Functional anatomy of the postcranial skeleton of *Styriofelis lorteti* (Carnivora, Felidae, Felinae) from the Middle Miocene (MN 6) locality of Sansan (Gers, France)

Anatomía functional del esqueleto post-craneal de Styriofelis lorteti (Carnivora, Felidae, Felinae) del Mioceno Medio (MN 6) de Sansan (Gers, France)

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ABSTRACT

The postcranial skeleton of the European Middle Miocene feline *Styriofelis lorteti* has been traditionally known on the basis of fragmentary fossils mainly from the French locality of Sansan. The discovery of an almost complete skeleton in the same site in the excavations of 1990 opened the possibility of unprecedented assessment of the morphology and function of this early felid. In this paper we describe this material, and compare it with a sample of modern and fossil felids, finding a combination of a generally modern morphology, with moderate adaptations to terrestrial locomotion, besides a set of primitive characters linking *S. lorteti* with earlier felids like *Proailurus lemanensis*.

Keywords: Felidae, Felinae, Middle Miocene, Functional Anatomy.

RESUMEN

El esqueleto post-craneal del felino *Styriofelis lorteti*, del Mioceno medio de Europa, ha sido tradicionalmente conocido en base a fósiles fragmentarios, procedentes principalmente del yacimiento francés de Sansan. El descubrimiento en este yacimiento de un esqueleto casi completo, durante la campaña de 1990, abrió la posibilidad de llevar a cabo un análisis sin precedentes de la morfología y función de este félido primitivo. En este trabajo se describe este material, comparándose con una muestra de felinos fósiles y actuales, hallándose una combinación entre una morfología general moderna, con adaptaciones moderadas para la locomoción terrestre, junto con una serie de caracteres primitivos que relacionan a *S. lorteti* con los félidos más antiguos como *Proailurus lemanensis*.

Palabras clave: Felidae, Felinae, Mioceno medio, Anatomía funcional.

Introduction

The fossil record of Felinae from the Early and Middle Miocene of Europe is relatively well-known (Thenius, 1949; Viret, 1951; Beaumont, 1961; Ginsburg, 1961, 1983, 1999, 2002; Crusafont & Ginsburg, 1973; Rothwell, 2001, 2003; Werdelin *et al*., 2010), with 4 species classically included in the genus *Pseudaelurus* (only the type locality is indicated): *P. romieviensis* (Roman & Viret, 1934) from La Romieu (France, MN 4), *P. turnauensis* (Hoernes, 1882) from Göriach (Germany, MN 5), *P. transitorius* Deperet, 1892 from La Grive-Saint-Alban (France, MN 7/8), and *P. lorteti* Gaillard, 1899 from La Grive-Saint-Alban (France, MN 7/8). All these species basically show the same morpho-

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logical dental pattern, and, apart from their size, there are no major differences between them. A fifth species of the genus, *P. quadridentatus* (Blainville, 1843) from Sansan (France, MN 6), which is the type species of the genus, is actually an early form of sabre-toothed felid and probably is near the origin of the subfamily Machairodontinae (Beaumont, 1978; Salesa *et al.*, 2010a; Werdelin *et al.*, 2010).

Most 19th century authors tended to place all early felids in the genus *Felis*, while in the 20th century the trend was to include all primitive species from the Early and Middle Miocene in the genus *Pseudaelurus*. Over time some specialists recognized the need to acknowledge the morphological diversity among these taxa, leading to a long and sometimes confusing taxonomy. In 1929 Kretzoi proposed the genus *Styriofelis* for *Felis turnauensis*, based on the absence of p2, the short mandibular post-canine diastema, and the relatively low talonid on m1. Later authors (Thenius 1949; Crusafont-Pairó & Ginsburg 1973) concluded that these characters were basically the same that Gervais used in 1850 to separate *Felis* from *Pseudaelurus*, and although this was not correct, they considered *Styriofelis* as a junior synonym of *Pseudaelurus*.

Later, Kretzoi (1938) proposed the genus *Miopanthera* for *Pseudaeulurus lorteti*, based on the general morphology of the dentition, which he considered close to the pantherin morphotype, and the presence of a vertical groove in the canine. In 1951, Viret proposed the new subgenus *Schizailurus* to separate the genus *Pseudaelurus* into two subgenera: *Pseudaelurus* (*Pseudaelurus*) *quadridentatus*, which would be related to the sabre-toothed felid *Metailurus*, and *Pseudaelurus* (*Schizailurus*), which, including the rest of species, would be the starting point of the feline lineage. Viret did not use the available taxon *Styriofelis*, and thus, as pointed out by other authors (Werdelin *et al.*, 2010) *Schizailurus* would be a junior synonym of the former.

In 1950, Dehm studied a huge felid collection from Wintershof-West (Germany, MN 3), pointing to the existence of a strong morphological variability within the sample, due to the presence of a combination of very primitive characters (such as the presence of m2, uniradiculated P1 and p1, birradiculated P2 and p2, and a strong talonid on m1) alongside some very derived features (such as the absence of metaconid on m1). Dehm (1950) considered this variability to be a consequence of a "phase

of chaotic evolution" experimented by the small species of *Pseudaelurus* at that time, and included the whole sample within the species *Pseudaelurus transitorius*. Nevertheless, in our view, a more likely explanation for the variability within the felid sample from Wintershof-West is the presence of two forms, a primitive one, probably related to the genus *Proailurus*, and a more derived species, more similar to modern felids, and closely related to *P. turnauensis*. Most authors consider *P. transitorius* as a junior synonym of *P. turnauensis*, which seems a satisfactory interpretation of the more derived specimens in the Wintershof-West sample, while the more primitive *Proailurus*-like specimens require further analysis.

Beaumont (1964) elevated *Schizailurus* to the category of genus, "due to its position as an important intermediate state between *Proailurus* and *Felis*", but ignoring the existence of the available genus *Styriofelis*. However, as mentioned by Werdelin *et al.* (2010), *Schizailurus* is an objective junior synonym of *Miopanthera*, as they were proposed for the same type species, and the latter would be a subjective junior synonym of *Styriofelis*. The status of *P. romieviensis* remains unclear due to fragmentary nature of the sample. In 2002, Ginsburg recovered the two genera of Kretzoi, using them as subgenera, and provided the following taxonomy: *Pseudaelurus romieviensis*, *Pseudaelurus quadridentatus*, *Pseudaelurus* (*Styriofelis*) *turnauensis*, and *Pseudaelurus* (*Miophantera*) *lorteti*. Nevertheless, whilst Ginsburg (2002) made an exercise in restrain when keeping these taxa at the subgeneric level, the morphological differences amply justify elevating them to the genus rank.

Most of these previous studies have dealt with cranial or dental material, and little is known about the postcranial anatomy of these early felids, and some interesting questions, such as the origin of the postcranial adaptations of felids, or the polarity of some characters, have remained unsolved. Therefore, the main aim of the present study is the description of the new postcranial fossils of *S. lorteti* from Sansan, in order to shed some light on all these open questions, carrying out one of the first assessments on the functional anatomy of the skeleton of this Middle Miocene felid.

A few years after the discovery of the skeleton, Leonard Ginsburg generously provided one of us (MA) with preliminary measurements and images of the material, which served as the basis for the first, anatomically grounded reconstruction of this

species (Turner & Antón, 1997). With the more detailed observations made in this study we can now offer a revised and updated reconstruction of the skeleton and life appearance of this early member of the Felinae.

The Sansan specimen of *S. lorteti* also includes cranial and dental material, but its description will be the subject of a future paper.

Material and methods

The fossils of *Styriofelis lorteti* described in the present paper come from the Middle Miocene (MN 6) fossil locality of Sansan (France), and were found during the excavations of July 1990, conducted by L. Ginsburg (MNHN, Museum national d'Histoire naturelle, Paris) and F. Duranthon (Museum d'Histoire naturelle, Toulouse). The specimen belongs to the collections of the Museum d'Histoire naturelle de Toulouse (MHNT) but is now deposited in the MNHN for study. The specimen belongs to the collections of the Museum d'Histoire naturelle de Toulouse (MHNT) but is now deposited in the MNHN for study. The specimen has the collection number SAN 879, and it is composed of the following: a complete but laterally compressed cranium and mandible with left C-M1, right I1, C, P1, left and right i1-m1; 15 fragmentary vertebrae: 5 more or less fragmentary thoracics (3 pre-diaphragmatic thoracics, the diaphragmatic, 1 post-diaphragmatic thoracic), 4 lumbars, the sacrum, 5 caudals; 1 sternebra; left clavicula; left ulna, proximal fragment of right ulna, left radius, right Mc I, left Mc II, left and right Mc IV, left and right Mc V, fragmentary coxal, right femur, subcomplete left femur, right tibia, right calcaneum, left navicular, right ectocuneiform, subcomplete right Mt III and proximal fragment of left Mt III, right Mt IV and subcomplete left Mt IV, left and right Mt V, 6 proximal phalanges, 4 medial phalanges, and two distal phalanges. Comparisons were made with extant felines and with the viverrid *Genetta genetta*; this comparative material belongs to the collections of the Museo Anatómico, Facultad de Medicina, Universidad de Valladolid (Spain) (with the acronym MAV), and Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain) (with the acronym MNCN). The following specimens were used: *Genetta genetta* (two individuals, both males: MNCN-14233 and MNCN-5444), *Caracal caracal* (1 female individual, MAV-1518), *Leptailurus serval* (two individuals: MAV-1547, male, and MAV-271, female), *Lynx pardinus* (two individuals: MNCN-16806, male, and MNCN-16812, female), *Lynx lynx* (one female individual, MAV-3542), *Lynx rufus* (one male individual, MNCN-14252), *Felis silvestris* (1 male individual, MNCN-172), *Leopardus wiedii* (one individual, unknown sex, MNCN-65), and *Oncifelis geoffroyi* (two individuals: MAV-1166, female, and MAV-1172, male). Comparisons with extant felines are made throughout the description, whilst *G. genetta* is used as a reference in the discussion because this viverrid species illustrates the primitive model of arboreal-scansorial Feliformia.

Measurements of the complete long bones, calcaneus and metapodials were taken (Table 1) with a digital caliper, as shown in fig. 1. For the anatomical descriptions we have followed the nomenclature from the *Nomina Anatomica Veterinaria* (2005).

