SHORT COMMUNICATION

Three Ways To Be a Saber-Toothed Cat

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Abstract Saber-toothed carnivores, until now, have been divided into two groups: scimitar-toothed cats with shorter, coarsely serrated canines coupled with long legs for fast running, and dirk-toothed cats with more elongate, finely serrated canines coupled to short legs built for power rather than speed. In the Pleistocene of North America, as in Europe, the scimitar-cat was *Homotherium*; the North American dirk-tooth was *Smilodon*. We now describe a new sabercat from the Early Pleistocene of Florida, combining the scimitar-tooth canine with the short, massive limbs of a dirk-tooth predator. This presents a third way to construct a saber-toothed carnivore.

Introduction

We introduce a saber-toothed cat from the Early Pleistocene (Irvingtonian) of North America that presents a new evolutionary strategy for the saber-toothed adaptation, combining the highly effective prey manipulation of the dirk-toothed *Smilodon* with the specialized killing bite of a scimitar-toothed *Homotherium*. We suggest that this new cat was the most formidable feline predator of its time. Its closest competitor was the dirk-toothed *Smilodon gracilis*, an animal about the size of the jaguar, *Panthera onca*. The only other lion-sized cat in the early Pleistocene of North America was *Homotherium*, but this long-legged scimitar-tooth was much less robust and probably did not overlap ecologically with the new form (Meade 1961; Rawn-Schatzinger 1992). When biting, the long sabers of dirk-toothed cats may have cut parallel slits for some distance before the relatively smaller incisors could be applied. In scimitar-toothed cats the shorter canines and longer incisors worked more as a unit, first cutting parallel slits with the canines, immediately followed by the incisor arc removing the strip of flesh. Such a large open wound would have bled profusely, traumatizing the victim. If the incisors and canines acted in unison, the torsional forces on individual teeth would have been reduced, resulting in fewer restrictions on bite placement. In felids the size of the sagittal crest is directly proportional to the forces exerted by the temporalis musculature. Scimitar-toothed cats have a sagittal crest that is generally less pronounced than that in their dirk-toothed contemporaries. In a modification of the typical scimitar-tooth condition, the new cat from Florida exhibits both an elongated sagittal crest and an enlarged temporalis muscle that would have permitted a stronger bite. In addition, although the canines are shorter than in the average homothere, the incisor arc is more procumbent. Unlike other saber-toothed cats, the occipital region of the new type is both elongated and inclined rather than shortened, and vertical. This arrangement allows the movement of the temporalis to scribe a larger arc as the jaw closes, increasing the force generated at the anterior

