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Larry D. Martin

University of Kansas Main Campus

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FUNCTIONAL MORPHOLOGY AND THE EVOLUTION OF CATS

Larry D. Martin

Museum of Natural History and
Department of Systematics and Ecology
University of Kansas
Lawrence, Kansas 66045

Three basic morphotypes are proposed for cats on the basis of their upper canines: 1) conical-toothed cats with short, unserrated canines having a round cross-section; 2) scimitar-toothed cats having short, broad canines, usually with very coarse serrations; and 3) dirk-toothed cats having long, slender canines which usually have fine serrations. Commonly all three morphotypes occur together in the same fauna. The method of prey capture was probably different for each morphotype. Both types of saber-toothed cats appear to have specialized on large prey, but it seems unlikely that they utilized the same prey. Scimitar-toothed cats are long-limbed, and were probably pursuit predators. Dirk-toothed cats are short-limbed and must have ambushed their prey.

The separation of cats into two families, Nimravidae and Felidae, is accepted. Felid cats have a *septum bullae* in the auditory bulla and a cruciate sulcus on the brain. Nimravid cats generally lack complete bullae, and when they are present there is no septum. Nimravid cats also lack the cruciate sulcus on the brain.

† † †

INTRODUCTION

C. B. Schultz, M. R. Schultz, and I (1970) described a new group of bizarre saber-toothed cats, the Barbourofelini. This ultimately required a review of all the fossil saber-toothed cats and finally led to an examination of most of the fossil Felidae. Results of this work have been published in four papers with Schultz. Although much remains to be done, this paper is a preliminary synthesis of my overall conclusions.

Saber-toothed cats belong to that small group of extinct animals that has caught the public fancy and with the dinosaurs is often cited as an example of over-specialization which resulted in extinction. What is not generally understood is how numerous and diverse saber-toothed cats were and how successfully adapted they must have been. For at least the first 20 million years of feloid history, saber-teeth are the only cats for which we have a record. Recent cats represent a feloid radiation which began only about 15 million years ago and which did not achieve its present dominance until the last few

million years. The adaptive significance of saber-teeth may be that they permit an animal to kill larger prey or to inflict a more severe wound than its proportions would otherwise permit. However, such an adaptation may have led to reduced ability to catch relatively small prey such as that with which cats with more "normal" canines had their early success.

MORPHOLOGY AND BEHAVIOR

Canine Shape

All cats belong to one of three basic morphotypes, which can be recognized in many of their skeletal elements, but which is best typified by the shape of their upper canines (Fig. 1). The upper canine of all modern cats is round in cross-section and forms a posteriorly recurved cone. I refer to cats of this type as conical-toothed. Cats whose upper canines have a flattened cross-section are called saber-toothed cats. The latter can be easily separated into two groups on the basis of their canines. In one group we have cats with relatively short, broad canines that usually bear coarse crenulations. These I call scimitar-toothed cats. The other group (dirk-toothed cats) has long, narrow upper canines with very fine or no crenulations (*Megantereon*). Kurtén (1968) originated these two terms for his Homotherini and Smilodontini respectively, but I have expanded their usage to include in each group all cats that have the required canine morphology regardless of phylogenetic relationship. I do not believe that it is important that the knives Kurtén used for his analogy are not closely similar to the actual saber-toothed canines. The names are now well-enough established in the literature that new terms would only cause confusion. The functional analogy is at least approximate in the sense that a scimitar is a slashing weapon while the dirk is a short, straight-stabbing dagger. Because the cutting edge of a canine is on the inside of its curvature neither weapon is much like a saber-toothed cat's canine. Conical-toothed cats are not certainly known before the

Hemingfordian and its Eurasian equivalent, the Burdigalian. Scimitar-toothed and dirk-toothed cats both appear in the North American Early Oligocene (Chadronian) and may occur in the Late Eocene of Eurasia. Commonly, both types of saber-toothed cats occur together; and, after the appearance of the conical-toothed cats, it is usual to find all three morphotypes in the same fauna. The fact that they commonly occur together suggests that they had successfully partitioned the resources of their environment.

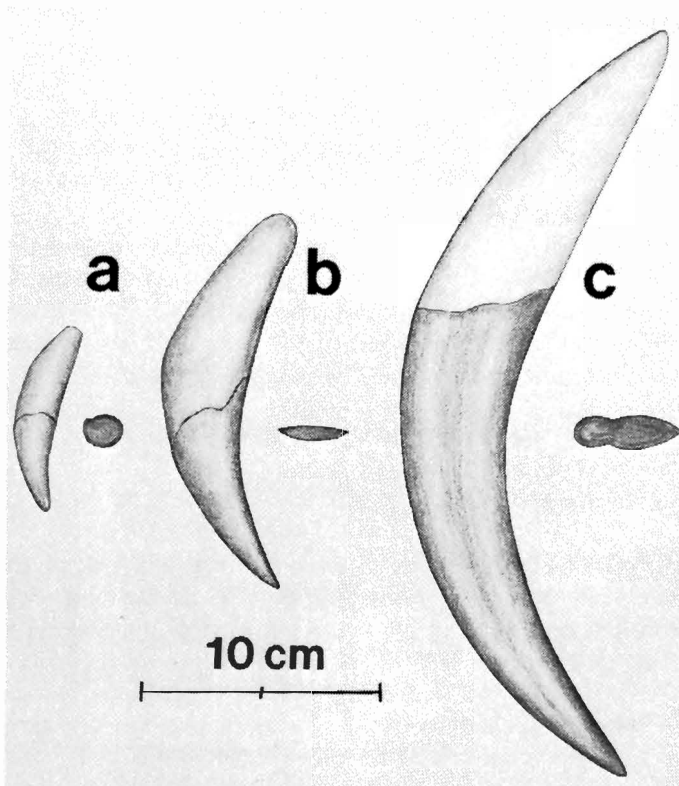


FIGURE 1. Labial and cross-sectional views of upper canines. a. Conical-toothed cat, *Panthera leo*. b. Scimitar-toothed cat, *Machairodus coloradensis*. c. Dirk-toothed cat, *Barbourofelis fricki*.

Conical-toothed Cats

Conical-toothed cats stalk their prey until they are able to close with it quickly. Although they may be capable of great speed, they tire quickly and do not pursue their prey as canids do. Leyhausen (1965) has shown that modern cats have two basic modes of killing. One of these is instinctive and involves biting the back of the neck in such a way as to damage the spinal cord. The other involves biting the throat and is learned. The dorsal neck-bite is preferred for smaller prey but against larger prey, the throat-bite is employed.

One may even speculate that the high napes and heavy manes found on necks of many ungulates and the ability of so many forms to lay their horns over the back of the necks might be a response to this type of attack. Both methods may result in a quick kill as the throat-bite severs (or at least obstructs) the larynx, carotid arteries, and jugular veins. Even if these structures are not severed, a firm grip on the throat closes the larynx and carotids resulting in unconsciousness and death.