Table 1.—**Measurements in mm of the studied postcranial elements of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France)**

	PW	PL	DEW	DFW	L	
Left Radius	17.4	11.5	22.1	15.1	143.8	

	OH	TH	MW	L		
Ulna	27.4	13.4	17.5	176.4		

	PEW	PEL	CW	CL	DEW	ML
Right Metacarpal I	9.3	7.1	–	–	7.6	20.0
Left Metacarpal II	7.7	12.6	7.1	6.4	8.8	44.4
Left Metacarpal IV	9.0	10.8	5.8	5.7	9.2	50.3
Right Metacarpal IV	8.8	10.8	5.7	5.7	9.1	50.3
Left Metacarpal V	7.3	10.0	5.6	5.1	8.2	37.9
Right Metacarpal V	7.2	10.0	5.5	5.0	7.5	38.0
Left Metatarsal III	13.3	–	8.9	7.8	9.8	78.4
Right Metatarsal III	12.2	16.5	–	–	–	–
Left Metatarsal IV	8.5	12.6	7.1	7.7	9.3	79.2
Right Metatarsal IV	8.5	12.6	–	–	–	–
Left Metatarsal V	9.4	11.8	5.6	5.2	8.8	73.2
Right Metatarsal V	9.5	10.9	5.6	5.5	9.2	72.9

	LP	AC	AD	LD	MA	L
Right Femur	37.0	17.5	–	23.0	15.3	199.8
Left Femur	–	–	34.5	23.0	–	–

	PEW	PELT	DEW	CCL	L	
Right Tibia	37.4	23.0	34.1	14.7	195.5	

	LH	TFMW	DEW	TL	TW	MH
Right Calcaneus	48.3	20.7	17.8	15.2	13.7	50.1

Morphological Observations on the Postcranial Anatomy of *Styriofelis lorteti*

Thoracic vertebrae

At least five thoracic vertebrae of *S. lorteti* are available, although only one, interpreted as being approximately the sixth thoracic vertebra, preserves some structures, such as the transverse processes and the cranial articular surfaces (fig. 2A). The overall morphology is very similar to that observed in the compared species, although the transverse processes are relatively larger. The cranial articular processes in *S. lorteti* and *L. rufus* are parallel, with their caudal borders widely separated. In *L. lynx* these surfaces are disposed in V, and their caudal
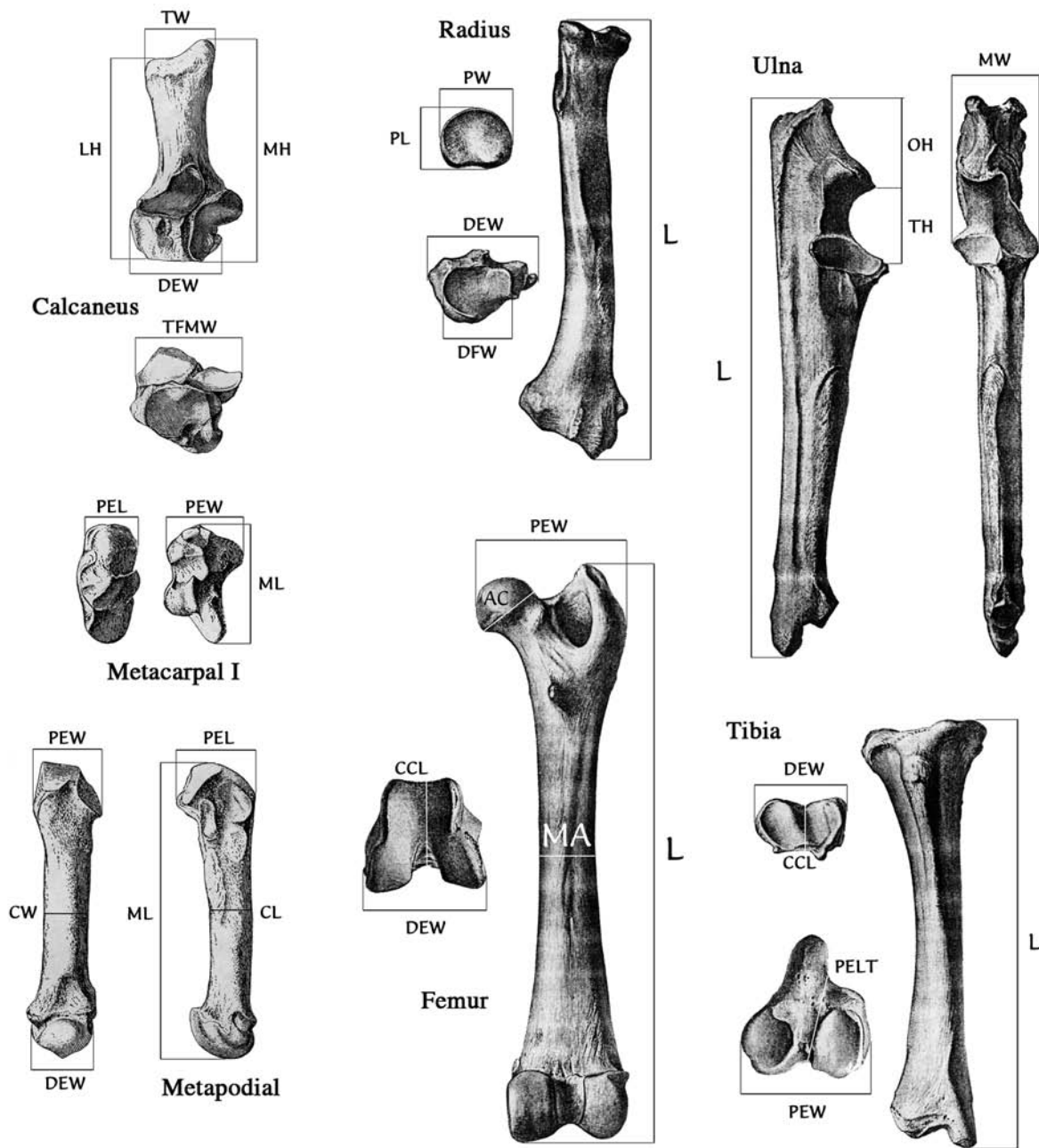
Fig. 1.—Measurements for each skeletal element: Calcaneus (TW, Tuber calcanei width; LH, lateral height; MW, medial height; DEW, distal epiphysis width; TFMW, talar facets maximum width), Metapodials (PEL, proximal epiphysis length; PEW, proximal epiphysis width; ML, maximum length; DEW, distal epiphysis width; CL, diaphysis length at the level of the medium point; CW, diaphysis width at the level of the medium point), Radius (L, maximum length; PW, proximal width; PL, proximal length; DEW, distal epiphysis width; DFW, distal facet width), Ulna (L, maximum length; MW, maximum width at the level of the coronoid process; OH, olecranon height; TH, trochlear notch height), Femur (L, maximum length; AC, femoral head diameter; PEW, proximal epiphysis width; MA, diaphysis width at the level of the medium point; CCL, cranio-caudal length; DEW, distal epiphysis width), and Tibia (L, maximum length; PEW, proximal epiphysis width; CCL, cranio-caudal length; PELT, cranio-caudal length of the proximal epiphysis on the medial side of the tibial tuberosity; DEW, distal epiphysis width).
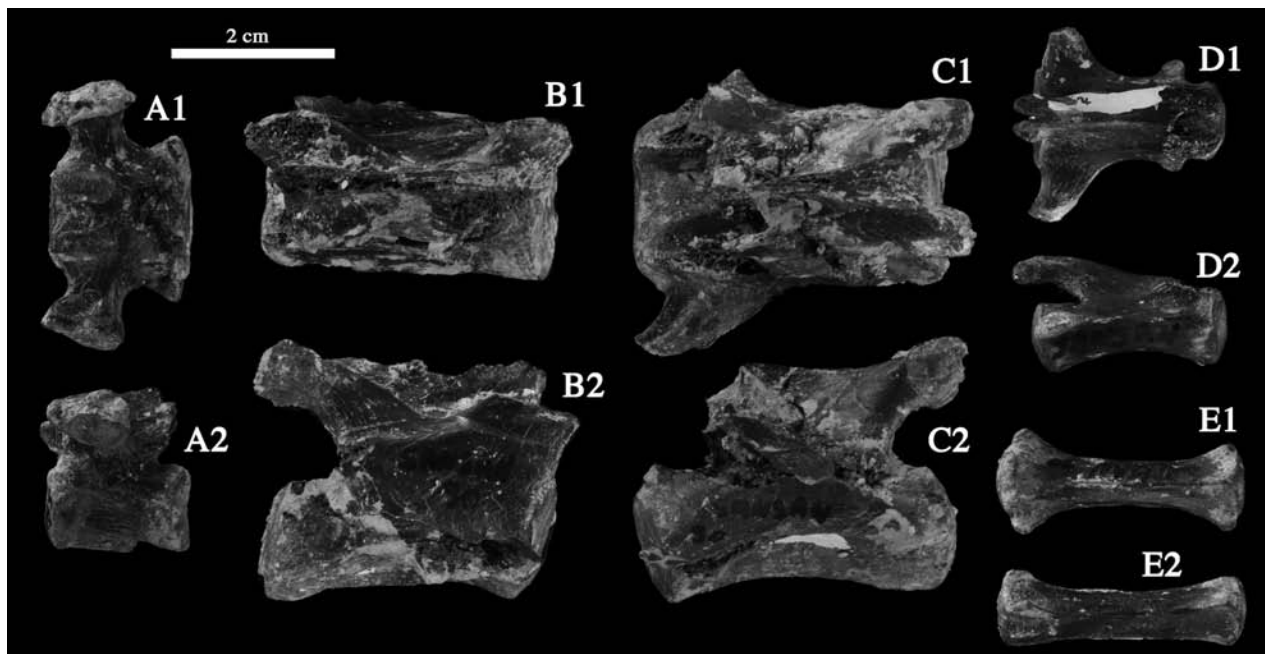
Fig. 2.—Vertebrae of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A, sixth thoracic vertebra, A1, dorsal view, A2, left view. B, C, lumbar vertebrae, B1, dorsal view; B2, right view of the same piece; C1, dorsal view; C2, left view of the same piece. D, sixth caudal vertebra, D1, dorsal view; D2, left view. E, distal caudal vertebra, E1, dorsal view; E2, left view.

borders contact. In *L. pardinus, C. caracal, L. serval, O. geoffroyi* and *F. silvestris*, the cranial articular surfaces are disposed in V, but their caudal borders are well separated, thus showing some kind of intermediate morphology between both groups.

Lumbar vertebrae

Four lumbar vertebrae were recovered with the Sansan skeleton, but their preservation is very poor so that only two of them are described here. In spite of their damaged state, two other lumbar vertebrae have a measurable corpus length, a measurement that has been taken into account for preparation of the skeletal and life restorations offered here in fig. 3. The studied vertebrae are damaged, and most of their structures are broken (fig. 2B, C). Both transverse processes are severely broken, so it is difficult to infer the position of the vertebrae within the lumbar series; nevertheless, one of the 2 vertebrae preserves the left transverse process, which is larger than the typical transverse process observed in the first and second lumbar vertebrae of *L. lynx, L. rufus, L. pardinus, C. caracal, L. serval* and *F. silvestris*. The vertebral body is relatively long, as observed within the sample of extant felines. On dorsal view, the caudal articular processes
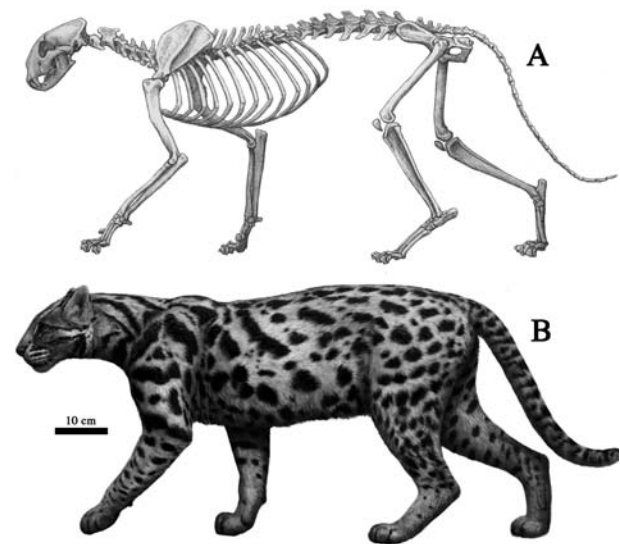