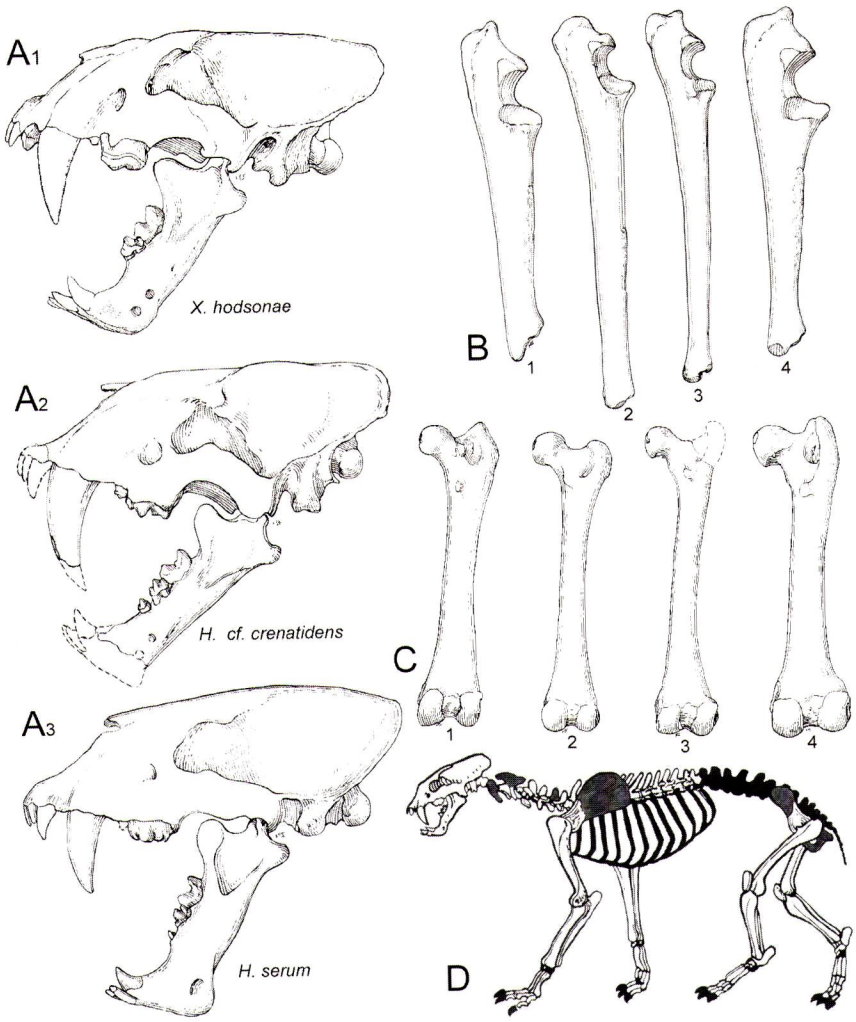

Fig. 1. A) Lateral view of skulls and mandibles. *1 Xenosmilus hodsonae* (Holotype) BIOPSI 101; *2 Homotherium* cf. *crenatidens*, University of Idaho (UI 11861); *3 Homotherium serum*, (TMM 933-3582); B) Radial view of ulnae. *1 Smilodon fatalis* (based upon Merriam and Stock 1932); *2 Homotherium serum* (TMM 933-3231; based upon Rawn-Schatzinger 1992); *3 Homotherium* cf. *crenatidens* (UI 11851); *4 Xenosmilus hodsonae* (Holotype) BIOPSI 101; C) Posterior view of femora. *1 Smilodon fatalis*; *2 Homotherium serum* (TMM 933-1570); *3 Homotherium* cf. *crenatidens* (UI 11861); *4 Xenosmilus hodsonae* (Holotype) BIOPSI 101; D) Restored skeleton of *Xenosmilus hodsonae*. *Black* missing elements

teeth (incisors and canines) rather than at the carnassials. It may be that this anterior component of the bite was more important in feeding than in other saber-toothed cats, where the carnassials act as the main meat-cutting apparatus.

The shortened limbs indicate that the new cat resembled *Smilodon* in occupying areas of dense vegetation. Osteological details show that this new form is a close sister group to the typical scimitar-toothed-*Homotherium* (Martin 1980; Martin et al. 1988), but that it diverged from that lineage and followed an evolutionary pathway in which its postcranial skeleton was convergent to that of dirk-toothed cats such as *Smilodon fatalis* (Merriam and Stock, 1932). This association of structural characters has produced a previously unrecognized body form for saber-toothed carnivores and represents a third and new genus and species of saber-tooth for the North American Ice Ages. All three kinds of saber-toothed cats coexisted in North America in the early Pleistocene. This new cat is presently the only short-legged taxon within the Homotherini, and is known only from Florida. We can describe this animal as follows:

- Systematic paleontology: class, Mammalia; order, Carnivora; family, Felidae (Gray 1821); tribe, Homotherini (Fabrini 1890) M; *Xenosmilus hodsonae* gen. et sp. nov.
- Etymology: *xenos* (Greek) strange; *smilos* (Greek) knife; *Hodsonae* for Debra Hodson.
- Holotype: BIOPSI (Babiarz Institute of Paleontological Studies), 101; a nearly complete skeleton (Fig. 1D) except for the lumbar vertebrae, sternum, ribs, and tail. The specimen is deposited in the Museum of Geology, Arizona State University.
- Paratype: University of Florida, UF 60,000, partial skeleton, including skull and mandible.

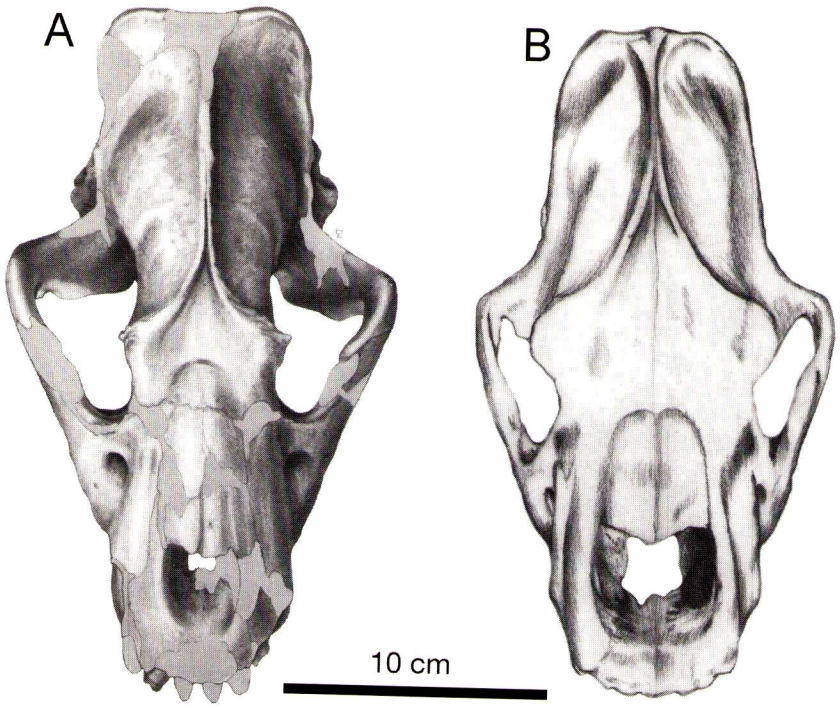

Fig. 2. A,B. Dorsal view of skulls showing frontal expansion in *Homotherium*. A) *Xenosmilus hodsonae* (Holotype) BIOPSI 101. B) *Homotherium serum*, Texas Memorial Museum (TMM 933-3582)

- Type locality: University of Florida collecting site (commercial limestone quarry, Haile 21A) Alachua County, Florida.
- Horizon: undifferentiated sinkhole fill sediments in the Eocene Ocala limestone.

