

# The Habits and Adaptation of the Oligocene Saber Tooth Carnivore, *Hoplophoneus*

By JEAN HOUGH

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*A study of the anatomy and hunting habits of  
Hoplophoneus, with comparisons to both fossil  
and present-day relatives*



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## CONTENTS

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	Page		Page
Abstract.....	125	The structure of <i>Hoplophoneus</i> —Continued	
Introduction.....	125	Range of variation.....	128
Habits and adaptation of Recent Felidae.....	126	Cranial characters.....	129
Predation.....	126	<i>Hoplophoneus primaevus primaevus</i> Leidy.....	129
<i>Panthera</i> .....	126	<i>Hoplophoneus primaevus latidens</i> Thorpe.....	130
<i>Felis</i> .....	126	Dentition.....	130
<i>Acinonyx</i> .....	127	Axial skeleton.....	130
Cranial variation.....	127	Appendicular skeleton.....	131
Dentition.....	127	Mode of life of <i>Hoplophoneus</i> .....	132
Structure of the limbs.....	128	Comparison of <i>Smilodon</i> and <i>Hoplophoneus</i> .....	133
The structure of <i>Hoplophoneus</i> .....	128	References cited.....	135
General characters.....	128		

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## ILLUSTRATIONS

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	Page
PLATES 26-28. Views of <i>Hoplophoneus mentalis</i> Sinclair.....	Fol. 137
29. Fore limb bones of <i>Hoplophoneus primaevus latidens</i> Thorpe.....	Fol. 137
30. Hind limb bones of <i>Hoplophoneus primaevus latidens</i> Thorpe.....	Fol. 137
31. Vertebral column of <i>Hoplophoneus primaevus latidens</i> Thorpe.....	Fol. 137

# THE HABITS AND ADAPTATION OF THE OLIGOCENE SABER TOOTH CARNIVORE, *HOPLOPHONEUS*

By JEAN HOUGH

## ABSTRACT

Most restorations of the Oligocene saber tooth carnivore, *Hoplophoneus*, depict it as very feline in pose and appearance. A detailed comparative study of the osteology seems to show that this is erroneous. Actually, the head is large, the neck long and straight, the legs short. The radius, which is a short stout bone, articulates with the cuneiform as well as with the scapholunar. The shafts of the radius and ulna are thus held in an oblique position, with the elbow joint everted and the foot turned inward. The manus is pentadactyl, with divergent digits, and a *semiopposable pollex*.

The hindquarters slope abruptly, bringing the hind limbs forward under the body in a slinking pose. The tibia, which is the longest bone in the body of *Felis*, is shorter than the femur in *Hoplophoneus*. The knee joint, like the elbow, is everted; the hind foot, like the forefoot, plantigrade.

The dentition is characterized by a reduction of the premolars and molars and carnassialization of the remaining cheek teeth as extreme as that of *Felis*. The upper canines are elongate sabers, the lower canines short and incisorlike. The lower jaw is very deep vertically, especially at the symphysis. A lobelike flange from the external, anterior border forms a sheath for the upper canine.

The contours of the skull resemble those of *Panthera*. This combination of characters—pentadactyl scansorial feet with an extreme carnivorous dentition—is unknown among modern carnivores and consequently difficult to interpret. It would seem, however, that the actual mode of attack, dropping on the back of prey, or using the long canines to pierce the throat in a head-on approach was similar to that of *Felis* but that the more highly developed and typical feline habits, such as the stalk in ambush, and running leap at the victim so highly developed in *Panthera* had not yet evolved.

Although the saber teeth in all genera seem to have been used as stabbing weapons, the mode of their use must have differed widely. Especially, the habits and mode of attack of the gigantic *Smilodon* of the Rancho la Brea tar pits must have differed from the Oligocene hoplophoneids, most of which were not much larger than a big lynx. The sabers in *Smilodon* are extremely large in proportion to the skull size (index canine diameter: prothion-basion length is 14.4:15.7), heavy and recurved. Evidently, the growth period was long. There is evidence that breakage was frequent. The period when the canines were at their maximum efficiency was thus apparently very short. Even with all of the mechanical adaptations in the structure of the skull which made possible the use of such huge teeth, they must have been awkward weapons in an ordinary attack. It is suggested, therefore, that they may have been used primarily in sexual combat between males, and as a means of obtaining food only in unusual circumstances. One such situation existed at Rancho la Brea, where large numbers of the bigger herbivores were rendered helpless by miring in the asphalt. Under these conditions, with the victim unable to run away or put up a very violent struggle, a strike with the huge, unwieldy canines could be made at leisure and there

would be no need for a quick withdrawal—difficult because of the length and recurvature of the teeth. It may have been that kills were made by animals with mature, fully effective canines and the food provided used by the young and aged individuals.

The role of *Smilodon* in the Pleistocene fauna was quite different from that of *Hoplophoneus* in the Oligocene fauna. The former had to compete with *Panthera atrox*, the lynx, and the jaguar, all much more intelligent and highly evolved animals. Although the machairodont still held its own in numbers, it apparently did so only by an excessive specialization.

There were no true cats, dogs, or modern carnivores of any sort in the Oligocene. *Hoplophoneus* had no competitors higher in the evolutionary scale than itself. Stupid, slow, and awkward though it may have been in comparison with modern cats, it was nevertheless the most active flesh-eater of the time.

## INTRODUCTION

The various genera of Oligocene carnivores are near enough to modern forms, in an evolutionary sense, that the structure of the dentition, of the basicranium, or of the limbs, in almost every instance allies them with one or another of the present day families. The combinations in which these characters occur are different in all the genera. In *Daphoenus* the auditory region is extremely like that of the viverrid, *Nandinia*—the dentition and limb structure a mixture of canine and ursine characters. *Zodiolestes* has a procyonid type of auditory region although the dentition is mustelid. In *Phlaocyon*, on the other hand, the dentition is procyonid and the auditory and limb structure are canid. The saber tooth carnivores usually included in the Felidae are no exception to this general rule. *Hoplophoneus*, *Eusmilis* and *Dinictis* have a type of dentition which is feline, both in the reduction in the number of teeth and in the extreme carnassialization. The elongation of the upper canines is also, in a sense, an exaggeration of a feline specialization, because in all of the family the upper canines are relatively longer and stouter than the lower. However, in all Oligocene forms, especially in *Hoplophoneus*, the details of the dentition are quite dissimilar to those of true felids. The other adaptive characters (shape and proportion of the skull, relative size of the head and body, limb structure and foot structure) are even more widely divergent.

These differences are obscured by the common assumption that the Oligocene saber tooth carnivores are "cats," primitive to be sure, but nevertheless true felids on their way to evolving into the modern forms. This

is wholly untrue of *Hoplophoneus*. In fact, the term "saber tooth tiger" applied to this genus is such an extreme misnomer that its use ought to be discouraged even for purposes of popular exposition. *Dinictis* is perhaps somewhat more "feline" but still far from typical, its habits and appearance more nearly approximating those of the cheetah, as Matthew (1910) suggested. Even so, the resemblance is analogous only, with no close correspondence in detail of the skull or limbs.

In line with the general notion that *Hoplophoneus* was very catlike, skeletons are usually mounted with the feet in a digitigrade position and the back and neck arched in as feline a fashion as possible. A complete skeleton of the oldest known machairodont, *Hoplophoneus mentalis* Sinclair, however, which has been skillfully mounted by John Clark and is now in the University of Colorado Museum at Boulder (pls. 26, 27, 28) was found articulated. This skeleton, together with another virtually complete one of the same species in the museum of the South Dakota School of Mines, and several articulated skeletons of the Brule subspecies, *H. primaevus latidens* Thorpe, in the United States National Museum show that, in fact, the feet were plantigrade and the pose of the limbs very different from that of the modern Felidae. As no detailed comparative study of the limb structure of the various species has been published, and there is abundant material for such a study, a more complete description seems desirable. To emphasize the divergence in adaptation of *Hoplophoneus* from *Felis* or *Panthera*, descriptions of the habits of the modern genera are included.