The upper and lower canines of conical-toothed cats are of about equal size and serve to anchor the cat while the jaws lock onto the neck of the prey. The leopard also uses its forepaws to fasten itself to its victim and bites through the neck from above (Turnbull-Kemp, 1967). It attacks the throat of large animals. Tigers attack from either the side or the rear of their prey, grip it with the forepaws, and bite the throat of large prey or the nape of the neck of small prey (Perry, 1965:188). However, they have difficulty killing the large, native bovids of India; usually they hamstring them and then attack the neck or stomach (Perry, 1965). Tigers are extremely powerful animals; Perry (1965:123) described an instance in which a wounded tigress seized a young working elephant by the base of its trunk and jerked it onto its side. Tigers do not usually prey on elephants; the only reports of successful predation were of very young individuals killed by being bitten through the back of the neck. Small- to medium-sized prey are usually pulled down and then bitten in the neck. Schaller (1972) examined several hundred lion-kills, but found no substantive evidence that lions deliberately broke the necks of their prey. They are, however, often forced to strangle large prey, as are all large cats, by maintaining their grip until the prey strangles, when they fail to get an immediate kill with the throat-bite. Both lions and tigers keep their hind feet on the ground when attacking prey and do not spring onto the back of the prey animal as is sometimes depicted. This gives them more control than they would otherwise have. Clearly modern felids are not well-adapted to take prey with very large, massive necks, and these prey (elephants, rhinoceroses, and some large bovids) are presently almost free of felid predation.

Conical-toothed cats are remarkably homogeneous in osteological characters, a fact that has been the bane of students of their paleontology and systematics. All have posteriorly recurved, conical canines that have lateral grooves and two ridges that meet to form a lateral triangle and which are not serrated. The upper and lower canines are about equal in size, and the upper canines fit behind the lowers. The incisors are small, spatulate (usually with three cusps), and arranged in a straight line. The premolars, P^{3-4} and P_{2-4} are always large and with multiple roots. The P_4 may not overlap the upper carnassial (P^4). The lower carnassial (M_1) has a deep, narrow carnassial notch. The upper carnassial nearly always has a large, anterior protocone (except in *Acinonyx*). The face may

be short as in *Acinonyx* or long as in *Panthera leo*. The occiput is inclined posteriorly to the upper tooth row, the paramastoids and the paraoccipitals are small and separate, and the auditory bullae are large and inflated. The upper carnassial is always ventral to the glenoid fossa. The very small felids sometimes have a complete postorbital bar, but the orbit is never walled posteriorly. The limbs are variable in length ranging from the relatively short, robust limbs of the jaguar, *Panthera onca*, to the highly elongated limbs of the cheetah, *Acinonyx jubatus*. Except for *Acinonyx*, which has apparently secondarily lost them, all conical-tooth cats have retractile claws. They are all digitigrade, but a few, like the ocelot, have remarkable powers of flexion of their feet.

Saber-toothed Cats

Most of the derived features found in the skulls of saber-toothed cats are related to functional problems caused by the elongated upper canines, and they become progressively more specialized as the canines become longer. The maximum possible gape in conical-toothed felids is about 65° for *Panthera leo*; in *Smilodon* the gape is increased to about 100° (Kurtén, 1952), and *Barbourofelis fricki* manages something more than 115° .

These very large gapes subject the temporal muscles to considerable stretching. I interpret the reduction of the coronoid process (Fig. 2) as a response to this stretching. A small coronoid would reduce the angular distance the insertion area must travel, and is not an indication of weak musculature as Kurtén (1952) has suggested. The temporal muscles were probably strong as their origins are very large and the insertions may have been tendinous. The insertions of all muscles which elevate the mandible are more posterior than in conical-toothed cats. This results in a loss of mechanical advantage but permits a greater range of movement of the mandible and causes less stretching of the muscles involved.

The loss of mechanical advantage is partially compensated for by moving the carnassials posteriorly and by a relative increase in size of the muscles involved (as indicated by the size of their origins and insertions). The glenoid fossa is lowered in dirk-toothed cats until it is on the same level as the cutting edge of the upper carnassial. According to Kurtén (1952:46) this, and the elevation of the occipital region, provides a more vertical and hence more effective force upon the short coronoid process. It would also move the lower canine more ventrally and less posteriorly for a given angle of rotation. A similar adaptation has been described for peccaries (Herring, 1972). As the jaw is rotated posteriorly the angle strikes the posterior surface of the postglenoid process. Matthew (1910) suggested that the angle of the jaw is reduced and twisted outward in saber-toothed cats to prevent this from happening before an adequate gape is achieved (see Fig. 2).

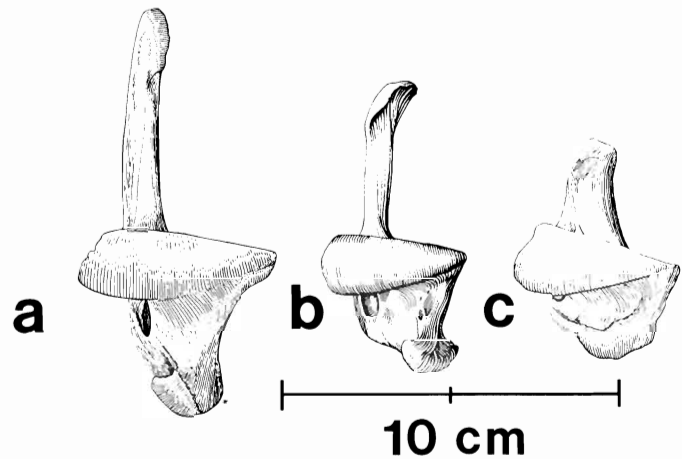


FIGURE 2. Posterior views of rami. a. Conical-toothed cat, *Panthera leo*. b. Scimitar-toothed cat, *Machairodus coloradensis*. c. Dirk-toothed cat, *Barbourofelis fricki*.

The idea that saber-toothed cats had a weak bite and did not use their carnassials very much seems to be poorly founded when one considers that the most extreme examples of carnassialization known in carnivores occur within this group. The movement of the carnassial posteriorly towards the fulcrum is accompanied by reduction of the anterior premolars until in *Barbourofelis* the P^3 is a small, single-rooted, peglike tooth while the upper carnassial is enormously enlarged (more than 6 cm long). In the lower jaw the P_3 is reduced to a single-rooted tooth while the P_4 tilts posteriorly and overlaps the carnassial (M_1). P_4 and M_1 act as a single tooth when they occlude with the enlarged upper carnassial (Fig. 3). The region where the P_4 overlaps M_1 effectively becomes the carnassial notch in the lower jaw, and dirk-toothed cats are characterized by having shallow carnassial notches on M_1 .

Saber-toothed cats were probably unable to tear flesh directly off the bone, as do other carnivores, because the upper canines would get in the way. I also regard it extremely unlikely that the sabers were employed for cutting out pieces of meat as has been suggested (Kurtén, 1952; Bohlin, 1940). Food must have been taken into the side of the mouth. Perhaps to facilitate this, the upper and lower incisors and the lower canines are prognathous, arranged in a semicircle, sharp pointed, and recurved posteriorly (Fig. 4). They may have been used to pull flesh away from the bone so that it could be put into the side of the mouth. Food might have been taken in directly over the incisors, if a long, protrusible tongue were present; however, it is difficult to see how the carnassials could have come into play with that method. I doubt that either this method or specialized blood-sucking (Merriam and Stock, 1932) were important attributes of food ingestion in saber-toothed cats.