Fig. 3.—Skeletal (A) and life reconstruction (B) of *Styriofelis lorteti*, based on the specimen SAN 879 from Sansan (France). The skeleton reveals body proportions broadly similar to modern felines of comparable size, but with somewhat shorter forelimbs and metapodials. Such proportions are less robust than those of either the primitive felid *Proailurus lemanensis* or the early machairodonts such as *Promegantereon ogygia*. The reconstructed first digit of the hind feet is hypothetical, but strongly indicated by the morphology of Mt II. The hypothetical coat colour pattern shown in the life reconstruction is congruent with the phylogenetic inferences about coat pattern evolution in felids proposed by Werdelin *et al.* (2010) (artwork by M. Antón).
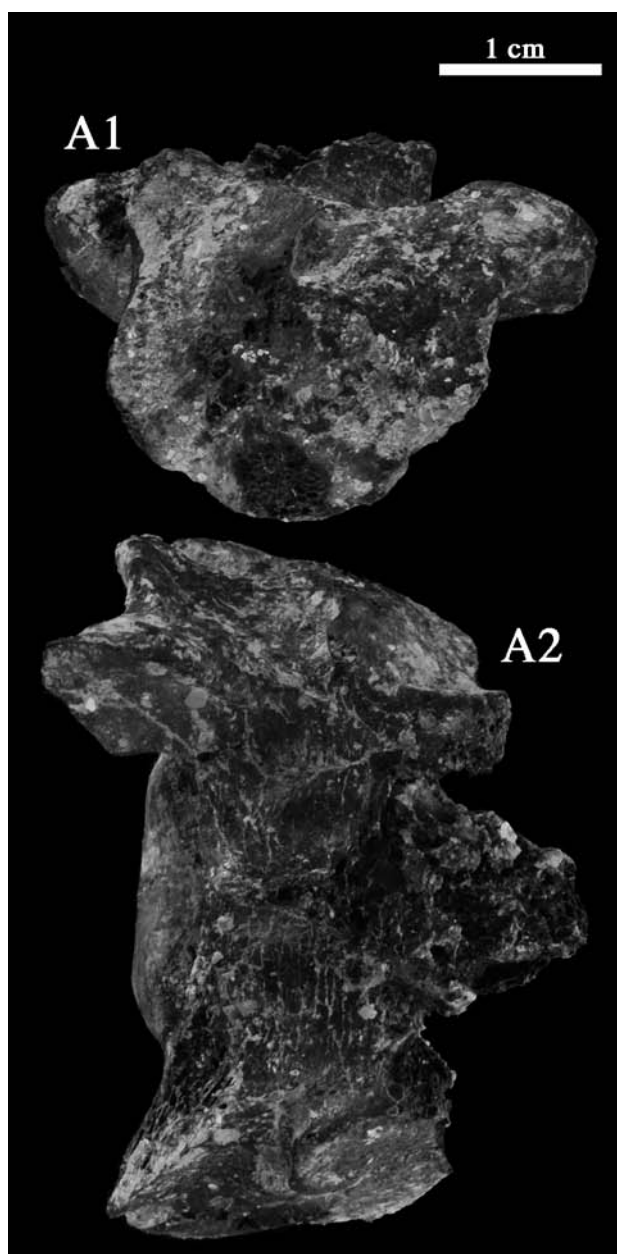
Fig. 4.—Sacrum of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, left view; A2, dorsal view.

are well separated by a round notch, as in all the compared felines except *F. silvestris*, which shows a relatively narrower, triangular notch.

Sacrum

The available sacrum of *S. lorteti* is relatively well preserved, but it lacks most of its caudal half

(fig. 4), so the fossil does not provide relevant information on the development of the tail, or on the morphology of the spinous processes. Both cranial articular processes and the wings of the sacrum are similarly disposed and developed as in all the compared species. A small fragment of one spinous process is preserved, but it is insufficient to make even an estimation of its length.

Caudal vertebrae

The sample from Sansan includes five caudal vertebrae of *S. lorteti*, belonging to different portions of the tail. Two of them correspond to the proximal region: one, very damaged, is interpreted as being the first or second caudal vertebra, but the other one shows an intermediate morphology between that of the fourth and sixth caudal vertebra of an extant feline with a moderate to long tail, such as *F. silvestris* or *L. serval*; this specimen has large caudal transverse processes, as the fourth caudal vertebra of these species, but also shows well developed cranial transverse processes (fig. 2D), which are absent in the first five vertebrae of all the compared species, and present from the sixth; also the caudal articular processes show an intermediate size between those of the fourth and the sixth caudals of a feline.

The other 3 caudal vertebrae correspond to the distal third of the tail, being relatively long and slender (fig. 2E), allowing the interpretation of *S. lorteti* as having a tail as long as that of a typical feline such as *F. silvestris*.

Radius

The radius of *S. lorteti* resembles that of a medium-sized feline, such as *L. lynx*, *L. rufus*, *L. pardinus*, *C. caracal*, *L. serval* and *F. silvestris*, although it is relatively more robust (fig. 5). The diaphysis is dorso-palmarly compressed, and describes a gentle curvature. The proximal epiphysis is concave, elliptical, its plane being slightly medially inclined; its medial border develops a marked medial projection, whereas the lateral one does not stand out from the diaphysis border. The radial tuberosity is well developed, being proximo-distally elongated.

The distal epiphysis is well developed medio-laterally, the medial border being distally projected in a large radial styloid process. The lateral facet for
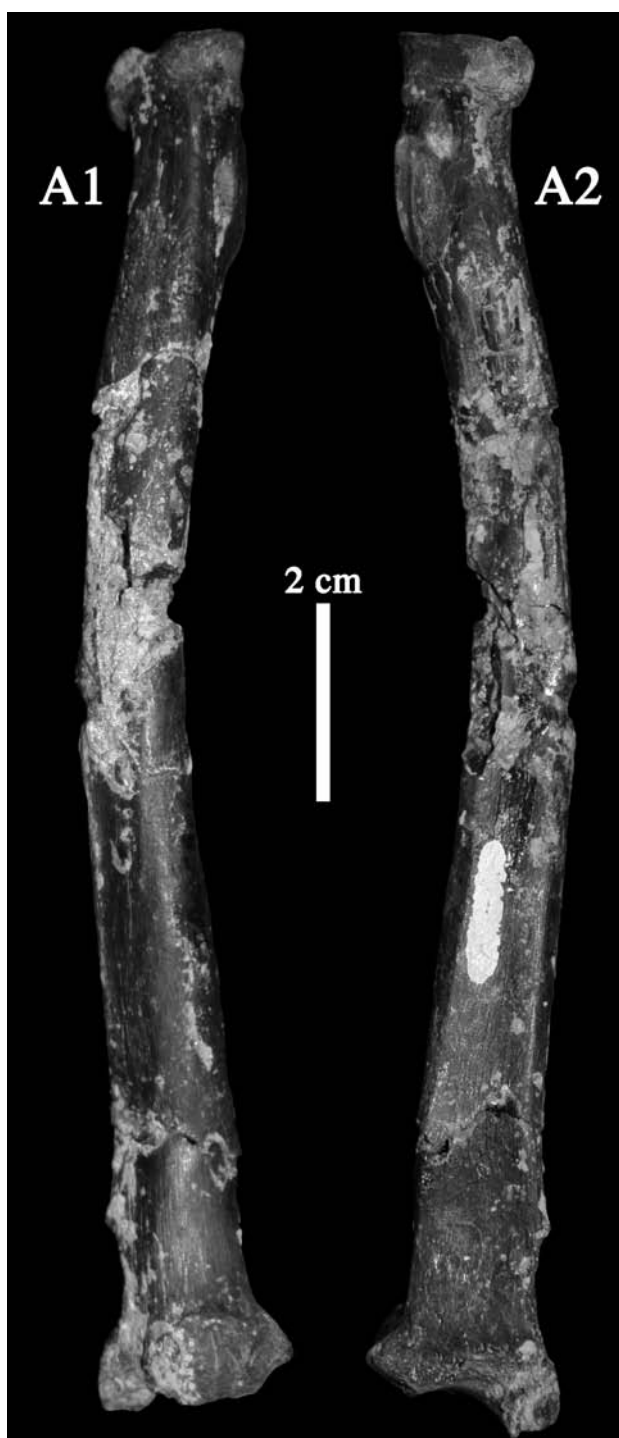
Fig. 5.—Left radius of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, dorsal view; A2, palmar view.

distal epiphysis, a central ridge is developed for the passage of the tendons of several extensor muscles; in this character *S. lorteti* differs from *L. lynx, L. rufus, L. pardinus, C. caracal, L. serval* and *F. silvestris*, as these species have a second ridge, located on the lateral margin of this dorsal face, barely hinted in *S. lorteti*. The distal articular surface for scapholunar is concave, and, although it is not complete, it is clearly narrower than those of the compared felines, showing an almost round profile, instead of the latero-medially elongated shape observed in the former.

Ulna

The ulna of *S. lorteti* is relatively more robust than those of the extant compared felines. The diaphysis shows a gentle caudal convex curvature in its proximal half, and it is markedly latero-medially flattened (fig. 6). In its lateral surface there is a rough scar for the attachment of the muscle *abductor digiti I longus* (=*extensor carpi obliquus*) (Barone, 2000), proximo-distally elongated, and more marked, and cranio-caudally longer than in *L. lynx, L. pardinus, L. rufus, C. caracal* and *L. serval*. This lateral surface also shows a ridge along its caudal margin, as in *L. rufus, L. pardinus, C. caracal* and *L. serval* (which is absent in *L. lynx*, and very smooth in *F. silvestris*); this ridge delimits a proximo-distally elongated groove for the attachment of the muscle *extensor digiti II*. On the medial surface of the diaphysis, there is another ridge, restricted to the distal area, whose cranial surface is the attachment area for the muscle *pronator quadratus*. This ridge is more developed in *S. lorteti* than in any other of the compared species.

