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SABER-TOOTHED CARNIVORES

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University of Florida

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Florida Paleontological Society Inc.

Official News

FINAL ANNOUNCEMENT

This is the last issue of *THE PLASTER JACKET* that will be distributed free of charge. Due to budgetary limitations, all successive issues will be distributed to individual and institutional members in good standing. The FPS derives its revenues solely from membership support. If you have not already done so and wish to join the FPS, see membership information on outside back cover.

4TH ANNUAL PALEONTOLOGICAL MEETINGS

The 4th Annual Paleontological Meeting will be held on Saturday, 20 October 1979, at the University of Florida. Registration will begin at 8:00 AM outside the Auditorium in the J.W. Reitz Union. If you are interested in presenting a talk (about 15-20 minutes in length), a poster display, exhibiting specimens, or want to preregister, fill out the enclosed form and return it to Howard Converse, Secretary-Treasurer. Standard 2" x 2" carousel projectors will be available for showing slides.

SUGGESTIONS FOR FPS LOGO

The FPS would like to choose a logo. If you have a suggestion, please mail an illustration to Howard Converse, Secretary-Treasurer, before 15 October. Slides will be made of each logo suggested, and the members present at the October Annual Meeting will vote for their choice.

(Bruce J. MacFadden, Editor)

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SABER-TOOTHED CARNIVORES

Jon A. Baskin[1]

Saber-toothed carnivores are among the most fascinating of fossils. They are highly prized as specimens, not only because of their general rarity, but also because of the interest they stimulate when trying to interpret their life histories. There has been much discussion and argument about how saber-tooths hunted and killed their prey, and in some cases how they died and accumulated as fossils. The stereotype of the saber-tooth is *Smilodon*, the saber-toothed "tiger," best known from the late Pleistocene tar pits of Rancho La Brea in Los Angeles. However, there have been many other carnivores with saber-like upper canines, some of them true cats like *Smilodon*, but many of them not. The evolution of greatly enlarged upper canines has occurred independently at least four times in meat-eating mammals: in the late Miocene and Pliocene South American marsupial *Thylacosmilus*, in the

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North American Eocene creodont *Apataelurus*, in the Oligocene through Miocene paleofelids, and in the Miocene through Pleistocene machairodontine neofelids. There are no strictly saber-toothed carnivores alive today. However the East Asian clouded leopard, *Neofelis nebulosa* has enlarged flattened upper canines. The clouded leopard almost certainly evolved from an ancestor with normal cat-like canines, testifying to the persistent tendency for the evolution of saber-like canines in carnivores.

ADAPTATIONS OF SABER-TOOTHED CARNIVORES

There have been many theories on what and how saber-tooths, especially *Smilodon*, ate. Some have suggested that they were carrion feeders, that their canines were not strong enough to stab living prey without the likelihood of the canines breaking. The main function of the canine was supposed to be the slicing of soft flesh. Simpson has demonstrated that the elongate, curved canines of saber-tooths and the associated specializations of their bones and muscles are perfectly adapted for stabbing. There is a whole adaptive complex of characters that work together with the greatly enlarged upper canines that has also evolved independently in the different lines of saber-toothed carnivores. In these animals, the lower jaw has to be able to swing clear of the enlarged upper canines so that they can function as efficient stabbing blades. Some earlier authors have doubted whether saber-tooths could have opened their mouths wide enough in order to function in this way. Matthew was one of the first to point out the specialized adaptations in the skulls of saber-tooths that allow them to open their mouths much wider than is possible in other mammalian carnivores (Fig. 1). The glenoid fossa, the region of the skull that articulates with the lower jaw, is moved down often below the auditory bulla. In the lower jaw, the coronoid and angular

