Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontinae), a sabrecat from the Late Pliocene – Early Pleistocene of Senéze, France

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Megantereon cultridens was a derived, Late Pliocene to Early Pleistocene sabrecat, and although fossils of animals referred to the genus and species have been found at several locations throughout Eurasia, most are fragmentary. However, the specimen SE311 from Senéze in France represents an almost complete and well-preserved skeleton, and this is only known from very few other sabrecats, thus providing a rare glimpse into the full anatomy of an unusual and derived sabrecat. In this monograph, we provide a complete overview of the anatomy of *Megantereon cultridens* SE311, and compare it with extant large felids, and the few other derived sabrecats from which ample fossil material is known, although most frequently representing several specimens. SE311 was a large specimen of *M. cultridens* and would have had a body mass of 100–110 kg and a head–body length or around 160 cm, which is similar to a small lioness or large male jaguar. *Megantereon* sp. were sexually dimorphic, and the size of SE311 suggests that it was a male. As with several other derived sabrecats, it was powerfully built, and had particularly robust forequarters with very well-developed muscle attachment sites, indicating a powerful forelimb and shoulder musculature. The neck was proportionally much longer than in extant felids, and the thoracic and particularly lumbar region was proportionally shorter, mimicking the condition in other derived sabrecats from which large parts of the vertebral column is known. *Megantereon* probably lived in open-forest environments and preyed on cervids, which were dispatched with a shearing bite from the hypertrophied and blade-like upper canines to the throat of the prey, while the prey was held immobile with the massive forelimbs, thus minimizing the risk of damage to the fangs. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **151**, 833–884.

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INTRODUCTION

The sabretoothed, or machairodont, felids were once a numerous and by all measures successful group of medium-sized to large predators throughout North America, Eurasia and Africa in the Miocene to Late Pleistocene, and during most of this long time span they appear to have been distinctly more common than members of the extant clade of felids, the conical-toothed, or feline felids in that their fossils are much more commonly found (Emerson & Radinsky, 1980; Radinsky & Emerson, 1982; Turner & Antón, 1997; Martin, 1998). Accordingly, they almost certainly were an important part of large predator diversity, and it is thus of interest for understanding ecosystem evolution in the Late Tertiary to document their morphological adaptations and evolutionary history.

The genus *Megantereon* was a widespread group of medium-sized, derived sabrecats, which occurred throughout the Old World in the Pliocene–Pleistocene (Berta & Galiano, 1983; Turner, 1987; Turner & Antón, 1997; Palmquist *et al.*, 2007). Although they appear to have been widespread and thus an

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important part of the large-predator fauna, most finds are very fragmentary. One notable exception is the specimen SE311 of *Megantereon cultridens* from Senéze, France, which is a nearly complete and generally well-preserved skeleton of a large, fully adult individual. Largely complete or even partial skeletons of sabretoothed felids are extremely rare, and are only known from a few specimens of *Smilodon populator* (Méndez-Alzola, 1941) and *Homotherium crenatidens/latidens* (Ballesio, 1963). Even the hugely abundant *Smilodon fatalis* from the La Brea tar pits of North America (Merriam & Stock, 1932; Miller, 1968; Akersten, 1985; Stock & Harris, 1992) is only known from a single, partial skeleton (Cox & Jefferson, 1988), which is less complete than *M. cultridens* SE311. Despite its completeness and obvious significance for understanding sabretooth morphology, SE311 has received only a cursory description by Schaub (1925).

THE LOCALITY OF SENÉZE

The locality of Senèze is an old maar (infilled volcanic crater lake) of Late Villafranchian age, dating to around 2.2–1.5 Mya (http://web.gc.cuny.edu/Anthropology/field_seneze.html). Accordingly, the recovered fauna need not all have been contemporaneous. The Senèze site has been excavated since 1892, when M. Boule informed the Muséum national d'Histoire Naturelle in Paris about an elephant discovery (Stehlin, 1923). Most of the excavations were made between 1910 and 1940 by local farmers, and yielded large amounts of fossil material, which was sold to several museums, for instance in Lyon, Basel and Paris. Unfortunately, as most excavators were non-professionals, little is known about the conditions and specific locations of many of the specimens from the locality. This also includes the skeleton of *Megantereon cultridens*, of which is only known that the specimen was purchased by the Natural History Museum in Basel sometime prior to 1923. Recently (2000), excavations were resumed by the Senèze Research Project, a collaborative Franco-American project under the supervision of Drs Eric Delson (City University of New York), Martine Faure and Claude Guérin (Universités de Lyon) (see http://web.gc.cuny.edu/Anthropology/field_seneze.html).

MEGANTEREON

The type specimen of *Megantereon* was called *Ursus cultridens* (Cuvier, 1824), as Cuvier thought the fragments of the canines and the associated drawings he studied were the remains a bear. In a study of the palaeofauna of Perrier, Croizet & Jobert (1828) described two varieties of *U. cultridens* based

on canines, and they described a new species based on a mandibular ramus as *Felis megantereon*, and also proposed a new generic name, *Megantereon*. Almost simultaneously, Bravard (1828) concluded that the canines and the mandible referred to *U. cultridens* and *F. megantereon* (*Megantereon*) apparently belonged to a portion of a felid skull, which he had collected (Ficcarelli, 1979). Bravard proposed the name *Felis cultridens* for the serrated canines, and *Megantereon megantereon* for the non-serrated canines, which subsequently has caused some confusion. As the specimens belong to a cat and not a bear, *Megantereon* has priority, and the specific name *cultridens* has priority to *megantereon*, which is to be regarded as a *nomen nodum*. Accordingly, the systematic palaeontology of *Megantereon* is

Order: Carnivora Bowdich, 1821
Family: Felidae Gray, 1821
Subfamily: Machairodontinae Gill, 1871
Genus: *Megantereon* Croizet & Jobert, 1828
Species: *cultridens* Cuvier, 1824
Etymology: *Mega-* (gr.) large, *-terion* (gr.) tool ~ large tool

In this paper, we describe the skeleton of *Megantereon cultridens* SE311 in detail, and compare it with the few other well-known sabrecats, and with a selection of extant large felids. Skull and dental terminology are based on Crouch (1969) and Osborn (1907), respectively, and soft tissue terminology is based on Schumacher (1961), Crouch (1969), Turnbull (1970) and Done *et al.* (2000). We also analyse its morphology and attempt to reconstruct aspects of its palaeobiology. Throughout the paper, we compare skeletal element sizes with those of other felids. This was done by means of one-way ANOVA and *post-hoc* Tukey HSD tests, or one-sample *t*-tests, as appropriate, on $\log_{10}$-transformed values, whereas ratios were angular (arcsine) transformed to restore normality (Sokal & Rohlf, 1995).

OSTEOLOGY OF *MEGANTEREON*
SKULL AND UPPER DENTITION

The skull of *Megantereon cultridens* SE311 (Fig. 1; Table 1) has been figured in several publications over the years, e.g. Piveteau (1961), Kurtén (1968) and, most recently, Palmquist *et al.* (2007). It differs from other sabrecats, with the sole exception of some specimens of *Smilodon populator*, in having a nearly vertical occiput relative to the long axis of the skull. Unfortunately, much of the skull is heavily restored, as also pointed out by Antón & Werdelin (1998), and the area behind the coronal suture on the left side, the entire right side, most of the palatal region and
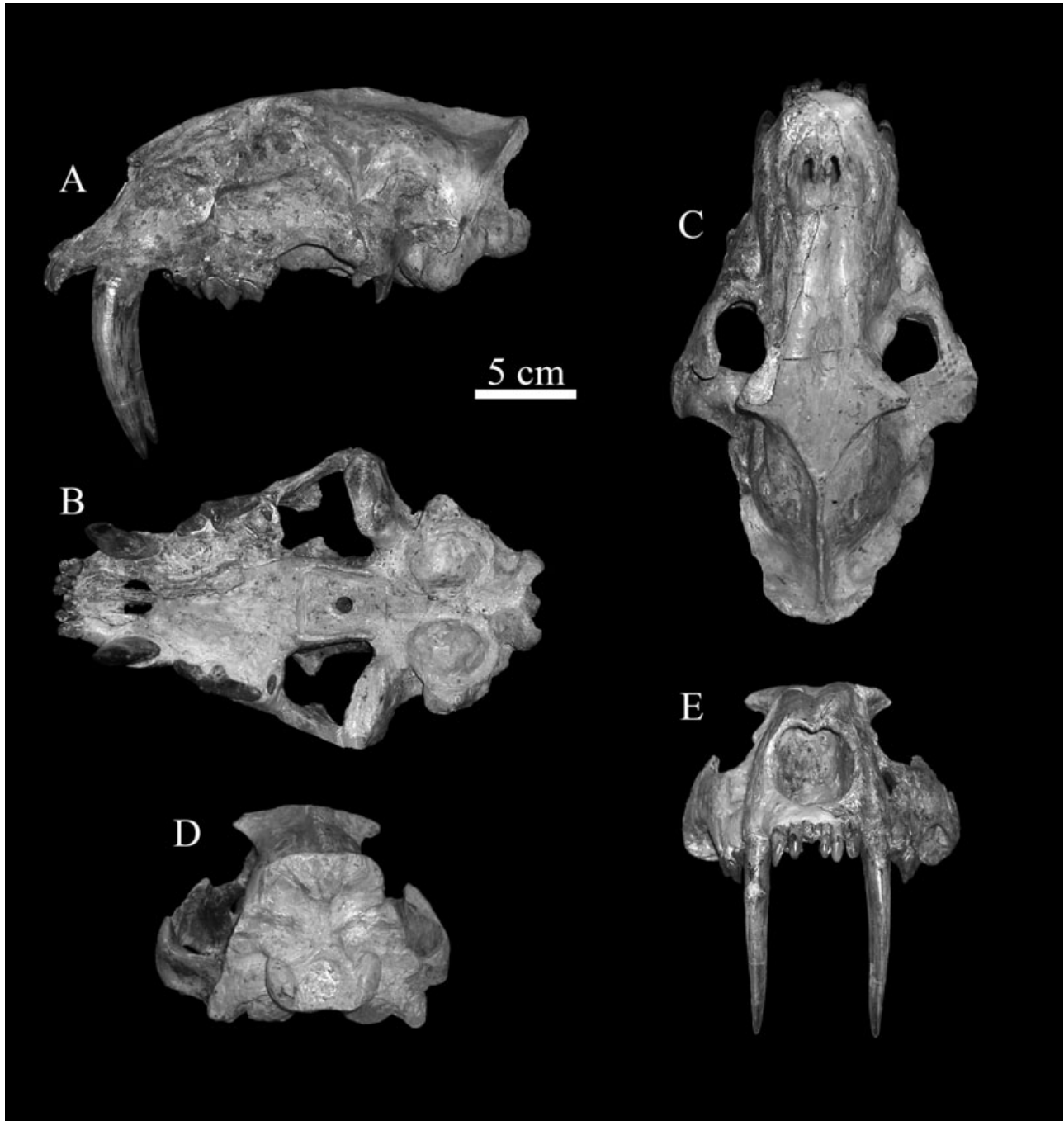
Figure 1. Skull of *Megantereon cultridens* SE311 in left lateral (A), ventral (B), dorsal (C), posterior (D) and anterior (E) view. Notice the obvious restoration of the entire posterior part of the skull.

the entire basicranial region are restored (Figs 1, 2). Other skulls of *Megantereon* sp., which we concur with Turner & Antón (1997) are also referable to *M. cultridens*, indicate that the occipital region was probably posteriorly inclined (Vekua, 1995; Antón & Werdelin, 1998), for instance MNHNPer2001a (Museum national d'Histoire Naturelle, Paris; pers.

obs). The dentition in SE311 is, however, excellently preserved. The resemblance to *S. populator* in the restored areas is probably not accidental. In his brief report, Schaub (1925: 255–256) states that 'Zum vergleich steht mir neben rezenten Feliden der Gipsabguss des Skeletts von *Smilodon neogaeus* [= *S. populator*] Lund . . . zur Verfügung' ('For com-

Table 1. Measurements (mm) of the skull and left mandibular ramus of *Megantereon cultridens* SE311

Skull		Mandible	
L*	238.7	L‡	159.2
ZW	150.8	D ant P_3	32.4
Jj–P^4	73.8	LM ant P_3	11.1
Jj–C^1	123.7	D P_3/P_4	29.1
Jj–I^3	147.9	LM P_3/P_4	12.1
Di P^3–C^1	12.2	D P_4/M_1	31.1
I^1 L	12.2	LM P_4/M_1	13.8
I^2 L	13.0	D post M_1	31.3
I^3 L	14.6	LM post M_1	16.0
C^1:		Cor	27.0
L	93.5	MAM§	18.6
AP	24.6	MAT§	37.5
LM	13.6	I_1 L	11.4
P^3:		I_2 L	12.0
AP	13.6	I_3 L	13.5
LM	7.5	C_1 L	19.5
P^4:		P_3:	
AP	31.7	AP	11.9
LM†	9.3	LM	5.5
		P_4:	
		AP	20.9
		LM	8.6
		M_1:	
		AP	21.8
		LM	9.7

*As reconstructed.
†Excluding the protocone.
‡Anterior part of symphysis restored.
§See Emerson & Radinsky (1980).
Abbreviations: ant, anterior to; AP, anteroposterior diameter; cor, height of coronoid process above jaw condyle; D, dorsoventral depth; Di P_3–C_1, diastema between third upper premolar and upper canine; Jj–C_1, anteroposterior distance from centre of jaw cotyle to centre of upper canine; Jj–I_3, anteroposterior distance from centre of jaw cotyle to centre of third upper incisor; Jj–P_4, anteroposterior distance from centre of jaw cotyle to upper carnassial paracone; L, anteroposterior length; LM, labiolingual diameter; MAM, inferred moment arm of the masseter about the temporomandibular joint; MAT, inferred moment arm of the temporalis about the temporomandibular joint; post, posterior to; ZW, width across zygomatic arches.

parative purposes, besides recent felids, I have a plaster cast of the skeleton of *Smilodon neogaeus* [= *S. populator*] Lund . . . at my disposal'). It thus appears likely that *Smilodon* was used as a template for reconstruction the skull of SE311 (Fig. 2A–D).

The left premaxilla is virtually complete with the exception of the labial part in front of the I^1 alveolus.

Of the right premaxilla, only the area between I^1, I^2 and the incisive foramen is preserved (Fig. 1A, B, E). The left premaxilla is partly preserved from the premaxillary suture to the sutures of the nasal and frontal bones, along with nearly all of the ventral part. The left palate is only preserved adjacent to the left M^1 alveolus. The left jugal is preserved in the area surrounding the preorbital foramen and the upper part adjacent to the sutures of the remaining part of the zygomatic arch, including the postorbital process.

The zygomatic arch is distinctly antereroposteriorly shorter than in comparably sized extant large felids, and is also distinctly taller dorsoventrally, which resembles the condition in other derived sabrecats, such as *Smilodon*. Medially, there are distinct muscle scars for the origin of the m. masseter (both pars profunda and pars superficialis) The preorbital foramen is slightly larger than in extant large felids of similar size, but not quite as hypertrophied as in *Smilodon* and *Homotherium*. The area immediately anteroventrally to the foramen is not sculptured, and, accordingly, lacks any distinctive signs of having had muscular attachments. Naples & Martin (2000) suggested that the hypertrophied preorbital foramina of derived machairodonts and nimravids were indicative of a condition known as hysticomorphy, where the anterior masseter passes through the foramen, as in certain extant rodents. This appears not to have been the case in *Megantereon*.

Only the lowermost part of the left temporal (squamous portion) is preserved, extending caudally to the squamous suture, and a small part of the occipital crest is also preserved. The majority of the left glenoid fossa is preserved, with the exception of the innermost part adjacent to the orbitosphenoid. Both the pre- and the post-glenoid processes are preserved; the post-glenoid process is distinctly ventrally deflected, which is a condition common to all derived sabrecats and nimravids, and is probably an adaptation for attaining a large gape (Emerson & Radinsky, 1980; Christiansen, 2006; see also Fig. 29, below). Around half of the left frontal is preserved, including most of the anterior postorbital process and orbital foramen, adjacent to the palatine, along with the ethmoid and lacrimal. The left nasal is preserved along the sutures towards the maxilla and the frontal, but unfortunately not the portion that was to reach the internasal suture. The facial part of the skull appears to display a less posterior inclination of the facial part relative to the basicranial part of the skull than reported for *Homotherium* and *Smilodon* (Emerson & Radinsky, 1980; Christiansen, 2006), which is a further adaptation for attaining a large gape, but the marked degree of restoration makes this tentative.

Although the palate is only partly preserved, it is evident that *Megantereon* did not possess the
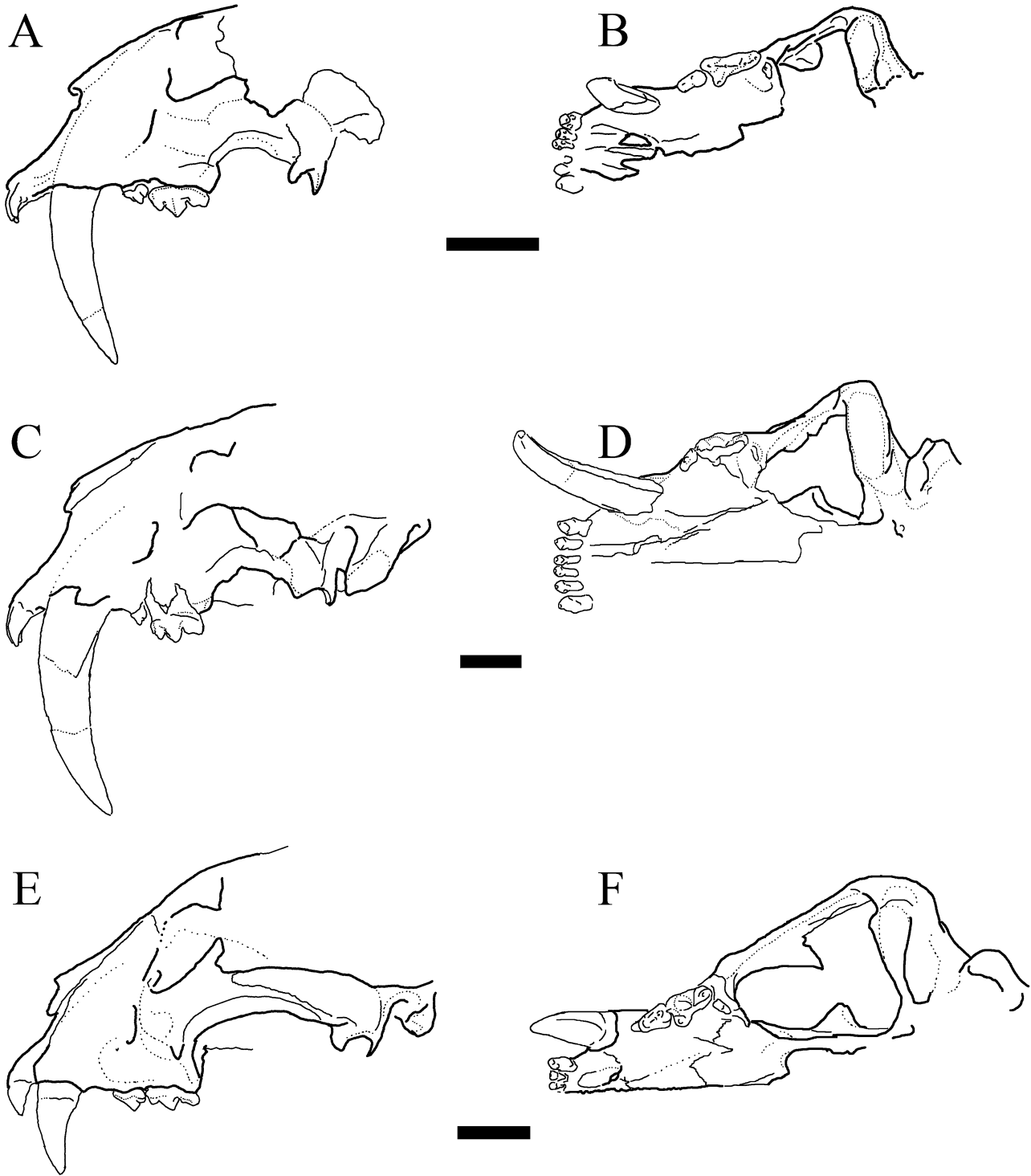
Figure 2. Comparative skull morphology of *Megantereon cultridens* SE311 (A, left lateral, and B, ventral view), *Smilodon populator* CN52 (C, left lateral, and D, ventral view) and a jaguar (*Panthera onca*) CN843 (E, left lateral, and F, ventral view). Scale bars = 5 cm. Only the portions which are preserved in *Megantereon* are indicated for all three species.
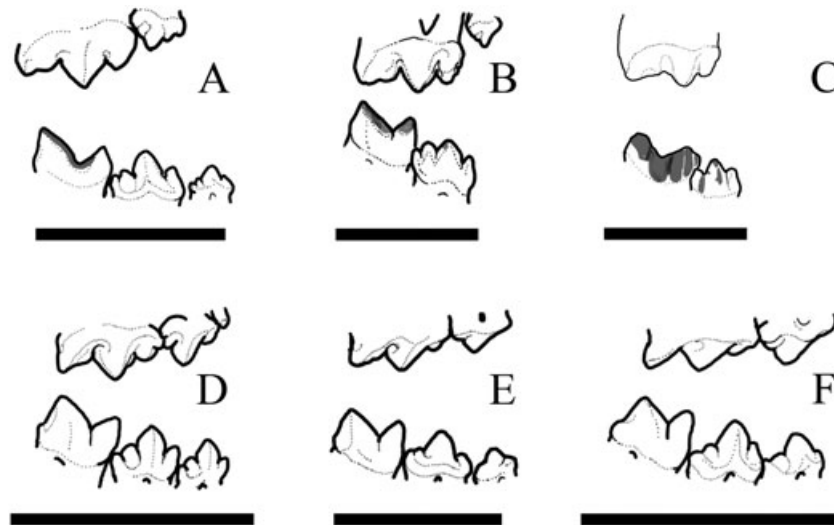
Figure 3. Comparative morphology of the upper and lower premolars and molars of M*egantereon cultridens* SE311 (A), *Smilodon populator* CN52 (B), *Homotherium serum* TMM 933–65 (P_4) and TMM933-3353 (P_4, M_1) (C), cheetah (*Acinonyx jubatus*) CN3793 (D), tiger (*Panthera tigris*) CN18 (E), and puma (*Puma concolor*) CN1673 (F). Scale bars = 5 cm. Labial attritional wear facets are indicated on the lower dentition.

palatal ridges that are present in *Smilodon* (Fig. 1B, D). The nasal aperture appears to have been distinctly proportionally larger than in extant felids, and broadly comparable with the equally hypertrophied apertures in *Smilodon* and *Homotherium*. The rostrum is comparable with the Dminisi specimen, described by Vekua (1995) as *M. megantereon* (= *M. cultridens*) and to the Perrier specimen MNHNPer2001a, although *M. 'megantereon'* lacks the nasals. The temporal fenestra are incompletely preserved (Fig. 1B, C), but it is fairly obvious that the size of the temporal musculature must have been distinctly less than in extant large felids (Fig. 2), and the bite force probably correspondingly lower.

All incisors are preserved, with the exception of the right I^1, where the crown is broken off, and the left I^3, where the tip of the main cusp is broken off. The preserved incisors are large, pointed and tricuspid, with one main cusp and two posterior accessory cusps, as commonly seen in other derived machairodonts. This condition differs from that of modern felids, which all have proportionally smaller, transversely spatulate I^1 and I^2, and where only I^3 is reminiscent of the shape observed in *Megantereon* and other derived sabrecats (Fig. 1B, E). The incisor arcade is procumbent and rounded, as in other derived sabrecats (Biknevicius, Van Valkenburgh & Walker, 1996), creating a conspicuously large diastema to the upper canine (Table 1), but is less anteriorly protruding than in *Homotherium*.

Both canines are well preserved, and only the tips were broken off but have subsequently been glued back together. They are enormously elongate and blade-like (Table 1), and entirely different from those of any extant carnivoran, and among sabrecats, only *Smilodon* has upper canines of comparable length. The cemento-enamel junction is located far from the alveolar margin, but less so at the mesial and distal crests than at the vestibular and lingual crests, as also found in *Smilodon* (Riviere & Wheeler, 2005; our pers. observ.). The canines, along with the rest of the dentition, lack crenulations, and appear largely unworn. In *Smilodon*, the canines tend to be slightly crenulated, and the incisors may also have slight crenulations along the cutting edges. In *Homotherium*, however, the entire dentition tends to be more or less serrated, especially the canines.

SE311 lacks a P^2, which is commonly found in extant lynxes (Werdelin, 1987), whereas most other modern felids have just a vestigial P^2. In *Smilodon* and *Homotherium*, it is absent. Both the left and the right P^3 are preserved, and are laterally compressed with a small parastyle, a reduced paracone and a small metastyle (Fig. 3). The cingulum is distally distinct, as in extant *Acinonyx*. The size of the parastyle and metastyle are not unusual compared with pantherine cats, but the paracone is distinctly smaller than observed in modern felids. Accordingly, the tooth as such is only slightly reduced, but not to the extent seen in *Smilodon* or *Homotherium*, in which the tooth is vestigial.

Both carnassials (P^4) are preserved, and are very large and mesiodistally elongate (Figs 1A, B, 2A, B, 3A; Table 1) with a distinct parastyle, a paracone, a metastyle blade and a small protocone. The presence of a cusped protocone differs from the condition
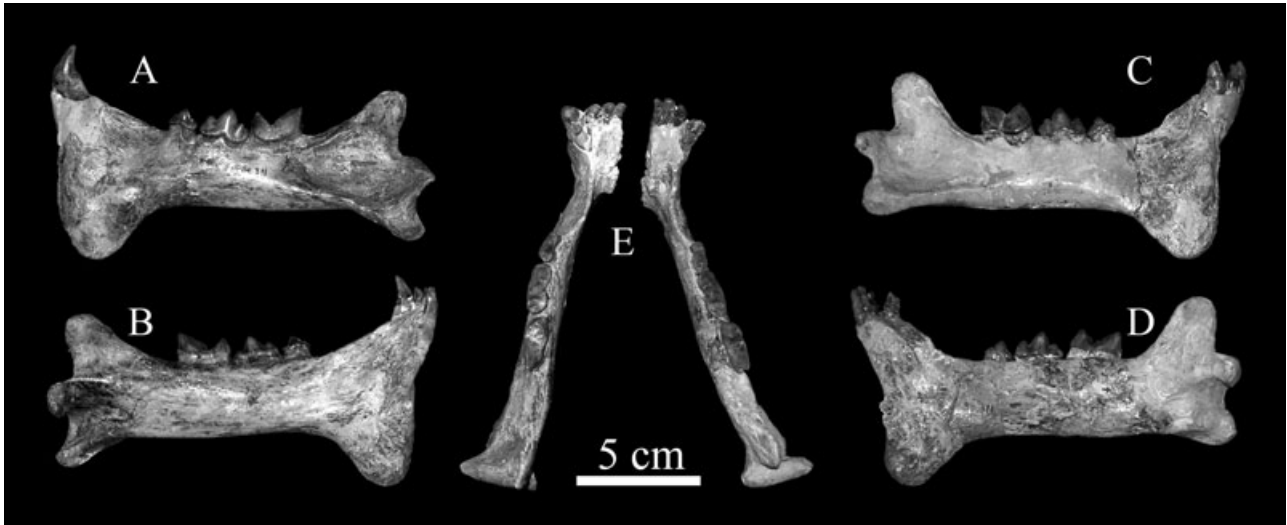
Figure 4. Hemimandibles of *Megantereon cultridens* SE311. Left mandible ramus in lateral (A) and medial (B) view; right mandible ramus in lateral (C) and medial (D) view; dorsal view (D) of lower jaw rami.

observed in several other, derived sabrecats, such as *Smilodon* and *Homotherium*, but also from advanced forms of *Machairodus*, where this cusp is absent. No ectoparastyle is present, contrasting with several other machairodonts. Owing to the better developed parastyle, with distinct sheering crests, and the small protocone, the tooth overall has a more blade-like appearance than in any pantherine, bearing a closer resemblance to the carnassial of *Acinonyx jubatus*, but it is not as advanced as observed in *Smilodon* or *Homotherium*. Both M^1 are preserved and are much reduced, but no more than often seen in extant felids.