The olecranon is well developed, very similarly to that of other felines, although its proximal border, in lateral or medial views, is clearly inclined caudally, whereas in the feline sample this border is more or less horizontal. The olecranon displays a pair of tubercles that correspond to the attachment areas for several muscles involved in extension of the forearm, mainly the *anconeus*, which attaches on the lateral tubercle, and the medial branch of the *triceps brachii*, which attaches on the medial tubercle (Gonyea, 1978; Barone, 2000). In the case of *S. lorteti* and *F. silvestris*, the medial tubercle is well developed, being markedly projected proximally, surpassing the level of the lateral tubercle; in *L. pardinus* this medial tubercle is almost absent,

articulation with the ulna is elliptical, dorso-palmarly elongated, and it is located close to the distal border of the epiphysis. On the dorsal face of the
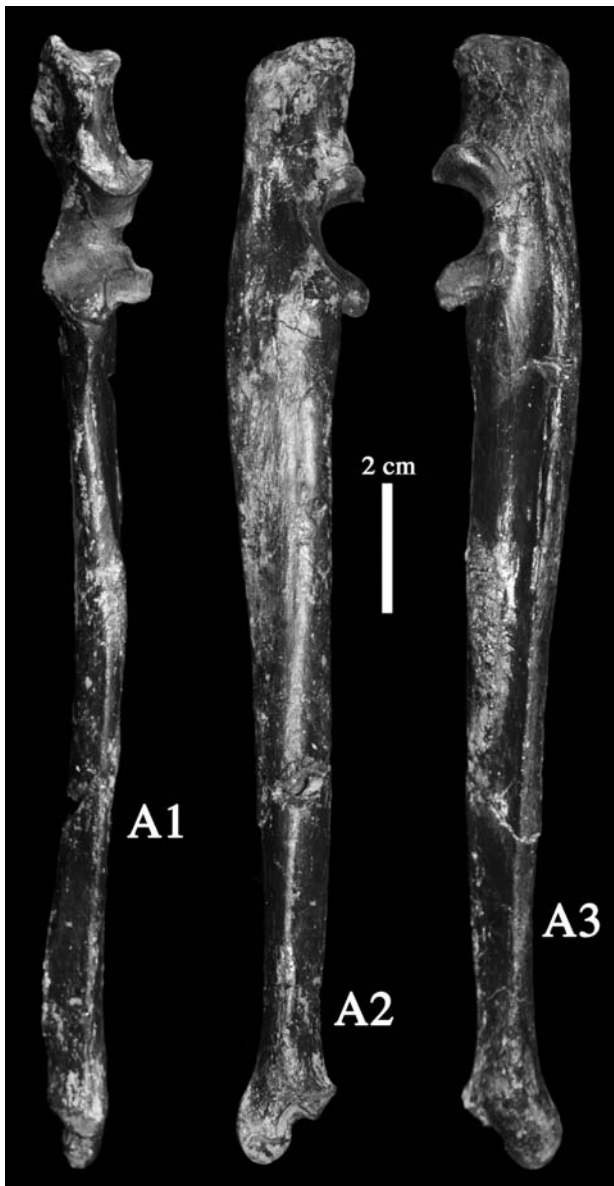
Fig. 6.—Left ulna of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, dorsal view; A2, medial view; A3, lateral view.

whereas in *L. lynx*, *L. rufus*, and *C. caracal*, both tubercles show the same proximal development. In *L. serval* the medial tubercle slightly surpasses the level of the lateral one, but lacking the strong proximal projection seen in *S. lorteti* and *F. silvestris*.

The distal epiphysis of the ulna of *S. lorteti* shows the basic feline morphology, although there are small differences: it is relatively larger and thicker in cranial view, and the facet for the radius is larger; also, the transition between this distal epi-

physis and the diaphysis lacks the constriction observed in the feline sample.

Metacarpal I

The metacarpal I of *S. lorteti* (fig. 7A) shows a similar morphology than that seen in the compared sample of felines. It is a short metacarpal, with a central constriction, more marked than in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal* and *L. serval*. The Mc I of *F. silvestris* shows a similarly developed constriction as that observed in *S. lorteti*, although the bone is markedly longer and slender.

Metacarpal II

The metacarpal II (fig. 7B) of *S. lorteti* is relatively more robust when compared to those of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris*. It is, however, very similar in morphology. Its proximal articular surface is trapezoid in shape, with its dorsal border medio-laterally wider than the palmar one. The dorsal face of the proximal epiphysis shows a marked groove for the passage of the radial artery (Reighard & Jennings, 1901), as in the other compared felines, but, distally to this structure, there is a large, round scar for the muscle *extensor carpi radialis longus*, much smaller in *L. lynx*, *L. pardinus*, *C. caracal*, *L. serval*, *L. wiedii* and *O. geoffroyi,* and almost absent in *F. silvestris* and *L. rufus*. In lateral view, the proximal epiphysis of the Mc II is slightly dorso-palmarly longer in *S. lorteti* than in the compared felines, with the palmar tubercle lacking the disto-palmar orientation seen in the latter, as it is palmarly oriented; the dorsal groove for articulation with the medial face of the Mc III is more excavated than in *L. lynx*, *L. rufus*, *L. pardinus*, *C. caracal*, *L. serval* and *F. silvestris*, and its dorsal border is more distally projected. In medial view, the proximal epiphysis shows a large, round facet for articulation with the trapezium that surpasses the level of the proximal border, as in the compared felines. Distally to this facet, there is a rough tubercle for the attachment of the short interosseous ligament connecting Mc I and Mc II. In the palmar border, there is a small but distinct facet for the attachment of the tendon of muscle *flexor carpi radialis*; this facet is located in *S. lorteti* more proximally than in the compared felines, as in the former the distal border of the facet does not surpasses the level of the dorsal tubercle, whereas in

Fig. 7.—Metacarpals of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, dorsal view of right Mc I; A2, palmar view of right Mc I; B1, medial view of left Mc II; B2, lateral view of left Mc II; C1, medial view of left Mc IV; C2, lateral view of left Mc IV; D1, lateral view of right Mc V; D2, medial view of right Mc V.

the latter the facet is located at the same level than the tubercle. Also, whereas in *C. caracal* this facet is proximo-distally elongated, in the rest, including *S. lorteti*, is more or less round.

Metacarpal IV

The metacarpal IV of *S. lorteti* (fig. 7C) is relatively more robust when compared to those of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris*. Its proximal articulation surface has a central dorso-palmar step that divides it in two distinct articular areas: a lateral surface for the unciform, and a medial one for the Mc III. This morphology is also seen in the compared sample of felines, although in *S. lorteti* this surface is medio-laterally wider. The medial articulation facets for Mc III are larger than those of any other of the compared felines, especially the palmar one, which is clearly divided in two areas, a proximal surface for the magnum and a distal one for the Mc III; this palmar facet is triangle shaped in *S. lorteti* and the compared felines, but it is remarkable than in *L. lynx* and *L. pardinus* it is clearly reduced in size. The lateral face shows a very similar aspect in all the compared species, with a marked central depression and a large facet developed along the proximal and dorsal margins, for articulation with the Mc V.

Metacarpal V

The metacarpal V of *S. lorteti* (fig. 7D) is very short and robust if compared to those of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris,* but very similar in overall morphology. Its proximal articulation surface is a semicircle with a dorsal facet projecting medially. On the lateral face of the proximal epiphysis there is an elliptical facet for the attachment of the muscle *extensor carpi ulnaris*, dorso-palmarly elongated in *S. lorteti* and *L. serval*, and round and larger in *L. lynx*, *L. rufus*, *L. pardinus*, *C. caracal* and *F. silvestris*. The medial face of the proximal epiphysis shows a very similar model in all the species, with a central medially expanded bony sheet, and a smooth face occupying both proximal and dorsal margins. The only remarkable difference is the presence in *S. lorteti* of a well-developed scar on the palmar border for the attachment of a muscle *interosseus*, very reduced in the rest of the species.

Femur

The femur of *S. lorteti* (fig. 8) is as slender as those of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* or *F. silvestris*. In fact, its overall morphology is very similar to that of any of the compared
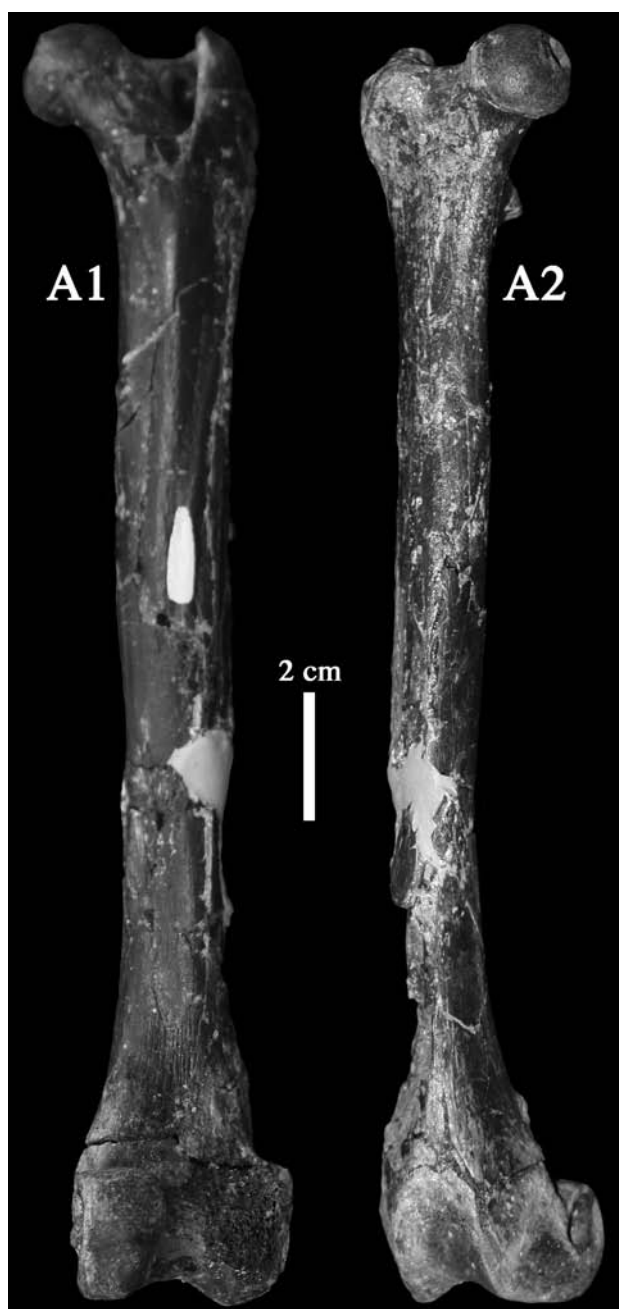
Fig. 8.—Right femur of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, caudal view; A2, cranial view.

felines, even in the disposition or development of minute structures. The proximal epiphysis shows a round lesser trochanter, slightly caudo-medially projected, and a well developed greater trochanter, which does not surpasses the level of the proximal border of the head; the trochanteric fossa is deep, proximo-distally elongated, and shows a ridged

intertrochanteric crest. On the lateral border of this proximal epiphysis, a marked gluteal tuberosity for the attachment of the muscle *gluteus superficialis* is observed.

The distal epiphysis shows a deep cranial trochlea, with ridged margins. On its caudal face, both medial and lateral condyles axis are inclined laterally, as in the compared felines.

Tibia

The tibia of *S. lorteti* is also slender (fig. 9), with a straight diaphysis and a caudally curved proximal epiphysis. The proximal epiphysis shows a triangular shaped proximal surface, with two clear articular facets (medial and lateral) separated by a rough groove; its cranial border projects markedly, but much less than in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, and *L. serval*, also lacking the typical cranio-lateral constriction observed in these species for the passage of the tendon of the muscle *extensor digitorum longus*; the projection seen in *F. silvestris* is moderate, as in *S. lorteti*, but this species does show the constriction. In medial view the proximal epiphysis is clearly cranio-caudally shorter than that of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, and *L. serval*, resembling *F. silvestris* in this character and also in the presence of a larger facet for the muscle *semimembranosus*, relatively reduced in the former species. In lateral view the proximal epiphysis of *S. lorteti* is cranio-caudally longer than the medial one, and similar to that of the compared species, although the lateral border is proximo-distally higher in *S. lorteti*. This is as well observed in cranial view, and also the clear medial inclination of the proximal surface, whereas in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris* this surface is basically horizontal. Nevertheless, this latter species shows also a proximo-distally high lateral border.