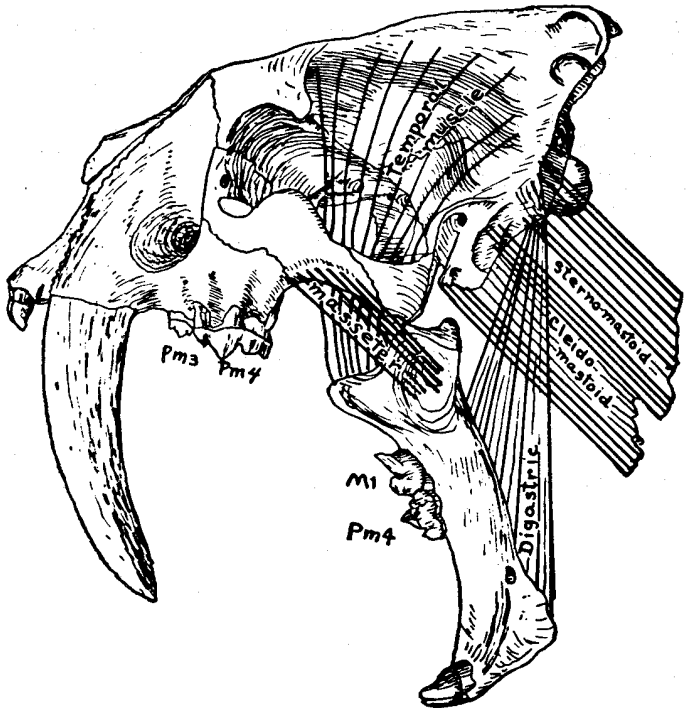

Figure 1. Skull of *Smilodon*, showing muscles of jaws (after Matthew).

processes are reduced to help increase the gape. The coronoid process is the place of insertion of the temporal muscle, the largest and most important muscle for closing the jaw in carnivores. Because the coronoid process is reduced, some authors have argued that the temporal muscle is too reduced and the lower jaw too weak to efficiently cut meat. Recently Turnbull has shown that at least in *Thylacosmilus*, there is no evidence of the temporalis being reduced in mass. The large saggital crests of most placental saber-tooths argue for a large temporal muscle to pull

directly up on the lower jaw. The premolars and molars of saber-tooths tend to be more blade-like than in other carnivores and therefore better adapted for slicing meat. This tendency reaches its extreme in the long, straight, shearing cheek-teeth of *Barbourofelis* and *Ischyrosmilus*.

Simpson thoroughly analyzed the action of stabbing in the saber-tooths and showed that it involved a rotary motion around the curved canines. This permited perfectly efficient stabbing with no slicing action that might have strained the canines. The head movement was controlled by extremely powerful muscles that were capable of making precise strikes. In saber-tooths, the mastoid processes are greatly enlarged for the attachment of these greatly enlarged muscles. The power to flex the neck and stab with the canines was further increased by having the mastoids situated farther below the occipital condyles than in ordinary carnivores, thus increasing the mechanical advantage of the strike.

Other adaptations of saber-toothed carnivores include reduction of the lower canines so that they are usually only slightly larger than the third lower incisor. In feline cats the lower canines are enlarged and, together with the upper canines, are used to kill by seizing their prey by the neck and biting; saber-tooths kill by stabbing with the upper canines alone. In some saber-tooths, there is a flange on the lower jaw to protect the sabers, but this does not appear to be necessary, since it is poorly developed in *Smilodon*.

Saber-toothed carnivores have extremely powerful forelimbs that were used to hold on to and pull down large prey animals. Prey probably included large, thick-skinned ungulates, such as rhinoceroses, ground sloths, and elephants, that greatly exceeded the carnivore in body size. The muscular front legs, which have large, sharp, retractile claws in the cats, would next be used to immobilize the prey so that the

saber-tooth could make an accurate, fatal stab through the neck or throat. Some saber-tooths, such as the marsupial *Thylacosmilus* or the scimitar-toothed cats, could also use the sabers for slashing or slicing, but this was secondary to stabbing. The carnivore would then use its blade-like cheek-teeth to slice off pieces of meat.

A HISTORY OF SABER-TOOTHED CARNIVORES

The dominant carnivorous or meat-eating mammals today are members of the Order Carnivora. The Order Carnivora is a natural group, that is, its members have a common ancestor not shared by any other mammal. *PLASTER JACKET 11* by Norm Tessman discusses terrestrial Carnivora; *PLASTER JACKET 27* by Clayton Ray, marine Carnivora. Not all members of the Order Carnivora are carnivorous. For instance, the aardwolf *Proteles*, a relative of the hyenas, is insectivorous. Its diet consists almost entirely of termites. Most bears tend to be omnivorous, eating a wide range of plants and animals. Some, such as *Ailuropoda*, the panda, are almost completely herbivorous, subsisting mainly on grasses, leaves, stems, and flowers. Conversely, not all carnivores are members of the Order Carnivora. There are carnivorous birds, such as owls and hawks, and carnivorous reptiles, such as snakes and some lizards. There are also mammals from other orders besides the Carnivora that are carnivores. Whales (see *PLASTER JACKET 29*) are marine mammalian carnivores of the Order Cetacea. *Sarcophilus*, the Tasmanian devil, and *Thylacinus*, the Tasmanian "wolf," now probably extinct, are marsupial carnivores. These two are closely related to opossums, phalangers, and kangaroos, not to members of the Order Carnivora, such as cats or dogs which they superficially resemble.