#### HABITS AND ADAPTATION OF RECENT FELIDAE

The Felidae were designated by Cuvier as the exemplar or archetype of the Carnivora, a category which included the Carnivora of modern classification and also carnivorous marsupials. The idea of an archetype in the way the French naturalist used the term is, of course, outmoded, but in a broader sense the cats can be said to be the ideal type of carnivorous mammal and to exemplify that habit in one of its most extreme adaptations. The "great" cats are the largest and most powerful predatory animals (with the possible exception of the bears); all of the Felidae are more exclusively flesh eating than the Canidae; of all of the Carnivora their dentition is the most uniformly specialized for that mode of life. To use the adaptive peak imagery, the Felidae, like the Canidae, may be said to be grouped around one major adaptive peak, the characteristics of which are determined by the method of securing prey.

All the Felidae (except the cheetah) use essentially the same method of securing prey—from the lion to the lynx they capture their victims by a silent, gliding stalk

from ambush followed by a swift dash and attack. The details vary from individual to individual and species to species, according to the necessities of the environment and the relative sizes of predator and prey.

*Panthera*.—The large cats, especially the lion and the tiger, usually attack by leaping from the ground onto the back of the animal which is then gored through the throat or nape by the powerful canines. With these teeth embedded in the flesh the neck is broken by a wrenching twist and the victim brought to the ground, in part by its own struggles and in part by the weight of the attacker. Both lions and tigers prey on very large animals such as bison, buffalo, and even (Pocock, Peacock, Blanford, and others) adult cow elephants, as well as the less powerful artiodactyla such as deer, antelope, and wild pigs. With the largest animals hamstringing may be resorted to and the victim felled before the kill is made. The hunt may be social—that is, participated in by two or more individuals—two males, a male and female during the breeding season, or (most commonly) a female and half-grown cubs.

The smaller species, lacking the size of the lion and the tiger, make the final leap from a rocky ledge or overhanging branch rather than from the ground. Gravity thus adds force to the weight of the cat.

All of the *Panthera* drag their kill to some place of concealment. A deer or antelope provides food for several days, or as long as it is eatable. If the carcass is very large it may feed a whole family. Therefore, size of prey is important not only with regard to ease of attack but also to amount of food furnished. It is difficult for a full-grown lion and impossible for a lioness with cubs to obtain enough small animals for subsistence unless they are very abundant and incapable of defense by flight. The capture of a rabbit requires as much time and almost as much effort as that of a deer. Two rabbits a day are semistarvation diet, and hunting is almost continuous. This is an important point in considering some of the reasons for the extinction of the extraordinarily large Pleistocene felids. The size of predator invariably declines with the size of the prey not only because larger size is not needed but because it is an obstacle in the way of obtaining sufficient food.

*Felis*.—The wild cats included in the genus *Felis* range in size from *Prionailurus* (15 to 18 inches in length) to the puma, which may reach a head-and-body length of 5 feet. Thus, some species of *Felis* are as large as the smaller species of *Panthera*, but most are moderate sized or small. The habits vary not only from species to species but even among races of the same species. Some, such as the marbled cat, are strictly forest-dwelling, where they feed on small mammals such as squirrels and rats, or on pheasant and other birds. Others, such as *Felis chaus*, live in bush jungle and the long-grass reed banks near lakes and

marshes. A few, such as *F. (Otocolobus) manul*, and some species of lynx inhabit rocky districts. All of the environments have in common the presence of some sort of cover. Only the caracal inhabits really open country, in this respect resembling the cheetah but lacking the typical adaptations of that genus.

These cats hunt in much the same way as *Panthera*. There is always the stalk or wait in ambush, the swift dash and attack. If the prey is larger than the predator, as is the case with the larger herbivora, there is a drop from a tree or rocky ledge and in some instances a head-on attack. Against small mammals and birds the kill is made by a "pounce" in which the victim is stunned by a blow from the paw.

*Acinonyx*.—The cheetah or hunting leopard is the only felid that captures its prey by running it down. It inhabits open country—commonly grassy plains near low hills. When the prey is once sighted from behind cover of a rocky ledge the cheetah speeds after it, carrying the pursuit a much greater distance than usual with cats, and making the final attack more in the manner of a dog. The speed is very great. The cheetah is said to be able to cover 100 yards in  $4\frac{1}{2}$  seconds which is "faster than the fastest greyhound and twice the speed of the fastest human sprinter" (Pocock, 1939). Enlarged nasal passages assure sufficient supply of air for this burst of speed but, because there are no physiological modifications for endurance, the maximum speed can be maintained for only a short time. Even in this one "cursorial" cat, therefore, the adaptation is very imperfect in comparison with that of animals in which the habit is really well developed such as the Canidae and swifter ungulates. Nevertheless, the cheetah does represent a felid which has "wandered," so to speak, from the adaptive peak representative of the family and is well on its way to climbing another.

#### CRANIAL VARIATION

In all felids the skull is broader and shorter than that of the Canidae or that of the Viverridae. The facial region is short, with a steep upper profile. Generally, the cranial portion of the skull is also short and highly inflated. There is a strong flexure between the cranial and facial portions, resulting in the very characteristic upper profile. The muzzle is never as long and slender as that of the wolf, and among domestic breeds none show anything like the extremes of the Canidae. Nevertheless, there is some variation. The species of *Panthera* have the longer, lower cranium, the longer muzzle, and the less abrupt cranial flexure, whereas the smaller species tend to have a shorter muzzle, broader palate, and more rounded cranium, and more sharply domed profile. These features are apparently intimately associated with the habits described in the preceding section. A domed skull and high orbits enable the animal

to sight prey while keeping the entire body and most of the head concealed, and are most highly developed in forms such as *Acinonyx* that habitually peers over rocks while waiting in ambush for its victims.

An exaggeration of this type of development is found in Pallas' cat (*Otocolobus manul*). The forehead in this species is exceptionally flat and the eyes are placed wide apart and practically at the top of the skull. This cat habitually lies stretched out on a large branch with the head resting on the forepaws and is virtually invisible.

Among the smaller cats, *Felis yagouaroundi*, an aberrant species not much larger than a domestic cat, and a native of South America and Mexico, is at the opposite extreme. The habits of this animal resemble those of a marten, and the head is elongate with almost musteline proportions, and very large in contrast to the short limbs.

#### DENTITION

The dentition of the Felidae represents the extreme of carnassialization and is structurally adapted in a most efficient way for their particular mode of attack. With one exception, the typical pattern prevails to some degree throughout the family, even in the smaller species where the canines are reduced in size and can be no longer used as stabbing weapons. In all cats, but especially in the larger species, the upper canines are longer than the lower, stout, oval in cross section, and taper abruptly to a point. The edges of the incisors form a straight line at the extreme anterior margin of the jaw. The alveolar margin of these teeth is below the level of that of the canine. The forward position of the incisors leaves a diastema in front of the canine, the loss of the first premolar and reduction of the second leaves a similar post-canine space. From this point the alveolar margin of the upper teeth curves downward. The edges of the lower incisors are raised above the level of the cheek teeth and the alveolar margin of the lower dentition curves upward. The carnassials are high, trenchant teeth placed at the angle of the jaw.  $M^1$  is reduced to a nonfunctional nubbin,  $M^2$  is absent. The only point of contact between the upper and lower teeth is thus between the carnassials at the extreme posterior of the jaw and the incisors and canines at the extreme anterior point. When the jaws are closed a wide gape remains between them. This gape together with the post-canine space is designed to give the greatest possible penetration and grasping power to the canines. It is present in all living felids except the cheetah but is especially well developed in *Panthera*.

This specialization enables these cats, first, to pierce the skin of the large herbivores on which they feed, and second, to keep the teeth firmly embedded in the flesh during the neck-breaking process—no small feat considered that the victim is not standing passively waiting to be killed but is struggling desperately with all weapons it possesses: hoofs, horns, and muscular strength.

In many of the smaller felines the canines are less well-developed, and the post-canine space is correspondingly reduced. Commonly, this is accompanied by a shortening of the muzzle. In the lynx, both the upper and the lower canines are very long, and the post-canine space is large. However, the alveolar margin of the upper and lower dentition is nearly straight, and there is little of the characteristic gape of the *Panthera*.

In the cheetah, the canines are little longer than is common in most fissipedes, the tooth row is crowded and the post-canine space entirely lost. As there is little gape between the jaws the occlusion of the teeth resembles that of the Canidae.