MANDIBLE AND LOWER DENTITION

The left hemimandible is nearly complete with the exception of the labial part at the canine alveolus (Fig. 4A, B; Table 1). The right hemimandible (Fig. 4C, D) is much more fragmentary. Labially, the anterior portion is preserved, although not the area below the teeth, and lingually the ramus is preserved to just posterior to the carnassial, although with some restoration around the symphysis. The posterior part of the hemimandible, the angular process, condyle and the coronoid process is entirely restored, and looks similar to preserved portions of its left counterpart, although the coronoid process has been made larger (compare Fig. 4A, C). The dental formula for *Megantereon* SE311 (3/3 1/1 2/2 1/1) differs from those of extant pantherines (3/3 1/1 3/3 1/1). The mandible of the Dmanisi *Megantereon* (Vekua, 1995) is similar to that of SE311, with the exception of P_3 being more reduced in the former, and clearly offset from P_4. This could merely be intraspecific variation, and not nec-

essarily an argument for species differentiation. In MNHNPer2001b, P_3 is only slightly more reduced than in SE311, but is no more offset from P_4.

The large, rather robust incisors form a broad, protruding, subcircular battery, which includes the lower canine. Immediately posterior to the canine, the mandibular corpus curves lingually. An unusually large and distinct, but labiolingually thin mandibular flange is present, and it is distinctly larger than observed in *Homotherium* or *Smilodon gracilis*, resembling the condition commonly observed in certain nimravids, such as *Hoplophoneus* and *Eusmilus*. This morphology is entirely absent in any extant carnivoran. The symphyseal plates are very tall and nearly vertical, but rather shallow. The plates display a high degree of rugosity, as commonly seen in large felids, but lack the distal depth of extant large felids. A single, large mental foramen is present.

Viewed dorsally (Fig. 4E), the mandibular corpus curves distinctly medially around the premolars and carnassial, a condition known as carnassial rotation (Figs 4E, 5C, G, K; Bryant & Russell, 1995), resulting in a vestibular outwards turning of the teeth. The mandibular fossa is deep, but lower than observed in pantherines, owing to the much reduced coronoid process. The fossa reaches far anteriorly and protrudes below M_1, which is unusual in pantherines, but common in other derived sabrecats. The coronoid process is about the same height relative to the length of the ramus (Table 1) as in *Smilodon* and *Homotherium*, but is relatively shorter in the anteroposterior direction, rendering it more gracile in appearance than in the latter forms (Fig. 5A, E). The condylar process is transversely shorter and stouter
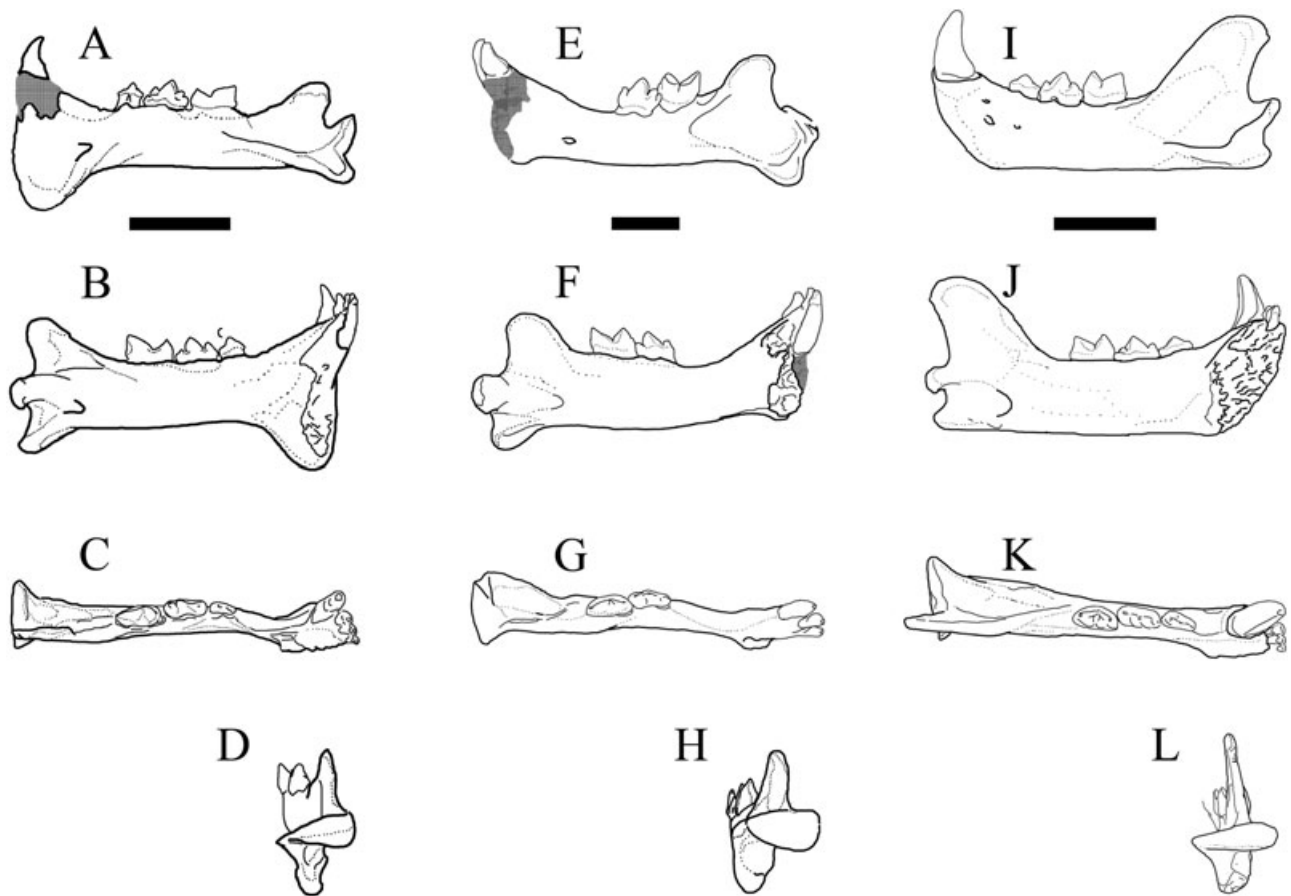
Figure 5. Comparative mandibular morphology of *Megantereon cultridens* SE311 (A, labial; B, lingual; C, dorsal; and D, posterior view), *Smilodon populator* L5350 (E, labial; F, lingual; G, dorsal; and H, posterior view), and jaguar (*Panthera onca*) CN5658 (I, labial; J, lingual; K, dorsal; and L, posterior view). Scale bars = 5 cm. Restored areas are indicated by cross-hatching.

than observed in pantherines, but not as stout as in *Smilodon* and *Homotherium*. The angular process is ventrally deflected and lingually directed, resulting in the jaw condyle protruding posteriorly to the angular process, a condition also found in other derived machairodonts, but unusual in pantherines (Figs 4A, B, 5I, J).

All teeth are preserved and no empty alveoli are present. The incisors are pointed and procumbent, as in other derived sabrecats (Biknevicius *et al.*, 1996), with a main cusp and two posterior accessory cusps. I_3 is the largest, followed by I_2 and I_1 (Table 1). The canine is much reduced in height, comparable with the condition in some species of *Machairodus*, but not completely incisiform as observed in *Smilodon* or *Homotherium*, as the canine is substantially larger than I_3 (Table 1; Fig. 5A, E). The teeth lack crenulations. P_3 is reduced in size, but distinctly larger than the P_3 of the Dmanisi specimen of *Megantereon* (Vekua, 1995; see also Dzaparidze *et al.*, 1992). It is

also directly adjacent to P_4, whereas in the former the two are separated by a large diastema. The tooth has a minute parastyle, a paracone and a small metastyle. This is similar to MNHNPer 2001b.

P_4 has a distinct parastyle, a paracone and a small metastyle. The cusps are more pointed than in extant pantherines (Fig. 3A, E, F) and are posteriorly inclined, but less so than in *Smilodon*, where the cusps of P_4 overlap with those of M_1, thus in effect creating one long shearing blade. The cheetah also has pointed cusps (Fig. 3D), but these are more blade-like, unlike the condition in *Megantereon* and other machairodonts. Contrary to the condition in *Smilodon* and *Homotherium*, the tooth is unworn (Fig. 3A–C). M_1 has a distinct paraconid and protoconid, but no discernible talonid. The tooth displays distinct wear facets (Fig. 3A), and a deep, worn, carnassial notch, distinctly deeper than usually observed in *Smilodon*, but not comparable to the extreme wear frequently present in *Homotherium* (Fig. 3C) where
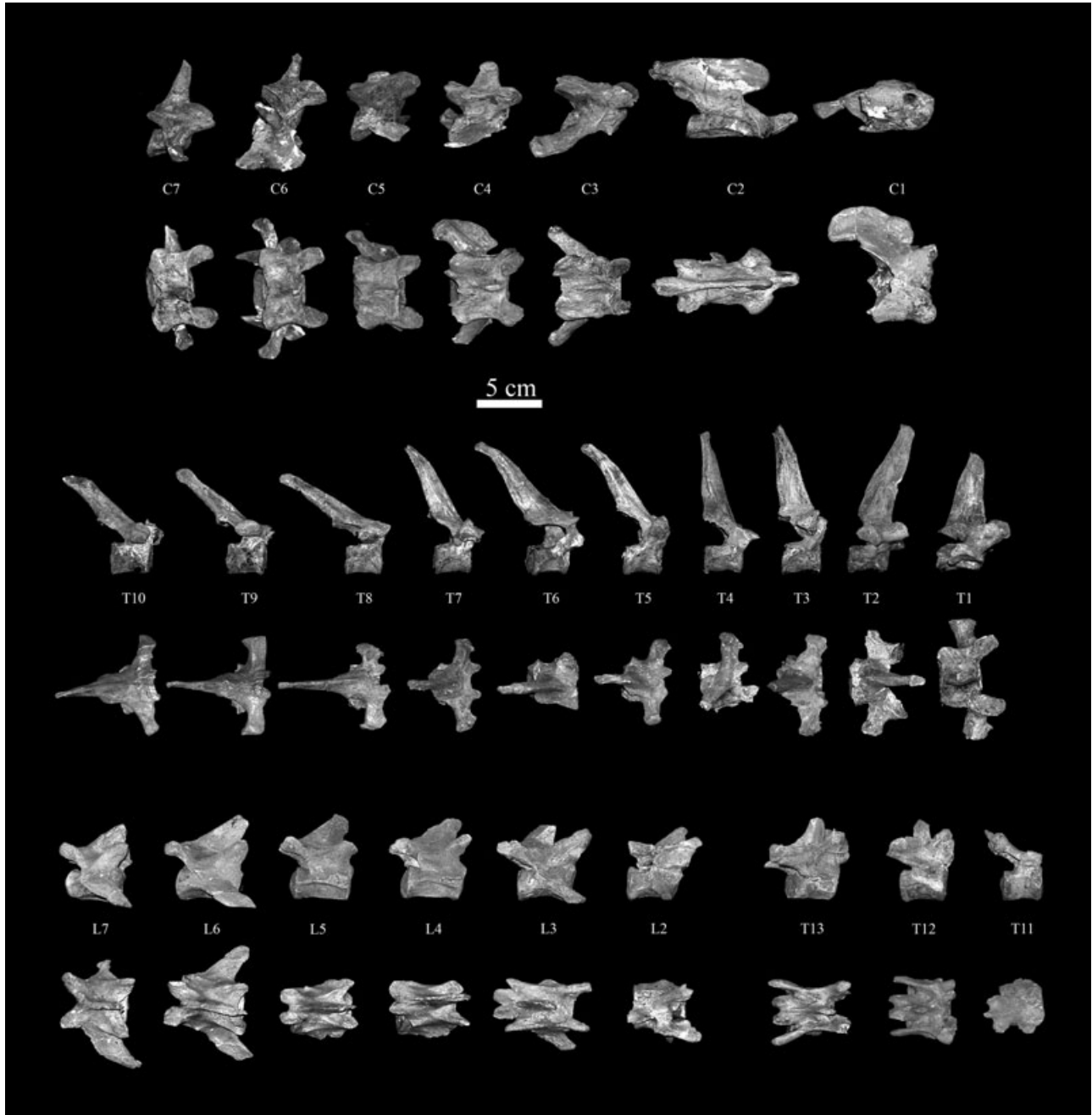
Figure 6. The presacral vertebral column of *Megantereon cultridens* SE311 in right lateral and dorsal view. Abbreviations: C, cervical vertebra; T, thoracal dorsal vertebra; L, lumbar dorsal vertebra.

the general shape of the tooth is often entirely altered by attrition (rather than abrasion, as indicated by the clearly visible traces of the P[4] cusps). This could indicate that *Meganteron*, like *Smilodon*, processed carcasses in a different manner from *Homotherium*. The wear on the carnassials in machairodonts is not comparable to the condition of the spotted hyena (*Crocuta crocuta*), where the carnassial cusps are

worn down by attrition, whereas wear in the former is always distinctly angular.

AXIAL SKELETON

The presacral vertebral column in *Megantereon cultridens* SE311 is almost complete (Fig. 6; Table 2), and the vertebral pattern of extant felids of seven

Table 2. Measurements (mm) of the vertebral series of *Megantereon cultridens* SE311

	Lz	Lc	Ch	Ns	Tp	Azw	Pzw
C1		50.7					
C2	76.0	84.9	19.0	19.1		51.7	42.2
C3	60.5	46.3	18.4		93.1	43.2	51.1
C4	54.8	45.6	20.7	20.3		59.1	55.2
C5	50.7	40.4	22.7			55.7	57.0
C6	49.1	37.7	22.3	24.9	105.0	60.2	62.1
C7	49.5	32.1	20.5	32.9+	88.8	59.4	59.0
T1	49.1	35.1	20.4	51.5+	86.5	57.3	41.6
T2	34.8	29.4	19.6	67.1	77.5+	31.0	
T3	33.7	27.9	21.8	55.4+	69.2	32.6	20.5
T4	39.8	28.2	19.7	55.3		24.8	21.2
T5	37.3	30.9	23.6	57.3	66.8		22.8
T6	42.4	34.2	23.6	74.0		26.2	23.2
T7	44.4	29.7	23.6	54.3+	71.9	27.4	24.6
T8	45.1	30.1	22.7	53.7	67.6	24.5	22.4
T9	45.1	31.7	24.8	47.4	76.9	21.9	21.1
T10	47.3	33.0	25.3	40.5+	78.3	24.9	23.7
T11		32.4	22.6				
T12	51.7	36.9	24.6	19.3		26.3	20.4
T13	64.7	36.6	23.5	24.5		25.9	22.4
L2	57.8	41.4	27.0	22.9			
L3	74.8	46.6	25.0	24.9		38.5	24.0
L4	67.1	53.0	28.3	33.6		38.1+	28.8
L5	65.7	52.1	26.4	32.8		37.1	30.1
L6	69.1	53.2	28.6	44.9		44.2+	38.2
L7	61.9	48.8	25.1	30.1+		51.0	47.2

The measurements given are as preserved, and in several cases the actual value should have been slightly higher, as indicated by a plus symbol.

Abbreviations: Azw, width across prezygapophyses; C, cervical vertebra; Ch, posterior height of centrum; L, lumbar vertebra; Lc, length of centrum; Lz, length of centrum from anterior margin of prezygapophysis to posterior margin of postzygapophysis; Ns, height of neural spine along its longitudinal axis; Pzw, width across postzygapophyses; T, thoracal vertebra; Tp, width across transverse processes.

cervical, 13 thoracic, seven lumbar and three sacral vertebrae is also present in *Megantereon*. As in other felids, the centra are generally amphiplatyan, albeit with gentle opisthocoeli in the cervicals. The apparent completeness of the presacral vertebral column of SE311 tends, however, to conceal the fact that several vertebrae are less well preserved, and in some cases key features are not discernible. Fortunately, most vertebrae are well preserved, and although several have been restored, this usually only amounts to cosmetic restoration. In several specimens of *Smilodon fatalis*, there is evidence of an extra thoracic dorsal or, alternatively, of one fewer lumbar dorsal vertebra (Merriam & Stock, 1932), but this is not the case in *Megantereon*, despite controversy about the identity of one of the dorsals, as noted below.

The vertebral column of well-known sabretoothed felids appears to differ from the morphology observed in large felines, such as extant and extinct *Panthera*, especially with regards to proportions and morphology of the cervical vertebrae (Schaub, 1925; Merriam & Stock, 1932; Rawn-Schatzinger, 1992; Turner & Antón, 1997; Antón & Galobart, 1999). However, a detailed comparison of vertebral proportions with extant large felids has not previously been made for any of the few sabrecats for which such a comparison is possible. For the purpose of this study, we measured the centrum length, posterior centrum height, width across the transverse processes (where applicable) and height of the neural spine of all 27 presacral vertebrae in 18 specimens of extant large felids (five *Panthera leo*; three *P. onca*, three *P. pardus*, four *P. tigris* and three *Puma concolor*), to which the vertebral proportions of *Megantereon* were then compared. Despite the frequent divergence of the vertebral proportions in *Megantereon* from extant
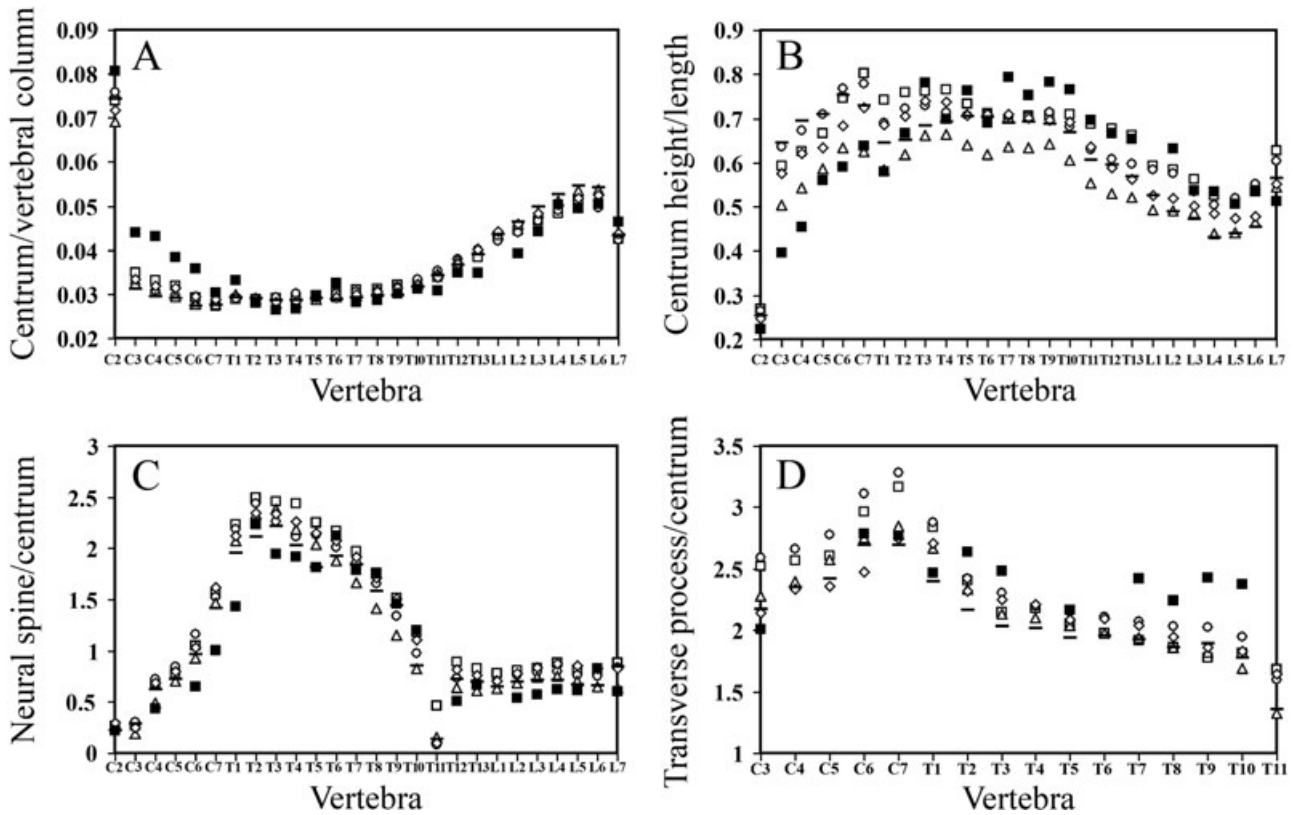
Figure 7. Vertebral dimensions along the vertebral column in *Megantereon cultridens* SE311 and averages of extant large felids. The included specimens of extant felids are listed in Table 5. A, length of centrum to length of the entire vertebral column; B, posterior height of centrum to length of centrum; C, height of neural spine to length of centrum; D, width across the transverse process to length of centrum. Symbols and abbreviation: C, T and L, cervical vertebra, thoracal vertebra, and lumbar vertebra, respectively; ■, *Megantereon cultridens* SE311; □, *Panthera leo* (N = 5); ○, *Panthera onca* (N = 3); △, *Panthera pardus* (N = 3); ◇, *Panthera tigris* (N = 4); –, *Puma concolor* (N = 3). The values for *Megantereon* were computed using a vertebral column length of 1053.2 mm, as in Table 5, where the sizes of the included specimens can also be seen.

large felids, especially with respect to the cervicals, *Megantereon* was built much along the lines of extant large felines, as shown by the uniformity of pattern of vertebral proportions along the presacral vertebral column (Fig. 7).

Cervical vertebrae

Schaub (1925) was the first to note the apparent hypertrophy of the anterior cervicals of *M. cultridens* SE311. All seven cervical vertebrae are present, and in general they are well preserved, although minor restoration has been carried out in several places. It is apparent that the cervicals, and not merely the anterior ones, are indeed proportionally larger than corresponding vertebrae in extant felids (Fig. 7A). In *Megantereon*, the great length of the cervical centra also makes them appear slightly gracile compared with extant large felids when comparing centrum

length to posterior centrum height (Fig. 7B), or the height of the neural spine compared with centrum length (Fig. 7C). However, the transverse processes, when preserved, are well developed, and even fall within the range of extant large felids, despite the size of the vertebral centra (Fig. 7D). The proportional size differences and divergent morphology of sabretoothed felid cervicals from extant felids has been attributed to the differences in the functional morphology of the upper cervical region, which is inferred to have resulted in different bite mechanics, as discussed under the palaeobiology section below.

Atlas (C1)

The atlas of *Megantereon* is a large, heavily constructed bone, and the vertebral body is distinctly more dorsoventrally massive than in extant large

felids, but bears a close resemblance to the morphology in *Smilodon* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992; see also Antón & Galobart, 1999). Unfortunately, the atlas in *Megantereon* is one of the least well preserved vertebrae. The corpus is large and massive and the medial tuberosity is long, low and massive, as in *Smilodon* (Merriam & Stock, 1932). The vertebral arch is much less deeply intended than in *Homotherium* (Rawn-Schatzinger, 1992), again resembling the condition in *Smilodon* (Merriam & Stock, 1932). The articular facets for the occipital condyles are deeply concave and are overhung by a wall of bone along the dorsal margin, as in other felids. The neural canal is subcircular, as in other felids. As in other felids, the entrance to the neural canal of the vertebrarterial canal is situated anterolaterally on the dorsal side of the atlas corpus and exits posterolaterally on the ventral side of the corpus. Ventrally there is a posterior lip for articulation with a notch basally on the axis odontoid process, as in other felids.

The most distinguishing feature of the atlas in derived sabretoothed felids, and the character in which they display the greatest divergence from the condition in extant felids, are the hypertrophied atlas wings. Unfortunately, the allegedly preserved left atlas wing of *Megantereon*, which resembles those of *Smilodon* (Figs 6, 8A, F) is entirely reconstructed. From the broken bases along the atlas corpus it is, however, evident that the transverse possesses must have been large, and the morphology of the closely related *Smilodon* and *Homotherium*, along with inferences of upper cervical function in derived sabretoothed felids (Turner & Antón, 1997; Antón & Galobart, 1999; Antón *et al.*, 2004; Salesa *et al.*, 2005), makes it likely that the processes were turned posteriorly, unlike the condition in extant felids. Strictly speaking, however, this is not discernible from the preserved specimen. As noted above, the similarity of non-preserved characters in *Megantereon* to corresponding characters in *Smilodon* is probably not accidental. In extant felids, the atlas wings rarely extend much posterior to the posteriormost extent of the articulating facets for the axis (Fig. 8K, P).

Axis (C2)
The axis of *Megantereon* is a very large and rather solidly constructed bone, as in other derived sabrecats. At a total length of nearly 85 mm, including the odontoid process (Table 2), it is larger than the largest specimens of *Homotherium* from the Friesenhahn Cave (Rawn-Schatzinger, 1992), despite this sabrecat being larger than *Megantereon* (Turner & Antón, 1997), and it is within the low range of *Smilodon fatalis* specimens from Rancho La Brea

(Merriam & Stock, 1932). Among extant felids, it is far larger than the axis in pumas (52.5–57.9 mm), leopards (49.2–59.5 mm) and jaguars (58.1–63.4 mm), and is comparable with male lions (e.g. CN1440: 85.5 mm, and CN6043: 86.9 mm) and almost the size of Siberian tigers (e.g. CN5698: 90.6 mm). The ventral keel along the centrum is well developed compared with extant large felids, indicating a strong attachment for the m. longus colli (Barone, 1967; Crouch, 1969; Done *et al.*, 2000). Among extant large cats, only *Acinonyx* has prominent ventral keels on the cervical centra.

As in other felids, the odontoid process is long and pointed at the anterior tip, but it forms a greater inclination to the long axis of the centrum than in *Smilodon* and extant large felids (Fig. 8B, G, L, Q), indicating a slightly more inclined position of the axis relative to the atlas. The anterior articulating surfaces for the atlas are very large and extend distinctly further dorsally than in extant felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932). Unlike *Smilodon* and extant felids, the dorsal part of the articulating surface is somewhat posteriorly inclined, resembling the condition in *Homotherium* (Rawn-Schatzinger, 1992). The postzygapophyses are very large and more elongate than in extant felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932), but are slightly more inclined, and distinctly more so than is usually the case in extant felids. In *Smilodon*, there is a large foramen for the vertebrarterial canal on the posterolateral face of the axis, but this is absent in *Megantereon*. In extant pantherines, the foramen is frequently present in lions and jaguars but often absent in leopards (Fig. 8B, G, L, Q). The transverse processes are preserved only as a fragment on the left side. The neural canal is taller relative to the transverse width than was the case in the atlas.