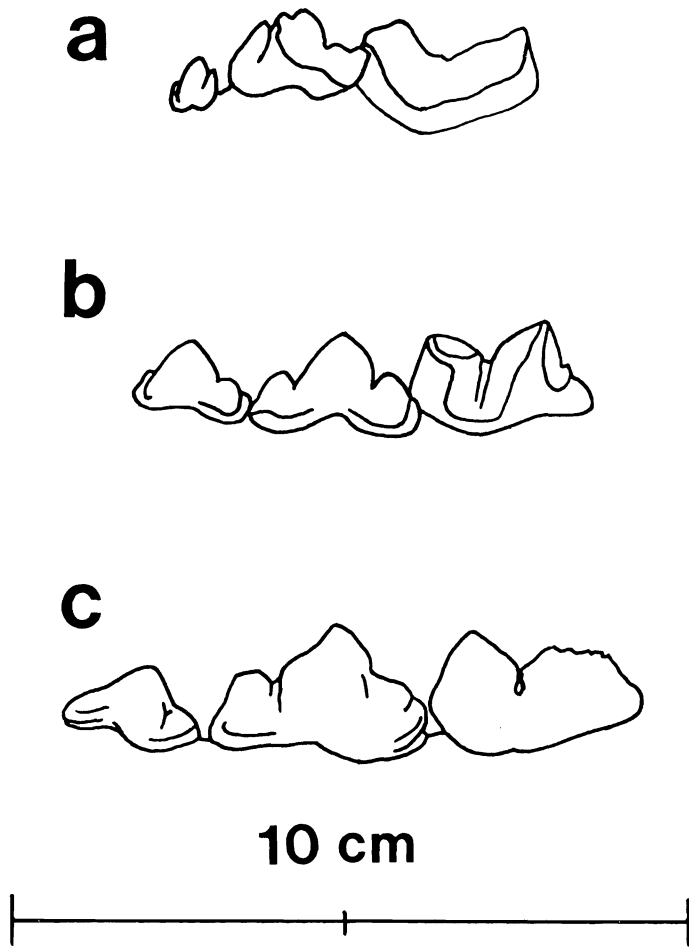


FIGURE 3. Labial views of P_{3-4} . a. Dirk-toothed cat, *Barbourofelis morrisoni*. b. Scimitar-toothed cat, *Machairodus aphanistus* (from Beaumont, 1975). c. Conical-toothed cat, *Panthera atrox* (from Merriam and Stock, 1932).

Carnassials in dirk-toothed cats were kept sharp by quickly wearing away the thin enamel on the upper lingual and lower labial sides of the carnassial, preserving the scissor-like action. This produces a dentine-enamel interface (the sharpest edge possible) that is ever-sharpening. It also promotes rapid wear on the carnassials, and this could have limited the life-span of a dirk-toothed cat.

The upper canines almost certainly lay exposed over the lower lip (the same position occupied by the upper canine in modern felines). Usually the upper canines lay against a dependent flange on the ramus (Fig. 5). This flange may have served to protect the saber; it may also have served to protect the cat from cutting itself with its own saber. The flange, however, creates a problem when the mouth is opened. As Kurtén (1952) pointed out, the flange limits the gape in that it would eventually strike the animal's chest. This problem can be alleviated by elevating the snout. In cats with large flanges, the *rectus capitis* muscles that elevate the snout have very large insertions, and in dirk-toothed cats the dorsal spine of the axis vertebra from which they originate is elongated (Fig. 6).

Elevation of the snout is limited by the contact of the back of the head against the neck. The amount of rotation possible is increased by elevating the primitively inclined occipital to a perpendicular position as the mandibular flange becomes longer. The occipital condyles also project well back away from the occipital region. Interestingly enough, similar adaptations in the occipital region of the skull and axis vertebra occur in *Spalax*, a fossorial rodent, that "digs" in part by elevating its snout.

The digastric muscles, which depress the lower jaw, have large insertions in saber-toothed cats which may help to explain the enlargement of the mastoid processes. Matthew (1910) interpreted the enlargement of these processes in terms

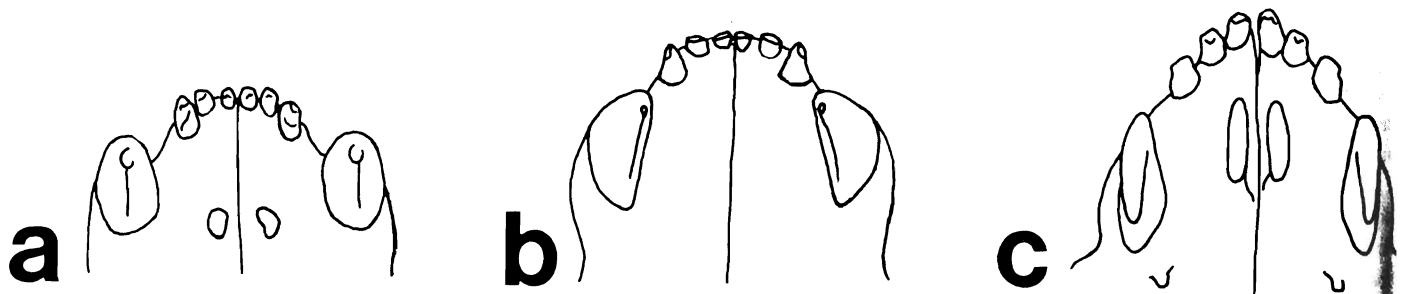


FIGURE 4. Ventral view of premaxillae with I^1-C . a. Conical-toothed cat, *Panthera atrox*. b. Scimitar-toothed cat, *Nimravus*. c. Dirk-toothed cat, *Barbourofelis morrisoni*.



FIGURE 5. Restoration of the head of *Barbourofelis fricki*.

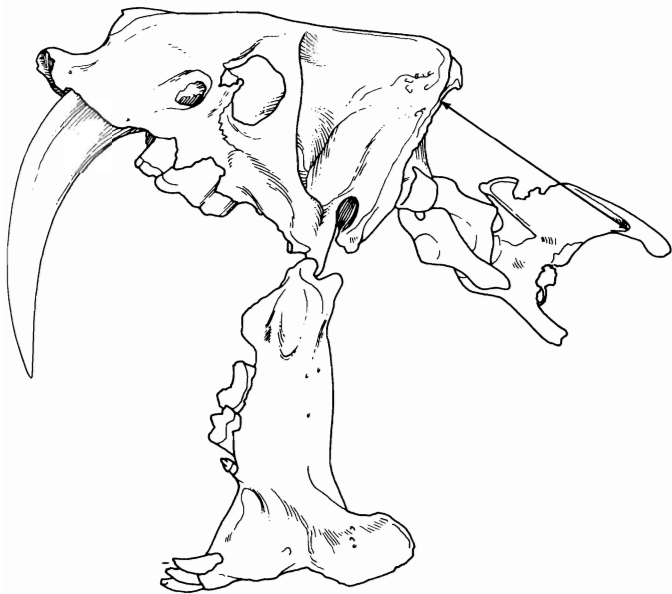


FIGURE 6. Lateral view of the skull and first two cervical vertebrae of *Barbourofelis fricki*. The arrow shows the route of the *rectus capitis* muscles.

of the development of the scalene musculature which depresses the head and inserts, in part, on the mastoid processes. However, the origins of the digastric muscles are also in this region and their large size may reflect the importance of the digastric in holding the lower jaws out of the way when the upper canines were in use.