In one species of *Panthera*, the clouded leopard, the upper canines reach a length three times the diameter of the base, which is the same proportion as in some dinictids. This is the only example of anything resembling "saber" teeth in modern genera.

The lower jaw of the clouded leopard also has points of resemblance with that of the machairodonts. The chin is described as "pronounced, flattish and nearly vertical in front, and the alveolus of the upper incisors is raised well above the socket of the canine so that when the mouth is closed the upper jaw is uptilted" (Pocock, 1939, p. 247). As will be seen, this is very similar to the structure of the lower jaw in *Hoplophoneus*.

#### STRUCTURE OF THE LIMBS

The limbs of the Felidae are less specialized than the dentition in contrast to those of some other carnivore families. They are sometimes described as "primitive." If by primitive is meant generalized, this is not true. Living cats, with the exception of the cheetah, do not have the cursorial adaptations so characteristic of the Canidae. Nevertheless, the compactness, slenderness, and mode of articulation of many of the bones do in many ways parallel that of the dogs. There is a much greater mobility and flexibility of the lower forefoot and paw, and these might be considered primitive features, but in the cats they are developed to such a degree of efficiency that they themselves constitute a specialization. The various devices that guarantee the retractibility of the claws also are specializations. In fact, it would be hard to find a forepaw other than that of the primates which is more specialized, in the sense that the structural details are highly adapted for speed, precision, and strength. These structures form an important part of the cat's mechanism for offense and defense. A tiger is said to be able to crush a man's skull with one blow of the huge paw delivered so swiftly that defense against it is impossible. Even a very small kitten uses its claws more effectively than a puppy. Undoubtedly the playful antics of cats serve to perfect the speed and coordination for which the structural details are so well adapted.

The cushioning of the paw by the soft three lobed plantar pads also is a feline characteristic and is responsible for the silence and elegance of the "stalk."

The hunting leopard alone among cats has lost—or never had—the greater part of these specializations. The short, stout, and almost straight claws are non-retractile, apparently because of the loss of an important part of the mechanism, the claw sheath—but another part, the flexor tendons running to the base of the terminal flange of each digit, is still present. The webs which in other cats extend to the digital pads, binding the metacarpals into a compact unit, are little developed and the digits consequently more spreading. The plantar pads are hard and compressed, more doglike than catlike. These features, together with the long legs, powerful hindquarters, and small head, are cursorial adaptations which make possible the enormous speed.

### THE STRUCTURE OF *HOPLOPHONEUS*

#### GENERAL CHARACTERS

*Hoplophoneus*, contrary to most restorations, was not very much like any of the modern Felidae. This is true of every important feature of the skeleton except for the dentition and the shape of the skull. In fact, "saber tooth badger" would come closer to describing the general aspect of the animal than "saber tooth tiger."

The head is large. The neck is long and straight. The cervical vertebrae are interlocked in such a way that the double curvature of the Felidae would be impossible. The back is arched, with the apex at about the ninth rib. From this point, the hindquarters slope sharply downward. The pelvis is broad, with a strong oblique inclination (about 45° from the horizontal), and the acetabulum is so placed that the hind limbs have a straddling position and are incapable of being drawn forward under the body in the typical felid fashion. The upper part of the leg is longer than the lower, the reverse of felid proportions. The thorax is shallow in comparison with that of *Felis* or *Canis*. The forelimbs are noticeably shorter than the hind, very stout, articulated in such a way that the elbow joint extends sideward and the lower part of the limbs and feet are turned inward. The pose is closely similar to that of such plantigrade animals as *Mustela* or *Taxidea*, especially the latter. Both fore and hind feet are strictly plantigrade.

#### RANGE OF VARIATION

The skulls of *Hoplophoneus* are greatly varied in size and details of form but, as Leidy pointed out, this variation is not greater than among individuals of *Felis concolor* (which Leidy called *Panthera*). The cranial variation in *Hoplophoneus* has been the subject of two

statistical studies (Simpson, 1941a, and Hough, 1949). These studies show that all specimens of *Hoplophoneus* collected from the Brule clay belong to one species, *H. primaevus*, which, however, has been subdivided into a number of geographic subspecies. These subspecies, which probably ranged over most of North America, include one or more of very large size, and at least one very small southern race. Two, occupying adjacent areas, are about the same size, but have clearly distinguishing cranial characters. The one, *Hoplophoneus primaevus primaevus* from South Dakota, included Leidy's original specimens, as well as the types of *H. insolens* Adams, *H. oreodontis* Cope, and *H. robustus* Adams. The other, *H. primaevus latidens* Thorpe includes Thorpe's types of *H. marshi*, *H. latidens*, and *H. molossus* from Colorado and Nebraska and a series of skulls and skeletons in the United States National Museum from Wyoming. *Hoplophoneus primaevus latidens* is closely allied to *H. mentalis* Sinclair from the Chadron formation, and is also primitive in having cranial characters nearer to those of the more generalized carnivores of the period, especially the daphoenids.

The variation in the proportions of the limb bones has not been so intensively studied. The work that has been done suggests that the amount of variation is not of great importance. Simpson (1941a) points out that in the specimens studied by him there is a general correlation (within a species) of the length and stoutness of limb bones in proportion to skull length. This is true of most Recent mammals. Small individuals tend to have relatively slender limbs but these limbs are shorter in proportion to skull length. The writer found this to be the case also for the United States National Museum specimens studied.

However, in the Chadron species, *Hoplophoneus mentalis* (insofar as can be determined from the few available specimens) there is positive difference in proportions, not correlated with size. The index, humerus length to femur length in *H. primaevus* is 85-87. That of *H. mentalis* is 94. In other words in the earlier form the fore and hind limbs are more nearly equal.

#### CRANIAL CHARACTERS

*Hoplophoneus primaevus primaevus* Leidy.—This type of skull was the one described by Leidy. He pointed out that the upper profile has about the same curvature as that in the skull of the puma, but the facial region is longer and straighter, and the cranium shorter. The nasal openings are narrower and are placed higher. As Leidy said (1869, p. 54):

The zygoma encloses a narrower space than in *F. concolor*, its posterior root has a deeper origin from the cranium and descends more in its outward course. Its anterior root below the orbit is shallow and thick.

The greatest difference between the two types of skulls, however, is in the proportions: in *Hoplophoneus* the muzzle is longer, narrower, and more tapering; the breadth across the postorbital processes is greater. There is a deep postorbital constriction with a narrow cranium so in dorsal view the skull has a wasp waist curvature. The capacity of the cranium is hardly one-third that of the puma. In fact, in this respect all of the Oligocene carnivores are nearer to the carnivorous marsupials such as *Thylacinus* or *Dasyurus* than to any of the placental families.

The base of the skull is narrower in proportion to its length than in the puma. The glenoid articulation has nearly the same form and direction as in the puma but is much lower, fully one inch below the basisphenoid. The post-glenoid tubercle is nearly like that of *Felis concolor*; the anterior one extends farther medio-laterally but is not as long or as distinct.

The mastoid processes are highly specialized in relation to the saber tooth dentition. This was not emphasized by Leidy but has since been the subject of much discussion by Matthew (1910) and others. The mastoid is produced into a rugose knob that projects downward and forward over the external auditory meatus in such a way as to make a deep, narrow passageway quite in contrast to the open circular aperture of *Felis*. The degree of development of this feature closely corresponds with the length of the canine teeth. When the sabers become very large, as in *Eusmilis* and *Smilodon*, the mastoid process extends so far forward as to be almost in contact with the base of the post-glenoid process.

The details of the auditory region are typical and uniform in all hoplophoneids. The cavity is very deep and narrow. There are never more than fragments of bulla preserved, but in many specimens these fragments suffice to show that there was a small, undivided discoid bulla similar to that of certain undescribed specimens from the Valentine in the Frick collection which are probably machairodonts. The paroccipital process is distinct in all of the early members of the subfamily, being a lobelike process similar to that of *Daphoenus*. The cranial foramina are more canoid than feloid as has been pointed out by Scott (1936) and others.

The mandible differs in many respects from that of modern cats. It is extremely thick and deep. Anteriorly, the depth is in remarkable contrast to that of *Felis*. The anterior face is a plane vertical surface 44 mm. high in a skull 188 mm. long. At the external corner of this vertical face the lobes for the protection of the upper canines project a distance of 13 mm. in the same skull. The ramus gradually narrows posteriorly, the least depth being just posterior to the last molar. The coronoid process is very low, lacking the

backward extension of that of *Felis*. It resembles that of the badger in general proportions but is relatively lower.