The neural spine appears very large, tall and winglike, but unfortunately the entire anterior part is reconstructed, and again resembles the condition of *Smilodon* (Fig. 8B, G). As in *Smilodon*, the posterior neural spine greatly overhangs the postzygapophyses, albeit less extremely. Merriam & Stock (1932) stated that this great posterior overhang in *Smilodon* 'presents a structure totally unlike that in the true felines' but this is only partly correct, since it is absent in the extinct *Panthera atrox* (Merriam & Stock, 1932) and in the extant lion, but is often present in jaguars, leopards and tigers (Fig. 8L, Q), albeit not developed to the extreme observed in *Smilodon* or *Megantereon*. Viewed dorsally, the posterior part of the neural spine in *Megantereon* becomes wide and triangular, although markedly less so than in *Smilodon*, and the posterior border is straighter than the sinusoid border of *Smilodon*.
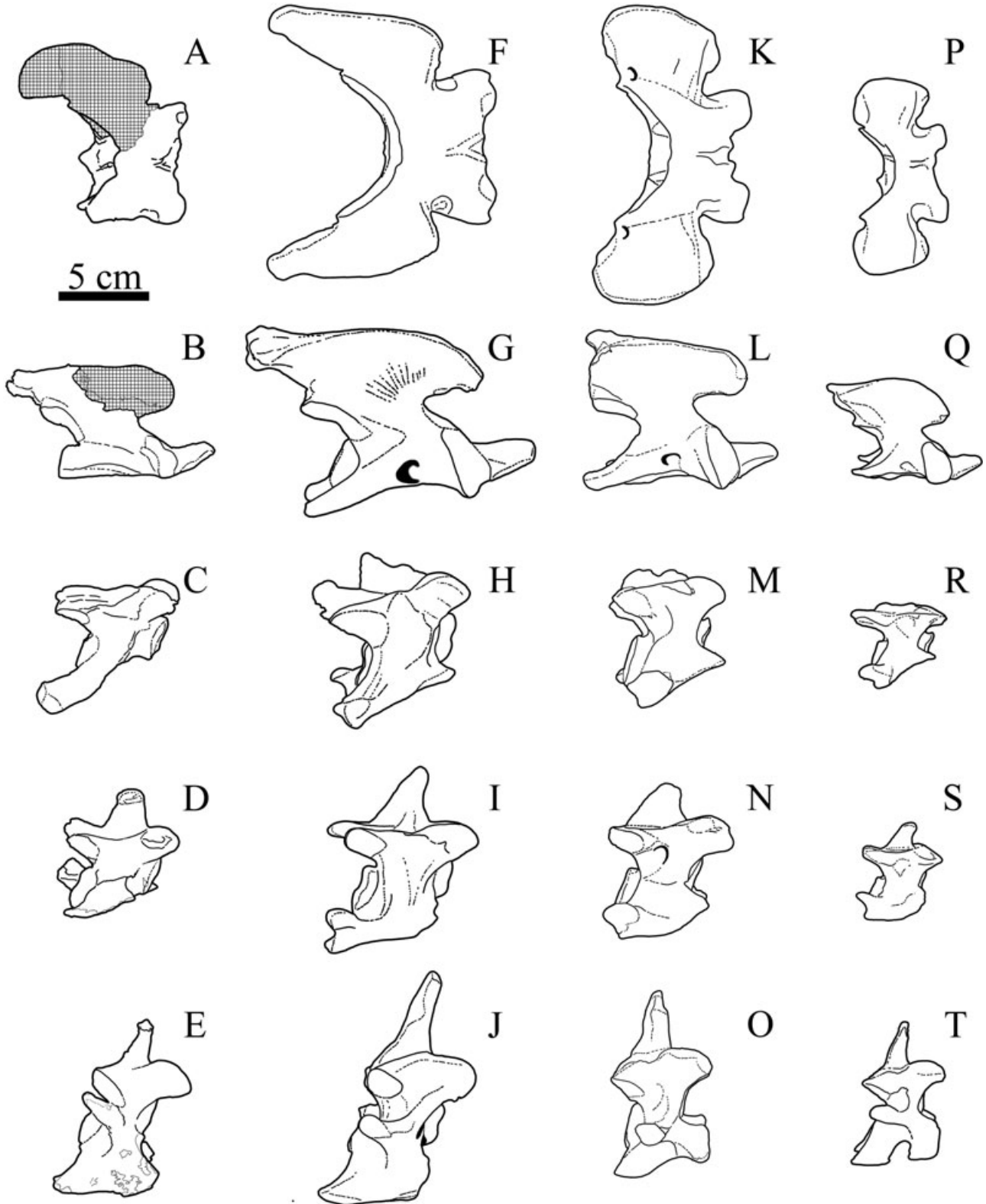
Figure 8. Comparative morphology of cervical vertebrae, all in right lateral view, except the atlas, which are in dorsal view. First row, atlas; second row, axis; third row, C3; fourth row, C4; fifth row, C6. A–E, *Megantereon cultridens* SE311; F–J, *Smilodon fatalis* (after Merriam & Stock, 1932); K–O, *Panthera leo* CN1440; P–T, *Panthera pardus* CN5662. Cross-hatching indicates restored areas.

Third cervical

The third cervical is well preserved. As in other felids, the centrum and its respective central articulating facets are greatly inclined. The most noticeable deviation from extant felids lies in the enormous development of the transverse processes, distinctly more so than in extant large felids and *Smilodon fatalis* (Fig. 8C, H, M, R). It is, however, comparable with the condition in the larger and more robust *Smilodon populator*. As in *Smilodon*, the transverse processes extend well posterior to the posterior face of the centrum, unlike the condition in extant felids. The diapophysial facet is markedly expanded compared with the process ramus, as in other felids, albeit more so than is usually the case in extant large felids. The hypertrophied transverse processes indicate particularly powerful m. longissimus cervicis and m. intertransversalis (Barone, 1967; Crouch, 1969; Done *et al*., 2000).

As in *Smilodon*, the posterior hyperapophyses are well developed and project posterodorsally as two elongate prongs. In extant felids they are more knob-like and less well developed. The neural spine is low but elongate, and is less well developed than in some specimens of *Smilodon* (Merriam & Stock, 1932) and most extant large felids. The neural canal is smaller and more rounded than is the case in the axis. A slit-like vertebrarterial foramen runs medial to a wall of bone along the dorsolateral side of the centrum, as in other felids. The ventral keel is also well developed. In dorsal view, C3 is markedly squarish in outline, but is less quadratic than in extant felids, owing to its proportionally greater centrum length (Fig. 7A). The prezygapophyses are large and oval, and are more inclined than often seen in extant felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932). This is also the case for the postzygapophyses. A round nutrient foramen extends into the base of the postzygapophysial pedicel, and in this position is often also found a foramen in extant felids, albeit much smaller.

Fourth cervical

The fourth cervical vertebra is also rather well preserved, although the right transverse process is incomplete. The central articulating facets are inclined relative to the long axis of the centrum, as in other felids. The neural spine is distinctly better developed than is the case in C3 and less anteriorly projecting than seen in *Smilodon* and most extant felids (Fig. 8D, I, N, S). The transverse processes are less well developed than was the case in C3. This is a deviation from the condition in *Smilodon*, in which the transverse processes of C4 are comparably developed with C3 (Merriam & Stock, 1932). Also unlike *Smilodon*, the diapophysial facet is not bifurcate. In

extant felids a bifurcate condition is frequently seen, albeit less extremely so than in *Smilodon*.

Ventrally, the inferior lamina is well developed, more so than in *Smilodon*. In extant felids, the inferior lamina is also usually well developed, albeit less so than in *Megantereon*. This indicates a strong development of the m. intertransversalis for twisting the cervicals about their long axis (Barone, 1967; Crouch, 1969; Done *et al*., 2000). The ventral keel is also well developed. The hyperapophyses are well developed, and resemble those of C3, although slightly thinner. The neural canal is more oval than is the case in C3. The prezygapophyses and postzygapophyses are more inclined than seen in extant large felids, and resemble the condition in *Smilodon*. The angular difference in inclination from the condition in extant large felids is, however, less than seen in C3.

Fifth cervical

Cervical five is quite well preserved, although the right transverse process is fragmentary and the neural spine has lost much of its height. It was, however, clearly well developed, as seen from its anteroposterior extension and lateromedial width. The centrum has inclined articulating facets, as in other felids. The lateral face of the centrum has undergone cosmetic restoration, and it is unknown whether a depression was present, as in *Smilodon* (Merriam & Stock, 1932). The left transverse process is less well developed than in C4, and distinctly less so than in *Smilodon*. The diapophysial facet is also not birfurcate, as in *Smilodon*. The dorsal transverse process lamella is not preserved, but since it is present in *Smilodon* and extant felids it can be inferred for *Megantereon* as well. The inferior lamella appears to have been rather well developed, but is not preserved in its entity on either side of the centrum. The above indicates a proportionally stronger development of the m scalenus primae costae than m. scalenus supracostalis (Barone, 1967; Crouch, 1969; Done *et al*., 2000). The prezygapophyses and postzygapophyses are slightly more inclined than in C4. The hyperapophyses are distinctly smaller than in C3 and C4.

Sixth cervical

Cervical six is well preserved and has only undergone cosmetic restoration along the inferior lamellae and transverse processes. It bears substantial resemblance to that of *Smilodon* (Fig. 8E, J), but the neural spine is less well developed and the postzygapophysis is proportionally larger and less steeply inclined. The transverse processes are well developed, but are slightly more gracile than the condition in *Smilodon*. In extant felids, the hyperapophyses are usually small, wing-like extensions dorsally to the postzyga-

pophyses, but in both *Megantereon* and *Smilodon* they are distinctly less well developed on C6 (Fig. 8E, J, O, T). The vascular foramen along the centrum is distinctly larger than in C4–5. The greatest divergence from extant felids is found in the enormous development of the inferior lamina (Fig. 8E). This indicates a more powerful development of the m scalenus primae costae than the m. scalenus supracostalis (Barone, 1967; Crouch, 1969; Done *et al.*, 2000). The lamella is less triangular than in *Smilodon* and does not extend as markedly posteroventrally.

Seventh cervical

Cervical seven is well preserved and only the tip of the neural spine and smaller sections of the left transverse process are missing. As in other felids, the centrum articulating facets are less steeply inclined compared with the long axis of the centrum than is the case in the preceding cervicals. Also, as in other felids, the neural spine is distinctly larger compared with centrum length than in the preceding cervicals (Fig. 7C). The postzygapophyses are less steeply inclined than in the preceding cervicals, unlike the condition often seen in extant felids, where there is less difference in inclination. The transverse processes are less well developed compared with centrum length than in *Smilodon* (Merriam & Stock, 1932), but comparable with the condition in extant large felids (Fig. 7D). There is no indication of an inferior lamella. The hyperapophyses are very small, and distinctly less well developed than in extant large felids. The neural canal is lateromedially wider than in the preceding cervicals. There is no vertebrarterial foramen along the sides of the centrum, as in extant large felids. In some specimens of *Smilodon* this feature may, however, occasionally be present (Merriam & Stock, 1932).

Dorsal vertebrae

In general, the dorsal vertebral column is well preserved, although several vertebrae have undergone cosmetic restoration. In some cases, for instance T2–7, a more extensive restoration around the neural arches has taken place, resulting in a peculiar anterior inclination of the neural spine of T2 (Figs 6, 9B). Generally, the dorsal vertebral column differs less in *Megantereon* from the proportions and morphology observed in extant large felids than do the cervicals. The centra are, however, often slightly more massive in comparison with their length, and the transverse processes are well developed compared with the length of the centrum (Fig. 7B, D). The neural spines appear well developed in *Megantereon*, but relative to centrum lengths they are, in fact, comparable with those of extant large felids, and in the anterior dorsals they are actually less well developed (Fig. 7C).

In *Smilodon*, the thoracic vertebrae usually have very well-developed neural spines (Fig. 9G–J; Merriam & Stock, 1932), but in *Homotherium* (Rawn-Schatzinger, 1992) they appear to be distinctly lower than in extant felids, and also *Megantereon*.

First thoracic

The first thoracic vertebra is solidly constructed; more so than in extant felids, and the neural spine, although lower than in extant felids, is very wide anteroposteriorly. It is, however, more lateromedially slender than the condition in *Smilodon* and the upper section appears to have been slightly less lateromedially dilated, although the apex is missing. The upper part of the neural spine of *Megantereon* is triangular in cross-section, resembling the condition in *Homotherium* (Rawn-Schatzinger, 1992). The transverse processes are short and massive, and are of similar width relative to centrum length to those of extant large felids (Fig. 7D), but are slightly less well developed than in *Smilodon*. The concave and elongate diapophysial facet is well developed and is almost the length of the centrum, indicating that the tuberculum of the first dorsal rib was large. The diapophysis in *Megantereon* is proportionally larger than those of extant felids, although tigers and lions sometimes also have very large diaphysial facets (Fig. 9A, M), and also than that of *Smilodon* (Fig. 9G).

The parapophysis is situated anteroventrally at the basis of the transverse process adjacent to the anterior articulating facet of the centrum, as in other felids, but is less well demarcated than in extant large felids and *Smilodon*, probably owing to postmortem abrasion. In *Smilodon*, there is a distinct ventral keel on T1 (Merriam & Stock, 1932), and this is frequently also seen in extant large felids, albeit less well developed. In *Megantereon*, a low ridge runs along the ventral part of the centrum, but it is less well developed than in *Smilodon*. The prezygapophyses are inclined to around a 45° angle, as in other felids. The postzygapophyses are, however, slightly more steeply inclined than in *Smilodon* and extant large felids. The neural canal is distinctly lateromedially oval, as in *Smilodon* and extant felids, and less circular than in *Homotherium* (Rawn-Schatzinger, 1992).

Second thoracic

The second thoracic vertebra is almost complete but for a small portion of the right transverse process. In *Homotherium*, T1 and T2 are very similar (Rawn-Schatzinger, 1992). This is not the case in *Megantereon*, *Smilodon* and extant large felids, where the neural spine of T2 is not just larger in absolute measure, but is distinctly larger proportionally to centrum length, and the transverse processes are
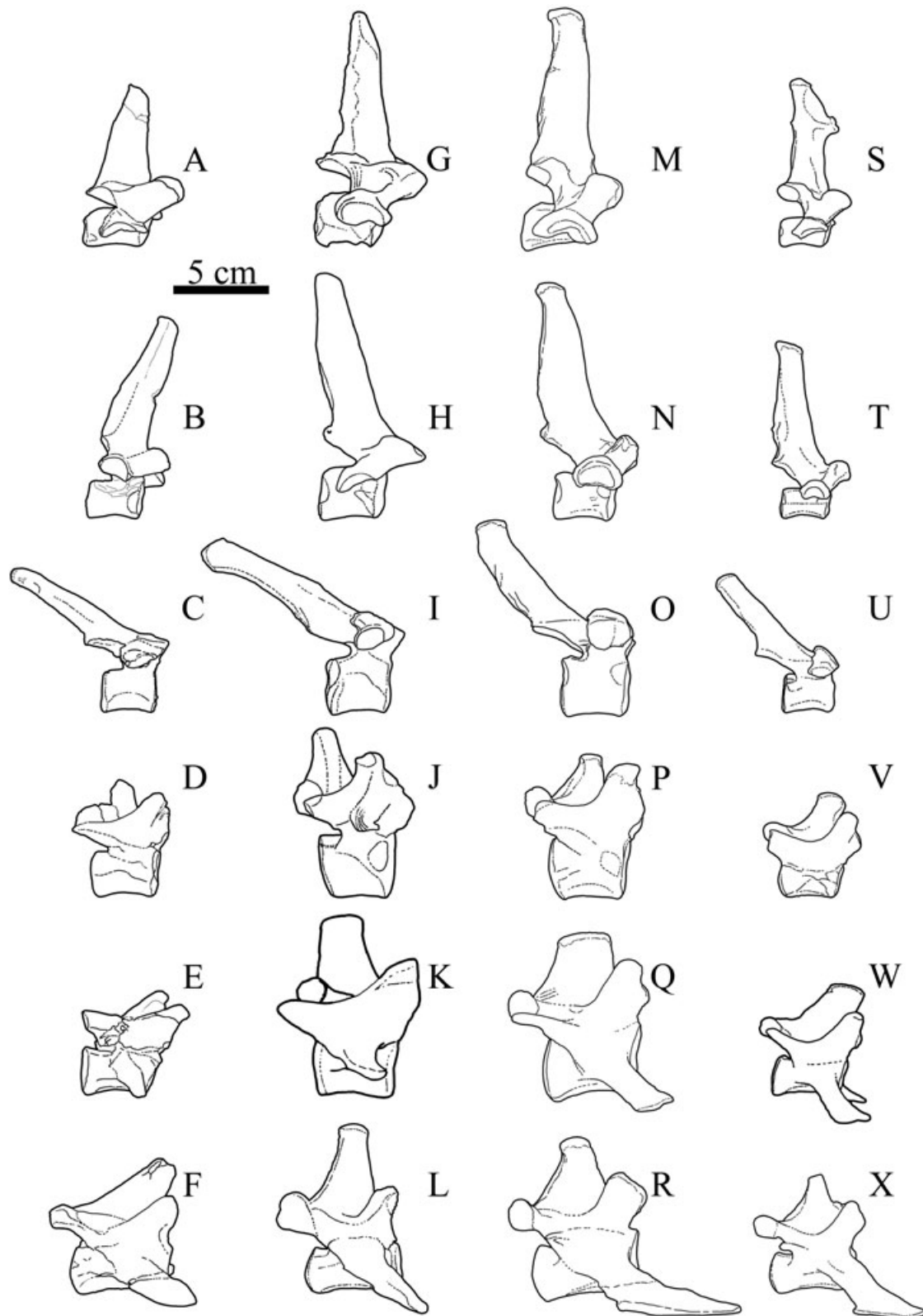
Figure 9. Comparative morphology of dorsal vertebrae, all in right lateral view. First row, T1; second row, T2; third row, T8; fourth row, T12; fifth row, L2; sixth row, L6. A–F, *Megantereon cultridens* SE311; G–L, *Smilodon fatalis* (after Merriam & Stock, 1932); M–R, *Panthera leo* CN1440; S–X, *Panthera pardus* CN5662.

proportionally distinctly more narrow compared with centrum length than is the case in T1 (Fig. 7C, D). In *Megantereon*, the difference in neural spine height relative to the length of the centrum is readily apparent (Figs 6, 9A, B), although the apex is missing in T1. This is both owing to the increased height of the spine itself relative to the spine of T1, as in other felids, but also owing to the centrum of T2 being distinctly longer relative to T1. Compared with the condition in extant felids, this is, however, not owing to a proportionally small T2 but a proportionally large T1 (Fig. 7A). In extant felids, the centrum of T2 can be both smaller, of similar size and larger than T1, but usually by no more than 1–2 mm, whereas the difference is > 5 mm in *Megantereon*. *Smilodon* and *Homotherium* appear to follow the condition observed in extant felids (Merriam & Stock, 1932; Rawn-Schatzinger, 1992).

The diaphysial facet is distinctly smaller than in T1, and more resembles the condition of other felids and faces more laterally than on T1, as in other felids. Also, the parapophysis has migrated to the anterolateral face of the centrum and is situated around the middle of the centrum, which is slightly lower than in *Smilodon* and extant large felids (Fig. 9B, H, N, T). The posterior demifacet is markedly larger on T2 than on T1.

Thoracic 3–10
The pattern along thoracic vertebrae 3 to 10 in *Megantereon* follows that of other felids. The parapophysis is situated at the upper, anterolateral part of the centrum on T3, and remains approximately in this position in the succeeding thoracics, as in other felids. The posterior demifacet tends to be situated slightly higher than on T2, but also remains in approximately the same position and is of a similar size throughout T3–10. The percentile length of the centra of T3–10 of the entire presacral vertebral column follows the patterns observed in extant large felids closely (Fig. 7A). The centra do, however, appear somewhat heavier in build than in extant felids, as seen from their greater dorsoventral diameters relative to length along T3–10 (Fig. 7B). The pre- and postzygapophyses are horizontally orientated and gently slope ventolaterally, and the postzygapophyses are usually slightly more inclined. This is similar to the condition in other felids.

The height of the neural spines along T3–10 relative to centrum length follows the pattern observed in extant large felids closely (Fig. 7C), although they are somewhat shorter in T3–5. As in other felids, the neural spines become progressively more posteriorly inclined towards the rear, having an inclination of around 35–40° to the long axis of the centrum in T8–10 (Fig. 9C, I, O, U). Where preserved (Fig. 6), the transverse processes are proportionally wider and

more heavy in overall build than in extant large felids (Fig. 7D), and they bear substantial resemblance to corresponding vertebrae in *Smilodon* (Merriam & Stock, 1932). The neural canal gradually becomes less oval further posteriorly and also decreases in absolute size.

The diaphyses show slightly varying degrees of posterior and lateral inclination along the thoracic vertebral column, but this is clearly both owing to some actual variation of the facets along the vertebral column, as seen in other sabrecats such as *Smilodon* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992), and extant large felids, but is in some cases also due to restoration, for instance on T6 (Fig. 6). The metapophyses are fairly prominent on T3–10, and in general become progressively larger towards the rear, as in *Smilodon* and extant large felids. This does not necessarily occur linearly, however, as the metapophysis is large on T7 and T10, but is less well developed on T8 and T9 (see Fig. 9C). Such variation is also seen in other felids. As in other felids there are no anapophyses prior to T11.

Eleventh thoracic
This vertebra is unfortunately not well preserved, and has been restored with peculiar-looking postzygapophyses situated on thin pedicels (Fig. 6). This imperfect preservation results in a morphology that is quite different from a posterior thoracic or lumbar vertebra in any felid. In the mounted skeleton of *Megantereon* (see Fig. 27, further below), it was placed as the third lumbar, but this is evidently incorrect. Although lacking the entire upper section above the neural arches, thus making identification difficult, the centrum bears a distinct parapophysis and shows evidence of having had rather thick transverse processes situated on the neural pedicels and not the lateral face of the centrum, and is thus congruent with T11 and not with a lumbar, or, for that matter T12 or T13. The vertebra is proportionally slightly shorter than in extant large felids (Fig. 7A) and is heavy in build (Fig. 7B). The posterior-most dorsals and lumbars also show the characteristic size increase compared with the thoracals observed in other felids.

According to Rawn-Schatzinger (1992), the transition from anterior-mid to posterior dorsals in *Homotherium* occurs at T12, where the prezygapophyses are orientated almost horizontally, as in the preceding dorsals, but the postzygapophyses are orientated sharply laterally, as in the succeeding dorsals and lumbars. This is an unusual condition. In *Megantereon*, *Smilodon* and extant felids, this transition occurs at T11. The transition is also evident in the position of the zygapophyses, in that the postzygapophyses are situated on elongate pedicels well above

the level of the prezygapophyses. In extant large felids, the transition is also evident in the great reduction of the neural spine compared with both preceding and succeeding vertebrae (Fig. 7C). In *Smilodon*, two morphs are present, one lacking and one possessing a well-developed neural spine on T11 (Merriam & Stock, 1932), but the state of preservation in *Megantereon* does not allow detailed comparison with either.

Twelfth thoracic

Thoracic vertebra 12 is well preserved, and bears resemblance to that of other felids (Figs 6, 9D, J, P, V). The metapophysis is well developed and rises to two-thirds of the height of the neural spine. In extant large felids, it often almost reaches the top of the neural spines. In extant felids, a wide, wing-like lamina extends from the anterior part of the centrum up along the metapophysis, and this is also the case in *Megantereon*. Although small portions are missing, it would appear that the lamina is slightly less well developed than in *Smilodon* (Fig. 9D, J) and comparable with the condition in extant large felids. The apex of the metapophysis is distinctly thickened, as in other felids. The anapophysis is also well developed, and appears better developed than in *Smilodon* (Fig. 9D, J) given that it virtually overlaps the postzygapophysis, as commonly seen in extant large felids (Fig. 9V). Viewed dorsally, the anapophyses appear proportionally slightly more slender than in *Smilodon* (Merriam & Stock, 1932), and broadly comparable with those of extant large felids. The apex is slightly thickened and rugose, as in other felids.

As in other felids, the intervertebral notch of T12 in *Megantereon* is distinctly V-shaped, and comparisons with *Smilodon*, *Homotherium* and extant felids imply that this was also the case for the notch on T11, although this section is not preserved. Unlike extant felids, the apex of the neural spine is not thickened. The parapophysis is well developed but the diapophysis is indistinct. This is also frequently the case in extant felids. In *Smilodon*, the facet may be present on both sides of the centrum, one side only, or absent, which appears to be the most common condition (Merriam & Stock, 1932).

Thirteenth thoracic

The last thoracic vertebra is also well preserved and bears great resemblance to T12. In contrast to the condition in extant felids, where the centrum of T13 is often 1–2 mm longer than in T12, the two are almost the same size in *Megantereon* (Table 2). As in other felids, the metapophyses are larger than on T12, as are the anapophyses. The neural spine is slightly more anteriorly inclined and the parapophysis is situated lower on the anterior face of the centrum, as in

other felids. The zygapophyses, metapophyses, anapophyses and neural spine appear slightly less well developed relative to centrum length than in *Smilodon* (Merriam & Stock, 1932).

Lumbar 2–7

The first lumbar vertebra is not preserved. The transverse processes are absent in L2, L4 and L5, and in L3 the apex of the right transverse process is missing. In L6, the apex of the right transverse process is missing, whereas almost the entire process is missing from L7. The metapophyses and anapophyses are fully preserved only on L3. On L2, most of the anapophyses are not preserved, and in L4–7 the anapophyses were evidently greatly reduced, perhaps even more so than in extant felids, where they merely constitute thin prongs. In contrast, the metapophyses of *Megantereon* remain well developed on all lumbars, although imperfectly preserved in L4–6. This is similar to the condition in other felids.

Apart from this, the vertebrae are generally well preserved and show the same overall pattern as other felids in becoming progressively larger from L2 to L6, and then sharply decreasing in centrum length at L7 (Table 2, Fig. 7A). The length of the centra relative to the entire presacral vertebral column, and the height of the posterior face of the centrum relative to centrum length closely follow the patterns observed in extant large felids. As in other felids, the transverse processes curve distinctly anteriorly and also become progressively larger towards the rear. In general, they appear comparably developed to the condition in *Smilodon*, and they are less anteriorly inclined than in extant felids, and more laterally orientated (Fig. 6). Overall, the lumbar transverse processes are distinctly less well developed in *Megantereon*, *Smilodon* and *Homotherium* relative to centrum size than in extant large felids (Figs 7C, 9F, L, R, X). The proportionally greater size of the lumbars (Fig. 7A) and markedly anterior inclination of the transverse processes (Fig. 9R, X) in extant large felids, however, result in their actually appearing more narrow relative to centrum size than in *Megantereon* (Fig. 7D).

The neural canal is distinctly oval in the anterior lumbars, which is accentuated towards the rear, where the neural canal is almost squarish, as in other felids. As in other felids, the zygapophyses are sharply inclined to approximately 60–70°, and increase in size from L2 to L4, after which they decrease slightly again. In general, they appear less well developed than in *Smilodon* (Merriam & Stock, 1932). The height of the neural spines increases towards the rear (Table 2), as in extant felids, but because the centra also become longer the ratio of neural spine height to centrum length changes less towards the rear. *Megantereon* follows the pattern
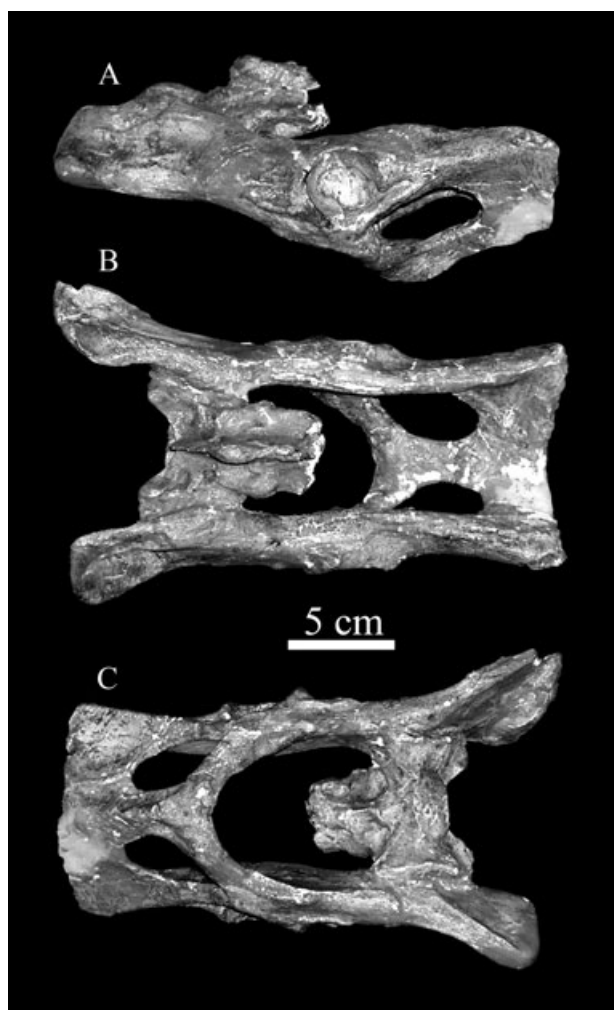
Figure 10. Pelvis of *Megantereon cultridens* SE311 in left lateral (A), dorsal (B) and ventral (C) view.

observed in extant felids closely, but its neural spines appear rather short, with the exception of L6 (Fig. 7C). As in other felids, the last lumbar is markedly shorter than L6 and has a much greater width across the postzygapophyses, providing strength and stability to the sacroiliac joint.

Sacrum

The three sacrals are firmly co-ossified to each other and to the lateral face of the iliac wings. The sacroiliac joint is very powerfully constructed (see also Schaub, 1925). The left sacroiliac joint has, however, undergone cosmetic restoration, as have parts of the surface and neural spines (Fig. 10B). The anterior sacral connects to the ilia with very strong transverse processes, and the neural spine is missing. The prezygapophyses are angled at around 50°, comparable with the condition frequently seen in other felids. They are more anteroposteriorly elongate than
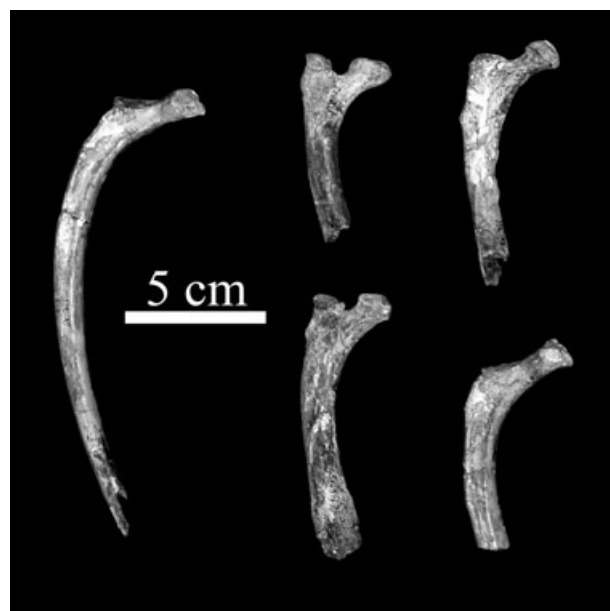

Figure 11. Rib elements of *Megantereon cultridens* SE311.

in *Smilodon*. The sacrum rapidly tapers posteriorly and the neural spines are moderately tall, less so than in *Smilodon* (Merriam & Stock, 1932), but like the condition in *Smilodon*, they are more massively built than in extant large felids. Ventrally, the anterior sacral centrum is gently convex, and as in other felids, sacrals two and three develop a prominent keel. Unfortunately, the posterior part of the last sacral is weathered, and the postzygapophyses are not preserved.