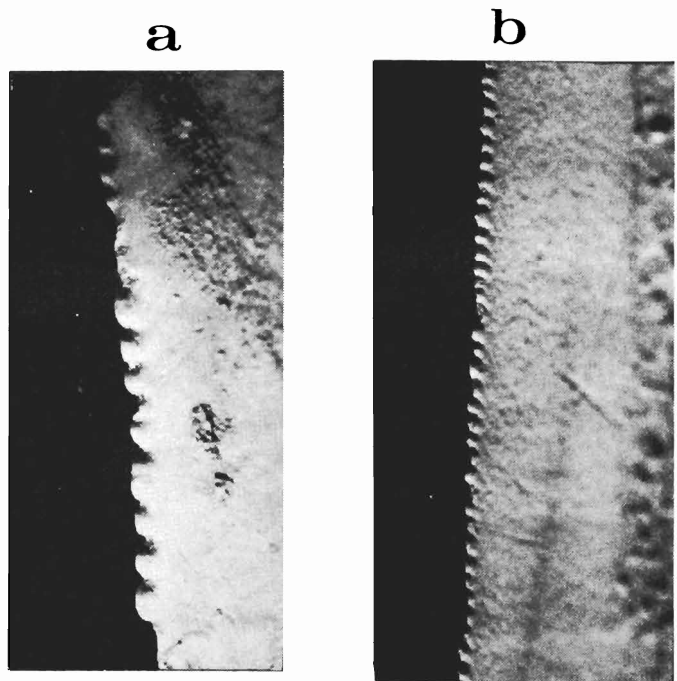


FIGURE 7. Serrations on the upper canines of saber-toothed cats. a. Scimitar-toothed cat, *Machairodus coloradensis*. b. Dirk-toothed cat, *Barbourofelis morrissi*.

The canine is usually slender and was subject to breakage in life, as attested by several broken canines in the collection of *Smilodon* from Rancho La Brea that show wear on the broken surface. In *Barbourofelis*, the canine bears inner and outer grooves that appear to be analogous to the blood grooves on swords and bayonets (Fig. 1). These grooves apparently facilitated penetration and promoted bleeding. Most saber-toothed cats bear serrations on the canines which aid in slicing. These serrations are large and broadly spaced in scimitar-toothed cats, suggesting a ripping effect, while in dirk-toothed cats they tend to be very fine and closely spaced for slicing (Fig. 7).

Simpson (1941) suggested that saber-toothed cats leaped on their prey and used the force of that impact to insert the canines, but I prefer Matthew's (1910) suggestion that the scalene musculature that depresses the head was used in stabbing. This view is supported by the enlargement and posterior extension of the transverse processes of the atlas and axis vertebrae which provide part of the area of insertion for these muscles (Fig. 8). Direct evidence for the strength of the stabbing force can be seen in several fossil skulls which show stab wounds in the forehead made by dirk-toothed cats. These include a skull of *Nimravus* stabbed by *Eusmilus*,

and a dire wolf with part of a *Smilodon* canine still imbedded in its forehead (Miller, 1969). The forehead includes some of the thickest bone in the skull and the fact that it was penetrated in all the above examples indicates that saber-toothed cats could stab with considerable force. However, because of the ever-present risk of breaking their upper canines, it is unlikely that stabbing was normally in an area where there was much risk of hitting bone. This and the probability that the wound would be superficial leaves only two areas available for attack by saber-toothed cats, the throat and the stomach.

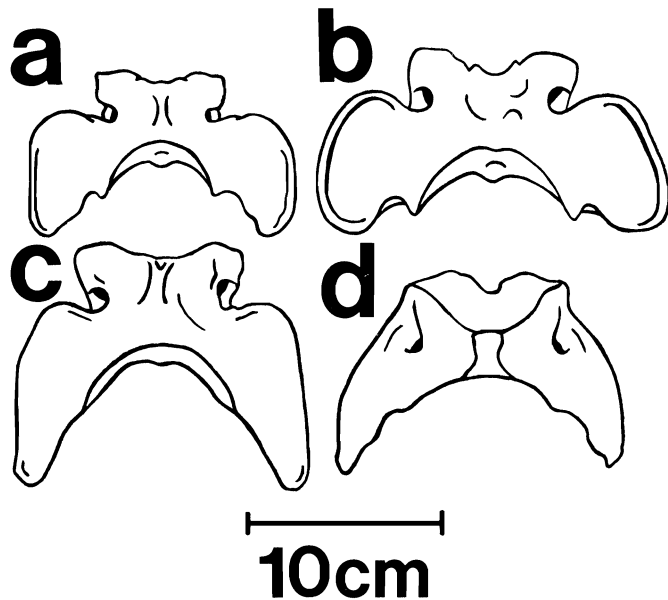


FIGURE 8. Dorsal views of cat atlas vertebrae. a. Scimitar-toothed cat, *Machairodus coloradensis*. b. Conical-toothed cat, *Panthera atrox*. c. Dirk-toothed cat *Smilodon floridanus*. d. Dirk-toothed cat, *Barbourofelis* sp.

The stomach is richly supplied with blood vessels and a long, tearing wound there would eventually result in exsanguination. However, unless the victim went into total shock, death would not be immediate and the prey might attempt escape. Pursuit of prey, even though wounded, would be unlikely by the short-legged, dirk-toothed cats. Lastly, the stomach is also defensible by the head in most potential prey and thus would be a higher risk area than the throat. Moreover, the curvature represented by the stomach area of a large ungulate would have too great a circumference for a dirk-toothed cat to get into its mouth so that it could stab effectively. In other words, I regard it extremely unlikely that dirk-toothed cats keyed on the stomach as an area of attack, but long-legged, scimitar-toothed cats might have attacked the stomach and then pursued the wounded prey.

This leaves the throat as the more likely target of attack especially for dirk-tooths. The saber-tooth adaptation may thus be viewed as an extension of the throat-bite, which permits the killing of an animal with a large neck. I suggest that saber-toothed cats would grasp prey in the manner described by Kurtén (1952) for bears attacking cattle; one paw thrown over the prey's shoulder and the other controlling the head. Probably the prey's head would be pushed to one side, contracting the neck and bringing the carotid artery and jugular vein to the surface. Both vessels are superficial but ventrally situated. It would be difficult and dangerous for a cat to stab the ventral surface of the throat from below, but a stab into the side of the neck would bring the canines down through the superficial musculature. Their recurvature would then bring the edge of the canine back under the carotid and jugular, slicing them and resulting in almost instantaneous death. The trachea might also have been cut, but this would not necessarily result in death. The larger the neck diameter of the prey species, the longer the canine of the predator would have to be. Although scimitar-toothed cats may have been more versatile, this mode of attack may have been the only one available to dirk-toothed cats.