The distal epiphysis of *S. lorteti* shows remarkable differences with that of the compared felines, mostly in distal view, as it is medio-laterally shorter than that of *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris*. This is due to the fact that the caudal margin of this distal articular surface is medio-laterally longer than that of any of the compared species, producing a lateral margin less inclined, and thus a more square distal articular facet.
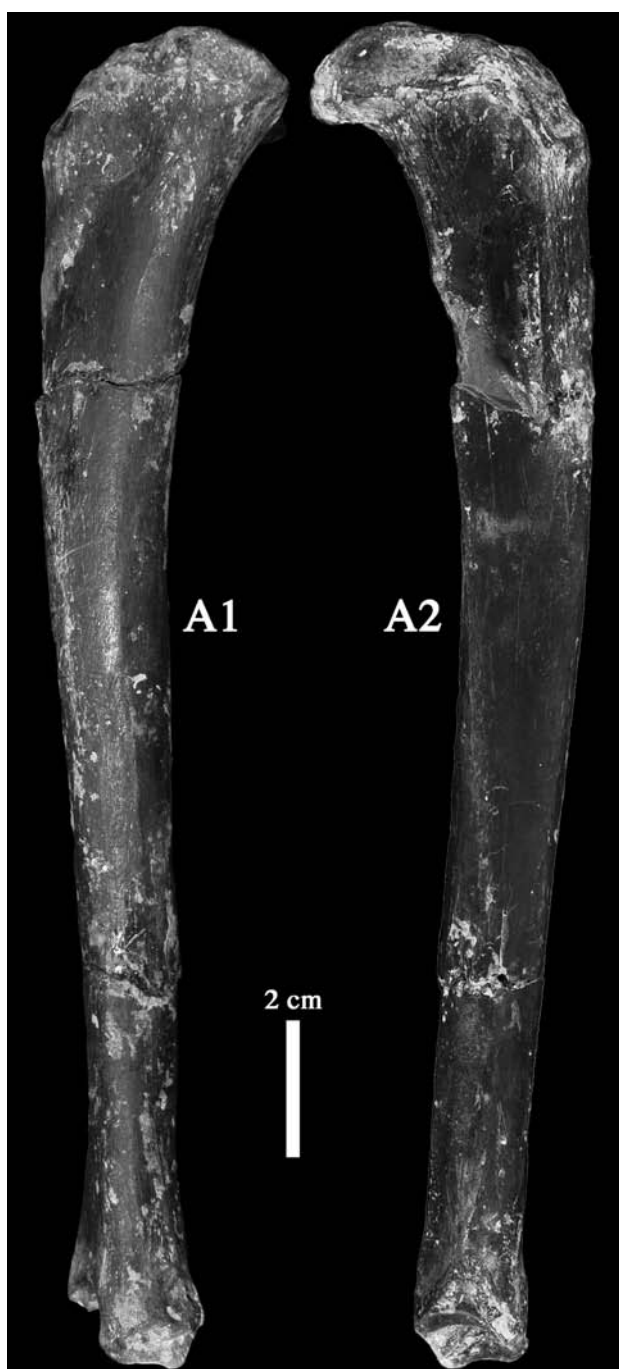
Fig. 9.—Right tibia of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A1, medial view; A2, lateral view.

Calcaneus

The calcaneus of *S. lorteti* resembles those of the compared felines, but shows some differences related to its higher robustness, such as a shorter and thicker tuber calcanei (fig. 10A). In dorsal view, the articular area for the astragalus is relatively medio-laterally wider than that of the compared felines, due to the fact that its lateral margin is not vertical, as in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris*, but clearly curved laterally. Besides, its medial margin is proximo-distally shorter. The medial facet of the *sustentaculum tali*, for articulation with the astragalus, is relatively larger and more rounded (in the compared felines is medio-laterally elongated). Also this facet, in medial view shows a different orientation in *S. lorteti* and *F. silvestris* than that observed in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, and *L. serval*, in the former being dorsally oriented, whereas in the latter it is dorso-medially.

In plantar view, the *sustentaculum tali* shows a greater proximo-distal and medial development in *S. lorteti* than in the other felines. The scar for the ligament *plantare longum*, located on the disto-plantar border, is more marked in *S. lorteti* than in the other species, probably reflecting the presence of a very strong ligament.

The fibular tubercle (disto-lateral expansion for the attachment of the ligament *collaterale tarsi laterale longum*) is also larger in *S. lorteti*, and thus implying the existence of a stronger ligament. On the other hand, the scar for the ligament *collaterale tarsi laterale brevis*, located proximally to the latter, is similarly developed in all the compared felines, including *S. lorteti*. Most of the lateral surface of the calcaneus of *S. lorteti* is occupied by a deep and wide groove, proximo-distally developed, for the attachment of the muscle *quadratus plantae*; this scar is significantly more developed in *S. lorteti* than in any other of the compared species, thus implying the existence of a larger muscle, unlike the extant species, which show a reduced muscle, whose attachment area is reduced to the distal border of the lateral face of the calcaneus.

The tuber calcanei of *S. lorteti* is round in proximal view, as in *L. lynx*, *L. pardinus*, *L. rufus*, *C. caracal*, *L. serval* and *F. silvestris*, with a marked groove developed across its plantar border, where the tendon of the muscle *gastrocnemius* attaches.

In distal view, no remarkable differences between the calcaneus of *S. lorteti* and those of the compared felines are found; it is worth mentioning the larger development of the fibular tubercle, already described above.
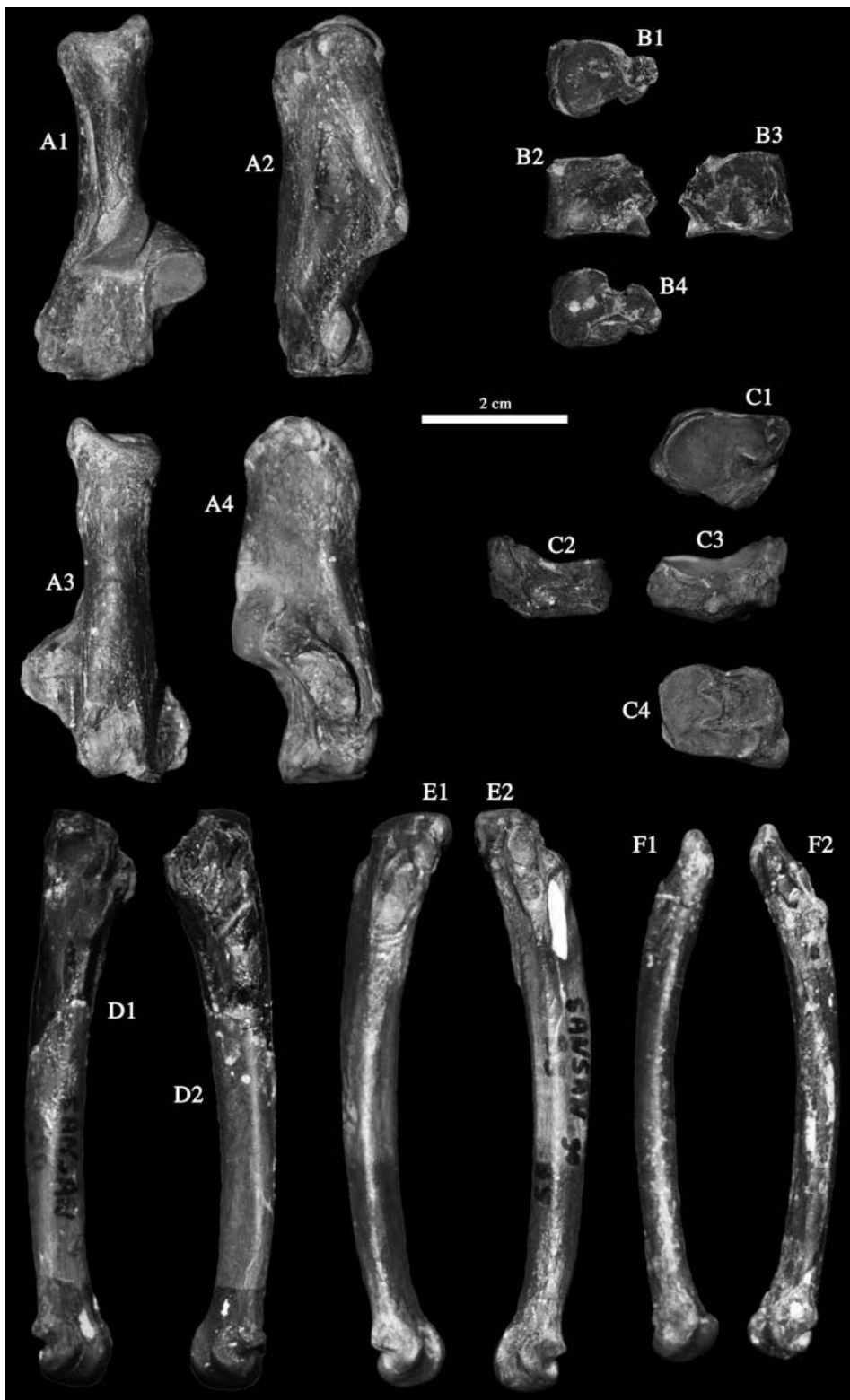
Fig. 10.—Tarsals and metatarsals of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). A, right calcaneus, A1, dorsal view; A2, lateral view; A3, plantar view; A4, medial view. B, right ectocuneiform, B1, proximal view; B2, medial view; B3, lateral view; B4, distal view. C, left navicular, C1, proximal view; C2, medial view; C3, lateral view; C4, distal view. D, left Mt III, D1, lateral view; D2, medial view. E, left Mt IV, E1, lateral view; E2, medial view. F, left Mt V, F1, lateral view; F2, medial view.

Navicular

The navicular of *S. lorteti* is also very similar to that of the compared sample of felines (fig. 10B). It is proximo-distally high, with a concave proximal articular facet for the astragalus, and a slightly convex distal surface with three articular facets for ecto-, meso- and entocuneiform. In all the compared species there is a large medio-plantar tubercle, proximally projected, and a latero-plantar tubercle for the attachment of the muscle *tibialis caudalis*, which is medio-laterally wider and proximo-distally lower in *S. lorteti* than in any other of the compared felines; thus, in the former this tubercle is rectangular, whereas in the latter its shape is more or less round.

In distal view the facets for the cuneiforms show some differences. In *S. lorteti*, the lateral facet for the ectocuneiform shows a marked notch in the middle of its plantar margin, whereas in the compared felines, this facet is round, lacking this notch; besides, in *S. lorteti* this facet shows less dorso-plantar development. The medial facet for the mesocuneiform, more or less rounded in *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal* and *F. silvestris*, shows a dorso-plantar elongation in *S. lorteti*. Finally, the medio-plantar facet for the entocuneiform is more or less round in all the compared species.

Ectocuneiform

The ectocuneiform of *S. lorteti* is very similar in shape and morphology to that of an extant feline (fig. 10C). Its proximal articulation facet has an irregular shape, more or less rounded, but with a straight medial border. All the extant compared species, except *C. caracal*, shows a medio-laterally narrower facet than that of *S. lorteti*, although in *L. wiedii* and *O. geoffroyi* this difference is even more evident. The plantar tubercle is broken in the only available piece of *S. lorteti*, but it was certainly more developed than in *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal, F. silvestris, O. geoffroyi* and *L. wiedii*, as its neck is relatively thicker. The distal articular facet is T shaped, with two round surfaces, one dorsally located, and another, much smaller, plantarly placed; both are separated by a marked constriction. The medial face of the ectocuneiform of *S. lorteti* shows relatively larger distal facets for Mt II than the compared sample, and a similar proximal facet for the mesocuneiform.