No caudals are preserved, but the tail of *Megantereon* was presumably short, owing to the strong posterior tapering of the sacrum, more so than in extant large felids and resembling the condition in *Smilodon* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992), and the fact that the tails also appear to have been short in these two closely related forms.

RIBS

There are a number of ribs preserved (Fig. 11), both from the anterior and the mid-posterior part of the ribcage, although a positive assignment of the elements is not possible, other than the first rib. The first rib was much straighter than the following and very short and heavy with a massive rugosity ventrally for the costal cartilage. Overall the ribs bear substantial resemblance to those of other felids.

SHOULDER GIRDLE AND STERNUM

The sternum is represented by the complete manubrium and four mesosternal elements (Fig. 12C–E).
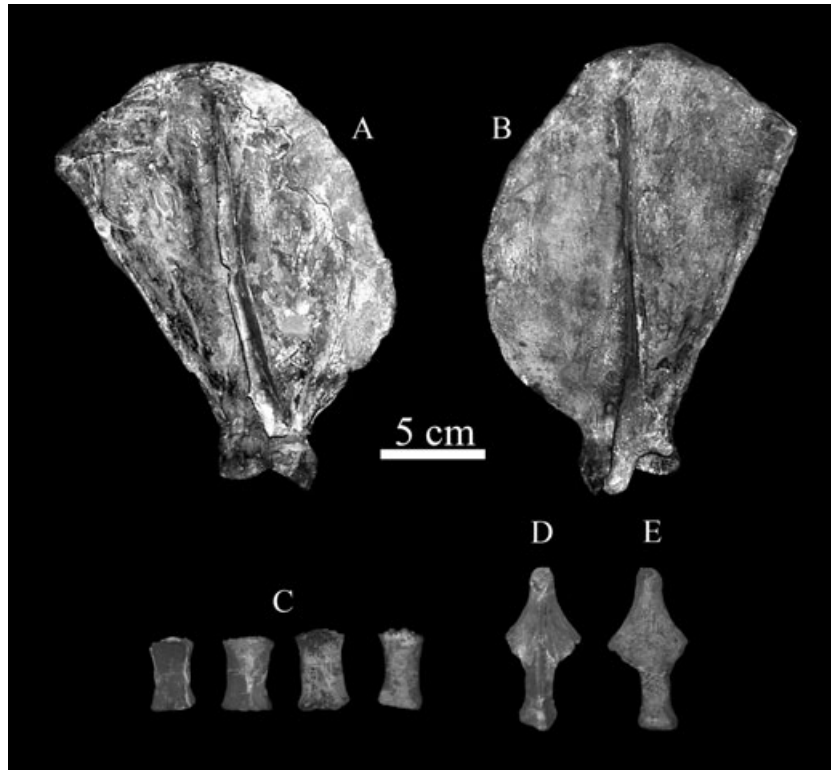
Figure 12. Scapulae and sternal elements of *Megantereon cultridens* SE311. Right scapula (A) and left scapula (B), both in lateral view; mesosternal elements (C); manubrium in ventral (D) and dorsal (E) view.

No parts of the xiphisternum are preserved. The anterior, triangular portion of the manubrium was originally broken away from the posterior, almost rectangular section, but has subsequently been glued back together. The bone has not been restored. Proportionally, it bears great resemblance to that of *Smilodon* (Merriam & Stock, 1932), except that it is slightly more slender. Typically of derived machairodont felids it is, however, much more heavy in build than in extant large felids, even large tigers, and only large, older male lions occasionally have manubria that approach, although do not reach, such heavy proportions.

The dorsal surface is bevelled with a prominent median ridge extending to the extreme apex. The ventral surface is gently concave. The posterior facet for the mesosternum is cut off squarely, and the rugose facets for the first costal cartilage are large and heavy. As in *Smilodon* and extant felids, the apex is rugose and incompletely formed, indicating cartilaginous covering in life. At a length of 77.1 mm, it is distinctly smaller than *Smilodon* manubria, which range from 100 to 141 mm (Merriam & Stock, 1932). It is comparable with those of lions ($N = 7$; 73.8–101.1 mm) and tigers ($N = 12$; 66.9–93.6 mm), and is much larger than in leopards ($N = 4$; 47.6–60.7 mm)

and jaguars ($N = 4$; 61.7–69.5 mm). The mesosternal elements resemble those of *Smilodon* and other large felids in being square and heavy, and in having a gently convex dorsal and gently concave ventral surface. The end facets for other sternal elements are rugose. The size (length × width at middle) of the four mesosternal elements are: 35.5×16.8 mm; 35.5×19.0 mm; 37.7×15.8 mm; and 38.3×19.4 mm.

Both scapulae are present and generally well preserved, although the left scapula is the better preserved of the two (Fig. 12A, B). The left scapula is virtually complete, although minor parts of the supraspinous and infraspinous fossae and scapular spine have been superficially restored. The dorsoventral length in straight line from the superior border to the lower margin of the glenoid fossa is 221.6 mm. The right scapula has undergone more extensive restoration, and the distal part of the scapular spine and acromion process are absent. The supraspinous fossa has been entirely restored along the anterodorsal border. As preserved, its dorsoventral length is 217.8 mm. Scapula length in *Megantereon* is comparable with lions ($N = 17$; ♀: 175.7–242.1 mm; ♂: 210.2–288.4 mm) and Bengal tigers ($N = 15$; ♀: 190.7–241.7 mm; ♂: 199.1–241.3 mm), and far larger than in leopards ($N = 16$; ♀: 123.2–150.8 mm; ♂:

144.6–170.3 mm), and jaguars ($N = 8$; ♀: 152.1–158.2 mm; ♂: 163.3–172.6 mm). Scapula length in *Smilodon* is 266–358 mm (Merriam & Stock, 1932), far exceeding the scapula size in even Siberian tigers ($N = 3$; ♂: 270.5–284.8 mm), despite *Smilodon* being lion-sized overall (Kurtén & Anderson, 1980; Akersten, 1985), albeit substantially more massive in build (Christiansen & Harris, 2005). This indicates that derived sabrecats had large scapulae for their body size.

The scapula is typically felid in overall morphology, but there are noticeable differences from both extant large felids and *Smilodon*. The cranial border is strongly curved, the caudal border is virtually straight from the caudal angle to the glenoid fossa and not sinusoid as in *Smilodon*, and the caudal angle is cut at an angle of ~104°. In all those characters, *Megantereon* bears a substantially closer resemblance to the condition in extant large felids than in *Smilodon* (Merriam & Stock, 1932). As in *Smilodon*, the spina scapula is rather straight and does not curve across the infraspinous fossa, as commonly seen in extant felids. The spina scapula reaches a maximum height of 36.9 mm in the left scapula. This is proportionally greater relative to scapula length than in *Smilodon*, and is similar to the proportions in *Neofelis nebulosa* ($P = 0.378$) and *Panthera tigris* ($P = 0.517$), but is less than in *Puma concolor* ($P = 0.001$), *Panthera leo* ($P = 0.022$), *P. onca* ($P = 0.018$) and *P. pardus* ($P = 0.043$). Accordingly, *Megantereon* has a proportionally lower spina scapula than several of the big cats (Fig. 13A).

Megantereon has a distinct, short and very heavy metacromion process, which constitutes a difference from *Smilodon*, in which this process is absent (Merriam & Stock, 1932). The acromion process is very large and heavy, distinctly more so than in *Smilodon* and extant large felids, indicating that the m. acromiodeltoideus (Barone, 1967; Crouch, 1969; Done *et al.*, 2000) was powerfully developed. The scapular notch is more clearly demarked than in *Smilodon*, resembling the condition in extant large felids. The supraglenoid tubercle is similar to those of other large felids. The scar for the m. biceps brachii is well developed, as in other large felids.

The scapula of *Smilodon* is markedly narrower than is the case in extant felids. The scapula of *Megantereon* is distinctly wider relative to overall length than in *Smilodon*, resembling the condition in extant large felids more closely. The infraspinous fossa in *Megantereon* appears comparably developed with the condition observed in *Smilodon*, but the supraspinous fossa is distinctly larger, indicating that *Megantereon* had more powerfully developed m. supraspinatus (Barone, 1967; Crouch, 1969; Done *et al.*, 2000) than did *Smilodon*. The scar for the m.
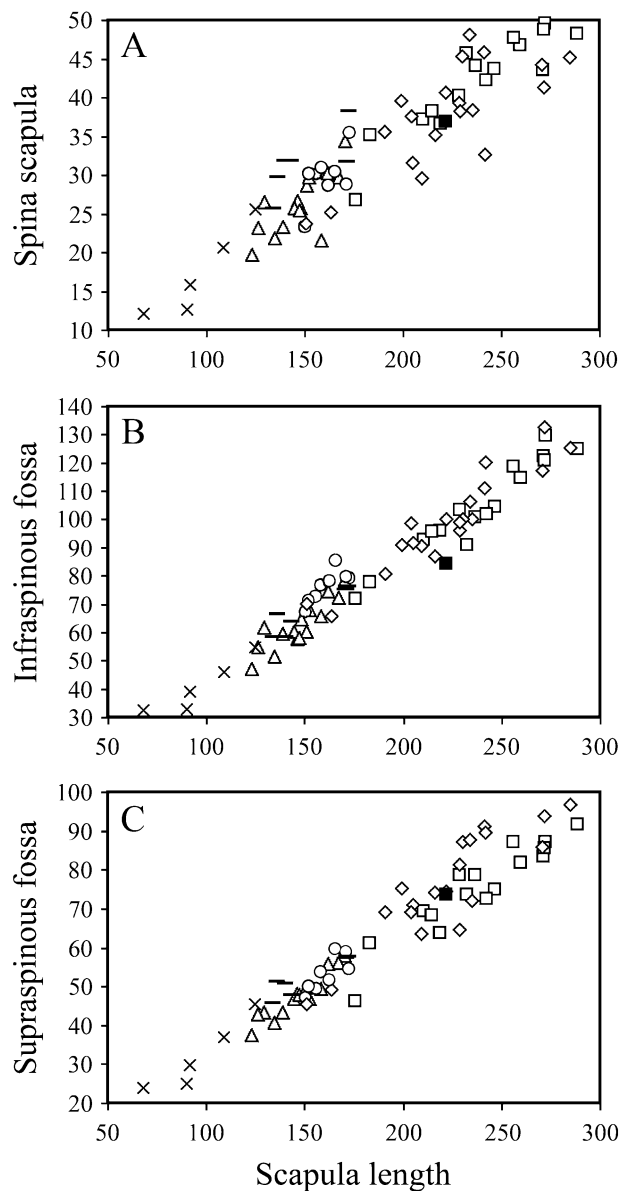

Figure 13. Scapula proportions (mm) in *Megantereon cultridens* SE311 and extant large felids. A, scapula length to maximum height of the spina scapula; B, scapula length to maximum height of the infraspinous fossa; C, scapula length to maximum height of the supraspinous fossa. Symbols: ■, *Megantereon cultridens* SE311; □, *Panthera leo* ($N = 17$); ○, *Panthera onca* ($N = 8$); △, *Panthera pardus* ($N = 16$); ◇, *Panthera tigris* ($N = 19$); ×, *Neofelis nebulosa* ($N = 5$); –, *Puma concolor* ($N = 6$).

teres major along the caudal border is distinctly larger in *Megantereon* than in *Smilodon*, and the scar for the m. triceps brachii is also large.

The above proportional differences are corroborated by analyses of fossae widths to scapula length in *Megantereon* and extant big cats. The infraspinous

fossa is narrower relative to scapula length in *Megantereon* (Fig. 13B) than in *Puma concolor* ($P = 0.001$) and all the pantherines ($P < 0.001$), but not in *Neofelis nebulosa* ($P = 0.062$). However, the supraspinous fossa is wider relative to scapula length in *Megantereon* (Fig. 13C) than in *Panthera leo* ($P = 0.014$) and *P. pardus* ($P = 0.029$), but not in *P. onca* ($P = 0.583$), *P. tigris* ($P = 0.330$), *Puma concolor* ($P = 0.092$) and *Neofelis nebulosa* ($P = 0.971$). This results in the ratio of the infraspinous to supraspinous fossa width being significantly lower in *Megantereon* than in *Puma concolor* ($P = 0.014$), *Neofelis nebulosa* ($P = 0.006$) and the pantherines ($P < 0.001$). This indicates that *Megantereon* had a more powerfully developed m. supraspinatus relative to the m. infraspinatus than in extant big cats, and also than in *Smilodon*.

FORELIMB

The forelimbs are almost complete (Fig. 14), although several smaller elements are missing from the left carpus and the preservation is often better in the right forelimb.

Humerus

Both humeri are well preserved, especially the right one (Fig. 14A–D), but in several places the surface of the left humerus is slightly weathered, as are parts of the distal trochlea. Humerus length (Table 3) is within the lower size range of lions ($N = 17$: 222.2–367.0 mm) and tigers ($N = 19$: 236.6–372.7 mm), and is far larger than in jaguars ($N = 8$: 195.8–238.7 mm), leopards ($N = 16$: 176.4–222.6 mm) and pumas ($N = 6$: 187.4–231.9 mm). It is also larger than in *Smilodon gracilis* ($N = 4$; 232.9–259.9 mm), but well below *S. fatalis* ($N = 7$: 352.5–381.6), and although smaller adult specimens are known (see Merriam & Stock, 1932), few appear to be as small as *Megantereon*. It is of course also below the values in the even larger sabrecat *S. populator* ($N = 4$; 333.5–387.5 mm), but only slightly smaller than small specimens of the otherwise large *Homotherium serum* (Turner & Antón, 1997), but as pointed out by Rawn-Schatzinger (1992), the humerus is short in this species compared with the epi- and metapodials.

As in other derived sabrecats, the humerus of *Megantereon* is very similar to those of extant big cats, albeit with exaggerated robustness overall. The ratio of humerus least circumference of the diaphysis relative to articular length in *Megantereon* (0.356; Fig. 15A) is distinctly higher than in *Panthera leo* (0.318 ± 0.005; $P < 0.001$), *P. onca* (0.322 ± 0.008; $P < 0.001$), *P. pardus* (0.290 ± 0.005; $P < 0.001$), *P. tigris* (0.303 ± 0.005; $P < 0.001$), *Neofelis nebulosa* (0.298 ± 0.010; $P = 0.009$) and *Puma concolor* (0.291 ± 0.009; $P < 0.001$), and even than in *Smilodon*

Table 3. Measurements (mm) of the forelimb bones of *Megantereon cultridens* SE311

	Left	Right
Humerus		
Articular length	262.4	262.5
Least circumference	93.5	87.3
Diaphysial AP	32.3	30.8
Diaphysial LM	27.2	24.8
Capitulum AP	27.3	26.8
Capitulum LM	27.2	26.6
Trochlea AP	31.0	31.1
Trochlea LM	15.3	15.1
Articular width	53.6	51.1
Distal width	77.4	79.3
Ulna		
Overall length	271.1	274.3
Circumference	70.2	74.3
Diaphysial AP	26.5	30.9
Diaphysial LM	18.2	16.4
Olecranon	56.6	58.3
Radius		
Overall length	216.2	220.7
Circumference	65.6	63.3
Diaphysial AP	15.7	14.9
Diaphysial LM	26.1	25.4
Metacarpals		
I length	–	30.3
II length	79.8	80.9
III length	88.8	89.4
IV length	85.0*	86.3
V length	71.5	71.7

*Proximal articulating surface weathered.
Diaphysial diameters are taken at the site of circumference, which is least circumference in the humerus, but are taken at midshaft in radius and ulna.
Abbreviations: AP, anteroposterior diameter; LM, lateromedial diameter.

gracilis (0.330 ± 0.011; $P = 0.047$) and *S. fatalis* (0.337 ± 0.008; $P = 0.027$). Only the very robust *S. populator* has a higher circumference/length ratio than *Megantereon* (0.401 ± 0.011; $P = 0.003$).

The humeral head is relatively wider than in extant large felids, as in *Smilodon fatalis* and *S. populator*, and the greater tuberosity is prominent, and much lateromedially wider than in extant large felids (Fig. 14B), even more so than is frequently the case in *S. fatalis*, but less than often seen in *S. populator*. The dorsal profile of the greater tuberosity in *S. fatalis* is less curved with a distinct median notch, whereas it is more evenly rounded in extant large felids. In *Megantereon*, the dorsal profile is also curved without a medial notch, but the tuberosity is distinctly larger than in extant large felids, and the

Figure 14. Left humerus and antebrachium and right metacarpals of *Megantereon cultridens* SE311. Humerus in anterior (A), posterior (B), medial (C) and lateral (D) view; ulna in medial (E), lateral (F) and anterior view (G); radius in lateral (H) and ulnar (I) view; metacarpals I-V in dorsal (J) and palmar (K) view.
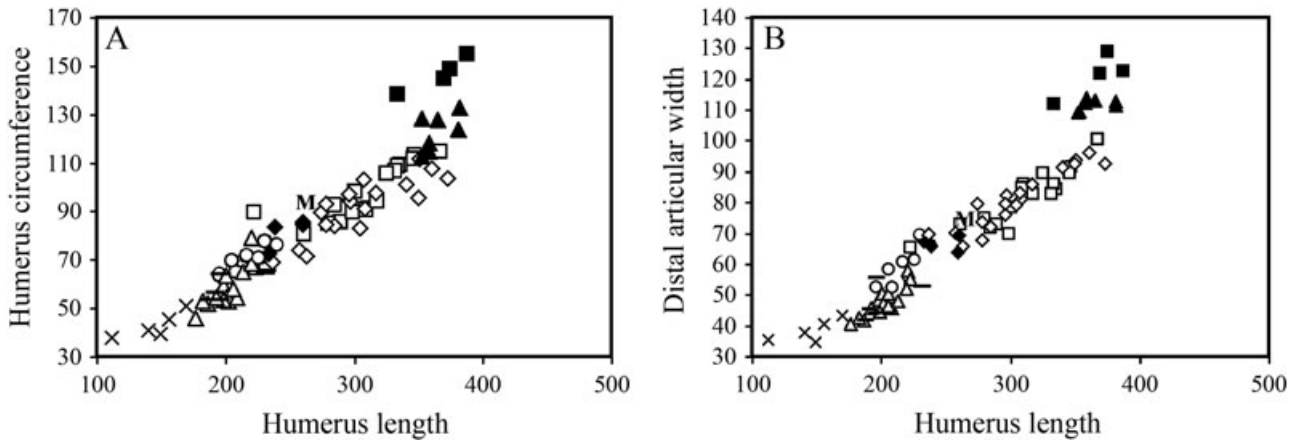
Figure 15. Articular length of the humerus to least circumference of the humeral diaphysis (A) and articular length of the humerus to the distal width of the humerus (B), all in mm. Symbols and abbreviation: M, *Megantereon cultridens* SE311; □, *Panthera leo* ($N = 17$); ○, *Panthera onca* ($N = 8$); △, *Panthera pardus* ($N = 16$); ◇, *Panthera tigris* ($N = 19$); ×, *Neofelis nebulosa* ($N = 5$); –, *Puma concolor* ($N = 6$); ▲, *Smilodon fatalis* ($N = 7$); ◆, *Smilodon gracilis* ($N = 4$); ■, *Smilodon populator* ($N = 4$).

anterior edge is less ventrally curving than is often the case in extant large felids. Viewed anteriorly (Fig. 14A), the tuberosity gradually descends from the level of insertion for m. supraspinatus towards the deltopectoral crista, and in this respect it bears a closer resemblance to the condition in extant large felids than *Smilodon fatalis*, where the proximal edge is more horizontal and abruptly descends towards the deltopectoral crista. Viewed anteriorly, the greater tuberosity crest is markedly thickened, distinctly more so than in extant felids and even *S. fatalis*, resembling the condition in *S. populator*. This indicates a particularly massive insertion for the m. deltoideus acromialis and m. pectoralis (Barone, 1967; Crouch, 1969; Done *et al.*, 2000), congruent with scapula morphology (above).

The facet for insertion of the m. supraspinatus (Fig. 14D) is large and appears distinctly more elongate than in extant large felids, but it is also frequently rather elongate in *Smilodon fatalis* and *S. populator*. The adjacent facets for insertion of m. infraspinatus and m. teres major are also distinctly larger than in extant large felids. The bicepital groove is large and wide, as in other large felids. The lesser tuberosity is better developed than in extant large felids (Fig. 14A), and is proportionally larger than in some, but not all, examined specimens of *Smilodon fatalis*. Curiously, the tubercle is frequently also very well developed in *S. gracilis*, and, as expected, in *S. populator*. This indicates a well-developed m. subscapularis in *Megantereon*, in accordance with scapula morphology (above).

The deltopectoral crista is very massive in *Megantereon*, and its length relative to the humerus has been used to infer locomotor behaviour in mammals
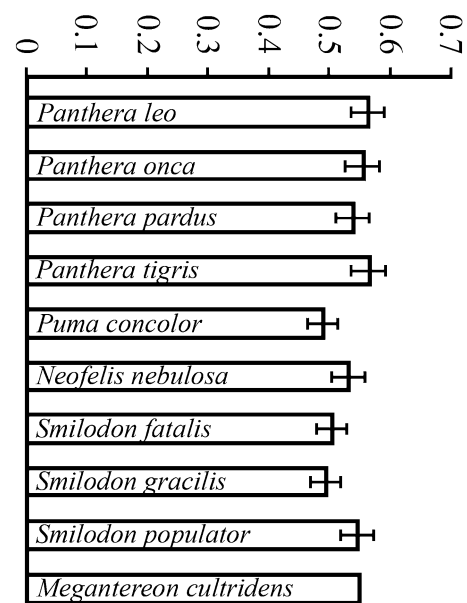

Figure 16. Deltoid length of humerus (length of deltoid crest from the proximal point of the humeral head/humerus articular length) in *Megantereon cultridens* SE311 and large felids. Specimen numbers are: *Panthera leo* ($N = 13$), *P. onca* ($N = 7$), *P. pardus* ($N = 11$), *P. tigris* ($N = 12$), *Neofelis nebulosa* ($N = 5$), *Puma concolor* ($N = 5$), *Smilodon fatalis* ($N = 7$), *S. gracilis* ($N = 3$) and *S. populator* ($N = 3$).

(see Elissamburu & Vizcaino, 2004). However, the distal extension of the crista to the length of the humerus (DLH; Fig. 16) in *Megantereon* (0.549) is similar to the values in most other large felids, both extant and extinct [*Panthera leo* ($P = 0.054$), *P. onca*

($P = 0.544$), *P. pardus* ($P = 0.329$), *P. tigris* ($P = 0.055$), *Neofelis nebulosa* ($P = 0.416$), *Smilodon fatalis* ($P = 0.064$) and *S. populator* ($P = 0.965$)], but DHL is lower in *Puma concolor* ($P = 0.022$) and *Smilodon gracilis* ($P = 0.015$). Accordingly, the deltopectoral crista does not extend further down the diaphysis than is the case in most other large felids (*contra* Schaub, 1925), probably for biomechanical reasons, as a distal extension provides a larger inlever and thus greater inforce, but also reduces the outvelocity and amplifies torsional moments (Hildebrand, 1988).

The distal end of the humerus is very wide. The distal width of the humerus relative to the articular length in *Megantereon* (0.282; Fig. 15B) is significantly higher than in *Panthera leo* (0.264 ± 0.014; $P < 0.001$), *P. pardus* (0.236 ± 0.012; $P < 0.001$), *P. tigris* (0.266 ± 0.013; $P < 0.001$) and *Puma concolor* (0.238 ± 0.023; $P = 0.006$), but is not significantly different from *Panthera onca* (0.273 ± 0.017; $P = 0.197$), *Neofelis nebulosa* (0.267 ± 0.030; $P = 0.343$) or *Smilodon gracilis* (0.270 ± 0.018; $P = 0.283$). Distal humeral width is proportionally greater in *S. fatalis* (0.307 ± 0.009; $P < 0.001$) and *S. populator* (0.332 ± 0.012; $P = 0.003$) than in *Megantereon*.

All felids have proportionally well-developed medial epicondyles, and, accordingly, powerfully developed m. flexor carpi radialis, digitorum profundus and superficialis, and m. pronator teres (Barone, 1967; Crouch, 1969; Done *et al.*, 2000), as the forelimbs are very important not only for climbing (see e.g. Taylor, 1974) but also for catching prey. *Megantereon* is no exception, but the medial epicondyle appears unusually well developed, distinctly more so than in even jaguars or tigers. In this respect, it bears resemblance to powerfully built specimens of *Smilodon fatalis* and, in particular, *S. populator*. The medial epicondyle is also very powerfully developed relative to extant large felids (Fig. 14B), indicating powerful m. extensor carpi ulnaris, digitorum communis, indicis, pollicis longus and minimi digitis. Overall, muscle attachments of the entire humerus appear powerfully developed compared with even jaguars, lions and tigers, resembling the condition in *Smilodon fatalis* and *S. populator*.

The olecranon fossa is proportionally wider and lower than in extant large felids, and its lateral face is distinctly flaring, unlike the condition in extant large felids, but this is also present in some specimens of *Smilodon fatalis* and *S. populator*. The radial fossa is wide and low, as in other large felids, and appears proportionally larger than in most extant large felids owing to the great width of the distal humerus. The coronoid fossa is distinctly taller than wide, unlike the condition in extant felids, resembling the condition in *Smilodon* sp. There is an elongate, slit-like entepicondylar foramen, but it is distinctly

smaller than usually seen in extant large felids, resembling the condition often seen in the three species of *Smilodon*.

The articulating facets for the antebrachium are large, and the capitulum is heavy and subcylindrical. The trochlea is narrower (Table 3), and projects distinctly beyond the capitulum. The long axis of the trochlea forms a moderately wide angle (33.7°) to the capitulum (Fig. 14A; see Heinrich & Rose, 1997). The angle is frequently shallower among extant large felids, but varies substantially intraspecifically, and the value in *Megantereon* is within the variation of extant large felids. In some extant felids, e.g. jaguars, the trochlea frequently extends only slightly ventrally to the capitulum, whereas in tigers it often extends distinctly beyond the capitulum. In all three species of *Smilodon* this variation is also present, although the trochlea of *S. fatalis* and *S. populator* usually extends further below the capitulum than in jaguars. There is no reason to infer differences in elbow function or limb posture in *Megantereon* from other large felids.

Radius
The radius differs from those of extant felids primarily in being distinctly heavier in build (Fig. 14H, I; Table 3), a feature which it has in common with *Smilodon fatalis* (Merriam & Stock, 1932), *S. gracilis* (Berta, 1987) and *S. populator* (our pers. obsserv.). The radial head is less flaring than in extant large felids, resembling the condition in *Smilodon fatalis* (Merriam & Stock, 1932), *S. gracilis* (Berta, 1987), *S. populator* and *Homotherium* (Rawn-Schatzinger, 1992). The biceps tuberosity is very prominent, distinctly more so than in *Homotherium* and *S. gracilis*, resembling the condition in *S. fatalis* and extant large felids and indicating a powerful m. biceps brachii (Barone, 1967; Crouch, 1969; Done *et al.*, 2000). The insertion scar for m. pronator teres is well developed, as in other felids, and is situated lower on the shaft than is frequently the case in tigers and lions, more resembling the condition in leopards and jaguars. The scar for the origin (not insertion, as stated in Berta, 1987) of m. abductor pollicis longus along the posterolateral side of the shaft is elongate and distinct, as in other large felids. The scar for the origin (not insertion, as stated in Berta, 1987) of m. flexor digitorum profundus is large and elongate, tapering towards the medial side of the posterior shaft, but is rather indistinct. This could be owing to slight postmortem weathering, in particular along the left radius, but the scar is frequently also indistinct in extant large felids.

The styloid process is distinctly shorter, thicker and blunter than in extant felids, resembling the condition in *Smilodon fatalis* (Merriam & Stock, 1932), and differing from the condition in *S. gracilis* (Berta,

1987) and *Homotherium* (Rawn-Schatzinger, 1992). The distal articulating facet is concave with clearly demarcated edges, and is wider laterally than medially, as in other felids. The area for the m. extensor carpi radialis in *Megantereon* appears to have been wider than in *Smilodon fatalis* (Merriam & Stock, 1932), *S. gracilis* (Berta, 1987) and *Homotherium* (Rawn-Schatzinger, 1992), but the margins of the scar are less well preserved.