The head—with the short facial region, huge canines, and enormous, highly prognathous lower jaw—must have been bizarre. These features are usually minimized in restorations which also give the impression that *Hoplophoneus* and *Smilodon* (to say nothing of *Dinictis* and *Eusmilis*) presented a very similar appearance. This could not have been the case. The contours of the skull are very different in all of these forms. In particular *Smilodon* and *Hoplophoneus* differ in the size and shape of the lower jaw.

*Hoplophoneus primaevus latidens* Thorpe.—In this subspecies the skull is typically much longer and lower. The upper profile is horizontal with the tip of theinion the highest point. The height is due mainly to the strong sagittal crest but the cranium is horizontal with no flexure between it and the cranial region. The latter is longer and straighter than in *H. primaevus primaevus*, and the zygoma are stronger and deeper and more closely pressed to the side of the skull. The muzzle is long, and narrower than that of any of the Felidae, although broad in comparison with that of the contemporary daphoenids or canids. In other respects, the proportions are very close to those of the larger specimens of *Daphoenus vetus* Leidy. The cranial capacity is very small. The postorbital constriction is narrow and in some skulls, probably males, very posterior in position.

The mandible has essentially the same characters as *H. primaevus primaevus* but because of its greater length the disproportion seems less.

The appearance of *H. primaevus latidens* and *H. mentalis* both must have been more canine than feline. Very probably neither had the whiskers and cleft rhinarium with which they are often pictured. It is much more probable that the muzzle resembled that of a musteline.

#### DENTITION

The large saberlike canines are the most prominent feature of the dentition. The length ranges from three to four times the basal diameter. In *Hoplophoneus*, in contrast to *Smilodon* or to *Eusmilis*, there is little recurvature. The cross section at the base is a narrow, compressed, oval, tapering gradually to a point at the tip. The sabers are not as compressed or scimitarlike as those of *Eusmilis*, but are longer, thinner (and taper less abruptly) than those of *Dinictis*. Both length and width of cross section are varied but, strangely enough, not so much as in the modern felids.

The lower canines are small teeth that differ very little from the lateral incisors. They shear against the upper lateral incisors rather than against the upper canines, which they barely touch. The incisors, upper and lower,

are stout, sharp, semiprocumbent teeth, arranged in a semicircle, and in some species, pointed—in contrast with the straight comblike arrangement in *Dinictis* and *Felis*.

Between the canines and the first premolar present (which is a minute nonfunctional tooth) there is a long post-canine space—much greater, of course, in the longer-jawed forms. The alveolar margin of the cheek teeth is almost straight, but the sockets are raised in such a way that when the mouth is closed the upper jaw is uptilted. The upper and lower jaws of the clouded leopard have similar relations.

There are only two functional cheek teeth, P<sup>4</sup> and one other premolar in the upper jaw, M<sup>1</sup> and one premolar in the lower jaw. The upper molar is a rudimentary tooth. Both functional cheek teeth are shearing teeth with the posterior one the principal carnassial. The anterior one is smaller but placed in line with the other in such a way that they present one shearing surface. Both teeth have a strong backward inclination. The roots are stout and recurved. With age, the upper teeth tend to rotate inward and the lower teeth outward. This insures a type of wear that keeps the edge always sharp. There is nothing of this sort in *Felis*. In the latter, too, the premolars anterior to the sectorial are grasping teeth used for holding food in the mouth. The incisors are weak and ineffective. The opposite is true in *Hoplophoneus*.

#### AXIAL SKELETON

In general, all of the elements of the axial skeleton of *Hoplophoneus* closely resemble those of *Smilodon* (pl. 31). However, the atlas is more like that of *Daphoenus*. The transverse processes in *Smilodon* are greatly extended posteriorly, tapering to a rounded edge. In *Hoplophoneus* the posterior extension is not so great, and the ends are truncated. Both in *Smilodon* and in *Hoplophoneus* the processes differ from those of *Felis* in lacking the anterior breadth which gives them a rectangular shape. In all specimens there is an atlantal foramen on one side and not on the other.

The axis vertebra resembles that of *Smilodon*, but the neural crest is proportionally higher and is extended into a longer, sharper spine. The anterior projection is less developed than in *Felis*. The opening of the neural canal is triangular, narrowing dorsally much more than in *Felis*. A deep, narrow groove is present on the under side of the neural spine where it projects over the posterior opening of the canal. The anterior articulating surfaces are close together and face more forward. The postzygapophyses are also closer together and face obliquely upward and laterally. In *Felis* their orientation is almost directly downward. The odontoid process is relatively stout. The anterior face slants obliquely upward. The transverse processes are broader and extend laterally and ventrally.

The cervical vertebrae behind the axis closely resemble those of *Smilodon*, even in detail. There is a general likeness to *Felis*. The dorsal surface is broad; the neural spine of Cervical III is very low (lower than in *Felis*), and that of Cervical IV pointed and tapering. In this vertebra there is a suggestion of bifurcation of the long and stout transverse processes that increases until in the sixth cervical a distinct dorsal and ventral process is formed. Such a bifurcation may be present also in *Smilodon* (Stock, 1932).

The thoracic vertebrae closely resemble those of *Smilodon* and do not differ markedly from *Felis*. The spines are somewhat longer and narrower than those of the Pleistocene genus but proportionally stouter than those of *Felis*. The centra are also somewhat broader and heavier.

The lumbar series in *Hoplophoneus*, as in *Smilodon*, is more firmly interlocked than in *Felis*, making the section more rigid. This is effected in part by the inward curvature of the zygapophyses, but principally by the position of the anapophyses. The latter are long and project backward, overlapping the metapophyses one-half to one-third of their antero-posterior breadth. Merriam and Stock (1932) pointed out this feature in *Smilodon*, and it is much more striking in *Hoplophoneus*.

The very sturdy sacrum closely resembles that of *Smilodon*. It is much narrower than in *Felis*, particularly toward the posterior where the zygapophyses are very close together. The spines are broader and higher than those of *Felis*, and are slightly inclined backward. In true felines the spines are much more slender and inclined forward.

There are 21 caudal vertebrae in *Hoplophoneus mentalis*. Probably, the number was varied. Most felines have 18 or 19, although there may be as many as 24. However, the tail in *Hoplophoneus* was shorter and more slender than in such forms as the puma, not only because there are fewer vertebrae, but because the individual vertebrae (especially those in the posterior half of the tail) are proportionally much shorter. The tail must have been a less mobile and important appendage in *Hoplophoneus* than in typical felines.

#### APPENDICULAR SKELETON

The scapula is narrower and more angular than that of *Felis*, and the vertebral border is sharply convex (pl. 29). The notch at its lower end (just below the coracoid process) is broad and shallow. The coracoid process is a rounded lobe, relatively larger than that of *Felis*. The axillary border is straight in its lower portion, but curves downward to form the process for the insertion of the teres major muscle. This process in *Hoplophoneus* is short and broad, much more like that of the American badger (*Taxidea taxus*) than *Felis*.

The spine is of almost even height throughout its length. The metacromion and acromion are not separate as in *Felis*, but confluent as in *Taxidea*. The glenoid fossa is an elongate oval, also resembling that of the badger rather than *Felis*.

The humerus of *Hoplophoneus* is very different from that of a cat; it is short and extraordinarily thick because of the enormous development of the deltoid and supinator crests. In *Felis* and *Canis* the shaft of the bone is long and slender, with an oval cross section. The deltoid crest is a triangular flattened area extending a little more than a third the length of the bone. The supinator crest is a slight ridge along the external condylar surface. In *Hoplophoneus* the deltoid area is two-thirds the length of the shaft and is extended into a process approximately 5-mm. above the body of the bone. The supinator crest extends from a point on the external condylar side about on a plane with the termination of the deltoid crest and forms a wing-like process to the external condyle. The prominence of these muscle attachment areas makes the humerus look like the peculiarly crooked humerus of the badger.