The cat's posture in such an attack would put unusual stress on the lumbar vertebrae, and these are more firmly interlocked in the dirk-toothed felids, *Hoplophoneus*, *Barbourofelis*, and *Smilodon*. All dirk-toothed cats for which skeletons are known have the distal segments of the legs shortened (Fig. 9), and the feet tend to approach a plantigrade condition [according to Hough (1950), plantigrade in *Hoplophoneus*]. The muscle attachments tend to be huge, and the limb bones are very massive. The whole skeleton resembles that of a badger or a wolverine rather than that of a lion or tiger. This suggests an extremely powerful animal that was not equipped for pursuit. Almost certainly, dirk-toothed cats ambushed their victims from concealment. This may also be reflected in the size of their brains, which are among the smallest in proportion to body size of any post-Eocene carnivore. It is likely that large brains of canids and modern large felids evolved partially in response to pursuit of prey in open country, while animals that ambush their prey may retain smaller brains.

Scimitar-toothed cats have specialized in the opposite direction from dirk-toothed cats and generally have longer legs than are found in conical-toothed cats. This suggests that they were more adapted for open country and active pursuit of their prey. Cats in general are not animals of totally open country; that adaptive zone has been filled by the highly cursorial canids. Felines are also generally not arboreal as are many of the mustelids and viverrids. No mustelid or viverrid is really cursorial, and no canid is arboreal. Cats may combine some of both, and it may be areas where trees and open areas mix that are the real adaptive areas of the Felidae.

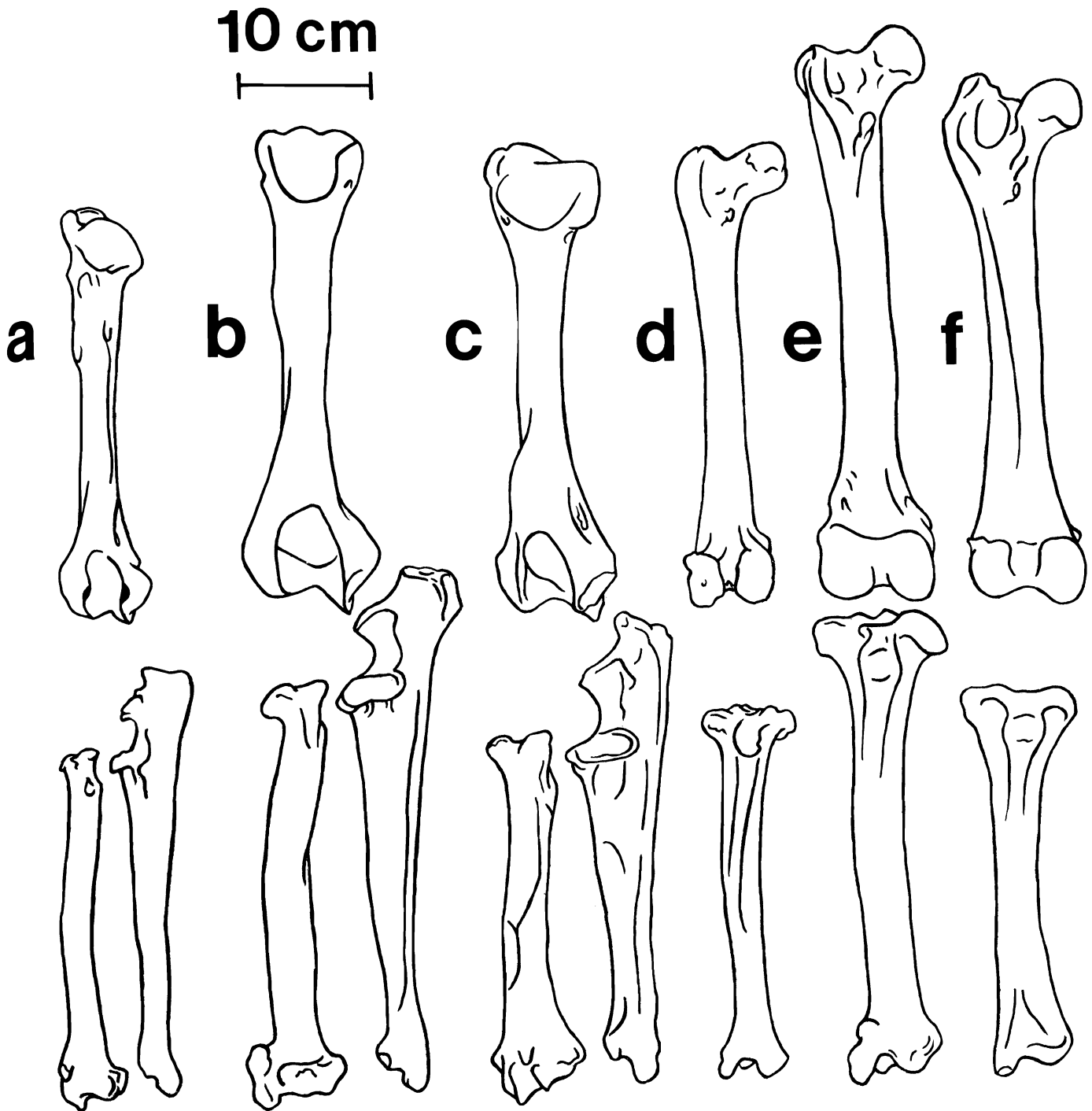


FIGURE 9. a-c. Bones of the front limb (humerus, radius, and ulna). d-f. Bones of the hind limb (femur and tibia). a and d, Scimitar-toothed cat, *Machairodus coloradensis* (from Dalquest, 1969); b and e, conical-toothed cat, *Panthera atrox*; c and f, dirk-toothed cat, *Smilodon floridanus* (b, c, e, f, from Merriam and Stock, 1932).

STRATIGRAPHIC DISTRIBUTIONS

The earliest known cats are from the Late Eocene or Early Oligocene of Eurasia and the Early Oligocene of North America. They appeared suddenly with most of their basic adaptations (retractile claws, sectorial carnassials, reduction of posterior molars, etc.) already well-developed. This fact makes it very difficult to relate them to the other Carnivora, and in fact the time of their separation from other carnivores is so remote that a separate miacid ancestor is possible. These earliest cats belong to the extinct family Nimravidae. They all have incomplete auditory bullae and long saber-teeth. In North America they divide into scimitar-toothed forms of the genus *Dinictis* with small paramastoid processes, small dependent flanges on the ramus, and moderately long limbs, and dirk-toothed cats belonging to *Hoplophoneus* and "*Eusmilus*" which have large paramastoid processes, large dependent flanges on the ramus, and short limbs. The diversity of these cats is fairly great, and cats probably represent a greater proportion of the large carnivore adaptive zone at this time than later when canids become more numerous.

In the Late Oligocene a miniature dirk-tooth cat developed which Macdonald (1963) named *Ekgmoiteptecela* but which is a "true" *Eusmilus*. This is a separate radiation of dirk-toothed cats that ranged in size from a large domestic cat to a small bobcat. In North America they are known from the Orellan through the Arikareean, and are known from similar-aged strata in Eurasia. Cats usually referred to *Eusmilus* in North America, "*Eusmilus*" *dakotensis*, are larger and more closely related to *Hoplophoneus*. They became extinct at the end of the Whitneyan.