Ulna
The left ulna (Fig. 14E–G) is completely preserved but the coronoid lip for the humeral trochlea has broken away from the proximal articulating cotyle in the right ulna. As with the radius, the ulna in *Megantereon* is powerfully built compared with those of extant large felids, but interspecific differences are present. The ratio of anteroposterior diameter of the ulnar diaphysis at midshaft to overall length (including the olecranon process) in *Megantereon* (0.098; Fig. 17A) is not significantly different from the proportions in *Smilodon gracilis* (0.102 ± 0.009; $P = 0.176$), *Panthera tigris* (0.098 ± 0.002; $P = 0.845$) and *P. onca* (0.103 ± 0.003; $P = 0.069$), but is significantly higher than in *P. leo* (0.086 ± 0.002; $P < 0.001$), *P. pardus* (0.086 ± 0.002; $P = 0.001$), *Neofelis nebulosa* (0.085 ± 0.004; $P = 0.024$) and *Puma concolor* (0.081 ± 0.004; $P = 0.001$). *Smilodon fatalis* has a significantly thicker ulna than *Megantereon* (0.112 ± 0.003; $P = 0.026$), but despite *S. populator* having the most massive ulnae of all (0.123 ± 0.006), low sample size ($N = 2$) prevents assumptions of significance from *Megantereon* ($P = 0.412$). The single included specimen of *Machairodus giganteus* was evidently

extremely large, but has a markedly thinner ulna (0.088), and proportionally appears more similar to *Homotherium* (Rawn-Schatzinger, 1992) or a lion (see also Turner & Antón, 1997).

The olecranon process of *Megantereon* is well developed, but not unusually so, and the posterior face of the ulna is markedly straight, more so than often seen in extant felids. The length of the olecranon process from the centre of rotation in the cotyle to the tip compared with total ulna length in *Megantereon* (0.209; Fig. 17B) is not significantly different from the averages in *Smilodon gracilis* (0.221 ± 0.009; $P = 0.144$), *S. populator* (0.220 ± 0.009; $P = 0.642$), *Panthera onca* (0.208 ± 0.004; $P = 0.803$),and *P. tigris* (0.211 ± 0.003; $P = 0.672$), and is significantly higher than in *P. leo* (0.191 ± 0.003; $P < 0.001$), *P. pardus* (0.180 ± 0.003; $P < 0.001$), *Neofelis nebulosa* (0.176 ± 0.005; $P < 0.001$), and *Puma concolor* (0.183 ± 0.005; $P < 0.001$), but lower than in *Smilodon fatalis* (0.235 ± 0.005; $P = 0.003$). The single specimen of *Machairodus giganteus* again appears very gracile with a proportionally small olecranon (0.163), resembling *Homotherium* (Rawn-Schatzinger, 1992). Although the olecranon is not markedly elongate, its transverse width, markedly greater than in extant felids, *Machairodus* and *Homotherium*, and similar to *Smilodon*, indicates that it constituted a very large area for insertion of m. triceps and was designed for withstanding substantial moments about the joint.

In *Megantereon*, the olecranon process is relatively straight, whereas it is angled somewhat more posteriorly in *Smilodon gracilis* (Fig. 18). The angle for the insertion of m. triceps, in this analysis the inferred centroid of the muscular inforce, is also rather low in
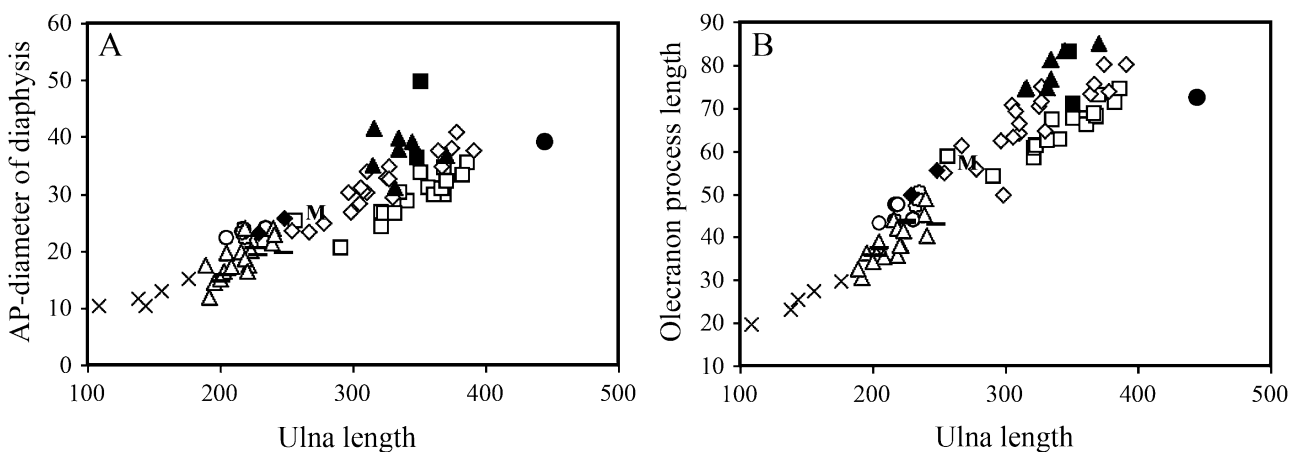

Figure 17. Total length of ulna to anteroposterior diameter of ulnar diaphysis at midshaft (A) and total length of ulna to olecranon process length from the centre of rotation in the articular cotyle to distal end (B), all in mm. Symbols and abbreviation: M, *Megantereon cultridens* SE311; □, *Panthera leo* ($N = 17$); ○, *Panthera onca* ($N = 8$); △, *Panthera pardus* ($N = 16$); ◇, *Panthera tigris* ($N = 19$); ×, *Neofelis nebulosa* ($N = 5$); –, *Puma concolor* ($N = 6$); ●, *Machairodus giganteus* ($N = 1$); ▲, *Smilodon fatalis* ($N = 7$); ◆, *Smilodon gracilis* ($N = 2$); ■, *Smilodon populator* ($N = 2$).
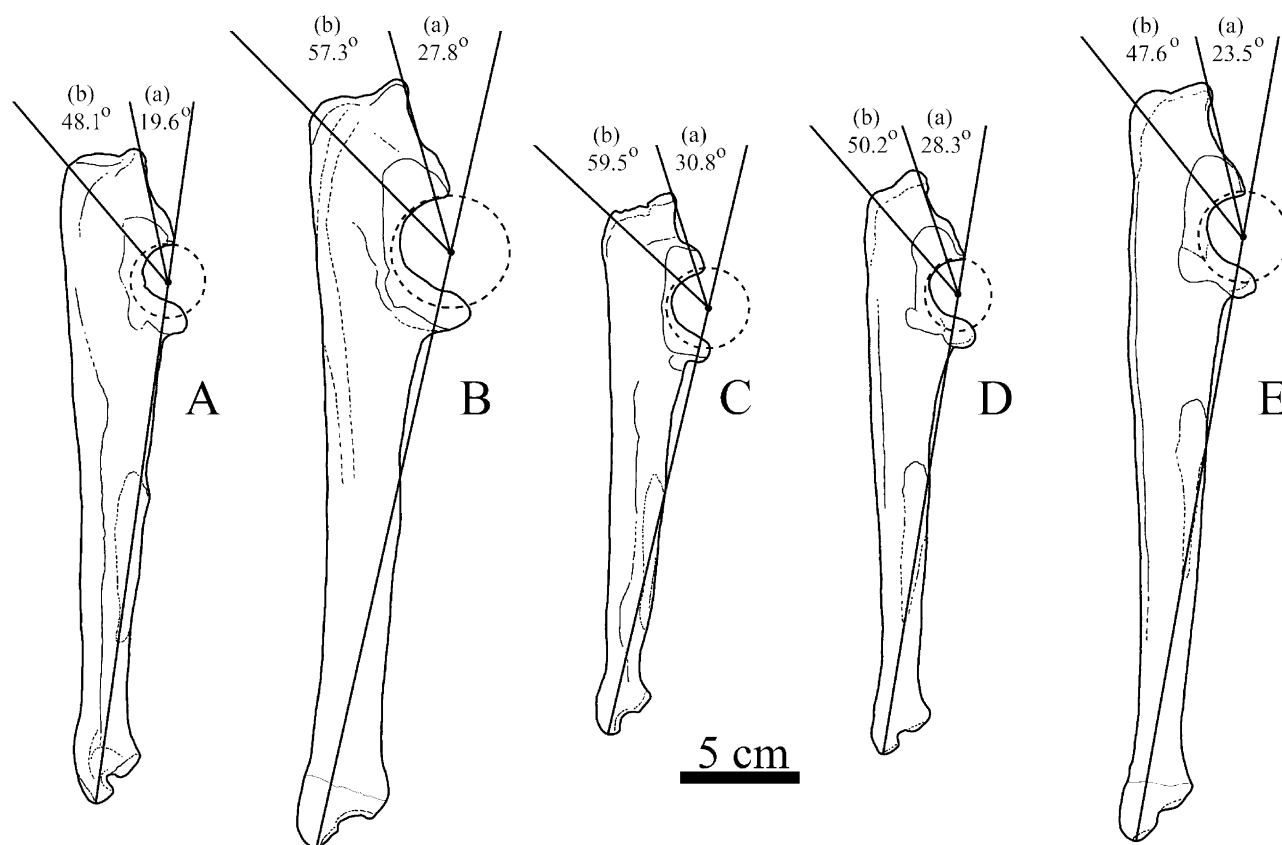
Figure 18. Comparative morphology of the ulna, lateral view. A, *Megantereon cultridens* SE311 [left]; B, *Smilodon fatalis* LACM-HC1505 [left]; C, *Smilodon gracilis* UF87279 [right]; D, *Panthera onca* CN5659 [right]; E, *Panthera tigris* CN5669 [right]. Angle (a) is between long axis of diaphysis and olecranon process (olecranon angle) and (b) is between long axis of diaphysis and insertion of m. triceps brachii caput longum (triceps angle).

Megantereon, albeit close to the angles in the other species. Van Valkenburgh (1987) found that olecranon angle to the long axis of the diaphysis was greater in terrestrial than scansorial and arboreal species, and that the angle increases with body size. However, the included felids are all large animals, and it is doubtful if *Megantereon* was scansorial or arboreal to any greater extent than extant big cats. Rather, the differences are most likely attributed to intraspecific variation; among extant large felids the olecranon process angle to the long axis of the ulna often shows substantial intraspecific variation.

The radial notch is deeply concave, as in other felids, and on the left ulna the wide coronoid lip for the humeral trochlea is completely preserved. It is less medially flaring than is frequently the case in extant large felids, and is less distally orientated than in extant large felids, more closely resembling the condition in *Smilodon*, especially *S. gracilis* (Berta, 1987). The anconeal process is well developed and deeply U-shaped, as in other felids, but unlike the condition in extant large felids, the medial part is not

markedly inclined with respect to the lateral part. In this latter respect, *Megantereon* resembles all three species of *Smilodon*. The scar for the m. brachialis and m. biceps brachii is very well developed, as in other large felids, but the insertion of the m. anconeus and origin of m. flexor carpi ulnaris (Barone, 1967; Crouch, 1969; Done *et al*., 2000) are indistinct, as is frequently the case in extant large felids. The styloid process is rather long and massive, and curves gently anteriorly.

Manus
The right manus is virtually complete and well preserved (Figs 14J, K, 19, 20), with only some cosmetic restoration of the proximal part of the palmar surface of metacarpal III. The right manus consists of the full carpus, metacaparpals I–V, and the proximal phalanx of digit I, the proximal and middle phalanx and claw sheath of digit II, the complete proximal and incomplete distal phalanx and claw sheath of digit III, the proximal and distal phalanx of digit IV and the claw sheath of digit V. The left manus is less complete,
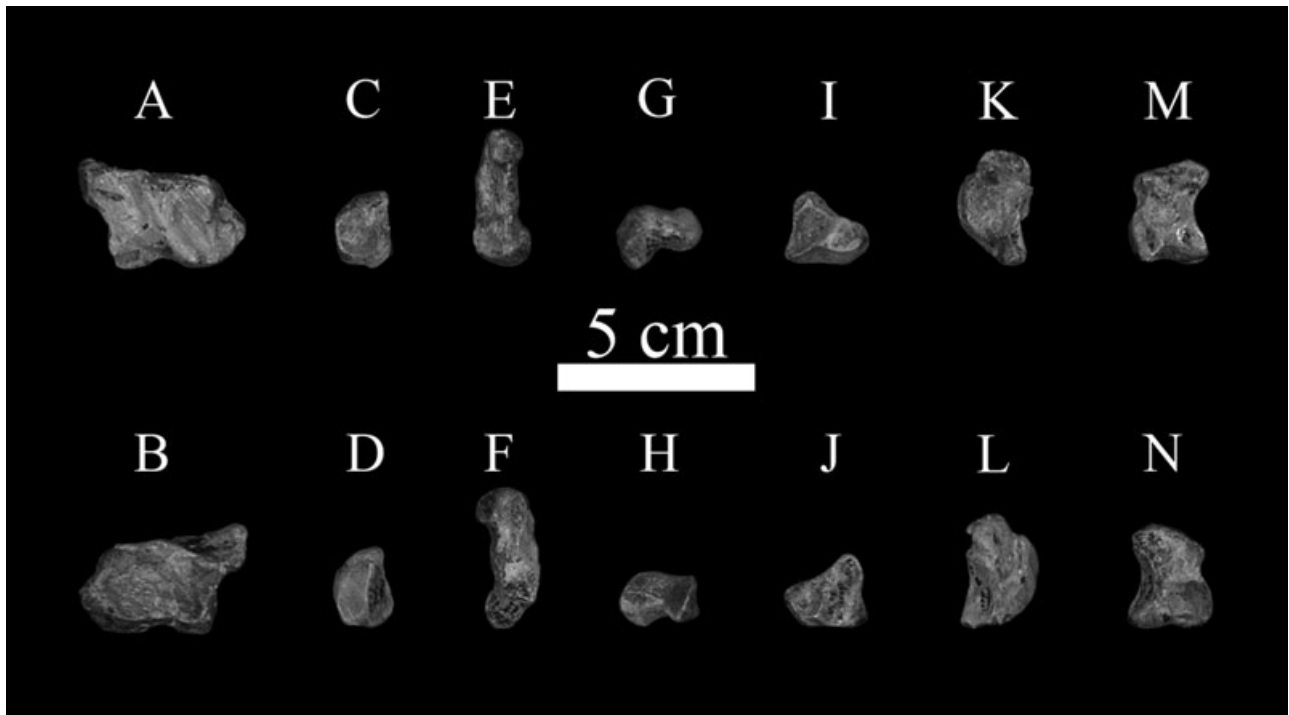
Figure 19. Right carpus of *Megantereon cultridens* SE311. Scapholunar (A, proximal view; B, distal view); cuneiform (C, inner view; D, outer view); pisiform (E, distal view; F, proximal view); trapezium (G, inner distal view; H, proximal view); trapezoid (I, proximal view; J, distal view); magnum (K, inner view; L, outer view); unciform (M, inner view; N, outer view).

consisting of the trapezoid, scapholunar and unciform, and metacarpals II–V, which are also well preserved with only cosmetic restoration in a few places. Note that in Schaub (1925: fig. 4) the articulated left manus ('Manus sin.' [= sinistre]) is shown in its entity, albeit excluding phalanges, but this is probably the left manus with missing elements restored, based on the preserved elements of the right manus

Scapholunar
The scapholunar (or Os scaphoideum and Os lunatum; or radiale and intermedium) is similar to those in other large felids. In proximal view (Fig. 19B) the large, squarish and gently convex articular facet for the radius takes up most of the surface, and it is wider than in extant large felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932; Berta, 1987). The proximal process is large with a large, lateral sesamoid facet, and curves more upwards than in *Smilodon fatalis* (Merriam & Stock, 1932), resembling *S. gracilis* (Berta, 1987) and extant large felids. The process is distinctly larger than in *Homotherium* (Rawn-Schatzinger, 1992). In distal view (Fig. 19A), the large articulating facets for the distal carpals extend across the entire corpus. Towards the ulnar side, the elongate facet for the

unciform is distinctly wider than in extant large felids, and the facet for articulation with the magnum is proximally wider and tapers less distally than in extant large felids. The adjacent facets for the trapezoid distally and trapezium dorsally are broadly similar to those of *Smilodon fatalis* (Merriam & Stock, 1932), and the trapezoid facet is wider than in *S. gracilis* (Berta, 1987). The bevelled ridge separating the two facets is less demarked than in extant felids.

Cuneiform
The cuneiform (or ulnare; or Os triquetrum) in *Megantereon* resembles that of other large felids, but is slightly more triangular in outline than in extant large felids and also than *Smilodon* (Merriam & Stock, 1932), owing to a large lip, but this is frequently also present in *Smilodon* and in extant large felids, albeit usually more pronounced in tigers than in lions. In medial view (Fig. 19C), the bowl-shaped articulating facet for the unciform is apparent, and it is distinctly oval in outline, as opposed to a more triangular outline, as in *Smilodon*, or a rectangular outline, as often seen in lions. Among extant felids the facet is, however, morphologically quite variable. In distal view (Fig. 19D), the two large articulating
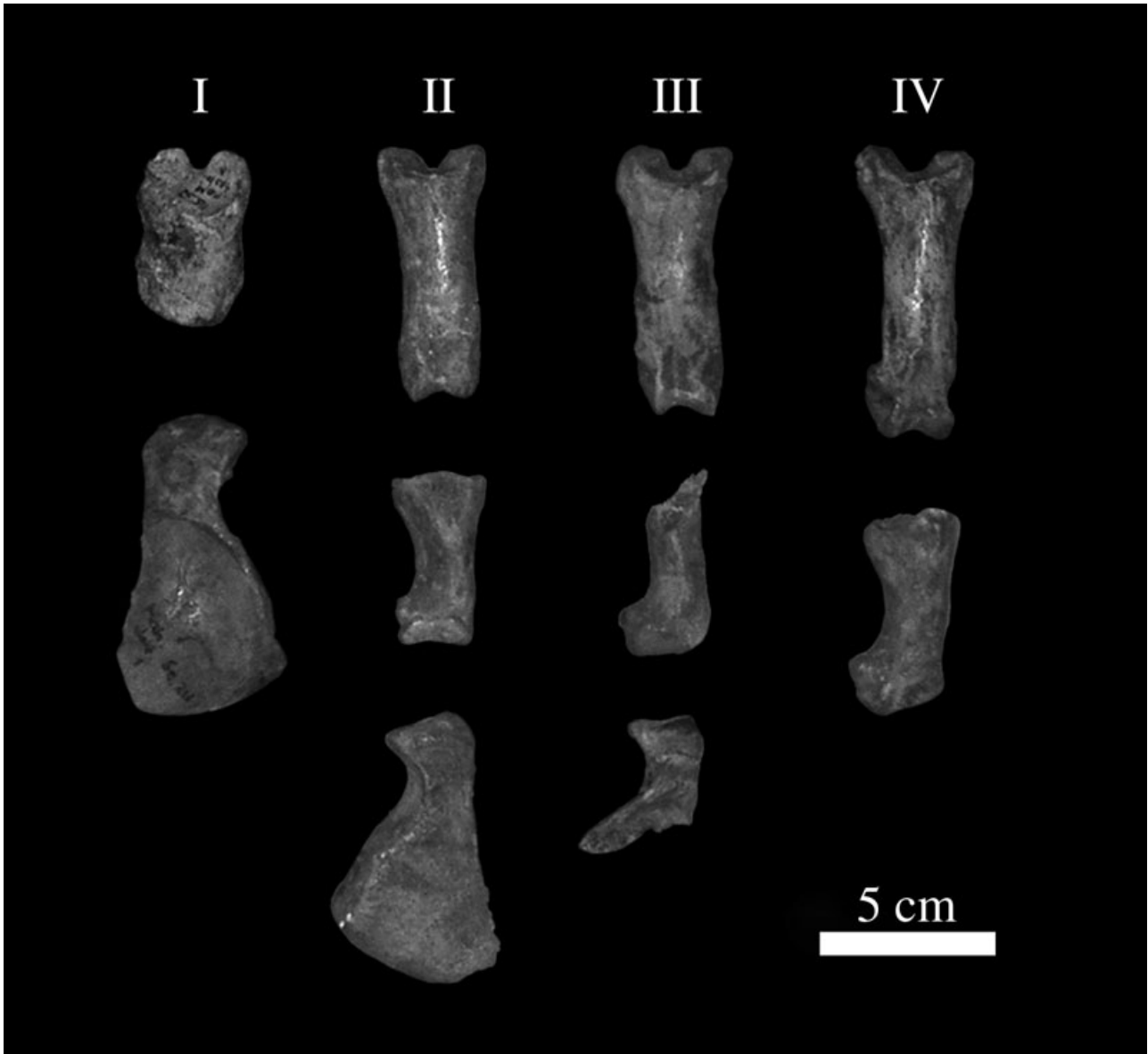
Figure 20. Manual phalanges of digits I–IV from the right manus of *Megantereon cultridens* SE311, viewed dorsally, except terminal phalanges, which are viewed laterally (I and III) and medially (II).

facets for the pisiform and ulna are visible. As in other felids, they are separated by a raised ridge and slope gently towards the sides, giving the distal face a triangular profile.

Pisiform
The pisiform (or Os pisiforme) of *Megantereon* is a long, stout bone, as in other large felids, but appears heavier in build than in leopards and jaguars, more resembling the condition in lions. It appears proportionally longer than in *Smilodon* and *Homotherium* (Rawn-Schatzinger, 1992). In distal view (Fig. 19E) the compact build of the bone is readily apparent. The

facet for the cuneiform on the radial face is narrower than in extant tigers and lions, more resembling the condition often seen in leopards, and is less keyhole-shaped than in *Smilodon*. The articulating facet for the ulna on the ulnar face is markedly less distally directed and flaring than in extant big cats, resembling the condition in *Smilodon* (Merriam & Stock, 1932). The proximal face of the bone (Fig. 19F) is unfortunately somewhat weathered.

Trapezium
The trapezium (or distal carpal I; or Os trapezium) is very stout, more so than even in *Smilodon* and large

male lions, and the outer edge is more rounded and less triangular than in *Smilodon*, *Panthera atrox* (Merriam & Stock, 1932) and extant lions, resembling the frequent condition in tigers and jaguars. In *Megantereon* and *Smilodon* (Merriam & Stock, 1932), the outer facets for the trapezoid and metacarpal II are largely confluent, and the metacarpal facet is elongate. As figured in Merriam & Stock (1932), the trapezoid facet is relatively wider in *Panthera atrox*, but in extant lions and tigers it is usually more elongate and rectangular, whereas the metacarpal II facet is oval and sometimes almost round, and thus very different from the condition in *P. atrox*. Facet morphology is, however, subject to substantial intraspecific variation among extant large felids. In inner distal view (Fig. 19G), the large facet for metacarpal I is distinct, and it bears great resemblance to those of other large felids. In proximal view (Fig. 19H) are two large, rectangular–oval facets for the scapholunar. In *Smilodon* (Merriam & Stock, 1932), the facets are confluent and deeply U-shaped, but as also noted by these authors, the facets are very variable in *P. atrox* (compare their fig. 80D, H). This is also the case in extant large felids. In lions, there may be two large, oval–triangular facets, or a U-shaped facet, as figured for *Smilodon* in Merriam & Stock (1932), whereas tigers and jaguars often have just one, saddle-shaped, rectangular facet.

Trapezoid
The trapezoid (or distal carpal II; or Os trapezoideum) is distinctly triangular in outline, as in *Smilodon*. Proximally (Fig. 19I), the saddle-shaped facet for the scapholunar takes up most of the surface, as in other felids. In *Megantereon*, the deeply concave portion of the facet is more pentagonal than in *Smilodon* (Merriam & Stock, 1932), whereas the smaller, weakly concave portion is oval–triangular, as in *Smilodon* and extant large felids. In *Panthera atrox* (Merriam & Stock, 1932) and extant pantherines, the deeply concave portion is more rectangular, and the weakly concave portion is proportionally larger than in *Megantereon* and *Smilodon*. Along the outer rim, the facet for the magnum is visible in *Megantereon*, but not in *Smilodon*. Occasionally, this is also the case in some lions, leopards, jaguars and tigers, although not as markedly as in *Megantereon*. The magnum facet is, however, more exposed in distal perspective, but owing to it being twisted about its long axis, it can occasionally extend onto the dorsal face also. In distal view (Fig. 19J), the facet for metacarpal II is triangular, as in other large felids, and as in *Smilodon* (Merriam & Stock, 1932), there is a notch in the facet. In *Panthera atrox* and extant pantherines the notch is either absent, or present but fairly small, as often seen in tigers and jaguars. Along the edge, the dis-

tally turned portion of the magnum facet is visible, and it is relatively larger than most often seen in extant pantherines. In inner view, the facet for the trapezium is subrectangular, resembling the condition in *Smilodon*, whereas it is often triangular and S-shaped in pantherines.

Magnum
The magnum (or distal carpal III; or Os capitatum) is very similar to those of extant large felids, and is robust, more so than in leopards, and more comparable with those of lions, jaguars and tigers. The inner side (Fig. 19K) is unfortunately slightly weathered, but the large round to drop-shaped facet for metacarpal II is similar in proportion and placement along the palmar side to those in other felids. The ligament pit is proportionally larger than often seen in extant felids. The facet for the trapezoid is very similar to other large felids, in being a raised, rectangular ridge, which is gently concave on top. The facet for the scapholunar extends along the proximal edge, and is fairly narrow, as in extant large felids. The facet for metacarpal III extends as a narrow, concave band along the distal edge. Along the outer side (Fig. 19L), the facet for the unciform is, unfortunately, not well preserved, but is appears to have been large, as in other large felids. Along the distal edge, the facet for metacarpal III flares more dorsally than is the case in *Smilodon* (Merriam & Stock, 1932). In *Panthera atrox* (Merriam & Stock, 1932) and extant pantherines, the facet is virtually unexposed along the outer face of the magnum, and is large, rectangular and distinctly concave in distal view. In *Megantereon*, it is more bowl-shaped, and the inner part of the facet is offset at a steeper angle to the distal portion of the facet.

Unciform
The unciform (or distal carpal 4 and 5; or Os hamatum) also bears a close resemblance to those of other large felids. In medial view (Fig. 19M), the facet for the magnum is wider than in *Smilodon* (Merriam & Stock, 1932) and lions and tigers, but some jaguars also have a wide facet. As in *Smilodon* and *Homotherium* (Rawn-Schatzinger, 1992), the facet for the scapholunar extends well onto the medial side, unlike the condition in extant large felids. In *Megantereon* and *Smilodon*, the lower edge of the facet is curved, whereas it is straighter in *Homotherium* (Rawn-Schatzinger, 1992) and extant large felids. In lateral view (Fig. 19N), the facet for the cuneiform is very wide, distinctly more so than in *Smilodon* (Merriam & Stock, 1932), *Homotherium* (Rawn-Schatzinger, 1992) and extant felids. The gently concave ligament fossa is very similar to that of *Smilodon* with a downward-curving, distal portion, and is not square

as in *Homotherium* and extant felids. As in *Smilodon* and *Homotherium*, the fossa is much larger than in extant big cats.

Metacarpals

The relative length of the metacarpals is I–V–II–IV–III (Table 3). In extant felids, metacarpal IV is frequently slightly longer than II, as is the case in *Smilodon* (Merriam & Stock, 1932), but in *Homotherium serum* metacarpal IV is the longest (Rawn-Schatzinger, 1992), an unusual condition among felids (the notion by Rawn-Schatzinger that metacarpal IV is longest in felids in general is incorrect). In *Homotherium latidens* metacarpal III is also the longest, however (Ballesio, 1963). The metacarpals of *Megantereon* are distinctly heavier in overall build than in extant large felids and *Homotherium*, although not quite as robust as in *Smilodon*. At a greatest length of around 89 mm, metacarpal III approaches the low size range of lions ($N = 15$: 89.3–125.7 mm) and tigers ($N = 19$: 88.8–124.3 mm), and is distinctly larger than in jaguars ($N = 8$: 59.4–75.9 mm) and leopards ($N = 16$: 57.6–80.1 mm). It is comparable with the upper size range in pumas ($N = 6$: 71.3–85.9 mm), which, however, have much more slender metacarpals than *Megantereon*. Metacarpal III length in *Megantereon* is also far less than in *Homotherium* (Rawn-Schatzinger, 1992: table 18: 112.0–127.5 mm). All metacarpals in *Megantereon* are, however, well within the size ranges of *Smilodon fatalis* (Merriam & Stock, 1932), indicating that *Megantereon* had proportionally longer metacarpals than did *Smilodon*, as the latter was a distinctly larger cat (Turner & Antón, 1997; Christiansen & Harris, 2005).