In general shape and proportions the ulna resembles that of the badger rather than of *Felis*. It is stouter and less tapered than in the latter, and the olecranon process is proportionally longer. The greatest difference from *Felis*, however, lies in the size and shape of the articular surfaces. The greater sigmoid cavity is oblique, narrower, and much deeper. The upper bounding process and the coronoid process that forms the lower border are about the same size. The lesser sigmoid cavity is a deeply concave rim of bone in *Felis*, but a flat triangular surface like that of the badger in *Hoplophoneus*. The bicipital groove is deep in *Felis* but very faint in *Hoplophoneus*, and this, too, is a likeness to *Taxidea taxus*.

The shaft of the radius resembles that of *Felis*, but the head is narrower, and there is virtually no neck. The margin of the head is flat, without the marked "lip" of *Felis*. The articular surface is much less concave. The tuberosity is somewhat smaller and the shaft below it is a little less flattened. The distal end is relatively broad. The surface for articulation with the scapho-lunar is more concave and the styloid process larger and stouter than in *Felis*. There is a small facet for articulation with the cuneiform.

The carpus resembles that of the badger but differs in the contacts of the bones and lacks the height and compactness of that of *Felis*. The scapho-lunar is proportionally large. It articulates with the trapezium, trapezoid and magnum in very broad contacts. The magnum is high, almost excluding the cuneiform from contact with the scapho-lunar. The contact of the cuneiform with the unciform is superior (or dorsal) rather than lateral as in *Felis*. There is a broad, concave

articular surface for the styloid process of the ulna and, medially, a smaller flattened facet for articulation with the radius. The shafts of the radius and ulna are thus held in an oblique position with the elbow directed outward. The unciform articulates with the fifth metacarpal, the magnum almost entirely with the fourth metacarpal, the trapezoid with the third metacarpal, the trapezium with the second and first metacarpal. The articulation with the first metacarpal is almost at a right angle with that of the second metacarpal so that the pollex is widely divergent from the other digits. The head of the pollex also articulates with the posterior palmar surface of the scapho-lunar. Therefore, in walking, the digits of the forefoot would be spread widely apart and the divergent thumb used to give a forward impetus to the gait. In climbing, the hand could encircle a small branch with the first digit opposing the others. Opossums, raccoons, squirrels, and other arboreal animals climb in this fashion.

Like the carpals, the metacarpals are broad and spreading. Metacarpal III and IV are of almost equal lengths and are the largest of the series. Metacarpal II and V are also paired as to length. Metacarpal I is the shortest, but is a stout bone almost two-thirds the length of Metacarpal II.

The claws are hooded, with the claw core about as large proportionately as that of *Felis*. Probably, the claws were long and beaklike as in *Felis*. The ungual phalanx closely resembles that of *Felis* both in general shape and structure of the articular surfaces. Probably, it was capable of being rolled back on the phalanx preceding it and the claws retracted in the same way that this action is accomplished in the modern cats.

The general outline of the pelvic girdle is like that of *Felis* but the details are quite different (pl. 30). The ilium much more closely resembles that of the badger. The outer surface is convex rather than concave as in *Felis*, and the posterior spinous process is expanded and situated relatively near the acetabulum as in *Taxidea*. The spine of the ischium is a large hooklike process, however, closely resembling that of *Felis*. In the badger this process is very small. The shape of the pubis and ischium, and the size of the obturator foramen also are very feline. The acetabulum is longer and narrower than that of *Felis*, and also shallower and more posteriorly placed. It is lower in position, and faces laterally and a little posteriorly. Because of this, the limbs when articulated are relatively wide apart and drawn under the body in a squatting pose. In *Felis* the acetabulum is high and faces forward so that the femora lie close to the body and in the normal running gait have a completely fore and aft motion.

The femur is feline in character and not at like that of *Taxidea*. The only significant differences from that of a cat are the presence of a large third trochanter

and the deeper separation of the head and greater tuberosity.

The tibia and fibula also are very feline. The surface of the distal end of the tibia which articulates with the tarsus is narrower and somewhat less concave but otherwise like that of *Felis*. The internal maleolus in *Hoplophoneus* is somewhat longer. The fibula is stouter and straighter, and lacks the sinuous curvature of *Felis*. The external maleolus is narrower than in *Felis* and as Scott (1936) points out there is no sulcus for the peroneal tendon.

The calcaneum differs from that of *Felis* in general shape and also in detail. The tuber calcis is narrower proximally and expanded distally. The outer articular surface for the astragalus is short and flat. In *Felis* this surface is a long tongue-like facet and very convex. The outer articular surface is narrower and flatter than in *Felis*. It is placed at a greater angle to the external facet so that the two are much farther apart than in *Felis*. The body of the bone is not spool shaped (as in *Felis* and almost all living carnivores) but more nearly cylindrical. The neck extends downward and laterally rather than postero-laterally. It is broader and less distinct from the head which is narrow and oval, rather than hemispherical like that of *Felis*.

The shape of the body of the bone and the position of the head are much more as in *Taxidea* than as in *Felis* but in *Taxidea* the neck extends almost directly forward whereas in *Hoplophoneus* the head is extended laterally and downward.

The facets for the articulation of the external and internal maleoli are more obliquely placed than in either *Felis* or *Taxidea*. Evidently the ankle of *Hoplophoneus* was articulated in such a way that the foot tended to point inward in walking. In fact, the posture of the foot from the evidence both of the articulation of the separate bones and of an articulated foot found in position was strikingly like that of the scansorial viverrine, *Arctictis*. The metatarsals in *Hoplophoneus* are long and slender as they are in *Arctictis* and agree in relative length. Metatarsal I is the shortest but is almost as long as Metatarsal II. Metatarsal III and IV are the longest and almost equal in length, while III and V (missing in the articulated foot) form a similar pair.

#### MODE OF LIFE OF HOPLOPHONEUS

The long, upper canines are the most conspicuous feature of *Hoplophoneus*. They are so conspicuous that they have been the subject of almost endless discussion with little consideration of other features of the dentition and skeleton. From the standpoint of interpreting the mode of life, however, it is the combination of characters that is most important. In *Hoplophoneus*, this combination is unusual.

The dentition is marked by an extreme development of the shearing function of the cheek teeth. This specialization, which appears in the earliest known forms, is certain evidence of an exclusively flesh diet. The lower Oligocene (Chadron) species have as elongate canines and as advanced a mechanical adaptation for their use as the middle and upper Oligocene (Brule) species; throughout the Oligocene there appears to have been little evolution in these features.

The shape of the skull is specialized, but differs from that of the true Felidae only in detail. Compared with the contemporary daphoenids or canids the forehead is domed, the frontal region high, and the nasals short and steeply sloping. The orbits are large, and placed higher in the skull than are those of *Daphoenus* or *Pseudocynodictis*. The nares are also comparatively large and highly placed. These features are by no means developed to the extent that they are in the modern Felidae, nor even to the degree found in the later dinictids, but they appear in the Chadron species and indicate at least an approach to feline habits. In the specimens that constitute Leidy's hypodigm of the Brule subspecies *H. primaevus primaevus* they are notably more highly evolved.

Associated with this comparatively catlike shape of the skull and the extreme carnassialization of the cheek teeth, there is a battery of stout, projecting semiprocurrent incisors unlike anything found among the Felidae.

The limb structure is definitely scansorial. The pentadactyl, grasping forefoot, with its divergent pollex, is well shown in the view of the mounted skeleton figured in plate 27. Both the structure of the humerus with its heavy deltoid and supinator crests, and of the foot structure are reminiscent of the Paleocene *Claenodon*. Neither the appearance nor the gait of *Hoplophoneus* could have been like that of a cat, even a very short legged one, and even less like that of a civet. The contours of the body must have been broad and the gait waddling, as indicated by the everted elbow and knee joints and inwardly directed feet. This type of limb structure combined with an extreme carnivorous type of dentition is extraordinary, and has no representation among modern animals. Apparently it results from a phenomenon observable in the history of many early Tertiary carnivores—the rapid evolution and high specialization of one set of structures, associated with extreme conservatism in others.