The first members of the Order Carnivora appeared in the Paleocene (about 55 million years ago). They were small and relatively unspecialized carnivores of

the family Miacidae. At that time they had not achieved the dominance among mammalian carnivores that they have today. Two other groups of mammals were also competing as carnivores during much of the early Cenozoic on the northern continents: the mesonychid condylarths, which are probably ancestral to the whales, and the Order Creodonta, a group of carnivorous mammals in which the carnassials, the shearing teeth, are not formed by the upper fourth premolar and lower first molar as in the Order Carnivora (see *PLASTER JACKET 11*) but by teeth farther back in the jaw. The Creodonta became extinct in North America during the Oligocene, but survived until the late Miocene in Africa and Asia, where they evolved into some of the largest carnivores ever known. One of the

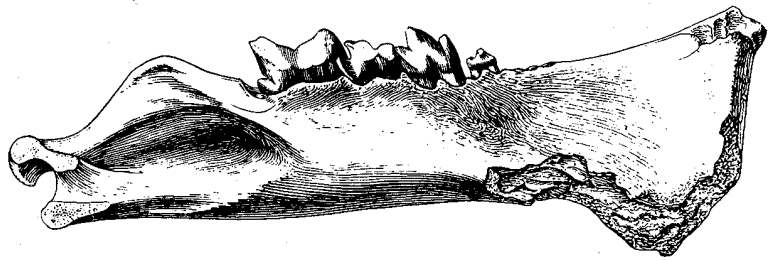

Figure 2. Lower jaw of the Eocene creodont *Apataelus kayi* (from Scott).

earliest saber-toothed carnivores is the creodont *Apataelurus kayi*. Although this animal is known only from a lower jaw (Fig. 2), it is almost certain from its structure that it belonged to a skull with elongated saber-like canines. The reduced coronoid and angular processes, long diastema, symphyseal flange, and reduced lower canine are all saber-tooth adaptations. *Apataelurus* had four premolars and two molars. The lower carnassial was the M_2 as in the Order Creodonta, not the M_1 as in the Order Carnivora.

Both South America and Australia were island continents throughout the Tertiary. Their mammalian faunas evolved independently of those of the northern continents. On Australia, where there were no placental mammals until the Pleistocene, marsupials filled the placental niches of herbivores, carnivores, and insectivores. In South America, there were native placental herbivores, but no placental carnivores. As in Australia, marsupials evolved into the large carnivores. At the end of the Pliocene (about 3 million years ago), North America became connected to South America, and North American mammals, including members of the Order Carnivora, migrated to South America, causing the extinction of the native South American carnivores and many of the large herbivores. Australia, which has remained an island continent, has had more of its native fauna survive. The dingo, a dog brought to Australia by the aborigines has probably caused the extinction of the marsupial carnivore *Thylacinus*, the Tasmanian or pouched "wolf."

One of the most remarkable carnivores known from anywhere is *Thylacosmilus* (Fig. 3) from the late Miocene and Pliocene of South America. This marsupial is a more highly specialized saber-tooth than any of its placental counterparts. Its canines were larger, more slender, and more securely anchored in the skull than in any placental saber-tooth. The canines continued to grow throughout life and were self-sharpening against the lower canines. The flange of the mandible, which protects the canine, was larger than in any placental, and the head and neck flexing musculature appears to have been more powerful. The cheek-teeth are not as specialized for slicing as in the saber-toothed cats, but the self-sharpening upper canines were probably able to slice as well as they could stab.