Metacarpal I bears substantial resemblance to that of *Smilodon* (Merriam & Stock, 1932), and is much more robust than in extant large felids and *Homotherium* (Rawn-Schatzinger, 1992). The dorsal facet for the trapezium is wide and appears slightly less concave than in *Smilodon* and extant large felids, and extends more distally than in either. As in *Smilodon*, there is a distinct dorsal ridge extending obliquely from the medial border of the trapezium facet, which is absent in extant felids. The distal tubercle is well developed, and the articulating facet for the first phalanx is wider and slightly heavier than in *Smilodon*, and distinctly larger than in *Homotherium* and extant big cats. The median keel of the articulation facet is also well developed.

Metacarpal II is the thickest metacarpal, and has a less triangular articulating facet for the trapezoid than in extant felids, as in *Smilodon* (Merriam & Stock, 1932; Berta, 1987), but the facet is concave, like in those taxa, and unlike the condition in *Homotherium* (Rawn-Schatzinger, 1992). As in other felids, there are heavy, rugose areas on the palmar face for insertion of the flexor musculature, and the projection for articulation with metacarpal III is heavier than in extant large felids. The proximomedial tubercle for the m. extensor carpi radialis is more pronounced than in extant felids, and the adjacent, trench-like groove for the radial artery is very pronounced, more so than in extant felids, *Smilodon* (Merriam & Stock, 1932; Berta, 1987) and *Homotherium* (Rawn-Schatzinger, 1992). The distal articulating facet for the proximal phalanx is medially asymmetrical and bears a very pronounced keel on the palmar surface, as in other felids.

Metacarpal III has a distinctly more pronounced articulating facet for metacarpal IV than does *Smilodon* (Merriam & Stock, 1932; Berta, 1987), *Homotherium* (Rawn-Schatzinger, 1992) and extant large felids, indicating a strong unison of the two. The medial facet for metacarpal II is less steeply inclined than in *Smilodon* and extant felids, and is not as dorsoventrally long either. The proximal articulating facet for the magnum is deeply concave with a gently raised median ridge. The proximolateral facet for the unciform is less triangular and more elongate than in extant large felids. The dorsopalmar, rugose area for insertion of the flexor muscles is less raised and triangular than is often the case in extant felids. The distal articulating facet bears a strong keel, and the facet is bulbous and taller than in extant felids and *Smilodon*.

Metacarpal IV is decidedly more slender than II and III. The articulating facet for metacarpal III is markedly more dorsally situated than is the case in *Smilodon* (Merriam & Stock, 1932; Berta, 1987), *Homotherium* (Rawn-Schatzinger, 1992) and extant large felids, probably owing to the pronounced facet on metacarpal III. The lateral articulating facet for metacarpal V is similar to that of *Smilodon*, and less smoothly rounded than in extant large felids. The proximal articulating facet for the unciform is smoothly convex, as in other felids, and unlike the condition in *Smilodon*, the facet forms a less steep angle with the metacarpal III facet, but is not as continuous with it as is the case in extant felids. The ventral, dorsal edge of the facet is distinctly more raised than in extant felids. Berta (1987) states that the posterior side of the proximal end of metacarpal IV not being broad is a characteristic of *Smilodon*, but this is also present in *Megantereon*. As in other felids, there is an elongate, rugose scar on the lateral face for insertion of the m. interosseus.

Metacarpal V has a less well-developed medial articulating tubercle for metacarpal IV than in extant large felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932; Berta, 1987). The convex articulating facet for the unciform is triangular in dorsal view, but is not as broad towards the palmar

surface compared with the dorsal surface as in extant felids. The proximal, lateral facets for the m. extensor carpi ulnaris are more raised than in extant felids. As in other felids, the distal articulating facet is markedly medially skewed, and the keel is only pronounced on the palmar face of the facet.

Phalanges

The phalanges of the right hand are almost completely preserved (Fig. 20), albeit lacking digit V. Morphologically, they bear great resemblance to those of extant felids. The most noticeable feature lies in the great development of the terminal phalanges, indicating that *Megantereon* had very powerfully developed claws on the forelimbs. We could not, however, affirm that the terminal phalanges had been correctly assigned to their respective digits, as the articulating facet of the proposed phalanx II of digit I was weathered, although their traditional placement appears likely (see below). Phalanx III of digit II appeared, however, to fit well onto the distal articulating facet of phalanx II.

The proximal phalanx of digit I is very similar to that of *Smilodon fatalis* (Merriam & Stock, 1932), and is very short, thick and heavy in build. The median ridge of the proximal articulating facet for the metacarpal is indistinct, as in extant large felids, and unlike *Smilodon*, where it is better developed. The distal articulating facet is wide and subcylindrical, and is wider dorsally than palmarly, as in other felids. The asymmetrical articulating facets in metacarpal I and the proximal phalanx are similar to those of extant felids, indicating that the digit functioned in a similar manner. The terminal phalanx assigned to this digit, although weathered, is probably the right one, as it is the largest of the terminal phalanges, as in other sabrecats where articulated mani have been recovered, such as *Smilodon* (Méndez-Alzola, 1941; Cox & Jefferson, 1988), *Homotherium* (Antón, Galobart & Turner, 2005), *Machairodus* (Gaudry, 1862) and *Lokotunailurus* (Antón, 2003; Werdelin, 2003). Sabrecats, accordingly, appear to have had very powerfully developed dewclaws.

Phalanges I are present in digits II–IV, and are morphologically very similar to those of extant large felids. Proximally, the articulating facet is deeply concave with a distinct median notch along the raised palmar face, and distally the facets are distinctly ginglymoid. This strongly indicates that motion was restricted to a dorso-palmar plane, lacking significant mediolateral or torsional components, and that the phalanges were built to withstand substantial force.

Two phalanges II from digits II and IV are completely preserved, and the majority, lacking only the proximal end, is preserved in digit III. Noticeable differences from extant felids are the very massive proportions of the phalanges, the pronounced development of the ligament scars on the proximal part of the dorsal surface, and the less pronounced dorsal lip of the proximal articulating surface. Significantly, the very wide distal articulating surfaces are strongly laterally skewed and asymmetrical, in that their lateral parts are ventrally turned compared with the medial part. This morphology is very similar to that of extant felids, and is a key feature in the claw retraction mechanism (Gonyea & Ashworth, 1975), strongly suggesting that this was also present in *Megantereon*.

PELVIS

The pelvis (Fig. 10) is well preserved and only the cranial ventral iliac spine on the right-hand side is missing. The area around the ischiadic tubers appears weathered, albeit only mildly so. The pelvis has undergone cosmetic restoration in relatively few places. More extensive restoration has taken place along the dorsal face of the left sacroiliac joint, the left tuber coxae and parts of the iliac crest, and the left ischium posterior to the acetabulum. As those parts are preserved in the right-hand side of the pelvis, this side had been used for modelling of missing parts. As preserved, the greatest length from the iliac crest to the ischiadic tuber is 260.8 mm, and external width is 167.7 mm (across tuber sacrale), 117.3 mm (across the acetabula) and 115.1 mm (across the ischiadic tubers). Pelvic length in *Megantereon* is comparable with the lower range in lions ($N = 11$; 245.4–333.2 mm) and tigers ($N = 13$; 256.5–345.3 mm) and is distinctly larger than in leopards ($N = 8$; 165.4–218.2 mm) and jaguars ($N = 7$; 200.5–226.9 mm). It is markedly less than in *Smilodon fatalis* (283–368 mm; Merriam & Stock, 1932), and *Homotherium* (322 mm; Rawn-Schatzinger, 1992).

The pelvis is typical for a large felid, but differs in several respects from those of extant felids. One difference lies in the overall proportions, as the pelvis of *Megantereon* is proportionally wider than in *Smilodon* (Merriam & Stock, 1932) and extant large felids. Overall, the pelvis also appears strongly built. The iliac wings are elongate and concave externally, as in other felids, and are longer compared with the pubo-ischiadic part of the pelvis than in *Smilodon*, and the anterior iliac crest is less pointed than in *Smilodon* (Merriam & Stock, 1932), resembling the condition in extant large felids more closely. The cranial dorsal iliac spine appears slightly more flaring than often seen in extant large felids, resembling the condition in *Smilodon*. The caudodorsal iliac spine is distinctly less clearly demarcated than in *Smilodon*, again resembling the condition in extant large felids. Medially, the iliac crest for the last sacral is less well

developed than often seen in extant large felids. The iliac tubercle is well developed, elongate and somewhat crest-like, resembling the condition in extant large felids more closely than in *Smilodon*, where it is wider and thicker (Merriam & Stock, 1932).

The lesser ischiadic notch is indistinct, and the ischiadic spine is less distinct than is often the case in extant large felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932). Despite slight weathering, the ischiadic tubers were evidently not nearly as posteriorly inclined as in *Smilodon* and extant felids, resulting in the ischiadic arch being only gently concave (Fig. 10B), an unusual condition in a large felid, and not deeply U-shaped, as in *Homotherium* (Rawn-Schatzinger, 1992), or V-shaped, as in *Smilodon* (Merriam & Stock, 1932) and extant felids. The ischiadic tuberosity is well developed, extending down the ischiadic arc, as in other felids.

The pubic pecten (brim) is straighter and shallower than in extant large felids, resembling the condition in *Smilodon*. The main difference from extant felids lies in the proportional length of the pubic symphysis. As in *Smilodon* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992), the symphysis in *Megantereon* is proportionally markedly shorter than in extant large felids, and the anterior face of the pubic brim terminates at around mid-level of the acetabulum, whereas in extant felids it terminates around the anterior rim of the acetabulum. The symphysis is also more anteriorly rounded than in extant felids, resembling the condition in *Smilodon* (Merriam & Stock, 1932). The obturator foramen is more elongate than in *Smilodon* and extant felids, although its morphology frequently varies, and measures 50.2×20.0 mm (length × height) on the left-hand side. The acetabulum is deeply concave and almost cylindrical, measuring 35.5×35.3 mm (length × height).

HIND LIMBS

Both hind limbs are largely complete, albeit without the fibulae, most of the smaller tarsal bones and phalanges. The hind limb long bones generally appear less heavy in build compared with those of extant large felids than was the case in the forelimb (but see below), in particular the humerus and radius. The hind limb appears to have been more gracile than the forelimb, and the metapodials proportionally rather elongate and slender. A right patella was present in the mounted skeleton, but could not be found. No evidence of fabellae is present.

Femur

Both femora are present and are generally well preserved. The right femur (Fig. 21A–D) has had cos-

metic restoration around the femoral head and along the anterolateral face around the middle of the diaphysis. The medial condyle is missing, but has been restored, albeit not to a credible morphology. The left femur has had more extensive restoration around the femoral neck, and the femoral head and distal condyles are weathered, and cosmetic restoration has been carried out at several places along the diaphysis and distal condyles. Femoral length in *Megantereon* (Table 4) is within the lower size range of lions ($N = 17$: 262.5–402.5 mm) and tigers ($N = 19$: 272.3–429.6 mm), and is larger than in jaguars ($N = 8$: 229.8–265.5 mm), leopards ($N = 16$: 200.9–255.3 mm) and pumas ($N = 6$: 226.3–274.3 mm). It is well below the values in *Smilodon fatalis* ($N = 7$: 370.5–423.5), although distinctly smaller adult specimens have been found than are present in our sample (see

Table 4. Measurements (mm) of the hind limb bones of *Megantereon cultridens* SE311

	Left	Right
Femur		
Articular length	285.8	286.6
Least circumference	82.5	82.3
Diaphysial AP	25.9	25.8
Diaphysial LM	26.6	26.6
Lateral condyle AP	42.1	40.1
Lateral condyle LM	20.7+	22.6
Medial condyle AP	36.1+	r
Medial condyle LM	19.8+	r
Distal width	63.7	63.8
Tibia		
Overall length	250.6	248.7
Circumference	77.2	74.7
Diaphysial AP	24.4	24.0
Diaphysial LM	24.7	23.5
Proximal width	65.5	65.2
Distal width	46.6	47.5
Calcaneum		
Total length	90.8	92.0*
Tuber length	46.4	47.8*
Metatarsals		
II length	84.2	84.3
III length	95.8	95.9
IV length	92.5	95.4
V length	87.0	86.9

*Distal end of tuber restored.
Diaphysial diameters are taken at the site of circumference, which is least circumference in the femur, but is taken at midshaft in the tibia.
Abbreviations: AP, anteroposterior diameter; LM, lateromedial diameter; r, restored. A plus sign indicates weathering, and that actual measurements should have been greater.

Figure 21. Right hind limb of *Megantereon cultridens* SE311. Femur in anterior (A), posterior (B), medial (C) and lateral (D) view; tibia in anterior (E), posterior (F), medial (G) and lateral (H) view; metatarsals I–IV in dorsal (I) and palmar (J) view.

Merriam & Stock, 1932), *S. populator* (*N* = 2; 390.2 and 395.0 mm; see Christiansen & Harris, 2005) and *Homotherium serum* (*N* = 5; 323.3–349.7 mm; Rawn-Schatzinger, 1992: table 23). The single specimen of *S. gracilis* available for this study (UF82652) is smaller than *Megantereon* (269.1 mm).

The femora are solid in build compared with those of extant large felids, and the least circumference of the femoral diaphysis to articular length of the femur in *Megantereon* (0.289; Fig. 22) is significantly higher than in *Panthera leo* (0.271 ± 0.004; $P < 0.001$), *P. onca* (0.263 ± 0.006; $P = 0.002$), *P. pardus* (0.246 ±
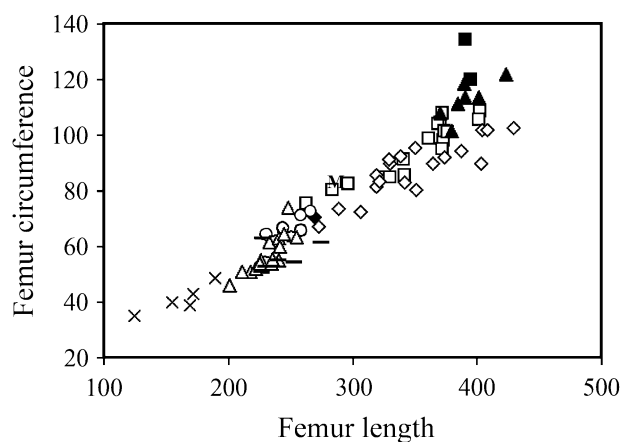
Figure 22. Articular length of femur to least circumference of femoral diaphysis, both in mm. Symbols and abbreviation: M, *Megantereon cultridens* SE311; □, *Panthera leo* (*N* = 17); ○, *Panthera onca* (*N* = 8); △, *Panthera pardus* (*N* = 16); ◇, *Panthera tigris* (*N* = 19); ×, *Neofelis nebulosa* (*N* = 5); –, *Puma concolor* (*N* = 6); ▲, *Smilodon fatalis* (*N* = 7); ◆, *Smilodon gracilis* (*N* = 1); ■, *Smilodon populator* (*N* = 2).

Figure 23. Distal extension of greater trochanter (length of greater trochanter from the proximal point of femoral head/femoral articular length) in *Megantereon cultridens* SE311 and large felids. Specimen numbers are: *Panthera leo* (*N* = 13), *P. onca* (*N* = 7), *P. pardus* (*N* = 11), *P. tigris* (*N* = 12), *Puma concolor* (*N* = 5), *Smilodon fatalis* (*N* = 7) and *S. gracilis* (*N* = 1).

0.004; *P* < 0.001), *P. tigris* (0.252 ± 0.004; *P* < 0.001), *Neofelis nebulosa* (0.255 ± 0.007; *P* = 0.015) and *Puma concolor* (0.234 ± 0.006; *P* = 0.002). The ratio in *Megantereon* is very similar to the average in *Smilodon fatalis* (0.288 ± 0.006; *P* = 0.830), and the single specimen of *S. gracilis* (0.262) appears distinctly more slender. As expected, *S. populator* had the highest circumference/length ratio average (0.324 ± 0.011), but the low sample size of two specimens meant that significance from *Megantereon* cannot be inferred (*P* = 0.329).

Overall, the femur of *Megantereon* is typical for a large felid, but several differences from extant large felids are evident. The comparatively slender femoral neck is distinctly longer than in extant large felids, all three species of *Smilodon* and *Homotherium* (Rawn-Schatzinger, 1992). The femoral head also appears to be turned more medially and ventrally relative to the long axis of the diaphysis than in other large felids. This could potentially indicate a slightly more crouched hind limb posture in *Megantereon*, although this is tentative. The greater trochanter rises to the level of the top of the femoral head, similar to the condition in extant felids, *Homotherium* (Rawn-Schatzinger, 1992) and *Smilodon gracilis*, and is not as elevated above the head as in *S. fatalis* and *S. populator*. Anterolaterally, the trochanter becomes more crest-like than in *Smilodon* and *Homotherium*, and also than the usual condition in extant large felids.

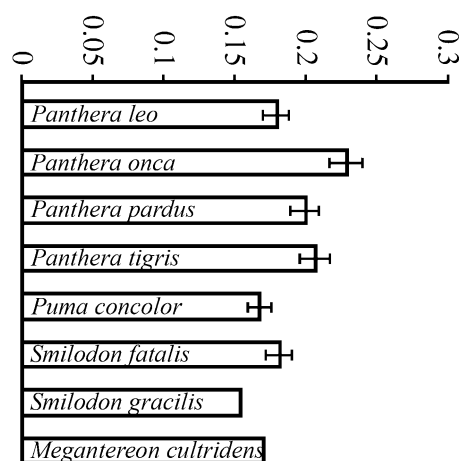The dorsoventral length of the greater trochanter from the proximal point of the femoral head divided by the articular length of the femur (distal extension of greater trochanter, or DMT; Fig. 23) has been used to infer locomotor behaviour in mammals, owing to inferences about mechanical inlevers for the limb muscles (Vizcaino & Milne, 2002; Elissamburu & Vizcaino, 2004). DMT is similar in *Megantereon* (0.170) to *Panthera leo* (*P* = 0.240), *Puma concolor* (*P* = 0.745) and *Smilodon fatalis* (*P* = 0.292), but is lower than in *Panthera onca* (*P* = 0.001), *P. pardus* (*P* = 0.003) and *P. tigris* (*P* = 0.002), where the greater trochanter extends further down the femoral diaphysis. The single DMT value in *Smilodon gracilis* (0.154) is lower than in *Megantereon*, but based on extant felids and *S. fatalis*, it would appear to lie within the intraspecific variation, indicating that they are probably not significantly different. Overall, DMT in *Megantereon* falls within the range of variation of large felids in general.

The area around the proximal prominent tuberosity is regrettably slightly weathered in the right femur and has been restored in the left. The tuberosity appears, however, to have been less well developed than in *S. fatalis* and *S. populator*, more closely resembling the condition in *S. gracilis* and extant large felids. The lesser trochanter is not situated as far below the intertrochanteric fossa as in *Smilodon fatalis* and *S. populator* (see also Merriam & Stock, 1932), again resembling the condition in *S. gracilis* and extant large felids more closely. The trochanter is very well developed, however, more so than is usually the case in extant large felids. The patellar trochlea is proportionally narrower in *Megantereon* than in

Smilodon fatalis and *S. populator*, resembling the condition in *S. gracilis* and extant large felids. The trochlea tapers gently dorsally, and is, accordingly, less squarish in outline than in *Smilodon fatalis*, *S. populator* and *Homotherium* (Rawn-Schatzinger, 1992), and also than in extant large felids.

The lateral supracondylar tuberosity is indistinct in the left femur, but is better preserved in the right. It appears well developed, as in all three species of *Smilodon*, extant lions, leopards and jaguars, but less so than is often seen in tigers. The medial supra-condylar tuberosity is smaller, and is also comparably developed with the condition in other large felids. The lateral condyle is complete in the right femur, and is proportionally wider and more squarish than in extant large felids, all three *Smilodon* species, *Machairodus* and *Homotherium* (Rawn-Schatzinger, 1992). The medial condyle is entirely restored in the right femur and is weathered in the left. In *Puma concolor* the average ratio of the width of the medial to lateral condyle is 0.963 ± 0.053 ($N = 6$), *Neofelis nebulosa* 1.071 ± 0.111 ($N = 5$), *Panthera leo* 0.994 ± 0.050 ($N = 17$), *P. onca* 1.048 ± 0.051 ($N = 8$), *P. pardus* 1.075 ± 0.062 ($N = 16$), *P. tigris* 0.961 ± 0.076 ($N = 19$) and *P. uncia* 1.159 ± 0.043 ($N = 10$). This contrasts with the preserved/restored morphology in *Megantereon*, where the medial is decidedly more slender (Table 4). This indicates that the medial condyle in *Megantereon* was also wide and heavy in build, and further indicates a sturdy knee joint.

Tibia

Both tibiae are generally well preserved (Fig. 21E–H), although both have been slightly restored around the proximal articulating cotyles. Like the other limb bones, the tibia of *Megantereon* is solidly built. The ratio of the circumference at the tibial midshaft to articular length of the tibia in *Megantereon* (0.308; Fig. 24) is significantly higher than in *Panthera leo* (0.275 ± 0.005; $P < 0.001$), *P. onca* (0.281 ± 0.007; $P = 0.001$), *P. pardus* (0.240 ± 0.005; $P < 0.001$), *P. tigris* (0.275 ± 0.005; $P < 0.001$), *Neofelis nebulosa* (0.260 ± 0.009; $P = 0.011$) and *Puma concolor* (0.236 ± 0.008; $P < 0.001$), but similar to the sabrecats *Smilodon gracilis* (0.290 ± 0.014; $P = 0.504$) and *Machairodus giganteus* (0.323 ± 0.011; $P = 0.114$). It is significantly less than in *Smilodon fatalis* (0.334 ± 0.008; $P < 0.001$). As expected, the ratio in the single specimen of *Smilodon populator* is distinctly higher (0.378).

The proximal articulating cotyles are large and wide, indicating a solidly constructed knee region. The intercondylar eminence is slightly weathered, but was low and rather narrow, as in extant large felids. The cnemial crista is distinctly lateromedially thicker than in extant large felids, resembling the condition
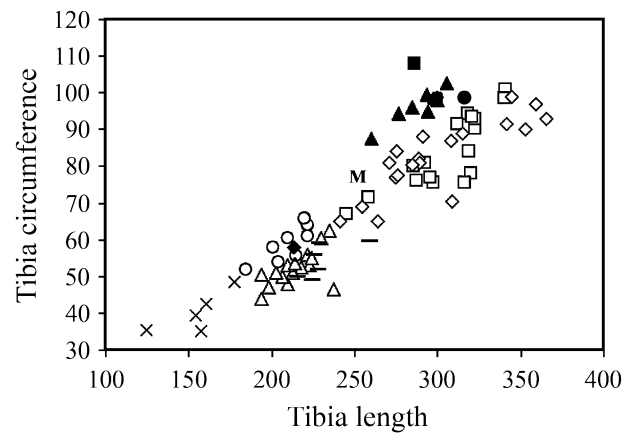

Figure 24. Articular length of tibia to tibial diaphysial circumference at midshaft, both in mm. Symbols and abbreviation: M, *Megantereon cultridens* SE311; □, *Panthera leo* ($N = 17$); ○, *Panthera onca* ($N = 8$); △, *Panthera pardus* ($N = 16$); ◇, *Panthera tigris* ($N = 19$); ×, *Neofelis nebulosa* ($N = 5$); –, *Puma concolor* ($N = 6$); ●, *Machairodus giganteus* ($N = 3$); ▲, *Smilodon fatalis* ($N = 7$); ◆, *Smilodon gracilis* ($N = 2$); ■, *Smilodon populator* ($N = 1$).

in *Smilodon fatalis* and *S. populator*. The crista extends almost halfway down the diaphysis, as in *Smilodon fatalis* and *S. populator*, and distinctly further than in extant large felids and *Homotherium* (Rawn-Schatzinger, 1992). This indicates powerfully developed epipodial extensors, such as the m. tibialis, and also a powerfully developed m. gastrocnemius, in accordance with calcaneal morphology (below), but also indicates a lower out-velocity of the epipodium (Hildebrand, 1988). The proximal lateral tuberosity is prominent, providing a strong attachment for ligaments. The popliteal notch is well developed in the right tibia, but the area is less well preserved in the left tibia.

In keeping with the overall limb morphology of *Megantereon*, the medial malleolus is moderately large and massive, as in *Smilodon fatalis* and *S. populator*, and is better developed than in *S. gracilis* and *Homotherium* (Rawn-Schatzinger, 1992). It is, however, incorrect to state that it 'projects further distally than in true cats' (Berta, 1987: p. 32), because this only holds true for certain specimens of some species, such as puma, leopard and jaguar, but not the tiger. The tubercles for m. tibialis caudalis and m. flexor digitorum longus (Barone, 1967; Crouch, 1969; Done *et al.*, 2000) are distinctly larger than in *Smilodon gracilis* and *Homotherium* (Rawn-Schatzinger, 1992), and this more closely resembles the condition in *Smilodon fatalis*, *S. populator* and extant pantherines, especially the tiger. The lateral malleolus is wide and heavy in build, closely resembling those of other large felids. The intermalleolar notch is more
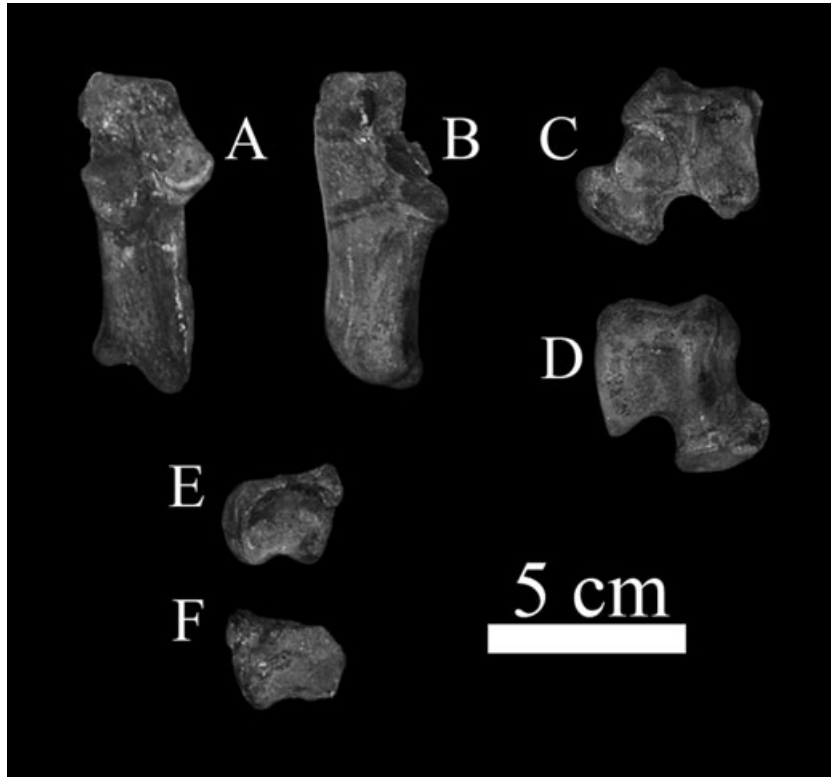
Figure 25. Tarsus of *Megantereon cultridens* SE311. Left calcaneum in dorsal (A) and lateral (B) view; right astragalus in plantar (C) and dorsal (D) view; right navicular in proximal (E) and distal (F) view.

deeply intended than in the three *Smilodon* species, and also *Homotherium*, and it bears a close resemblance to the notch in extant large felids, especially the tiger and lion, in is prominence and in being medially skewed.

Pes
The pes are well preserved, and consist of both astragali and calcanea, the left navicular (Fig. 25), and metatarsals II–V from both feet (Fig. 21I, J), whereas metatarsal I, which is rudimentary in other sabrecats, such as *Smilodon* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992), and also in modern felids, is not preserved. Both calcanea are well preserved, although the right calcaneum is slightly weathered and restored at the distal end of the tuber. Its overall length, however, appears to be fairly accurate (Table 4), as the restored portion appears correct. Both astragali are also well preserved, but the left astragalus is slightly weathered around the calcaneal articulating facets and has lost a small section of the corpus. The right navicular is also present. Curiously, the mesocuneiform is firmly attached to the articulating facet of the left metatarsal II.