The mental capacity in all hoplophoneids must have been extremely low. The braincase in the Brule species is not much larger than that of the contemporary hyaenodonts, and in the Chadron species it was smaller. Therefore, *Hoplophoneus* could not have had approached the true cats in speed, coordination, or cunning. Nevertheless with the formidable dentition, powerful forelimbs, and (probably) highly effective retrac-

tile claws, *Hoplophoneus* must have been an active predator—probably the most active of its time. The catlike dentition suggests that it killed in the same way, although there was nothing comparable to the wait in ambush, stalk, and dashing attack of the Felidae. The smaller subspecies may have been strictly arboreal, and they may have fed on rodents, birds, and reptiles much in the manner of the small species of *Felis* today. Probably, the larger hoplophoneids attacked the larger herbivores, especially the slow-moving, thick-skinned types (as Matthew suggested in 1910). The attack may have been made by a head-on charge in which the victim was seized by the throat, or by a drop from a tree branch or rocky ledge. In any case the canines could be used very effectively. They are not long enough in any known hoplophoneid to be unwieldly; they are thin and knifelike—after piercing the skin and muscle they could be readily maneuvered into interstices between bones or the cartilage and tendon of joints. There is little recurvature so that withdrawal would be easy. With the wide gape of the jaws the neck of the victim could be almost encompassed, the canines thrust deeply into the throat or nape of the neck, the strong lower jaw pressed upward, and the animal choked to death very speedily.

#### COMPARISON OF *SMILODON* AND *HOPLOPHONEUS*

It is often assumed, implicitly at least, that the sabers of *Smilodon* were used in much the same manner as those of *Hoplophoneus* and that the method of predation and type of victim was the same. Obviously this could not have been the case. Little *Hoplophoneus belli* of the Sespé or even the smaller subspecies of *H. primaevus primaevus* could not have attacked the same animals in the same manner as the gigantic machairodont of Rancho la Brea. Moreover, the same type of herbivores did not exist in the early Tertiary as in the Pleistocene, so that the role of *Smilodon* in the latter fauna was quite different from that of *Hoplophoneus* in the Chadron and Brule formations.

There is a vast amount of literature on the use of the saber teeth which it seems unnecessary to review here. The consensus among paleontologists who have studied the matter undoubtedly supports the stabbing theory, first presented by Matthew (1910) and ably supported by Simpson in his refutation of the slicing hypothesis of Bohlin (Simpson, 1949). There is also no doubt of the mechanical adaptation of the skull for the use of the teeth which in *Smilodon* reach such extraordinary proportions. They are not overspecializations in the sense that because of them the animal starved to death or could not open its mouth or was unable to use them effectively in an attack.

Nevertheless, as Merriam and Stock point out in their detailed and able discussion of the subject in the Felidae

of Rancho la Brea, there were certain limiting factors to their use. They required an extraordinary growth period.

These teeth are found to be represented by crowns 65 mm. in length in a kitten in which there is no indication of the formation of the enamel for the crown of the permanent carnassial. The permanent canine was not erupted and in full function until the other teeth had begun to show some evidence of wear.

On the other hand, a large number of old animals show loss of one or both canines by breakage. Merriam and Stock therefore concluded (1912, p. 55) that the peculiar mechanism of the animal was in active operation a relatively short time and suggest that the

degree of specialization exhibited was dangerously near the borderline of overspecialization or at any rate at a point where a slight change in environment might work a severe hardship.

Regardless of the mechanical efficiency of the sabers their thickness and recurvature must have made them difficult weapons to handle. Specializations of the skull which permitted a wide enough gape and a quick enough recovery to position to allow the animal to strike effectively could, and quite apparently did, take place. Nevertheless, choosing just the right position at which to strike, and particularly withdrawing such thick, elongate, recurved structures must have been a dangerous undertaking, except under certain favorable conditions.

The canines of the "great" cats of today are sharp, short, tubular teeth which can be used with the speed and efficiency of daggers. If the first strike is not successful they can be withdrawn and a second more effective one made. The head in all of the *Panthera* is small, the neck flexible. *Smilodon* on the contrary had to maneuver with bayonets—turned the wrong way. The very specialization necessary for the use of the huge teeth made the head unwieldy and the neck stiff. The strike could be made but once and from one position. Once the sabers were embedded they were there to stay, until the victim died. Were an attack to be made in the manner of the lion or the tiger, the struggles of the victim, the forward momentum of both predator and prey, as well as the manipulation of the teeth themselves in the act of withdrawal must have resulted almost invariably in breaking the neck of the predator, or the sabers, or both.

There are two situations, however, where these difficulties would be minimized. One is in sexual combat between males. Here the combatants are approximately the same size and use the same weapons. There is thus neither advantage nor disadvantage on either side. Moreover, the purpose of the attack is not to kill or fell the opponent but merely to drive him away. A severe blow, anywhere, on the top of the head for example, even if not lethal, would be sufficient to accomplish this.

The other favorable situation was at the tar pits of Rancho la Brea where the victims, mired in the asphalt, could not run away nor put up so violent a struggle as otherwise possible. They were also weakened in many cases by hunger, by thirst, by fright, and by wounds. The huge machairodonts could choose their own vantage point for an attack, taking all of the time necessary for the strike, and once the sabers were embedded, literally crush the animal until it bled to death. Merriam and Stock have described at some length an adaptation in the palate, which they think probably served to drain blood of the victim to the gullet of the attacker (Merriam and Stock, 1932, p. 36).

If *Smilodon* did bleed prey to death in this way, it might explain the weakness of the lower jaw and lack of a protective flange for the upper canine. Because in this type of attack the lower jaw is simply dropped down to allow free play of the canine and does not close upward against the upper jaw, the depth and strength of the jaw as it is in *Hoplophoneus* was not needed. A bony outgrowth, such as that of the flange to the mandible, develops ontogenetically by the mechanical stress exerted on the growing bone. The pressure of the elongating canine on the mandible, as that is forced up against it, would condition the growth of the flange. Thus, if no such pressure existed there would be no flange.

The incisors in *Smilodon* (and in all machairodonts) are long, sharp, stout teeth that show wear with age. The lower canine shears against the upper lateral incisor rather than the upper canine, especially in *Smilodon*. It seems probable, therefore, that the animal could tear flesh from prey by the use of these teeth alone without opening the mouth wide enough to allow full play of the canines. The food torn off by the incisors could be shifted back to the carnassial dentition without the aid of the canines. The peculiar wear of these teeth, which keeps them sharp even in old age, suggests that they played an important part in obtaining food. In youth, the relatively short canines could be used with the incisors, and as the period before the full eruption of the permanent canines includes a large part of the animal's life, this was the more common method of feeding. This same method could be continued, as pointed out above, even after the saber teeth reached full development.

It may have been that in many cases the kill was made by a mature animal and then participated in by young individuals in which the canines had not yet reached their full development, with the carcass left for the feeble, the old, and the crippled.

Of course, this mode of attack was not without its dangers. The predator was as frequently mired as the prey. Merriam and Stock point out that only an animal of the low mental capacity of *Smilodon* would have been so oblivious of the danger.