In the Felidae, the family of the Order Carnivora that contains the cats, the saber-toothed habit has evolved independently at least two and probably three

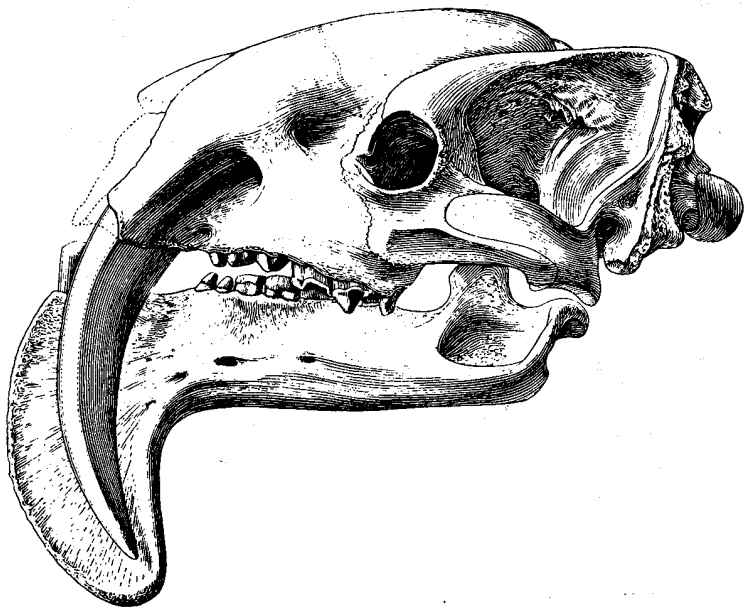

Figure 3. Skull of the South American marsupial *Thylacosmilus atrox* (from Riggs).

times. Some paleontologists have recognized separate Oligocene "paleofelid" and later Cenozoic "neofelid" radiations of cats. Both lines independently evolved saber-toothed carnivores. One of the legendary fossils among bone hunters is the skull of the saber-tooth *Pogonodon platycopis* that was found in 1879 perched on the summit of a 40-foot high rock spire in the late Oligocene John Day Formation of Oregon. Another paleofelid, *Eusmilus*, is not only one of the oldest known saber-tooths, it is also one of the most highly developed with greatly enlarged upper canines and a well developed flange on the lower jaw. Skulls of these paleofelid saber-tooths and "false saber-tooths" are not uncommon in the Oligocene Big Badlands of Nebraska and South Dakota. The last of the paleofelids was the

great saber-tooth, *Barbourofelis*. *Barbourofelis* is best known from the late Miocene of Nebraska, but has also been found in Florida (Fig. 4).

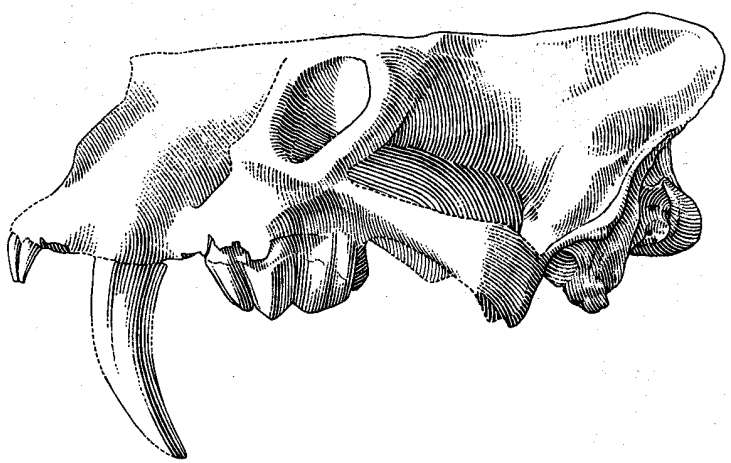

Figure 4. Skull of *Barbourofelis* (drawn by Lauren Keswick).

Among the neofelids, two types of sabercats have evolved. These have been described as the dirk- (or dagger-) toothed cats and the scimitar cats by Kurten. These are all extinct. Normal canine cats are the only neofelids living today. Saber-toothed neofelids evolved in the late Miocene, probably all in Eurasia, and invaded North America at least three times. The canines of dagger-toothed cats are very elongate with relatively thick oval cross-sections (Fig. 1). Two genera, *Megentereon* and *Smilodon*, are known from the Pliocene and Pleistocene of North America. *Smilodon* invaded South America at the beginning of the Pleistocene and may have competed with and caused the extinction of *Thylacosmilus*.

The scimitar-toothed cats are relatively rare in North America, but are better represented in Europe

Figure 5. Skull of the scimitar-toothed *Homotherium serum* (from Meade).

and Asia. These cats have canines that are shorter, more curved, and flatter than the dirk-toothed cats (Fig. 5). *Machairodus*, a relatively primitive scimitar cat, migrated to North America in the late Miocene; *Ischrosmilus*, in the Pliocene; and *Homotherium* (*Dinobastis*), in the Pleistocene.