The scimitar-toothed cat, *Dinictis*, appears to give rise to *Nimravus* in the Whitneyan as well as to *Pogonodon*, a scimitar-toothed cat with a distinct dependent flange on the ramus. *Nimravus* occurs in both North America and Eurasia. *Nimravus* is a scimitar-toothed cat that appears to have given rise to *Dinaelurus* as a side branch in the Arikareean in North America. *Dinaelurus* is a conical-toothed cat with relatively small canines and incisors. The skull is domed and the internal nares are enlarged which suggest cheetahlike adaptations although the limbs are presently unknown.

Nimravus, *Pogonodon*, *Dinaelurus*, and *Eusmilus* became extinct in North America at the end of the Arikareean. Cats are unknown from early and middle Hemingfordian deposits in North America. During this time a considerable amount of feloid evolution took place in Eurasia, including the development of the Barbourofelini, a lineage of dirk-toothed cats with grooved upper canines and enlarged origins for the superficial masseter muscles. The earliest known member of this line is *Sansanosmilus*. In the Clarendonian this lineage reached North America and culminated later in the most extreme case of

dirk-tooth specialization known, *Barbourofelis fricki* (Fig. 10). Among its more bizarre adaptations was the development of a postorbital bar walling off the back of the orbit in the North American species (Schultz *et al.*, 1970). This feature is not presently known outside of North America, possibly due to the lack of complete skulls, but the Barbourofelini are known from Europe, Asia, and possibly Africa.

The Barbourofelini give us our best insight into evolution in a dirk-tooth lineage. *Sansanosmilus* was a relatively robust cat about the size of a small puma. It did not have a postorbital bar; P³ and P₄ are large and double rooted; the auditory bullae are large and complete; the paraoccipital and paramastoid processes are small; the upper molar row is well below the glenoid fossa; the occipital region is inclined; the dependent flange is only moderately developed on the ramus; and the limbs are shortened as in a jaguar (Ginsburg, 1961). We are able to record a continuous but rapid change of these features to the full dirk-toothed condition. Coupled with these morphological changes is a remarkably rapid increase in size, which suggests a corresponding increase in prey size.

The Felidae are characterized by the presence of a septum bullae in the auditory bullae and the presence of a cruciate sulcus on the brain. *Pseudaelurus* is the basal stock, and the group quickly diversified into a series of conical and scimitar-toothed felids ranging in size from that of a domestic cat ("*Felis*" *stouti*) to the size of a small jaguar (*Pseudaelurus*). Most of the larger forms are scimitar-toothed cats although their canines may lack serrations. However, the North American Hemphillian form, *Nimravides*, has coarse posterior serrations on the upper canines. *Nimravides* is very long-limbed and about the size of an African lion (*Panthera leo*). In Eurasia there is a similar scimitar-toothed felid, *Dinofelis*, which totally lacks serrations. *Dinofelis* extends into the Villafranchian of Europe, Asia, and Africa and the Blancan of North America (Kurtén, 1972; Hemmer, 1965). *Nimravides* does not extend into the Blancan. Another group of scimitar-toothed cats is represented by *Machairodus*, which first appears in North America in the Hemphillian or Late Clarendonian. It also occurs in deposits of the same age in Europe, Asia, and Africa. It is a large slender-limbed cat (Fig. 11) with anterior and posterior serrations on both the upper and lower canines. Martin and Schultz (1975) showed that in North America it has been confused with *Nimravides*.

The Barbourofelini became extinct throughout the world at the end of the Kimballian. They were replaced by a new dirk-toothed lineage represented by *Megantereon megantereon* in the Villafranchian of Eurasia and *Megantereon hesperus* in the Blancan of North America (Schultz and Martin, 1970). *Megantereon* began as a short-faced, saber-toothed cat about the size of a mountain lion. It has shortened limbs, a moderate flange on the ramus, and a nearly perpendicular occipital

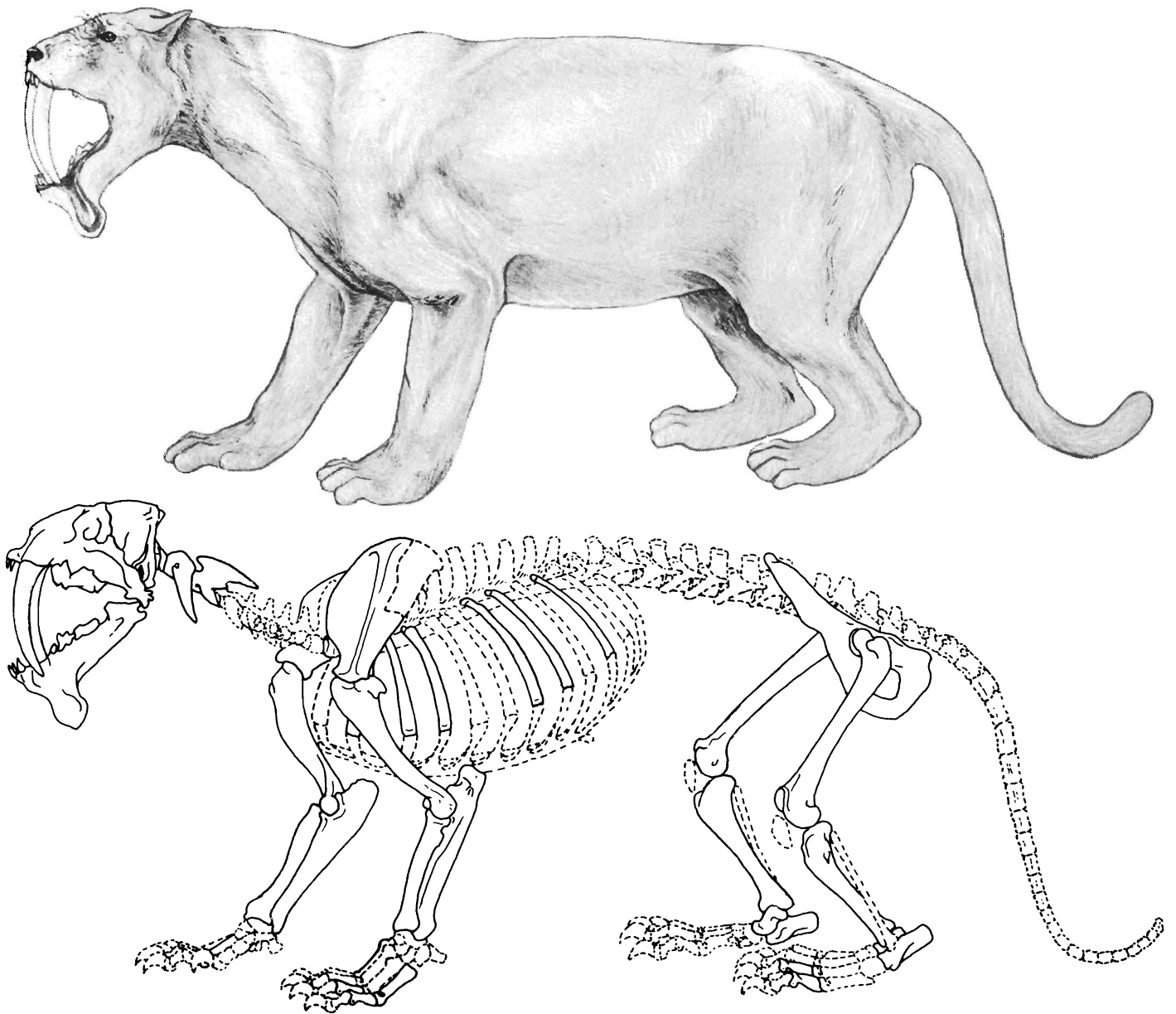


FIGURE 10. Life and skeletal restorations of *Barbuoufelis fricki*.

region. The upper canines are unserrated, and the P_3 is large and double-rooted. The brain has a cruciate sulcus, and the auditory bullae are divided.