The diagnosis is: extinct felid with short, broad, coarsely serrated, saberlike upper canines, third lower premolar (P_3) absent (Fig. 1A, 1); anterior margin of masseteric fossa (Merriam and Stock 1932); on ramus not pocketed as in *Homotherium serum* (Rawn-Schatzinger 1992; Fig. 1A 1–3); lower mandible has two large mental foramina below the diastema; relatively small head with large occipital condyles; cranium elongate with frontals much narrower than in *Homotherium* (Fig. 2A); temporal fossa elongated; apex of the occipital crest much posterior to the condyles (nearly even in *Homotherium*); width across the anterior articulating surface of axis vertebra greater than the average measured for either *Homotherium serum* or *Smilodon fatalis* (Martin 1980; Merriam and Stock 1932); neural canal of axis more triangular than in *Smilodon fatalis* with larger, elevated and oblong-shaped transverse foramina; distal segments (ulna, tibia) of limbs shortened and robust (Table 1); ulna straight and massive (Fig. 1B, 4); humeral articulation on the ulna larger than in *Smilodon fatalis*; olecranon process of ulna straight proximally as in *Homotherium*

Table 1. Selected measurements

	X. hodsonae BIOPSI 101	*H. ischyros* UI	*H. serum* TMM-3582	*H. serum* 3231
Length premaxillary to condyle	287.8	285.0	327.0	289.0
Width frontals	76.0	124.3	–	93.0
Width condyles	67.8	64.5	62.0	61.0
Length upper canine	81.3	"105"	68.0	–
AP diameter upper canine	36.8	35.0	26.5	32.8
AP diameter P_4	41.5	37.5	39.0	38.4
AP diameter M_1	31.5	30.2	–	30.6
Length humerus	360.0	328.0	–	358.0
Length ulna	320.0	"360"	–	376.0
Length femur	360.0	"389"	–	353.0
Length tibia	286	323	–	297.0

(pointed in *Smilodon*); styloid process blunt as in *Homotherium* (pointed in *Smilodon*); proximal breadth across radius is greater in *Smilodon* than *Xenosmilus*, but distal breadth is nearly identical; femur more stout than *Smilodon*, with patellar groove wider (Fig. 1C, 4); greater trochanter blunt as in *Homotherium* (opposed to pointed in *Smilodon*); trochanteric fossa deep (more shallow in *Smilodon*); trochanteric ridge prominent (less developed than *Smilodon*); strongly projecting lesser trochanter (reduced in *Smilodon*); distal end of femur relatively broad (narrower than *Smilodon*); tibia more robust than *Smilodon* with broader proximal and distal ends; proximal and distal ends of fibula resemble *Homotherium*, but exhibit a comparative decrease in total shaft length and increase in anterioposterior diameter at midshaft. Essentially, the postcranial skeleton of *Xenosmilus* is short and massive as in *Smilodon fatalis*, but resembles *Homotherium crenatidens* in detail.

Discussion

Xenosmilus has several features (absence of an anterior masseteric pocket and two mental foramina) that place it as primitive within the homothere clade. However, the elongated temporal fossa, loss of P_2, and shortened legs suggest that it took a different evolutionary direction from other homotheres. Until recently the skeleton of the American Pliocene *Homotherium* was incompletely known. It can now be described on the basis of an associated skeleton from Idaho (University of Idaho 11861). This specimen (Fig. 1A, 2) is closely similar to *Homotherium crenatidens* (Ballesio 1963) of the European Pliocene, but not to the new genus. The Late Pleistocene *H. serum* is osteologically similar to *H. crenatidens* and not to *Xenosmilus*. It ranged as far north as Alaska and was apparently closely related to the European *H. latidens*.

Unlike other saber-toothed cats, *Xenosmilus* has a relatively small head, yet the occipital condyles are unusually large for the skull size. Its ulnar length is even shorter when compared to the humerus than in *Smilodon fatalis*, and the femur is more stout. Overall *Xenosmilus* is more massive than *Smilodon* and would have had a more bearlike than catlike appearance. Such robust limbs suggest excellent prey manipulation and precision biting capabilities.

The combination of morphological features in *Xenosmilus* is a departure from the saber-tooth paradigm as we once understood it. This genus represents a previously unrecognized ambush predator about the size of a lion in the early Pleistocene of the North American southeast. The type and paratype skeletons were found in a cave deposit along with the remains of many large-bodied wild pigs (the peccary *Platygonus*). This was probably a den site and the peccaries a preferred prey. The discovery of *Xenosmilus* expands the concept of scimitar-toothed cats to include short-legged ambush predators along with the more typical long-legged genera.

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