SABER-TOOTHS OF FLORIDA

Carnivores are present in the oldest-known terrestrial Florida fauna, the late Oligocene I-75 locality, are common in several early Miocene localities, and are relatively abundant at Thomas Farm; but it is not until the late Miocene (about 9 million years ago) that saber-tooths, or any cat for that matter, are known from Florida. *Barbourofelis* is known from the Love Bone Bed. This saber-tooth has elongate flattened canines that have internal and external constrictions. The upper shearing carnassial is the most knife-like of the Carnivora. The P^3, the tooth in

front of the carnassial, is greatly reduced to make room for the long, narrow blade. The lower jaw has a well-developed flange to protect the saber. It is also the only known member of the Carnivora to have a post-orbital bar behind the eye. A post-orbital bar is also present in the saber-tooth marsupial *Thylacosmilus*. The function of the post-orbital bar in primates is to protect the eye from the temporal muscles, which bulge when they contract. In addition, in these two saber-tooths, the post-orbital bar may have given additional strength to the skull. A skull of *Barbourofelis* can be seen in the McGehee fossil site exhibit at the Florida State Museum.

Nimravides does not show all the adaptations of the saber-tooth cats. The coronoid process of the mandible is high. The mastoid processes are not enlarged. The upper carnassial is less blade-like. The lower canine is larger than the small incisors, but not as large relatively as in living cats. However, it does have enlarged, slightly flattened upper canines, and for that reason it is included here. In Florida, *Nimravides* is known from the late Miocene Love and Mixon's Bone Beds.

Machairodus is known from the latest Miocene (about 5 million years ago) Withlacoochee River 4A locality and possibly from Haile VI and Bone Valley. *Machairodus* is a latest Miocene immigrant from Eurasia. It has long, somewhat flattened upper canines, and the mandible has only a very slight flange. The third lower premolar is large and double-rooted in contrast to *Homotherium* or *Smilodon* in which it is extremely reduced or absent. The limbs are elongate and relatively slender.

Smilodon, the Pleistocene saber-toothed "tiger," is best known of the saber-tooths, because of the many specimens from the La Brea tar pits. It is no more closely related to the tiger than to any of the living cats, including the domestic house cat. *Smilodon* is the largest and most advanced of the dagger-toothed

cats. The dagger-toothed cats are heavily built, with relatively short, but powerful legs. Their upper canines are greatly elongated, but relatively thick. Two species of *Smilodon* have been described from Florida. *Smilodon floridanus* is known from several late Pleistocene localities in Florida, including the Ichetucknee River, Aucilla River, Seminole Field, and Haile quarries. *Smilodon floridanus* was first described by Joseph Leidy in 1889 on the basis of a fragmented skull from a fissure filling in a limestone quarry near Ocala. Recent work has demonstrated that *S. floridanus* is probably the correct specific name for late Pleistocene *Smilodon* from North America, including the saber-tooth from La Brea, which has been called *S. californicus*. A smaller species of *Smilodon*, *S. gracilis*, is known from Haile, Inglis, and the Santa Fe River. These localities are late Pliocene and early Pleistocene in age.

One of the rarest saber-tooths in North America is *Homotherium* (*Dinobastis*) *serum*. This scimitar-toothed cat had long powerful front legs. The upper canine is much less elongate than in *Smilodon*, but is broader, more flattened and has razor-sharp serrated cutting edges. The carnassial teeth are more blade-like than in *Smilodon*. In Florida, *Homotherium serum* is only known from Reddick of late Pleistocene age. It is represented there by several isolated teeth, apparently from one individual.

Saber-toothed cats became extinct in Florida at the end of the Pleistocene, as they did elsewhere in the New World. Their extinction coincides with that of many of the large ungulates, such as elephants and ground sloths. As most of the large prey species became extinct, their predators would also, if they could not find other prey. The earlier extinction of *Barbourofelis* in the late Miocene occurred at the same time large ungulate diversity in North America dropped. In the late Pleistocene there have been no associations of saber-tooths with early man. However, if early man is responsible for the extinction of the large ungulates, then man may also be indirectly responsible for the extinction of the magnificent saber-tooth.