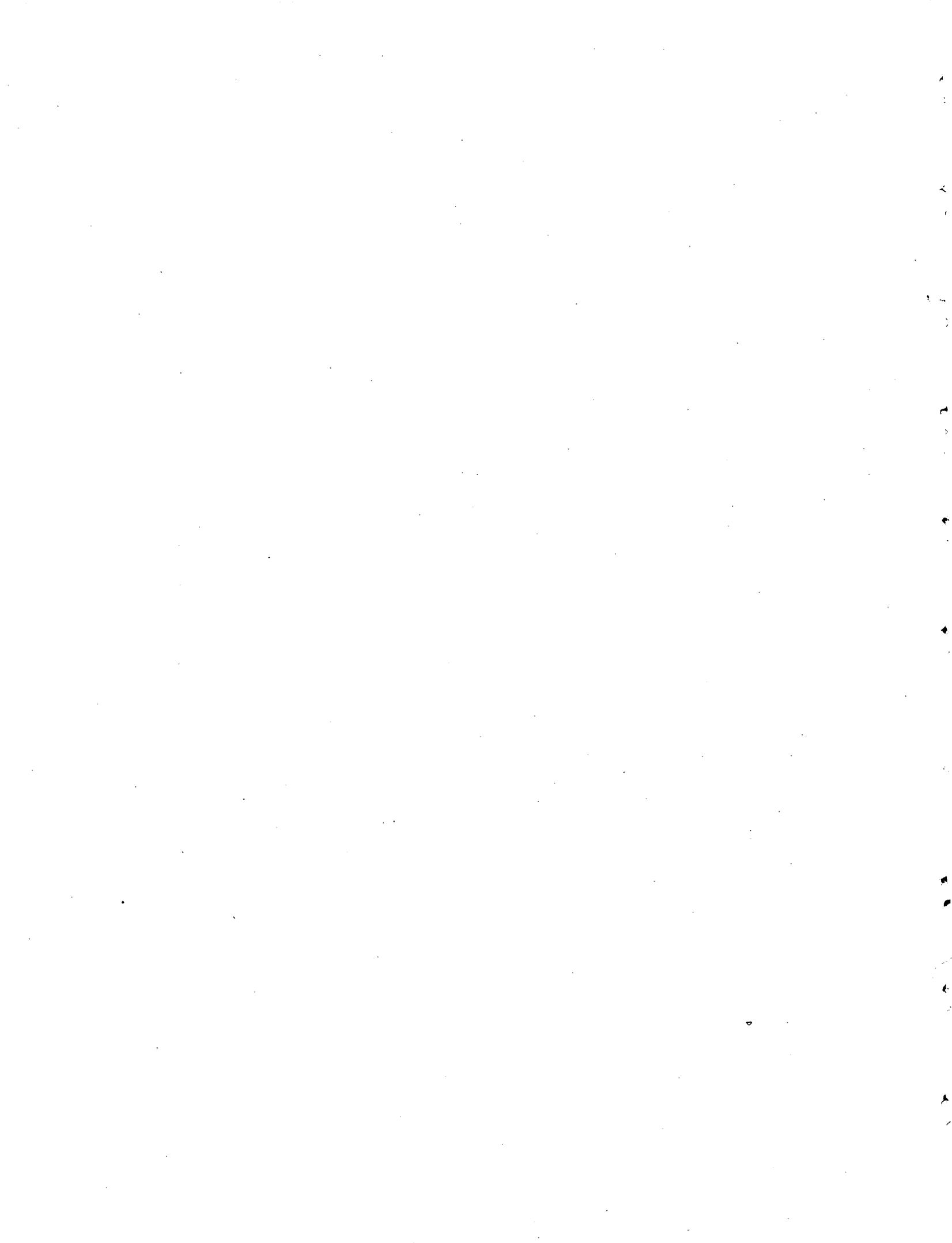
It should be remembered, also, that by the middle Pleistocene the true cats were making their competition felt. *Smilodon* was too large for effective ambush in trees, too stupid for the type of jungle stalking characteristic of the lion and tiger, and too slow to run down its victims. These modes of attack were being developed rapidly among the true Felidae: *Felis atrox*, the lynx, and the jaguar—remains of all of which are found at Rancho la Brea. It is evidence of the extraordinary adaptability of the machairodont stock and the effectiveness of the saber tooth mechanism that these animals were able to continue on in any habitat, under such stiff competition. Nevertheless, the balance was precarious and a shift of any sort in the environment, even the continued slow infiltration of the Felidae, would be sufficient to bring about extinction.

The role of *Hoplophoneus* in the Oligocene fauna was entirely different. During the early Tertiary there were no true cats, no dogs, nor indeed any highly evolved carnivores of any description. *Hoplophoneus* was unquestionably the most able and active predator in existence. Its only rivals were the small cynodonts whose role in the fauna was that of the mustelines of today—rather than the canids and the larger, but small-brained and ambulatory daphoenids with no particular equipment in the way of unusual strength or dental specialization or speed of limb. In fact, competition must have been largely between the saber tooth genera, *Hoplophoneus*, *Dinictis*, and *Eusmilis* themselves, with *Hoplophoneus* by far the most successful throughout Chadronian and Orellan time.

*Hoplophoneus* was in no way a generalized animal. It was highly specialized for a particular role in the fauna of the time. Certain characters (such as the narrow cranium or the foot structure, which do not show any of the specializations characteristic of modern Carnivora) may be considered generalized—but only in contrast with characters such as the dentition, that are more highly evolved. The combination of characters found in *Hoplophoneus* represents the culmination of a long evolutionary history from early creodont stock. It also represents the *beginning* of the machairodont phylum as is now known. This phylum in turn culminated in the Pleistocene saber tooth genera of North America and China.

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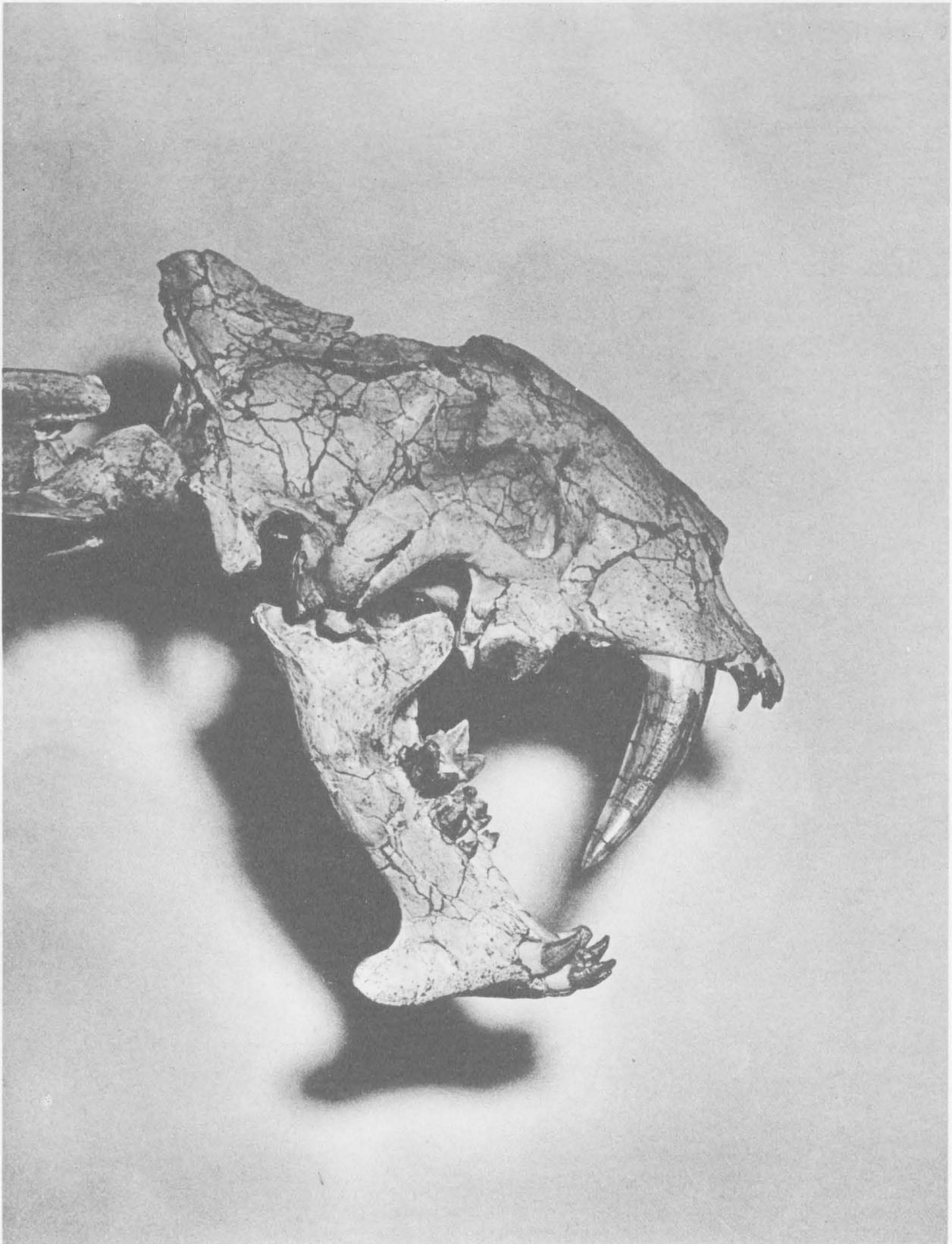
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PLATES 26-31