Astragalus
The astragalus (or tibiale) of *Megantereon* (Fig. 25C, D) is intermediate between those of *Smilodon* (Merriam & Stock, 1932; Berta, 1987) and extant felids, in having a rather shallow grooved tibial trochlea, as in *Smilodon*, but a relatively long neck, as in extant large felids, except *Panthera onca*. The anteromedial border of the head in *Megantereon* extends less distally on the neck than in *Smilodon*, resembling the condition in extant large felids. The navicular facet is shallower than in *Smilodon*, more closely resembling extant large felids, but is distinctly more round. In the latter respect it resembles *Smilodon* more than extant large felids. In calcaneal view (Fig. 25C), the astragalocalcanear articulating facet towards the fibular side is distinctly wider than in *Smilodon* (Merriam & Stock, 1932; Berta, 1987) and extant large felids, and is less medially directed posteriorly. The sustentacular articulating facet adjacent to the astragalar head is also very wide and almost circular, resembling the condition in *Smilodon fatalis* (Merriam & Stock, 1932), and is not as triangular as in extant large felids. It almost reaches the navicular facet, as in *Smilodon* and *Panthera onca*, unlike the other pantherines. The ligament pit between the two is more triangular

than in extant felids, and not as deep. There is no astragalar foramen.

Calcaneum

The most noticeable difference from the calcaneum (fibulare) in all three species of *Smilodon* is the moderately long calcaneal tuber, which proportionally resembles those of extant felids, providing a larger inlever for the m. gastrocnemius in *Megantereon*, and indicating a more powerful crus than in *Smilodon*. The articulating facets for the astragalus resemble those of *Smilodon* and to some extent jaguars more closely than the other pantherines (Fig. 25A). Medially, there is a distinct facet for the navicular, as in *Smilodon*, which is usually absent in extant pantherines, although it is sometimes present in jaguars. If present, it is distinctly smaller than in *Megantereon* and *Smilodon*. The sustentacular and navicular facets are either joined by a very slender section, or are separate in modern pantherines and *Panthera atrox* (Merriam & Stock, 1932), but are joined by a distinct section in jaguars, which is, however, not always narrow, as stated by Berta (1987). The latter condition is also present in *Smilodon gracilis* (Berta, 1987), whereas the section in *S. fatalis* (Merriam & Stock, 1932) and *S. populator* is very wide. In *Megantereon*, it is intermediate, wider than in jaguars, and narrower than in *S. fatalis* and *S. populator*.

The astragalocalcanear facet is distinctly wider than in *Smilodon gracilis* and extant felids, resembling the condition in *S. fatalis* and *S. populator*. It does not extend as far posteriorly as is often the case in extant pantherines, resembling the condition in *Smilodon*. The cuboid articulating facet is wide and shallowly concave, and is more rectangular than in extant large felids, resembling the condition in *Smilodon fatalis* and *S. populator*. The groove for the peronus tendon is well demarcated, as in other large felids. There are no marked differences in development of this groove in extant pantherines (*contra* Berta, 1987), and there is some intraspecific variation.

Navicular

The navicular (or centrale) is broadly similar to that of *Smilodon*, but there are differences in the nature of the articulating facets, and also from those of extant large felids. In proximal view (Fig. 25E), the bowl-shaped articulating facet for the astragalus occupies the majority of the surface, as in other felids, and the proximal plantar tuberosity is less pronounced than in extant pantherines and *Homotherium* (Rawn-Schatzinger, 1992), resembling the condition in *Smilodon*, especially *S. gracilis*, where it is slightly larger than in *S. fatalis* (Berta, 1987). In distal view (Fig. 25F), the large, gently convex articulating facets

for the ectocuneiform and mesocuneiform are confluent and divided only by a narrow ridge, as in extant pantherines, whereas there may be a strong ridge or gap between them in *Smilodon fatalis* (Merriam & Stock, 1932) and *Homotherium* (Rawn-Schatzinger, 1992). The facet for the entocuneiform is elongate, as in *Smilodon*, and not rounded, as in extant pantherines. In lateral perspective, *Smilodon* and *Homotherium* have distinct cuboid and calcaneal facets. Although indistinct, they are also present in *Megantereon*. Supposedly, the calcaneal facet is absent among extant pantherines (Merriam & Stock, 1932; Berta, 1987). However, tigers occasionally have a dorsally projecting part, clearly offset from the cuboid facet, and this is, in fact, a calcaneal facet.

Mesocuneiform

The left mesocuneiform (or distal tarsal II) is firmly attached to metatarsal II, making inspection of the distal articulating facets impossible. It is more rectangular than in *Smilodon fatalis*, resembling the condition in *Panthera atrox* (Merriam & Stock, 1932) and extant large felids more closely. Its metatarsal II articulating facet presumably resembled the mesocuneiform facet dorsally on the right metatarsal II (see below), which, unfortunately, is less well preserved than on the left, where it is obscured from view. The dorsal articulating facet for the navicular is wider than in extant large felids. The facet along the inner side for the ectocuneiform is indistinct, but appears to have been wider and less elongate than in extant large felids.

Metatarsals

Metatarsals II–V are present from both hind feet (Fig. 21I, J) and are well preserved, with only cosmetic restoration in several places, most notably along the dorsal face of the shaft of the left metatarsal IV. In several instances, however, the dorsal articulating surfaces are slightly weathered. Metatarsal I is absent and was evidently rudimentary, as in other felids, as indicated by lack of a medial articulating surface proximally on metatarsal II. Metatarsal III is the longest, although in the right foot, metatarsal IV is almost equally long, as frequently seen in extant felids, whereas there is a marked and peculiar discrepancy in length between the two in the left foot (Table 4). The relative length of the metatarsals is II–V–IV–III, as in extant felids.

At a length of around 96 mm, metatarsal III in *Megantereon* is similar to the upper size range in leopards ($N = 16$: 74.1–95.3 mm) and pumas ($N = 6$: 92.4–102.5 mm), below the range of lions ($N = 15$: 103.4–143.6 mm) and tigers ($N = 19$: 106.5–142.8 mm), and larger than in jaguars ($N = 8$: 73.8–90.5 mm). The lengths of all metatarsals in

Megantereon (Table 4) are well within the range of *Smilodon fatalis* (Merriam & Stock, 1932), indicating that the metatarsals were also proportionally more elongate than in this species, as with the metacarpals (above). As with the metacarpals, the metatarsals of *Megantereon* are more solidly built than in extant large felids, but are not quite as massive as in the three species of *Smilodon*.

Metatarsal II has a distinct proximal facet for the mesocuneiform, and as in *Smilodon* (Merriam & Stock, 1932) and extant felids, the facet is gently concave but the lateral wall of bone adjacent to the facet in *Megantereon* is distinctly thicker than in other felids. The facet is less well preserved on the right metatarsal. The scar for the plantar flexors is located more proximally, as in *Smilodon* (Merriam & Stock, 1932) and extant felids, and not further distally as in *Homotherium* (Rawn-Schatzinger, 1992). As in other felids, the distal articulating facet for the proximal phalanx is medially bevelled, but the median keel is decidedly less pronounced along the plantar side than in extant large felids.

Metatarsal III is not only the longest but also the most robust metatarsal. To some extent, this is similar to extant large felids, in that it is also often the case in tigers and lions, whereas the difference in robusticity is less pronounced in many leopards, jaguars and pumas. In dorsal view, the proximal end is greatly inclined, distinctly more so than in extant large felids, *Smilodon* (Merriam & Stock, 1932; Berta, 1987) and *Homotherium* (Rawn-Schatzinger, 1992). As in other felids, although not *Homotherium* (Rawn-Schatzinger, 1992), the proximal articulating facet for the ectocuneiform is keyhole-shaped, albeit less pronounced than in extant felids, and the plantar extension of the facet is set off towards the medial side. Proximolaterally, there is an oval and deeply concave articulating facet for metatarsal IV, and the two facets for metatarsal II are much smaller and divided by a trench, as in other felids. The plantar facet for metatarsal IV is located slightly dorsally to the dorsal one, as in extant felids, and unlike *Smilodon* (Merriam & Stock, 1932; Berta, 1987). The distal articulating facet for the proximal phalanx bears a thick, distinct median keel, and unlike metatarsal II, it is visible in dorsal view.

Metatarsal IV is distinctly less solidly built than metatarsal III, although being of subequal length. In dorsal view, the articulating facet for the cuboid slopes gently ventrally, but is inclined towards the plantar side, and has a slight heel along the plantar edge, as in other felids. It tapers somewhat more towards the plantar side than in extant felids. Proximomedially are two large, elongate articulating facets for metatarsal III. The dorsal one is not as bulbous as in extant felids, and the plantar one is gently concave, resembling the condition in extant felids. Proximolaterally are two articulating facets for metatarsal V, and as in extant big cats the dorsal one is larger and extends slightly further distally than the plantar one. The median keel on the distal articulating facet is pronounced as in metatarsal III.

Metatarsal V is both shorter and more slender than metatarsal IV, as in extant felids, and in contrast to the condition in *Smilodon*, where it is shorter and thicker (Merriam & Stock, 1932; Berta, 1987). As in other felids, the shaft is also more curved than was the case for the other metatarsals. In *Smilodon* (Merriam & Stock, 1932; Berta, 1987) and *Homotherium* (Rawn-Schatzinger, 1992), the dorsal facet for the cuboid lacks a raised lateral wing, but it is present in both extant felids and *Megantereon*. As in other felids, the facet is elongate, gently concave, and is gently inclined towards the plantar side. The medial articulating facets are less asymmetrical than in extant felids, in that the dorsal one is not situated markedly below the plantar one. In this respect, *Megantereon* is similar to *Smilodon* (Merriam & Stock, 1932; Berta, 1987). However, the dorsal facet is the largest, as in other felids. Merriam & Stock (1932) noted that the presence of a distinct ligament scar below the facets for metatarsal IV constituted a difference from *Panthera atrox*. It is not only present in *Megantereon* also, but is actually larger than in *Smilodon*. It is also present in extant pantherines, albeit less pronounced.

PALAEOBIOLOGY

BODY SIZE AND APPEARANCE OF *MEGANTEREON*

Megantereon cultridens has traditionally has been considered similar in body size to a male leopard (e.g. Schaub, 1925; Turner & Antón, 1997). This is probably correct for many specimens (see e.g. Vekua, 1995; Sardella, 1998; Palmquist *et al.*, 2007), but SE311 was clearly larger. Sunquist & Sunquist (2002) compiled head–body length (HBL) and body mass data from a variety of sources for all living felids, and gave the values for male pumas as 120–150 cm [body mass (BM): 50–75 kg), male leopards as 100–130 cm (BM: 40–70 kg), male jaguars from South America, where they attain their greatest body sizes, as 120–170 cm (BM: 70–120 kg), lionesses as 150–170 cm (BM: 110–160 kg) and Bengal and Siberian tigresses as 145–180 cm (BM: 100–170 kg).

Like other derived sabrecats (Anyonge, 1993; Turner & Antón, 1997; Christiansen & Harris, 2005), *Megantereon* was powerfully built, especially in the anterior part of the body. Christiansen & Harris (2005) provided a set of comprehensive equations for computation of body mass of extant and extinct felids,

and introduced a new multivariate method, in which the predictor variables for the reliability of the equations for mass prediction were incorporated into the computation, instead of merely being noted, as traditionally. When using their equations for prediction of the body mass of SE311 based on the better preserved limb bones from the left-hand side of the body, the results are remarkably homogeneous, and are 109.8 kg (humerus; 15 variables), 107.5 kg (ulna; three variables), 101.3 kg (femur; 12 variables) and 105.7 kg (tibia; six variables). This is clearly incongruent with even very large male leopards, and is similar to a large, male jaguar, or a rather small lioness or tigress. Such a notion is also in accord with the size comparisons given under description of the various skeletal elements (above). SE311 was, however, a large specimen when compared with other known specimens of *Megantereon* (e.g. Sardella, 1998). Other specimens, e.g. the specimen to which the skull MNHNPer2001a belongs (condylobasal length: 193.5 mm), would have a resulting inferred body mass of around 56.5 kg, providing it was allometrically similar to SE311. This specimen was, accordingly, leopard-sized. *Megantereon* sp. were sexually dimorphic (Palmquist *et al.*, 2007), as with extant large felids, and the size of SE311 suggests that it was a male.

The inference of *Megantereon* as similar in size to a small lioness or tigress is corroborated when comparing the osteological HBL, defined as the combined length of the skull and all the centra making up the presacral vertebral column, with similar data from extant large felids (Table 5). *Megantereon* has an osteological HBL of around 130 cm, as found when adding the centrum lengths of all the preserved presacral vertebrae, allowing for the missing L1, and adding the estimated length of the skull. When comparing to the osteological HBL values listed in Table 5, *Megantereon* is significantly larger than the averages for *Puma concolor* (898.1 mm; $P = 0.005$), *Panthera pardus* (964.6 mm; $P = 0.021$) and *P. onca* (1010.9 mm; $P = 0.006$), but is smaller than *P. leo* (1460.8 mm; $P = 0.032$) and *P. tigris* (1563.0 mm; $P = 0.046$).

However, live HBL would have been greater, as it is measured from the nose to the base of the tail, i.e. including the pelvis. This also accounts for the discrepancy in osteological vs. actual HBL of the extant felids in Table 5. Compared with the two lions and three tigers from which live HBL is known, it is evident that for an extant large felid, skeletal HBL is 25 cm (lion, CN7321) to 42 cm (tiger; CN5697) less than the HBL of the living animal, at least when HBL was measured after tranquilization, as was the case for the five specimens from the table. This implies that *Megantereon* would have had an HBL of around 160 cm, similar to a large male jaguar or a lioness or tigress, and distinctly larger than a leopard.

Megantereon, like the few other well-known derived sabrecats, appears to have been differently proportioned than extant large felids (see also Schaub, 1925; Turner & Antón, 1997). As restored, the skull in *Megantereon* is significantly smaller relative to the length of the vertebral column (0.227) than the averages (Table 5 and Fig. 26A) of the extant pantherines, *Panthera leo* (0.280; $P = 0.001$), *P. onca* (0.281; $P = 0.004$), *P. pardus* (0.248; $P = 0.001$) and *P. tigris* (0.258; $P = 0.005$), but not from the average in *Puma concolor* (0.231; $P = 0.640$), which, among others, is easily distinguished from *Panthera* by having a proportionally small, domed skull and a long dorsal vertebral column. Mounted skeletons and skeletal restorations of other derived sabrecats, such as *Smilodon*, *Homotherium* and *Machairodus* (Merriam & Stock, 1932; Méndez-Alzola, 1941; Ballesio, 1963; Turner & Antón, 1997; our pers. observ.), also indicate that these forms had smaller skulls relative to the size of their bodies than do extant large felids, with the probable exceptions of the puma and cheetah.

As noted by Schaub (1925), the cervical vertebral column in *Megantereon* is remarkably elongate compared with extant felids, in particular the anterior cervicals. This appears also to be the case in other derived machairodonts. In *Megantereon*, the cervicals make up around 32.1% of the length of the presacral vertebral column (Table 5). This appears comparable with reconstructions of *Smilodon* and *Homotherium* (Merriam & Stock, 1932; Méndez-Alzola, 1941; Ballesio, 1963; Rawn-Schatzinger, 1992; Turner & Antón, 1997; Antón & Galobart, 1999), but is distinctly longer than in extant large felids (Table 5; Fig. 26B). The neck in *Megantereon* makes up a significantly larger portion of the presacral vertebral column than in *Puma concolor* (0.251; $P = 0.003$), *Panthera leo* (0.263; $P < 0.001$), *P. onca* (0.257; $P = 0.002$), *P. pardus* (0.248; $P < 0.001$) and *P. tigris* (0.254; $P < 0.001$).

The length of the forelimb and hind limb relative to the length of the presacral vertebral column in *Megantereon* also differ from the averages of extant large felids (Table 5; Fig. 26D, E). The length of the forelimb in *Megantereon* is 0.544 of the length of the presacral vertebral column. This is significantly shorter than in *Puma concolor* (0.613; $P = 0.029$), *Panthera leo* (0.660; $P < 0.001$), *P. pardus* (0.595; $P = 0.019$) and *P. tigris* (0.611; $P = 0.001$), and also than *P. onca* ($P = 0.027$), which proportionally has the shortest forelimbs (0.587), in accordance with the traditionally held view of this large cat as being short-limbed and stocky (e.g. Gonyea, 1976a, b; Seymour, 1989; Nowak, 1991; Turner & Antón, 1997; Sunquist & Sunquist, 2002). The hind limb relative to the presacral vertebral column in *Megantereon*

Table 5. Physical sizes and proportions of *Megantereon cultridens* SE311 and extant large felids

	Vertebral column length							Osteological	Actual body size		
	Skull	BM	FL	HL	Neck	Thorax	Lumbar	HBL	HBL	SH	Tail
Megantereon cultridens	238.7		572.6	632.2	337.7	415.5	300*	1291.9*			
Puma concolor CN1663	155.2	45.7	437.5	547.8	173.3	276.0	237.8	842.3			
Puma concolor CN5664 (♀)	164.6		444.8	561.2	181.6	299.7	264.7	910.4			
Puma concolor CN886 (♂)	185.8		458.8	575.9	194.1	308.9	252.7	941.5			
Panthera leo CN887 (♀)	275.1		657.1	736.4	262.6	417.2	339.6	1294.5			
Panthera leo CN7364 (♀)	296.9	150	722.1	818.1	281.5	460.0	361.9	1400.3	180	–	80
Panthera leo CN1440 (♂)	341.7		776.4	832.0	309.2	471.0	367.0	1488.9			
Panthera leo CN6043 (♂)	325.0	170	796.1	885.2	310.0	489.4	395.4	1519.8			
Panthera leo CN7321 (♂)	359.7	203	814.9	880.2	339.2	504.2	397.6	1600.7	185	–	95
Panthera onca CN5658 (♀)	213.3		447.0	523.8	195.0	323.6	252.0	983.9			
Panthera onca CN5707 (♀)	222.4	51.5	448.2	513.8	200.0	323.3	249.1	994.8			
Panthera onca CN5660 (♂)	229.7	67.4	496.2	568.7	213.5	342.8	267.9	1053.9			
Panthera pardus CN5661 (♀)	188.2	61	447.3	545.5	186.6	313.7	257.8	946.3			
Panthera pardus CN7374 (♀)	177.5	434.6	520.9	176.3	290.0		247.2	891.0			
Panthera pardus CN5662 (♂)	210.1	60	495.7	581.3	212.5	348.5	285.3	1056.4			
Panthera tigris CN5669 (♀)	261.6	115	645.4	746.5	264.4	430.8	358.4	1315.2			
Panthera tigris CN5698 (♂)	350.9	220	786.5	891.4	328.3	533.5	440.6	1653.3	204	100	107.5
Panthera tigris CN5697 (♂)	334.2	221	811.4	934.2	329.7	531.9	440.7	1636.5	206	120	100
Panthera tigris CN6049 (♂)	337.8	225	788.9	904.1	341.1	532.6	435.5	1647.0	195	118	90

*Including missing L1. Actual length of L2–L7 is 295.1 mm.

All osteological measurements are in mm, body sizes are in cm, and body mass is in kg.

Abbreviations: BM, actual body mass; FL, forelimb length (humerus + radius + metacarpal III); HBL, head and body length; HL, hind limb length (femur + tibia + metatarsal III); SH, shoulder height; Skull, length of skull from premaxilla to the occipital condyles; Tail, length of tail.
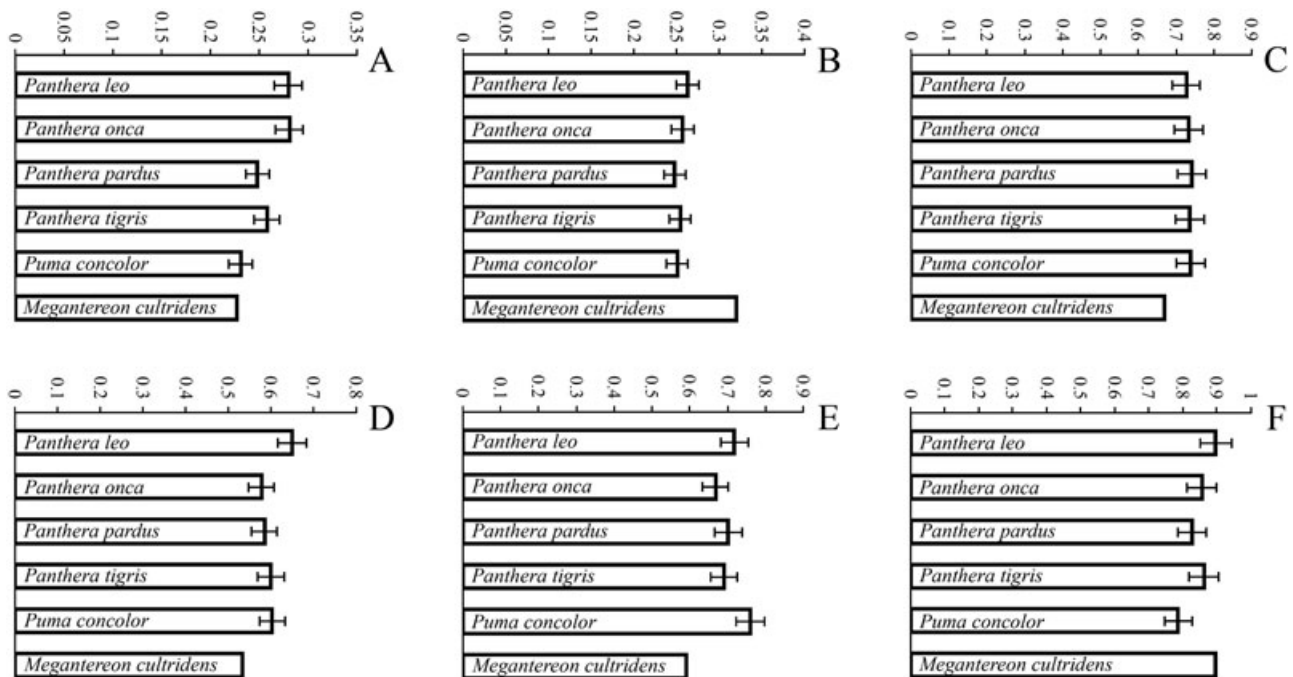
Figure 26. Vertebral and limb proportions in *Megantereon cultridens* SE311 and extant large felids, along with 95% confidence limits. A, skull length to the length of the presacral vertebral column; B, length of the cervical vertebral column to the length of the presacral vertebral column; C, length of the thoracal and lumbar vertebral column to the length of the presacral vertebral column; D, forelimb length to the length of the presacral vertebral column; E, hind limb length to the length of the presacral vertebral column; F, forelimb length to hind limb length. Forelimb length was computed as the length of humerus + radius + metacarpal III, and hind limb length as femur + tibia + metatarsal III. Specimens are listed in Table 5.

(0.600) is also significantly less than the averages in *Puma concolor* (0.771; $P = 0.006$), *Panthera leo* (0.728; $P < 0.001$), *P. pardus* (0.713; $P = 0.013$) and *P. tigris* (0.700; $P = 0.001$), and *P. onca* again has the lowest average value (0.678), which is still significantly higher than in *Meganterēon* ($P = 0.008$).

The above marked differences are, however, in part owing to *Meganterēon*'s long neck. If comparing the proportions of the limbs to the dorsal vertebral column only, the above pattern changes. The forelimb makes up 0.800 of the dorsal vertebral column in *Meganterēon*, which is significantly less than the averages in *Panthera leo* (0.895; $P = 0.001$) and *P. tigris* (0.819; $P = 0.049$), but not than *Puma concolor* (0.819; $P = 0.418$), *Panthera onca* (0.791; $P = 0.477$) or *P. pardus* (0.791; $P = 0.416$). Similarly, the hind limb makes up 0.884 of the dorsal vertebral column in *Meganterēon*, which is significantly less than in *Puma concolor* (1.029; $P = 0.020$), *Panthera leo* (0.988; $P < 0.001$) and *P. tigris* (0.939; $P = 0.010$), but not than *P. onca* (0.913; $P = 0.096$) or *P. pardus* (0.947; $P = 0.055$), the latter probably owing to small sample size. Accordingly, *Meganterēon* appears to have been a powerfully built, moderately elongate

felid with a small skull, a short tail, a very long and powerful neck, and rather short, powerful limbs (Fig. 27).

Locomotion in Meganterēon
Despite proportional and morphological differences from extant large felids, *Meganterēon* was, in effect, a big cat, and given its close morphological and phylogenetic affinity to extant felids, it appears defensible to argue that it also moved and lived in a broadly comparable manner. Much has been made of limb ratios in large felids, and also sabrecats, in attempts to explain their locomotory capabilities. Large, more slender sabrecats such as *Homotherium* and *Machairodus* have been claimed to have been cursorial (Rawn-Schatzinger, 1992; Anyonge, 1996), a problematic term in locomotor analyses (Stein & Casinos, 1997; Carrano, 1999). Traditionally, it is taken to imply animals that were inferred to be morphologically and ecologically adapted for running fast and far in open terrain (Gregory, 1912; Gambaryan, 1974; Stein & Casinos, 1997). In fact, no living felid is cursorial in that sense and all the great cats rely on a stealthy approach to get close to prey using ambush
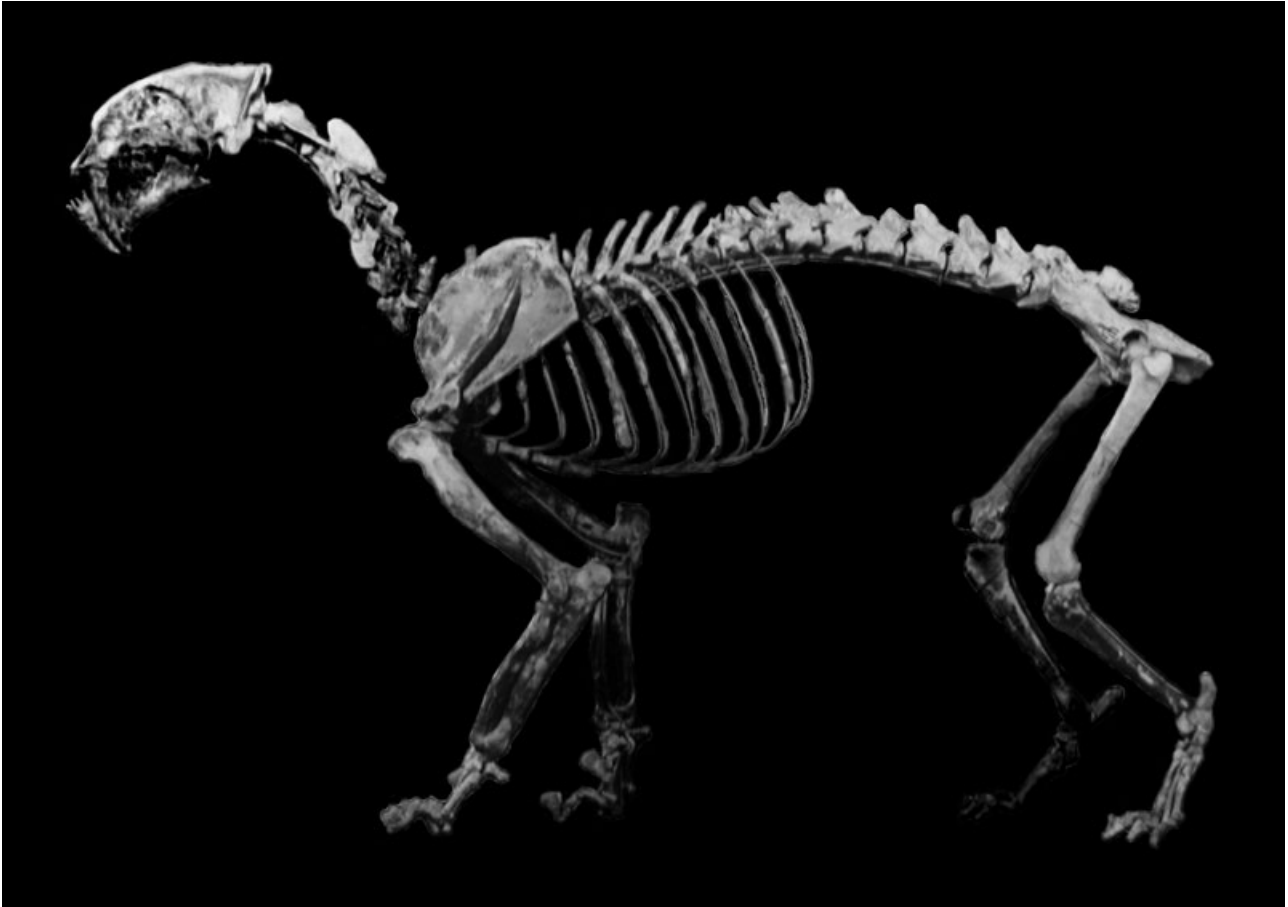
Figure 27. The skeleton of *Megantereon cultridens* SE311 as it stood when still mounted in the exhibitions at the Natural History Museum in Basel. As reconstructed, the skeleton has seven cervical, 12 thoracal and seven lumbar vertebrae, and is thus missing a posterior thoracal vertebra. The vertebra here placed as lumbar 3 is, however, the rather poorly preserved thoracic 11, and the actual missing vertebra is lumbar 1. Photo courtesy of Arne Ziems, curator, Natural History Museum, Basel.

cover, after which the pounce is initiated (for an overview see Sunquist & Sunquist, 2002). Even the cheetah, which is the world's fastest land animal (Nowak, 1991; Sharp, 1997; Christiansen, 2002), does not run fast and far, but also relies on stealth, followed by a very rapid, explosive rush over a rather short distance (Eaton, 1970; Ewer, 1973; Caro, 1994).