The lateral face has a similar morphology in all the species, although *S. lorteti* shows a relatively larger facet for the cuboid.

Metatarsal III

The metatarsal III of *S. lorteti* (fig. 10D) is relatively robust when compared to that of *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal* and *F. silvestris*. On the lateral face of the proximal epiphysis two concave and round grooved facets are present for the articulation with the Mt IV; that on the dorsal border is plantarly oriented, whereas that located on the plantar border is smaller and laterally oriented. On the plantar margin, distally located in relation to the former facet, there is a large, proximo-distally elongated scar for the attachment of one of the muscles *interossei*. The medial face of the proximal epiphysis develops two articular facets for the Mt II; both are triangular shaped, but whilst the dorsal facet is distally projected, the plantar one is dorso-plantarly elongated. Between both facets, a marked and rough groove is developed. On plantar view, a well-developed facet for the muscle *adductor digiti I* (=*adductor hallucis*) is present. This morphology is basically repeated in the compared felines.

Metatarsal IV

The metatarsal IV of *S. lorteti* (fig. 10E) is, like the Mt III, relatively robust when compared to that of *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal* and *F. silvestris*. Its proximal articulation surface has a rectangular shape, with its dorsal and plantar borders gently rounded, and a soft notch in the central part of its medial margin. The proximal epiphysis is slightly plantarly inclined in lateral or medial views, whereas in dorsal view it is laterally curved. The medial face of this epiphysis is occupied by the articular facets for Mt V, consisting on a central groove and two small rectangular facets, one dorsal and other plantar, located proximally to this groove; in the plantar border of the diaphysis, distally to these facets, there is a proximo-distally elongated scar for one of the muscles *interossei*. This morphology is shared by *S. lorteti* and all the compared felines.

The medial face of the proximal epiphysis of *S. lorteti* shows two facets for articulation with the Mt

III; that located dorsally is round, with ridged margins, and medio-dorsally oriented, as in *L. pardinus*, *L. rufus*, *L. serval*, and *C. caracal,* whereas in *L. lynx* and *F. silvestris* this facet shows a dorso-proximal orientation. This different orientation of the facet is evident in dorsal view, with the latter species showing a marked medially projected facet. The other articular facet, located on plantar margin, is elliptical and proximo-distally elongated, showing no remarkable differences among the compared sample.

Metatarsal V

As the previously described metatarsals of *S. lorteti*, the Mt V (fig. 10F) is relatively robust when compared to that of *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal* and *F. silvestris*. The proximal epiphysis is latero-plantarly curved in relation to the diaphysis; its proximal articulation surface for the cuboid is more or less square, being surrounded by two flattened tubercles, one lateral (for the attachment of the muscle *fibularis brevis*) and other medial (for the attachment of the muscle *fibularis longus*), separated by a small notch. In all the compared species the lateral tubercle is more projected proximally than the medial one, but the difference in height is more marked in *F. silvestris* than in any other of the compared species.

The medial face of the proximal epiphysis of the Mt V of *S. lorteti* has an irregular facet, proximo-distally elongated, and with a central constriction, for the articulation with the Mt IV. There is another articulation facet for the Mt IV, rectangular and proximo-distally elongated, located on the plantar border of this medial face. These two facets show a similar development in *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, *C. caracal* and *F. silvestris*.

The lateral face of the proximal epiphysis of the Mt V is occupied by the large tubercle for the attachment of the muscle *fibularis brevis*; from this lateral view, this structure is slenderer in *S. lorteti* and *F. silvestris* than in *L. lynx*, *L. pardinus*, *L. rufus*, *L. serval*, and *C. caracal,* as in these species is more round, and thus relatively more robust.

Functional implications of the postcranial anatomy of *Styriofelis lorteti*

The postcranial skeleton of *Styriofelis lorteti* resembles, in overall view, that of the extant *Felis*
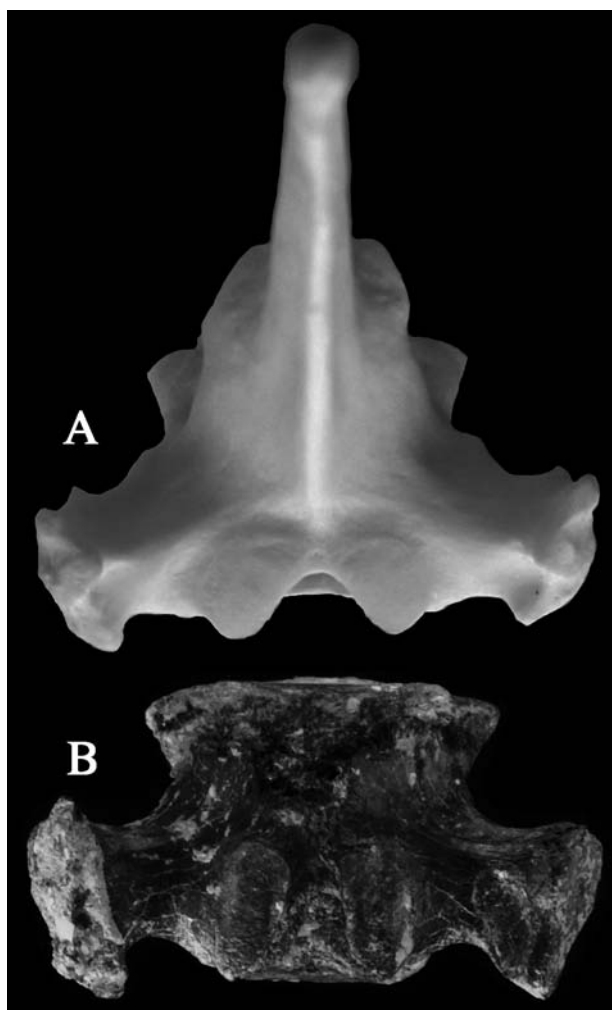

Fig. 11.—Dorsal view of A, sixth thoracic vertebra of *Lynx lynx*; B, thoracic vertebra of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France). The bones are showed at the same size.

silvestris, although its proportions are more robust and its size larger than this species.

Thoracic vertebrae

The different morphologies observed in the cranial articular processes of the thoracic vertebrae of the studied sample of felines are probably of lesser functional importance. The parallel and well separated cranial articular processes seen in *S. lorteti* and *L. rufus* could imply a cranio-caudally longer articulation area between adjacent vertebrae, which determines, in some way, the range of lateral and vertical flexion of the back (fig. 11). The

morphology of these processes in *G. genetta* is similar to those of *L. pardinus*, *C. caracal*, *L. serval*, *O. geoffroyi* and *F. silvestris*, this is, are disposed in V with their caudal borders well separated. Nevertheless, since two species with markedly different locomotor adaptations such as *G. genetta* (an arboreal species) and *L. pardinus* (a highly cursorial feline) share the same morphology, it is difficult to provide with a convincing functional explanation.

Lumbar vertebrae

Although the preserved lumbar vertebrae of *S. lorteti* are severely damaged, at least it can be seen that their relative length is comparable to that of any of the compared felines, indicating a long lumbar region and a flexible back, unlike the condition seen, for example, in derived machairodont felids, which display shortened, relatively stiff lumbar regions. There is another interesting character, namely the morphology of the notch separating both caudal articular processes, for which we have no clear interpretation. This character distinguishes *S. lorteti*, *L. serval,* and *C. caracal*, *L. lynx*, *L. rufus* and *L. pardinus*, from *F. silvestris*. In the first group, the notch has a round shape, whereas in the latter group the notch is triangle shaped, which produces a light but evident difference in its width. This could be related to the degree of lateral movements of the lumbar region, as during these movements, the neural process of a given lumbar vertebra accommodates in the notch of the precedent vertebra within the lumbar region. Thus, those species having wider notches would have a greater capacity for lateral flexion of this lumbar zone; nevertheless, as the round and wide notch is also found in *G. genetta*, and in highly arboreal felines such as *Oncifelis geoffroyi*, this could represent the primitive state for the Felidae, and the morphology observed in *F. silvestris* would be derived. Large extant felids such as *Puma concolor*, *Panthera onca* and *Acynonyx jubatus* show round and wide notches in the caudal articular processes of their lumbar vertebrae, but others like *Panthera pardus* show the same pattern of *F. silvestris*. Thus, considering the marked ecological differences between *A. jubatus* or *P. onca* (both with wide notches) it seems that there is not a satisfactory explanation for the observed differences in this character.
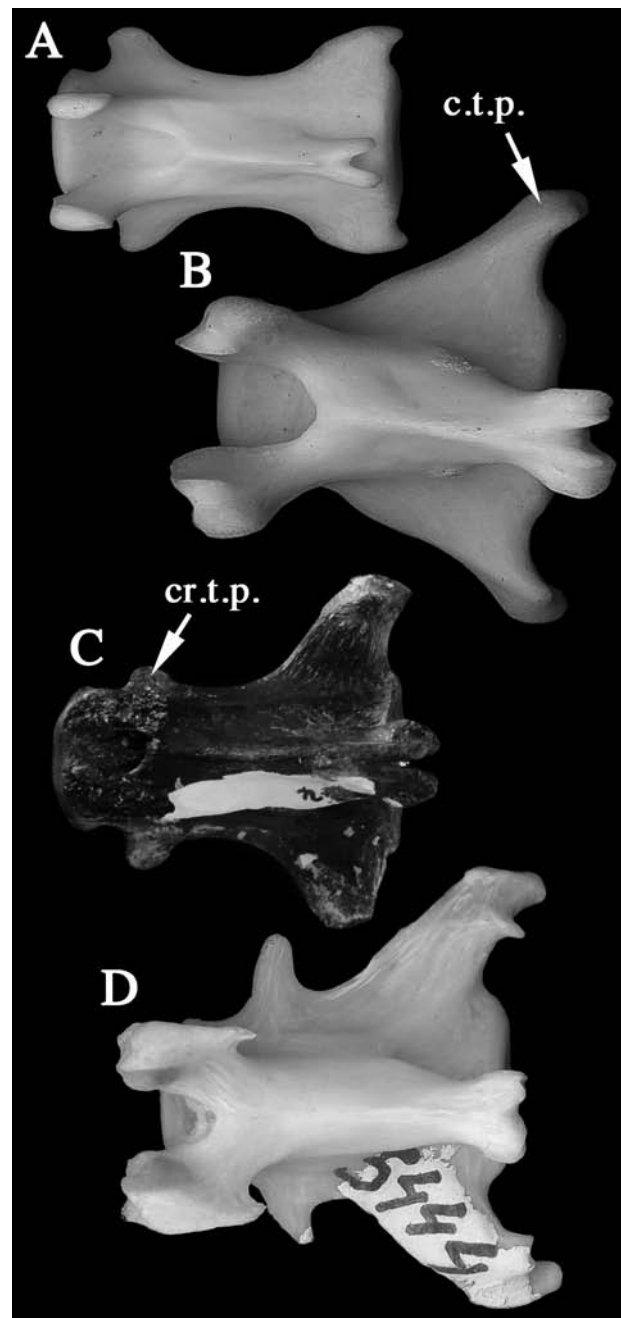

Fig. 12.—Dorsal view of A, sixth caudal vertebra of *Lynx lynx*; B, fourth caudal vertebra of *Lynx lynx*; C, proximal caudal vertebra of *Styriofelis lorteti*, specimen SAN 879, from Sansan (France); D, fourth caudal vertebra of *Genetta genetta*. The bones are showed at the same size (cr.t.p., cranial transverse process; c.t.p, caudal transverse process).

