula, with large postcapular fossa and teres major process, whereas in *M. anceps* these structures are clearly reduced. This indicates that these two species probably played different ecological roles within their ecosystems, although other important functional complexes should be considered before proposing any functional model for *M. anceps*. Argot (2010) studied an almost complete skeleton of *A. major*, proposing the hypothesis that this species "was a more efficient runner than are modern bears," so with *M. anceps* showing the above-mentioned features on its shoulder, it is highly probable that it were even more cursorial than the middle Miocene species.

Finally, when considering together the relatively primitive shoulder morphology of *M. anceps* and its hypercarnivorous dentition, which includes reduced post-carnassial teeth and markedly flattened upper canines (Peigné et al. 2008), this species reveals itself as a unique ecological type within Amphicyonidae. This combination of features suggests the importance of flesh in the diet of *M. anceps*, and supports the hypothesis that the need for an efficient hunting was the major evolutionary pressure determining the evolution of the appendicular skeleton of this amphicyonid. Nevertheless, any functional or ecological inference made from the study of such a concrete region as the shoulder must be taken with caution, and only future studies on the whole postcranial anatomy of *M. anceps* will allow a more complete understanding of the ecological role and locomotor adaptations of this unusual amphicyonid.

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