In North America we have a well-documented lineage leading from *Meganterion hesperus* through *M. gracilus* and *Smilodon fatalis* to *S. floridanus*. I refer the species *M. gracilus* to *Megantereon* rather than to *Smilodon*, where it is usually placed because of the lack of serrations on the upper canines, the relatively large dependent flange on the ramus, and the large P_3 which is double-rooted in some cases. In this lineage we see the development of most of the progressive dirk-toothed trends, but the dependent flange on the ramus is reduced

rather than enlarged, and the occipital region becomes more inclined at the same time. This reduction of the flange on the ramus is hard to explain except that it may have permitted *Smilodon* to attack with its mouth closed. *Megantereon* occurs in Eurasia, Africa, and North America, but *Smilodon* is known only from North and South America.

Along with *Megantereon*, we find a long-legged, short-tailed, scimitar-toothed cat (*Homotherium*) occurring in Eurasia, Africa, and North America. The North American form has been described as *Ischyrosmilus*, and I have generally supported the separation of the two genera (Schultz and Martin, 1970; Martin and Schultz, 1975), but I now regard

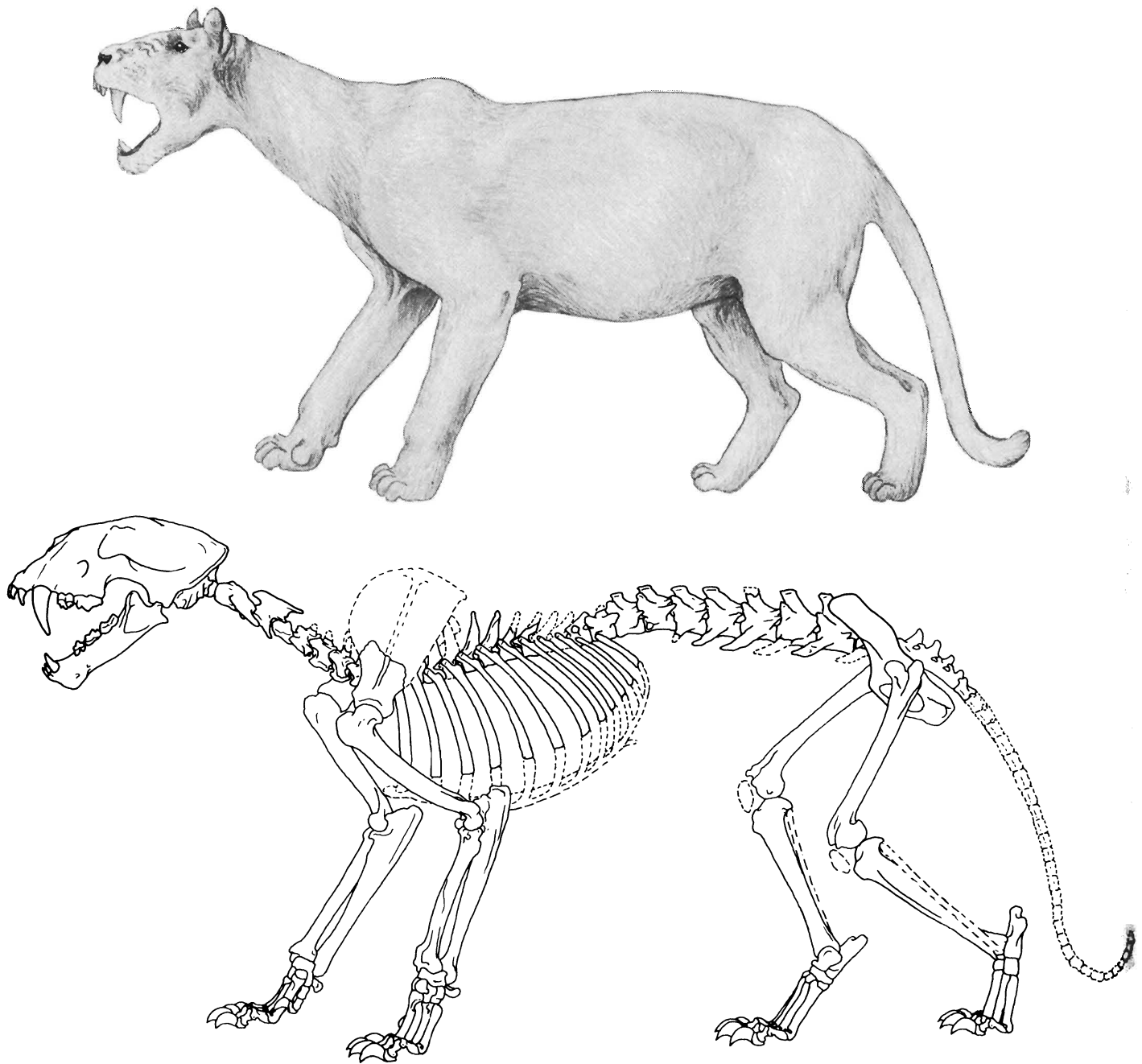


FIGURE 11. Life and skeletal restorations of *Machairodus coloradensis*.

them as congeneric. A related genus, *Dinobastis*, has a cruciate sulcus on the brain (based on the McPherson Equus Beds specimens of *Dinobastis*), and I regard *Homotherium* and *Dinobastis* as felids. Both have moderately developed dependent flanges on the rami, a small single-rooted P_3 , and large, coarsely serrated upper canines. *Dinobastis* has an unusually deep masseteric fossa on the ramus. Also occurring in the Villa-

franchian of Eurasia and Africa and the Blancan of North America is the scimitar-toothed cat, *Dinofelis*. *Dinofelis* is more feline in its proportions than *Homotherium*, and has unserrated upper canines.

Conical-toothed cats became firmly established in the Villafranchian and the Blancan with *Puma* and *Lynx* apparently