Caudal vertebrae

The morphology of the caudal vertebrae of *S. lorteti* suggests the presence of a moderate to long

tail, such as that of *L. serval* or *F. silvestris,* different from the short tail exhibited by *L. lynx*, which has relatively shorter proximal caudal vertebrae. One of the preserved proximal caudal vertebrae of *S. lorteti* has an intermediate morphology between that of the fourth and sixth caudal vertebrae of a typical long-tailed feline (fig. 12), which has not evident functional implications. The large cranial and caudal transverse processes would indicate the presence of strong muscles *coccygeus* and *sacrocaudalis ventralis lateralis* (both flexors of the tail), as they attach on these processes of the second to ninth caudal vertebrae (Reighard & Jennings, 1901; Evans, 1993). However, when the mentioned caudal vertebra of *S. lorteti* is compared to the proximal caudal vertebrae of *G. genetta* (fig. 12D), a very similar pattern is observed: the first three caudal vertebrae of *G. genetta* lack any cranial transverse processes, and the caudal transverse processes are large and wide; the fourth caudal vertebra shows an also large caudal process, but it has laterally projected cranial processes, in a very similar pattern than that of *S. lorteti* (fig. 12C, D). This similar pattern is probably reflecting the plesiomorphic morphology, more than a concrete functional adaptation.

Radius

Three main differences between the radius of *S. lorteti* and those of the compared felines have been described: 1) its relatively higher robustness, 2) the more rounded shape of its distal articular facet for the scapholunar, and 3) the absence of lateral ridge on the dorsal face of its distal epiphysis. The first difference would indicate the less cursorial locomotion of *S. lorteti* in relation to the extant feline species, and also a relatively stronger forelimb. The shape of the distal articular surface for the scapholunar can be related to the movements of pronation-supination of the hand, and thus, when this facet is round, the degree of rotation of the radius in relation to the carpals is higher than when the facet is square. All the compared felines show a rectangular distal surface in the radius, due to its latero-medial elongation; this morphology still allows a great degree of pronation-supination of the hand, as is observed when extant felids hunt using their grasping hands to subdue and hold prey before applying the killing bite; but it also produces a limitation in the rotation of the hand, at least when compared to the degree of movement that a round facet allows.
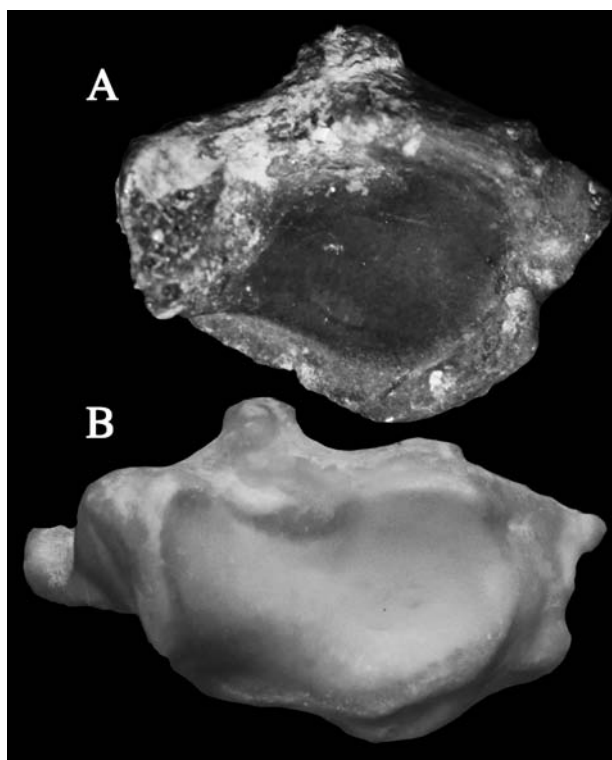

Fig. 13.—Distal view of the distal epiphysis of a left radius of *Styriofelis lorteti* (A) specimen SAN 879, from Sansan (France), and *Lynx lynx* (B), showed at the same size.

This may imply the necessity of higher control of the carpal rotation during terrestrial locomotion. The distal articular surface of the radius of *G. genetta* shows the same morphology as in *S. lorteti*, which could indicate that this is the primitive state for Felidae. Nevertheless, this primitive morphology has also functional implications, as the round distal surface of the radius allows a greater degree of rotation of the hand, which is important when the animal mainly walks on the branches of trees, and terrestrial locomotion is a secondary activity in the foraging strategies of a concrete species. Thus, the radius of *S. lorteti* would show a great capacity for pronation-supination movements of the hand, but also could be reflecting a primitive pattern, shared by arboreal viverrids (fig. 13).

Probably related to the round shape of the distal facet, and thus its shorter medio-lateral length, is the almost absence, in *S. lorteti*, of a lateral ridge on the dorsal surface of this epiphysis. The main function of this ridge is the formation of a groove for the passing of the tendon of the muscle *extensor digitorum lateralis* (Barone, 2000; Reighard & Jennings, 1901),
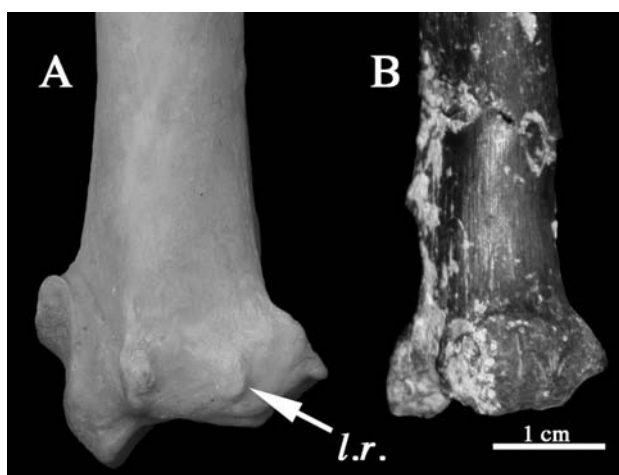
Fig. 14.—Dorsal view of the distal epiphysis of the left radius of *Lynx lynx* (A) and *Styriofelis lorteti* (B), specimen SAN 879, from Sansan (France), showing the development of the lateral ridge (*l. r.*) in the former species, and the absence in the latter. The bones are showed at the same size.

which would be relatively thinner in *S. lorteti* than in the compared felines (fig. 14). Nevertheless, all these latter species and *S. lorteti* do posses another ridge, on the middle of the dorsal surface of this epiphysis, which delimits a second groove, larger that the lateral, for the passing of the large and flat tendon of the muscle *extensor digitorum communis* (Barone, 2000; Reighard & Jennings, 1901). Both muscles have similar functions, but with some differences: the muscle *extensor digitorum lateralis* extends the fingers, but also contributes to the extension of the hand as a whole, whereas the muscle *extensor digitorum communis* (whose mass is larger than the former) extends the third phalanx on the second one, and this on the first phalanx, but it also extends each finger on its metacarpal, and contributes to the extension of the hand on the forearm (Barone, 2000). The separation of their tendons probably contributes to make their actions more precise, something probably important in both hunting and locomotor activities in modern felids. A primitive pattern, observed in *G. genetta* and *S. lorteti* would be the lacking of lateral ridge, and the existence of a common groove for the muscles *extensor digitorum communis* and *extensor digitorum lateralis*.

Ulna

The ulna of *S. lorteti* is relatively more robust than those of the extant compared felines, as is the case with the radius. One of the most interesting differences deals with the development of the scars for the muscles *abductor digiti I longus* and *pronator quadratus*. Both muscles are developed as muscular sheets whose fibres are oriented disto-medially, blending into a narrow but strong tendinous band that runs distally, becoming the tendon of the muscle at the level of the carpus (Evans, 1993; Vollmerhaus & Roos, 2001); thus, the cranio-caudally longer attachment surface of the muscle *abductor digiti I longus*, and the greater development of the ridge for the attachment of the muscle *pronator quadratus* on the ulna of *S. lorteti* probably indicates thicker muscle masses, and thus a stronger contraction, even if the tendons were not significantly different from those of other felines. The muscle *abductor digiti I longus* acts as an abductor and extensor of the thumb, whereas the muscle *pronator quadratus* is a pronator of the forearm (Barone, 2000), both actions being strongly related to the movements involved in the hunting and climbing activities. It is remarkable that in *G. genetta* the ridge for the attachment of the muscle *pronator quadratus* is as well developed as that of *S. lorteti,* whereas the scar for the muscle *abductor digiti I longus* is reduced to a round mark, very far from the elongated facet seen in the felines. This morphology would emphasise the importance of pronation in such an arboreal carnivore as the genet, whereas the abduction of the thumb, more related to hunting, is less critical. Thus, *S. lorteti* would retain the primitive morphology of the ridge for the muscle *pronator quadratus*, whereas the pressure for a more powerful abduction of the thumb would have favoured an increase in size of the muscle *abductor digiti I longus*, producing a larger and rougher scar on the ulna. The morphology observed in the three species of *Lynx*, and in *F. silvestris*, *C. caracal* and *L. serval*, with a reduced area for the attachment of this latter muscle, would be a consequence of their increased gracility in comparison to *S. lorteti*, whilst the pantherins such as *Panthera pardus*, or *P. onca,* as robust as *S. lorteti*, show the same pattern as the latter.

The morphology and development of the olecranon tubercles also have functional implications (fig. 15). The more proximally projected medial tubercle in *S. lorteti* and *F. silvestris* could imply a larger attachment surface for the tendon of the medial branch of the muscle *triceps brachii*, as it inserts along the dorsal half of the medio-proximal margin of the olecranon (Reighard & Jennings, 1901;
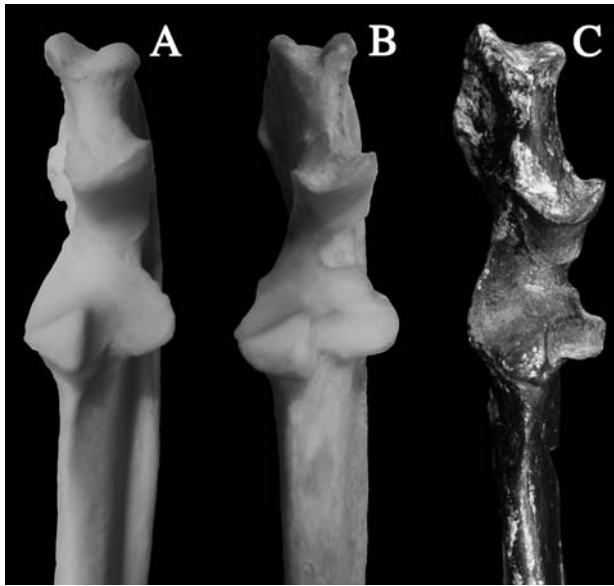
Fig. 15.—Dorsal view of the proximal epiphysis of the left ulnae of *Leptailurus serval* (A), *Lynx lynx* (B) and *Styriofelis lorteti* (C), specimen SAN 879, from Sansan (France), showing the different development of the tubercles of the olecranon. The bones are showed at the same size.
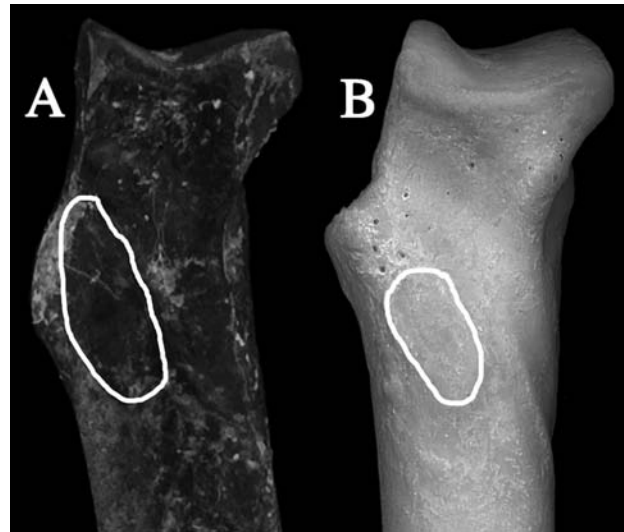

Fig. 16.—Dorsal view of the proximal epiphysis of the left Mc II of *Styriofelis lorteti* (A), specimen SAN 879, from Sansan (France), and *Lynx lynx* (B) showing the different development of the attachment area for the muscle *extensor carpi radialis longus* (white line). The bones are showed at the same size.