The heavy build and stocky limbs of some large sabrecats, such as *Megantereon* and *Smilodon*, although more pronounced, are broadly comparable with those of extant pantherines, especially the jaguar. There is little reason to suppose that they had a radically different hunting and locomotor style, also given the reliance of the forelimbs for prey capture in extant felids, and the constraints this places on adaptive alteration of forelimb morphology for different locomotor and hunting ecologies. Even the cheetah is built similarly to other living felids (*contra* Rawn-Schatzinger, 1992), except in having more slender and

elongate bones. The above was undoubtedly also the case in the large sabrecats, as also indicated by the uniformity of their retractile claws (Gonyea & Ashworth, 1975; Gonyea, 1976b). All living felids rely on stalking cover and employ an ambush mode of hunting (Sunquist & Sunquist, 2002). Sabrecat hunting ecology was probably no different.

Much has traditionally been made of certain limb ratios, especially the metatarsus/femur ratio, to predict locomotion and running capability in a variety of mammals (e.g. Gregory, 1912; Howell, 1944; Gambaryan, 1974; Coombs, 1978; Garland & Janis, 1993) and also large felids, including sabrecats (Schaub, 1925; Gonyea, 1976a, b; Rawn-Schatzinger, 1992; Anyonge, 1996). There are strictly mechanical reasons for supposing a tight relationship between limb morphology, including a variety of limb ratios, and peak running velocity, but the correlations are often modest, and phylogenetic affinity is responsible

Table 6. Averages and standard deviations, and *post-hoc* Tukey comparisons of the ratio of the length of the lumbar vertebral column to the length of the dorsal vertebral column in extant large felids and *Megantereon*

	Meg.	P. leo	P. onca	P. pardus	P. tigris	Puma
Megantereon	1.000					
Panthera leo	0.011	1.000				
Panthera onca	0.085	0.662	1.000			
Panthera pardus	0.001	0.109	0.018	1.000		
Panthera tigris	0.001	0.142	0.021	0.999	1.000	
Puma concolor	0.000	0.005	0.001	0.613	0.357	1.000

ANOVA: $F = 14.443$; $P < 0.001$.
For data see Table 5.
Megantereon cultridens: 0.419; *Panthera leo*: 0.443 ± 0.005; *Panthera onca*: 0.437 ± 0.002; *Panthera pardus*: 0.454 ± 0.006; *Panthera tigris*: 0.452 ± 0.002; *Puma concolor*: 0.461 ± 0.010.

for a substantial part of the purported form–function correlation (Christiansen, 2002). The close morphological and phylogenetic affinity of *Megantereon* and other sabrecats to extant large felids makes assumptions of broadly similar locomotor capabilities defensible.

As noted above, the limbs of *Megantereon* are differently proportioned compared with HBL in extant large felids. This is also the case for the length of the forelimb compared with the length of the hind limb (Table 5; Fig. 26F). The forelimb makes up 90.6% of the length of the hind limb in *Megantereon*, which is non-significantly different from the average in *Panthera leo* (0.903; $P = 0.698$), but is otherwise significantly higher than in other large felids, *Puma concolor* (0.806; $P = 0.002$), *Neofelis nebulosa* (0.823; $P = 0.003$), *Panthera onca* (0.865; $P < 0.001$), *P. pardus* (0.838; $P < 0.001$) and *P. tigris* (0.872; $P < 0.001$). Extant big cats are all adept jumpers, especially the puma (Young & Goldman, 1946; Wood, 1976; Sunquist & Sunquist, 2002), which has proportionally the longest hind limbs relative to the fore limbs. The snow leopard (*Panthera uncia*) also has a very good leaping ability (Hemmer, 1972; Wood, 1976), and in a sample of ten snow leopards (P. Christiansen, unpubl. data) the average fore to hindlimb ratio ± SD is 0.837 ± 0.013, in accordance with the above. Howell (1944) and Gonyea (1976a) argued that this is characteristic for species with good leaping ability. By this token, *Megantereon* would not have been a good leaper, which is corroborated by its heavily built forequarters, which appear less adapted for such athletic endeavours. However, the indices for jaguars and tigers are almost identical, as are those of pumas, snow leopards and clouded leopards, and there is universal agreement as to the good leaping ability of the tiger (Mazák, 1981), and it is regarded as a better leaper than the lion (Wood, 1976). Thus, inferences about the leaping ability of *Megantereon* remain tentative.

A long and flexible dorsal, and in particular lumbar, vertebral column is also indicative of bounding-gait running (Howell, 1944; Gambaryan, 1974; Hildebrand, 1988; Taylor, 1989) and has been associated with good leaping ability in felids (Gonyea, 1976a; Sunquist & Sunquist, 2002). This is also reflected in the neural spines, which are smaller in bounding runners. This is the condition of extant felids. In *Megantereon*, the neural spines along the lumbar vertebrae are low (Fig. 7C), but the lumbar vertebrae are not particularly large (Fig. 7A; see also Fig. 9). Indeed, the lumbar vertebral column in *Megantereon* is significantly shorter than in other big cats, with the exception of the jaguar (Tables 5, 6), and the puma has a longer lumbar region than the lion and jaguar. This indicates a non-galloping, bounding running gait in *Megantereon*, as in other felids, and less well-developed leaping ability, in accordance with the above.

Megantereon proportionally has a considerably longer calcaneal tuber than *Smilodon*, and as such should have been capable of a more forceful push-off by providing a longer inlever about the ankle joint. The calcaneal tuber is, however, not hypertrophied compared with those of extant large felids. *Megantereon* has a proportionally large scapula compared with the length of its forelimb (Fig. 28A). The length of the scapula makes up 0.386 of the length of the fore limb, which is significantly higher than in any of the extant large felids: *Puma concolor* (0.319; $P = 0.006$), *Neofelis nebulosa* (0.314; $P = 0.014$), *Panthera leo* (0.340; $P < 0.001$), *P. onca* (0.345; $P < 0.001$), *P. pardus* (0.331; $P < 0.001$) and *P. tigris* (0.328; $P < 0.001$). Along with the wide supraspinous fossa and hypertrophied acromion region, suggesting very powerful musculture, this indicates that *Megantereon* was adapted for exertion of great force from the forelimb, which is congruent with forelimb morphology.

The ratios of the major limb bones in *Megantereon* are intermediate between those of extant large felids
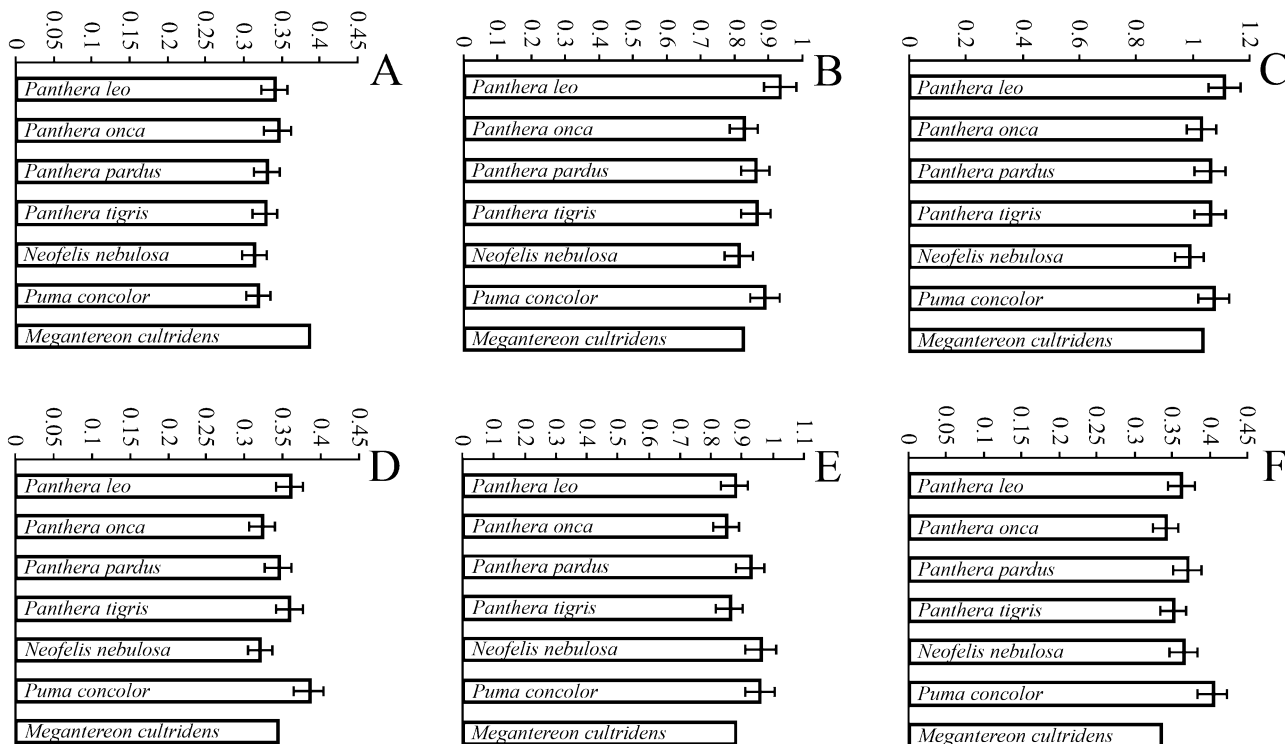
Figure 28. Fore and hind limb proportions in *Megantereon cultridens* SE311 and extant large felids, along with 95% confidence limits. A, scapula length to forelimb length; B, radius length to humerus length; C, ulna length to humerus length; D, metacarpal III length to humerus length; E, tibia length to femur length; F, metatarsal III length to femur length. Forelimb length was computed as the length of humerus + radius + metacarpal III. Specimen numbers are: *Panthera leo* (N = 16), *Panthera onca* (N = 8), *Panthera pardus* (N = 16), *Panthera tigris* (N = 19), *Neofelis nebulosa* (N = 5) and *Puma concolor* (N = 6).

(Tables 3–5; Fig. 28B–F). The radius/humerus ratio in *Megantereon* (0.824) is significantly lower than in *Panthera leo* (0.934; *P* < 0.001), *P. pardus* (0.861; *P* = 0.043) and *P. tigris* (0.863; *P* = 0.002), but is not significantly different from the averages in *Puma concolor* (0.888; *P* = 0.064) and *Neofelis nebulosa* (0.811; *P* = 0.097), and is virtually identical to the average in *Panthera onca* (0.825; *P* = 0.805). Similarly, the metacarpal III/humerus ratio of *Meganthereon* (0.343) is significantly lower than in *Puma concolor* (0.385; *P* = 0.011), *Panthera leo* (0.359; *P* = 0.004) and *P. tigris* (0.359; *P* = 0.010), higher than in *Neofelis nebulosa* (0.320; *P* = 0.096) and *Panthera onca* (0.323; *P* = 0.033), and virtually identical to the average in *P. pardus* (0.344; *P* = 0.822). The tibia/femur ratio in *Megantereon* (0.877) is non-significantly different from the average in *Puma concolor* (0.957; *P* = 0.120) and identical to that of *Panthera leo* (0.876; *P* = 0.931), it is lower than in *Neofelis nebulosa* (0.960; *P* = 0.016) and *Panthera pardus* (0.926; *P* < 0.001), but higher than in *P. onca* (0.848; *P* = 0.025) and *P. tigris* (0.860; *P* = 0.030). The metatarsal III/femur ratio of *Megantereon* (0.335) is

significantly lower than in *Puma concolor* (0.403; *P* < 0.001), *Panthera leo* (0.362; *P* = 0.010), *P. pardus* (0.370; *P* = 0.009) and *P. tigris* (0.351; *P* = 0.011), but non-significantly lower than in *Neofelis nebulosa* (0.365; *P* = 0.085) and virtually identical to the average in *Panthera onca* (0.338; *P* = 0.800).

In summary, it may be concluded that *Megantereon* was a heavily built big cat with rather short limbs, and that the long bone ratios are at the low end of the interspecific variation observed in extant felids. In these respects, *Megantereon* appears morphologically closest to the jaguar. Little is known about the jaguar's peak locomotor speed and leaping ability, but although it appears reasonable to infer that they are probably less than in pumas, tigers and leopards [Seymour (1989) and Sunquist & Sunquist (2002) both state that it is less supple than the leopard], the jaguar is still basically a big cat with a similar locomotor ecology. It is capable of bringing down very large prey, such as domestic cattle (Hoogesteijn, Hoogesteijn & Mondolfi, 1993), but usually hunts a wide variety of medium-sized prey (Leopold, 1959; Seymour, 1989). *Megantereon* most likely shared the

ecological characteristics of extant large felids in relying on cryptic stalking to get close to prey, followed by a rapid rush, although the latter may have been less forceful and explosive than seen in extant leopards, tigers and lions. We tentatively suggest that *Megantereon* was less fleet, and that its leaping ability was less than in extant lions, tigers and leopards, but that it relied on great strength for subduction of prey instead.

Habitat of Megantereon

Limb morphology has also often been used to infer form–ecology correlations among extant large felids, and to assign habitat preference to sabrecats (Gonyea, 1976a, b, 1978; Berta, 1987; Rawn-Schatzinger, 1992; Palmquist *et al*., 2003). As such, the jaguar is classified as a forest-dwelling species and the lion is classified as an open-country species, and differences in their limb morphology are then purported to be indicative of their habitat adaptations (Gonyea, 1976a, 1978). Accordingly, eventual similarities in sabrecats are taken as evidence for a particular habitat preference. By this token, *Megantereon*, and in particular *Smilodon*, are forest-adapted species (Gonyea, 1976b; Berta, 1987). However, this is incongruent with fossil plant evidence from Rancho La Brea, which indicates an open, coastal sage scrub community with riparian associations alongside the watercourses, and with chaparral and deep canyon floras in the mountains (Stock & Harris, 1992).

Such inconsistencies are hardly surprising. First, limb bone ratios constitute no causal explanation for habitat preference. The biomechanically selective advantage of a jaguar living in the rainforest having a slightly shorter tibia relative to the femur than a lion or leopard on the plains is elusive, especially given the often marked intraspecific variation in such ratios. Secondly, ratios are often size-related (e.g. Albrecht, Gelvin & Hartman, 1993; Christiansen, 2002), and this is not normally addressed in palaeobiological inferences. Thirdly, and most importantly, extant big cats, such as pumas, lions, tigers, jaguars and leopards, are found in a much wider variety of environments than is usually assumed, ranging from forest to scrub and even semi-deserts (e.g. Schaller, 1972; Seidensticker *et al*., 1973; Mazák, 1981; Anderson, 1983; Seymour, 1989; Srivastav & Srivastav, 1999; Sunquist & Sunquist, 2002; Divyabhanusinh, 2005). The exceptions are the clouded leopard, which appears to be a true forest cat, although not strictly arboreal (Prater, 1971; Sunquist & Sunquist, 2002), the high-altitude, mountainous snow leopard (Hemmer, 1972; Sunquist & Sunquist, 2002), and the cheetah (Caro, 1994), which inhabits open country. However, even cheetahs frequently inhabited other environments than the typical open plains of Africa, and lived in open-forest environments in Asia prior to their recent extinction by humans (Caro, 1994; Divyabhanusinh, 1995; Sunquist & Sunquist, 2002).

Rather, the common denominators are availability of appropriate stalking cover, a plentiful supply of large prey and accessible fresh water. Given this, extant large felids can and do live in a wide variety of environments. Stalking cover most often implies vegetation, but for the puma (Hibben, 1937; Young & Goldman, 1946; Wilson, 1984; Iriarte, Johnson & Franklin, 1991) and snow leopard (Hemmer, 1972; Sunquist & Sunquist, 2002), which often live in elevated, rugged and barren terrain, it often implies landscape topology, as these cats frequently rely on a stealthy approach using altitude and rocks, before launching a final, rapid attack from above. This implies that limb ratios as a basis for evaluation of sabrecat habitat preference is highly speculative.

More reliable evidence may be gained from faunistic studies. The fauna of the Senéze site is fairly well known and the composition of the mammalian fauna (Table 7), with macaques and a rather high diversity of deer, indicates a forested environment. Extant deer frequently live in forests (Nowak, 1991; Whitehead, 1993). The Barbary ape (*Macaca sylvanus*) primarily inhabits forest areas today (Nowak, 1991). The presence of a close relative of the extant Sumatra rhinoceros (*Dicerorhinus sumatrensis*) also indicates some sort of a forest environment, as this species lives in forests (Nowak, 1991). On the other hand, the presence of equids indicates a more open-type environment, as no extant equid typically inhabits forests (Nowak, 1991). However, the animals need not have been temporally sympatric even if they were geographically so, given that the Senéze fauna spans several hundreds of thousands of years. Several large carnivores were also present besides *Megantereon* (Table 7). Felids are represented by the scimitar-toothed *Homotherium* and the large cheetah *Acinonyx pardinensis*, but the fauna also included two large hyenas, *Pachycrocuta* and *Chasmaporthetes*. The presence of large cheetahs also suggests that the environment was not dense forest.

Predatory ecology

Extant large felids usually employ a suffocating bite to the throat of large prey, whereas smaller prey may be dispatched with a nape bite also (Sunquist & Sunquist, 2002). This is also the case in the jaguar, which, however, frequently also employs a powerful nape bite to large prey, in addition to a specialized skull bite, which is rarely seen in other large felids (Seymour, 1989; Hoogesteijn *et al*., 1993; Hoogesteijn & Mondolfi, 1996). The once popular notion of sabrecats stabbing their prey with their hypertrophied upper canines (e.g. Matthew, 1910; Simpson, 1941;

Table 7. Faunal list of the Senéze site, after Stehlin (1923) and Schaub (1943)

Order	Genus	Species
Primates	*Paradolichopithecus*	*arvernensis* (Depéret, 1929)
	Macaca	*sylvanus*
Proboscidea	*Mammuthus*	*meridionalis* (Nesti, 1825)
Perissodactyla	*Allohippus*	*stenonis senezensis* (Prat, 1964)
	Equus	*bressanus* (Viret, 1954)
	Equus	*stehlini* (Azzaroli, 1965)
	Dicerorhinus	*etruscus etruscus* (Falconer, 1859)
Artiodactyla	*Sus*	*strozzii* (Major, 1881)
	Croizetoceros	*ramosus minor* (Heintz, 1970)
	'Cervus'	*philisi philisi* (Schaub, 1941)
	Eucladoceros	*ctenoides senezensis* (Depéret, 1910)
	Libralces	*gallicus* (Azzaroli, 1952)
	Gazellospira	*torticornis* (Aymard, 1854)
	Procamptoceras	*brivatense* (Schaub, 1923)
	Megalovis	*latifrons* (Schaub, 1923)
	Gallogoral	*meneghinii* (Rütimeyer, 1878)
	Leptobos	*furtivus* (Duvernois, 1989)
		etruscus (Falconer, 1859)
	Pliotragus	*ardeus* (Depéret, 1884)
Carnivora	*Nyctereutes*	*megamastoides* (Pomel, 1842)
	Vulpes	*alopecoides* (Major, 1877)
	Canis	*senezensis* (Martin, 1973)
	Ursus	*etruscus* (Cuvier, 1824)
	Pachycrocuta	*perrieri* (Croizet & Jobert, 1828)
	Chasmaporthetes	*lunensis* (Del Campana, 1914)
	Acinonyx	*pardinensis* (Croizet & Jobert, 1828)
	Homotherium	*latidens* [*crenatidens*] (Fabrini, 1890)
	Megantereon	*cultridens* (Cuvier, 1824)
Lagomorpha	*Oryctolagus*	cf. *lacosti*
Rodentia	*Mimomys*	*pusillus*
		pitymyoides
		pliocaenicus
		newtoni
	Castoridae	indet.

Miller, 1984) is now abandoned. Rather, derived sabrecats probably used their large upper canines in a shearing-bite action with canine opposition to the throat of the prey, severing blood vessels and nerves and causing rapid collapse of the prey (Akersten, 1985; Bryant, 1996; Turner & Antón, 1997; Antón & Galobart, 1999; Antón *et al.*, 2004). Their skulls morphologically differed markedly from those of extant felids, and had a plethora of derived characters as adaptations for attaining a wide gape (Emerson & Radinsky, 1980; Bryant, 1996; Christiansen, 2006). *Megantereon* shared these characters, and could attain a very large gape compared with extant carnivores (Fig. 29; Christiansen & Adolfssen, 2005; Christiansen, 2006).

The large, strong and procumbent incisors of derived sabrecats would then function both to anchor the lower jaw in the skin of the prey at a high gape just prior to the canine shear bite, and thus provide a stabile section of the prey's flesh for the upper canines to shear through, and following the kill would be efficient for plucking off meat from the carcass (Biknevicius *et al.*, 1996; see also Van Valkenburgh, 1996). *Megantereon* is morphologically similar in all those respects to other derived sabrecats, and would most likely have shared this predatory mode. Bite mechanics appear to have differed from those of extant felids in other respects also. Akersten (1985) argued that the sabrecats had particularly strong cervical depressor muscles, which acted as an auxiliary force to drive the large upper canines into the flesh of the prey (see also Turner & Antón, 1997). Thus, bite forces from the primary jaw adductors were only partly responsible for the force of the killing bite.
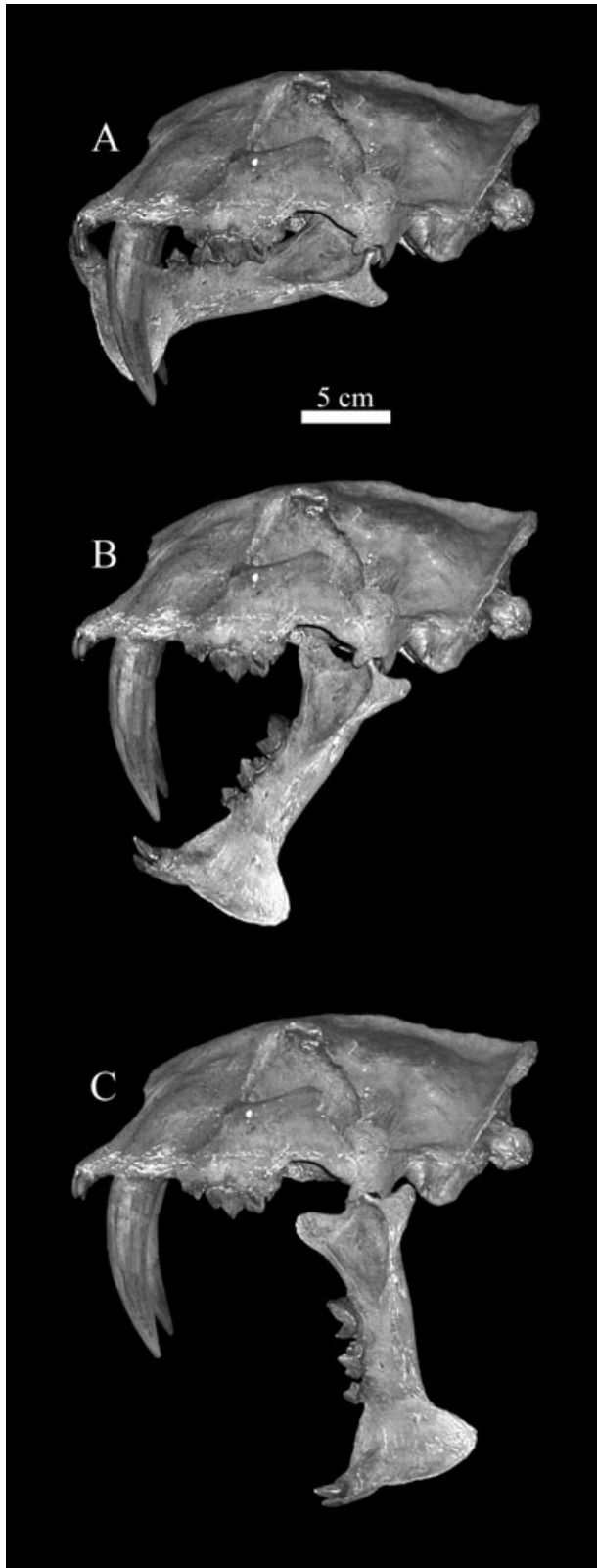
Figure 29. Cast of skull and lower jaw of *Megantereon cultridens* SE311 showing the lower jaw in normal posture at full occlusion (A), at the gape angle (~61°) at which the upper and lower canines clear each other (B), and at maximum inferred gape (~105°). A gape angle of 61° is broadly comparable with maximum gape in extant carnivores (Emerson & Radinsky, 1980; Akersten, 1985; Christiansen & Adolfssen, 2005). At maximal gape angle, the clearance between the upper and lower canines would be around 10 cm, comparable with the values in extant big cats (Christiansen & Adolfssen, 2005).

The hypertrophied cervicals of *Megantereon* and their rather strong transverse processes, especially on C3, the pronounced ventral keels on the centra, where preserved, and the great development of the inferior lamina on the posterior cervicals is similar to the condition of other derived sabrecats, such as *Homotherium*, *Smilodon* and *Machairodus giganteus*. Antón & Galobart (1999) and Antón *et al*. (2004) expanded on Akersten's (1985) arguments, and showed that the great development of the m. longus colli, as indicated by the ventral keels on the centra, and the m. scalenus on the posterior cervicals, as indicated by the large inferior laminae, indicated that sabrecats did indeed have very strong cervical flexors, but that the strong development of the m. intertransversalis, which act to twist the individual cervical vertebrae laterally (Barone, 1967; Crouch, 1969) suggested that they also had strong muscles for stabilizing the neck. This is all in agreement with a canine shear-bite (Antón & Galobart, 1999).

The hypertrophied mastoid process of derived sabrecats, and the associated changes in the also hypertrophied atlantomastoid musculature indicate a strong capacity for depressing the head, driving the large upper canines into the flesh of the prey, with an auxiliary force component from the more posterior neck flexors, while the stabilizing muscles ensured a more precise biting action (Akersten, 1985; Antón & Galobart, 1999; Antón *et al*., 2004). A significant component of this functional complex deals with the size of the mastoid process and sites of insertion for portions of the atlantomastoid muscles along the occipital crest relative to the occipital condyles (Antón & Galobart, 1999; Antón *et al*., 2004). Unfortunately, this region is not preserved in the skull of *Meganteron cultridens* SE311, but other skulls of *Megantereon* (e.g. MNHNPer2001a; see also Vekua, 1995; Turner & Antón, 1997; Palmquist *et al*., 2007) are similar in those characters to other derived sabrecats, and the preserved parts of the skull of SE311 strongly suggest that SE311 also augmented the force from the primary jaw adductors with a significant force component from the upper cervical muscles.

It is evident that the Senéze fauna contains a wide variety of prey species that appear suitable in size for *Megantereon*, such as many artiodactyls and equids (Table 7), and possibly juveniles of *Dicerorhinus* and *Mammuthus*. However, reliable proboscidean inferences have so far only been established for the larger, more gracile *Homotherium serum* (Rawn-Schatzinger, 1992; Marean & Ehrhardt, 1995), whereas carbon and nitrogen isotope analyses of bones from the larger and more robust *Smilodon fatalis* indicated that it primarily preyed on bison, camels, horses and groundsloths (Coltrain *et al.*, 2004), which were common in the La Brea fauna (Stock & Harris, 1992). Based on geochemical bone analyses, Palmquist *et al.* (2003) found that the closely related species *Megantereon whitei* in an Early Pleistocene site in Spain, which faunistically appears comparable with the Senéze fauna, primarily preyed on cervids, and given the faunistic composition of the Senéze site, this appears entirely plausible for *Megantereon cultridens* SE311 also. Palmquist *et al.* (2003) further found that *Homotherium latidens* probably preyed extensively on young *Mammuthus*, in accordance with the above. This could indicate some ecological separation and prey specialization, and resulting niche division, between the smaller and more powerfully built *Megantereon* and the larger, more gracile *Homotherium*, as has been discussed by Palmquist *et al.* (2003, 2007).

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