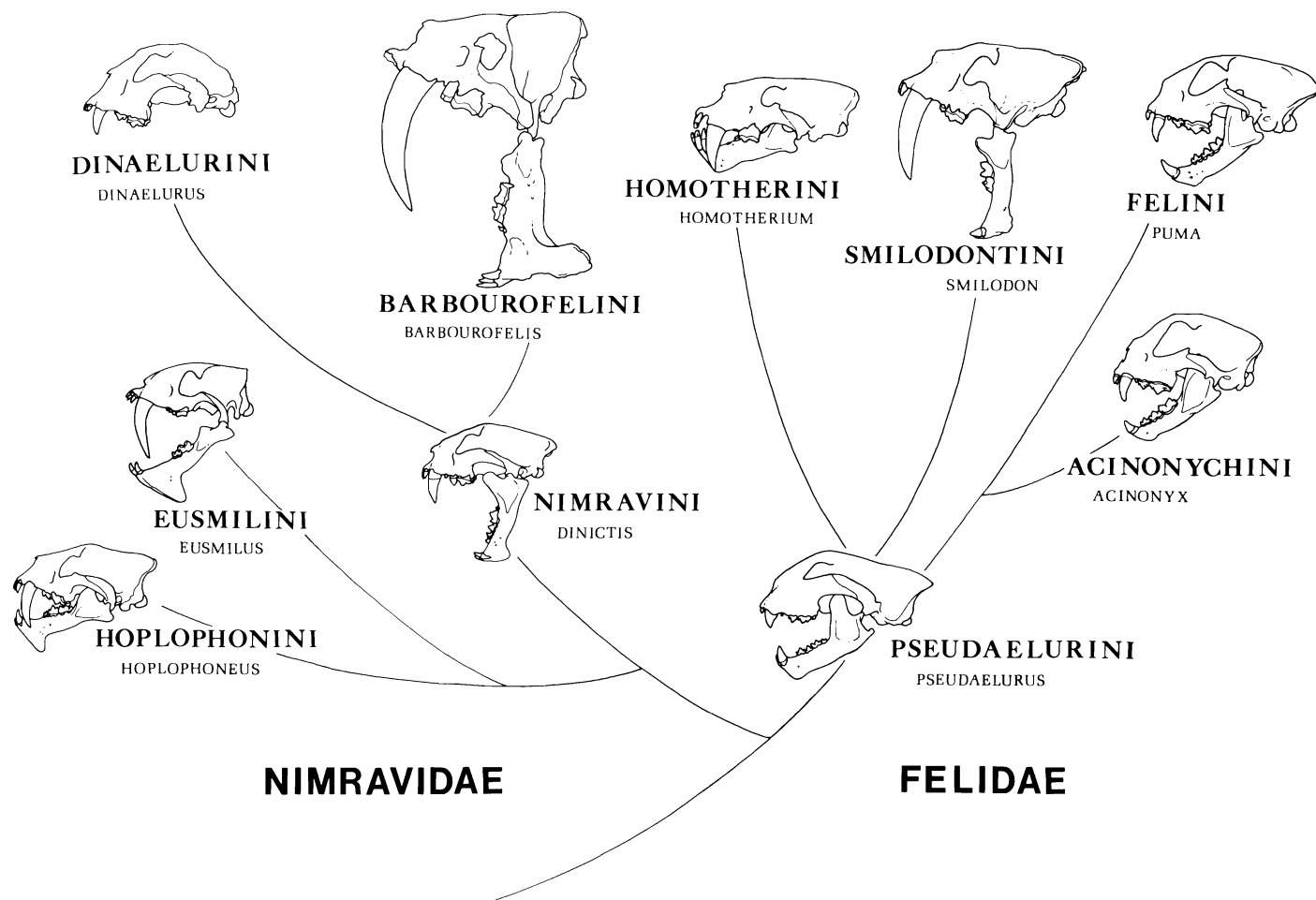


FIGURE 12. Suggested phylogeny of the Feloidae.

originating in North America and *Panthera* originating in Eurasia. The oldest known *Lynx* is *Lynx rexroadensis*, and a similar form must have entered Europe in the Villafranchian where we find *Lynx issiodorensis*. *Puma* remained restricted to North and South America, and in the Irvingtonian, *Panthera* entered North America in the form of *P. atrox* and *P. onca augusta*. Lions (*Panthera leo*, *P. atrox*, and *P. spelaea*) achieved the most extensive range to be occupied by any wild species of cat, occurring in Eurasia, Africa, and North and South America. The earliest cheetahs are in the Villafranchian of Eurasia, but North America apparently had cheetahlke cats (Martin *et al.*, 1977), with "*Felis*" *studer*i in the Blancan and "*F.*" *trumani* in the Late Pleistocene. Leopards (*Panthera*) also have a long history in Africa, first appearing in Villafranchian deposits. The history of the small felids is too complex and there are too few data to make a meaningful story. All of the saber-toothed cats became extinct at the end of the Pleistocene, but the conical-toothed cats, in general, suffered only restrictions of their ranges.

CLASSIFICATION

Definitive classification is not possible with our present knowledge of the fossil cats. Certainly the relationships of the Proailurinae need to be considered (I presently consider the subfamily as *incertae sedis*), and the nearness of the common ancestor of the Nimravidae and the Felidae evaluated. The taxonomic rank of various groupings of felids has varied almost absurdly with the large roaring cats sometimes included in *Felis* and sometimes (Kretzoi, 1929) put in their own subfamily, the Pantherinae. I have tried to keep a more intermediate position using tribes to indicate major adaptive lineages.

The phyletic relationships that I favored in the past followed the interpretations of Matthew (1910). Matthew argued that the Felidae were derived from the ancient saber-toothed cats through *Dinictis* and *Nimravus*. Both of these genera are scimitar-toothed cats in my scheme. Matthew's interpretation has been attacked by numerous authors who feel that

the ancient saber-toothed cats (paleofelids) differ sufficiently from the more modern cats (neofelids) to suggest that the derived characters shared by the two groups could be accounted for almost entirely by parallelism. This argument has been advanced by Beaumont (1961) and Hunt (1971; 1974a, 1974b).

These workers based their conclusions primarily on characters found in the basicranial and auditory regions of the skull. Hunt (1971) suggested that the auditory bulla of the paleofelids differs from that of the neofelids in: the presence of a rostral entotympanic; in the absence of a *septum bullae*; and in the presence of the ectotympanic as the major structural component of the auditory bulla. However, Hunt (1974a) has since demonstrated the presence of a rostral entotympanic containing the internal branch of the carotid in *Felis*, thus invalidating the first two distinctions. The only paleofelids for which complete auditory bullae are known are the Barbourfelini, and Hunt (1974b) suggested that in the Oligocene forms the ventral wall of the bulla was extremely thin and thus always broken. My studies of the auditory regions of *Dinictis*, *Hoplophoneus*, *Nimravus*, *Dinaelurus*, and *Eusmilus* do not support this view. In these forms, the bullae were incomplete with a large entotympanic and a small ectotympanic [contrary to Hunt (1971)]. I have not been able to distinguish a rostral entotympanic unless the single, large entotympanic element is one. The internal branch of the carotid does seem to have followed a shallow groove on its medial side. The ventral wall of the bulla was cartilagenous as in *Daphoenus*. No *septum bullae* occurs in any paleofelid, including *Barbourofelis*. This structure along with the cruciate sulcus on the brain (absent in all paleofelids for which the brain is known) provide shared derived characters to unite the Felidae. Their absence in the paleofelids is due to retention of primitive structures and is not useful in determining the nearness of the common ancestor between the two groups.

Shared derived characters that seem to unite the Feloidae are: the highly sectorial carnassials; retractile claws; loss of M^{2-3} ; and the conformation of the deciduous dentition. The carnassials provide rather weak evidence as this type of carnassial has developed independently in mustelids (*Mustelavus*), viverrids (*Cryptoprocta*), and canids (*Daphoenictis*). Loss of a structure also must be regarded with some suspicion. However, similarity among the deciduous dentitions is suggestive of relationship. The phylogeny I presently favor (Fig. 12) accepts a basic dichotomy between the Nimravidae and the Felidae, but still regards them as "sister groups."

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