Barone, 1967), but also a longer muscle, as the distance between its origin (the caudal surface of the proximal epiphysis of the humerus) and its attachment area is increased in comparison to those species lacking this projection; also, an increase in the distance between the rotation point of the forearm (the elbow) and the attachment point of the medial branch of the muscle *triceps brachii*, increases the effort arm of this muscle. Following the basic principles of leverage, this configuration also reduces the force that this muscle has to produce to extend the forearm (Salesa *et al.*, 2010b). As a consequence, the medial branch of the muscle *triceps brachii* in *S. lorteti* and *F. silvestris* would have a faster contraction, as the longer a muscle, the greater is the velocity of its contraction, since longer muscles have more sarcomeres in series, and their velocities are additive (Kardong, 2002). This pattern might be the primitive for Felidae, as it is shared by the primitive felid *Proailurus lemanensis*, or the earliest machairodontines *Pseudaelurus quadridentatus* and *Promegantereon ogygia* (Salesa *et al.*, 2010b). Following these assumptions, *L. lynx*, *L. rufus*, *L. pardinus*, and *C. caracal* would have a shorter (and slower) medial branch of the muscle *triceps brachii* than *S. lorteti* and *F. silvestris*, or at least its effort arm would be shorter. In terrestrial

viverrids, the attachment area for this branch shows strong differences in its development, from very reduced area in *Herpestes ichneumon*, to a much larger surface in *Ichneumia albicaudata* (Taylor, 1974); and among felids, the highly arboreal *Leopardus wiedii* (Alderton, 1998) shows a similar pattern than that observed on the more cursorial lynxes, thus preventing us from establishing a clear relationship between the attachment area of the medial branch of the muscle *triceps brachii* and any locomotor habit.

Metacarpals

The metacarpals of *S. lorteti* are more robust than those of the compared felines, which fits with the also relatively robust forelimb. There are some minor differences, but in general the metacarpal morphology of *S. lorteti* is very similar to that of other felines. One of the most remarkable features is the large, and round scar for the attachment of the muscle *extensor carpi radialis longus*, located on the dorsal face of the proximal epiphysis of the metacarpal II, which is much smaller in *L. lynx*, *L. pardinus*, *C. caracal*, *L. serval*, *L. wiedii* and *O. geoffroyi* than in *S. lorteti* (fig. 16), and almost absent in *G. genetta*, *F. silvestris* and *L. rufus*. Nevertheless, the great development observed in *S.*
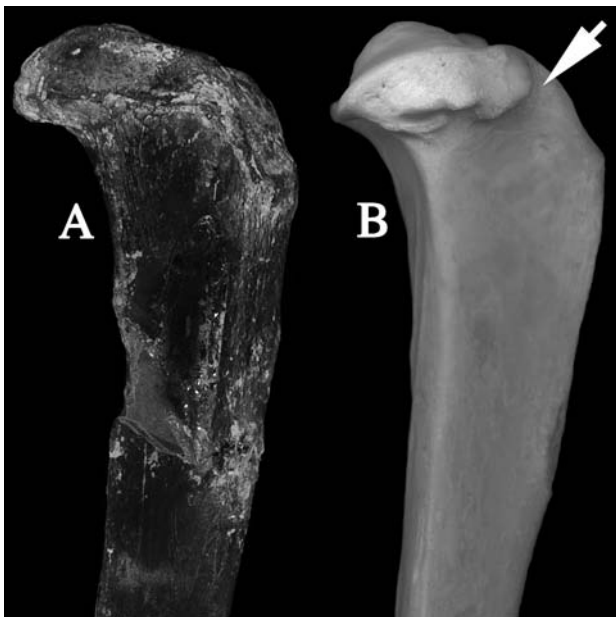
Fig. 17.—Lateral view of the proximal epiphysis of the left tibia of *Styriofelis lorteti* (A), specimen SAN 879, from Sansan (France), and *Lynx lynx* (B) showing the presence in the latter of a notch for the passage of the tendon of the muscle *extensor digitorum longus* (white arrow). The bones are showed at the same size.
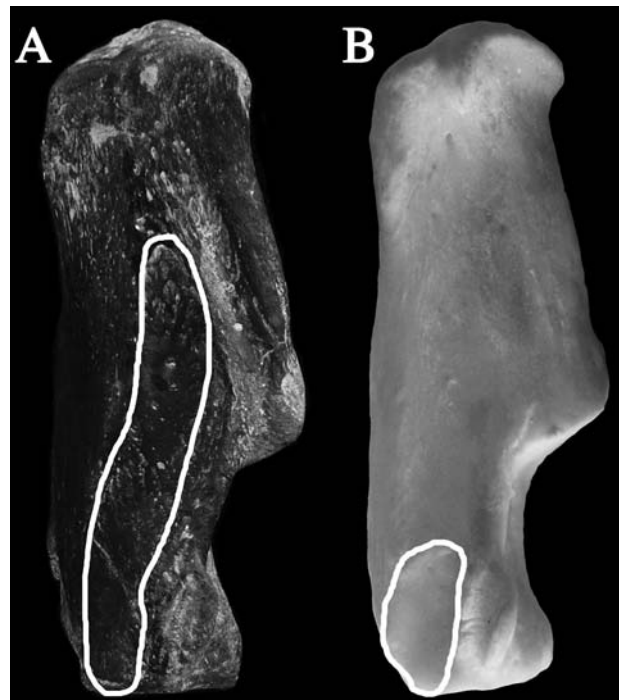

Fig. 18.—Lateral view of the right calcaneus of *Styriofelis lorteti* (A), specimen SAN 879, from Sansan (France), and *Lynx lynx* (B) showing the different development of the attachment area for the muscle *quadratus plantae* (white line). The bones are showed at the same size.

lorteti is comparable to that seen in the pantherins such as *P. pardus* or *P. onca*, and thus could have an allometric explanation. This muscle is an extensor of the carpal joint, and a flexor of the elbow (Evans, 1993) and would be relatively larger in the larger felids, as they support probably greater forces at the elbow and carpus.

Tibia

The absence of constriction for the passage of the tendon of the muscle *extensor digitorum longus*, shared by *S. lorteti* and *G. genetta*, would be thus a primitive character for Felidae (fig. 17). This muscle originates by a thin flat tendon from the lateral epiphysis of the femur, which becomes narrower and thicker as it passes through the articular capsule of the knee-joint, and over the mentioned constriction (Reighard & Jennings, 1901); the absence of this constriction probably implies the presence of a thinner or flat tendon of the muscle *extensor digitorum longus*. This muscle is an extensor of the phalanges of the foot, and a flexor of the tarsus (Reighard & Jennings, 1901; Evans, 1993; Barone, 2000), and a thinner tendon could represent a weaker origin point for the muscle.

Another interesting difference between the tibiae of *S. lorteti* and those of the compared felines is the morphology of the distal epiphysis, with a square shape in the former, instead of the more rectangular morphology observed in the latter group. This seems to be another primitive character for Felidae, as a square distal epiphysis is shared by *G. genetta* and earliest felid *Proailurus lemanensis*. Nevertheless, the differences do not seem to be highly significant, and could produce a minor difference in the maximum level of flexion of the astragalus on the tibia, although it also might reflect a higher degree of grasping capacity in the feet, typical of arboreal carnivores.

Calcaneus

Apart from the greater development of the attachment areas for several ligaments, the calcaneus of *S. lorteti* can be distinguished from those of extant felines by the larger lateral groove for the attachment of the muscle *quadratus plantae*, which would thus be larger as well (fig. 18). This muscle is an

accessory of the muscle *flexor longus digitorum*, having two important actions: it adjusts the oblique pull of this muscle, and also allows the foot to flex without the involvement of the muscle *flexor longus digitorum* (Reighard & Jennings, 1901; Barone, 1967; Turner & Antón, 1997; Vollmerhaus & Roos, 2001; Benjamin *et al.*, 2008); the muscle *quadratus plantae* is very reduced in extant felids (Barone, 1967; Vollmerhaus & Roos, 2001). Ginsburg (1961) associated the great development of this muscle with plantigrade locomotion, but in the case of early felids, which show several traits of digitigrady on its skeleton, this character has to be consider as primitive, explained by the retention of an empha-sized grasping function in the hind limb (Turner & Antón, 1997), and indicating a reduced capacity for pedal inversion but powerful flexion capability of the third phalanges of the foot (Cifelli, 1983). Du-ring subsequent evolution, as terrestrial locomotion became dominant in felids, the muscle *quadratus plantae* became less important and the muscle *fle-xor longus digitorum*, took over: this flexes the toes relative to the tibia, a propulsive rather than a grasp-ing function (Turner & Anton, 1997).

Metatarsals

The metatarsals of *S. lorteti* are shorter (and thus, more robust) than those of the compared species of extant felines, implying less cursorial abilities. The presence of a small tubercle for the muscle *fibularis brevis* on the lateral face of the proximal epiphysis of the Mt V is shared by *S. lorteti* and *F. silvestris*, and probably is another primitive character retained by the latter species, and modified in the more derived species included in the comparison sample.

Conclusions

The new postcranial fossils of *S. lorteti* from Sansan have allowed the first functional approach to the anatomy of its skeleton. In overall morpholo-gy, the postcranial bones of *S. lorteti* show a consi-derable resemblance to modern felines, with a long lumbar region and tail, and limbs well adapted to a digitigrade locomotion. However, after detailed comparison with modern felines of similar body size, *S. lorteti* reveals itself as having relatively robust and short metapodials (including Mc I) and limbs, with a higher capacity for pronation-supina-tion in the forelimbs and feet, and a stronger muscle *quadratus plantae* than in extant taxa. All these characters are strongly related to the hunting tech-niques of extant felids, but also to their climbing abilities, and their strong expression in *S. lorteti* suggests that either or both activities were empha-sised in this primitive feline. Some other features, such as the morphology of the caudal vertebrae or the tibia, or the development of the olecranon tuber-cles, might just reflect the primitiveness of *S. lorteti*.

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