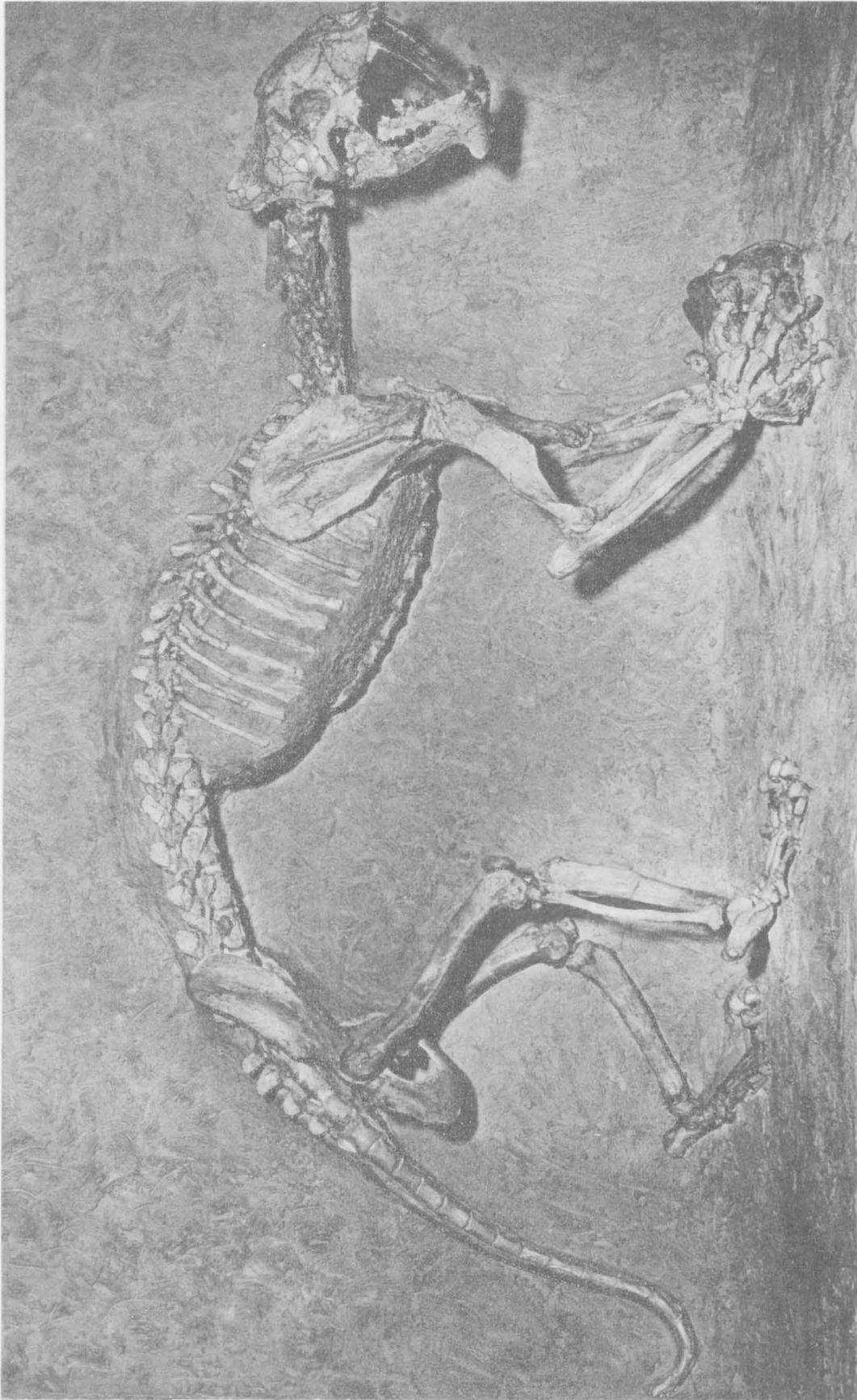
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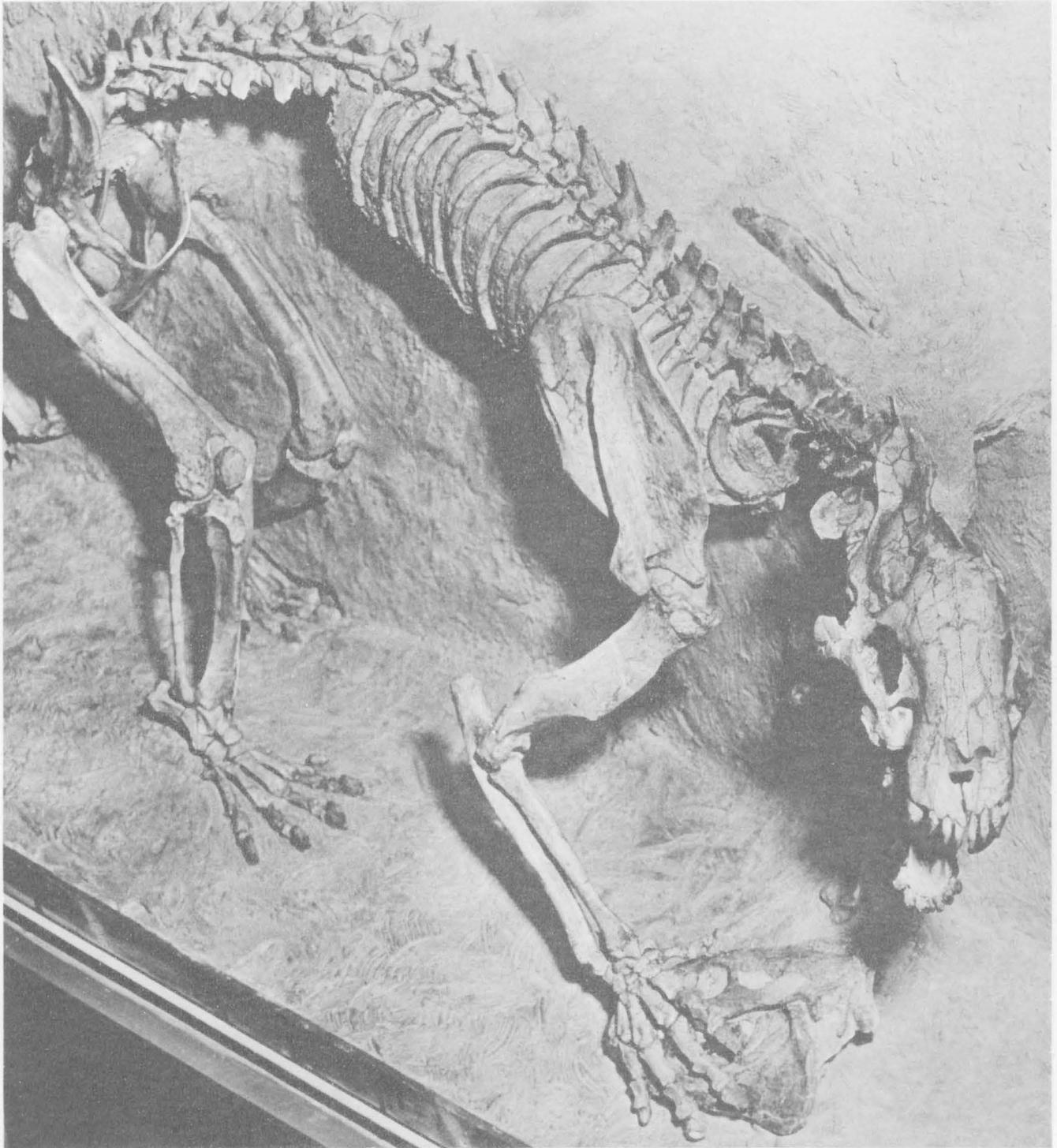
*HOPLOPHONEUS MENTALIS SINCLAIR*

(Side view of skull and lower jaw. Colorado Univ. Mus. 19163.)



*HOPLOPHONEUS MENTALIS* SINCLAIR

(Side view of skeleton mounted by John Clark, Colorado Univ. Mus. 19163.)



*HOPLOPHONEUS MENTALIS SINCLAIR*

(Antero-lateral view of mounted skeleton. Colorado Univ. Mus. 19163.)

PLATE 29

Fore limb bones of *Hoplophoneus primaevus latidens* Thorpe

[U. S. N. M. 18184]

FIGURE 1. Internal view of scapula.

FIGURE 2. External view of scapula.

FIGURE 3. Posterior view of radius.

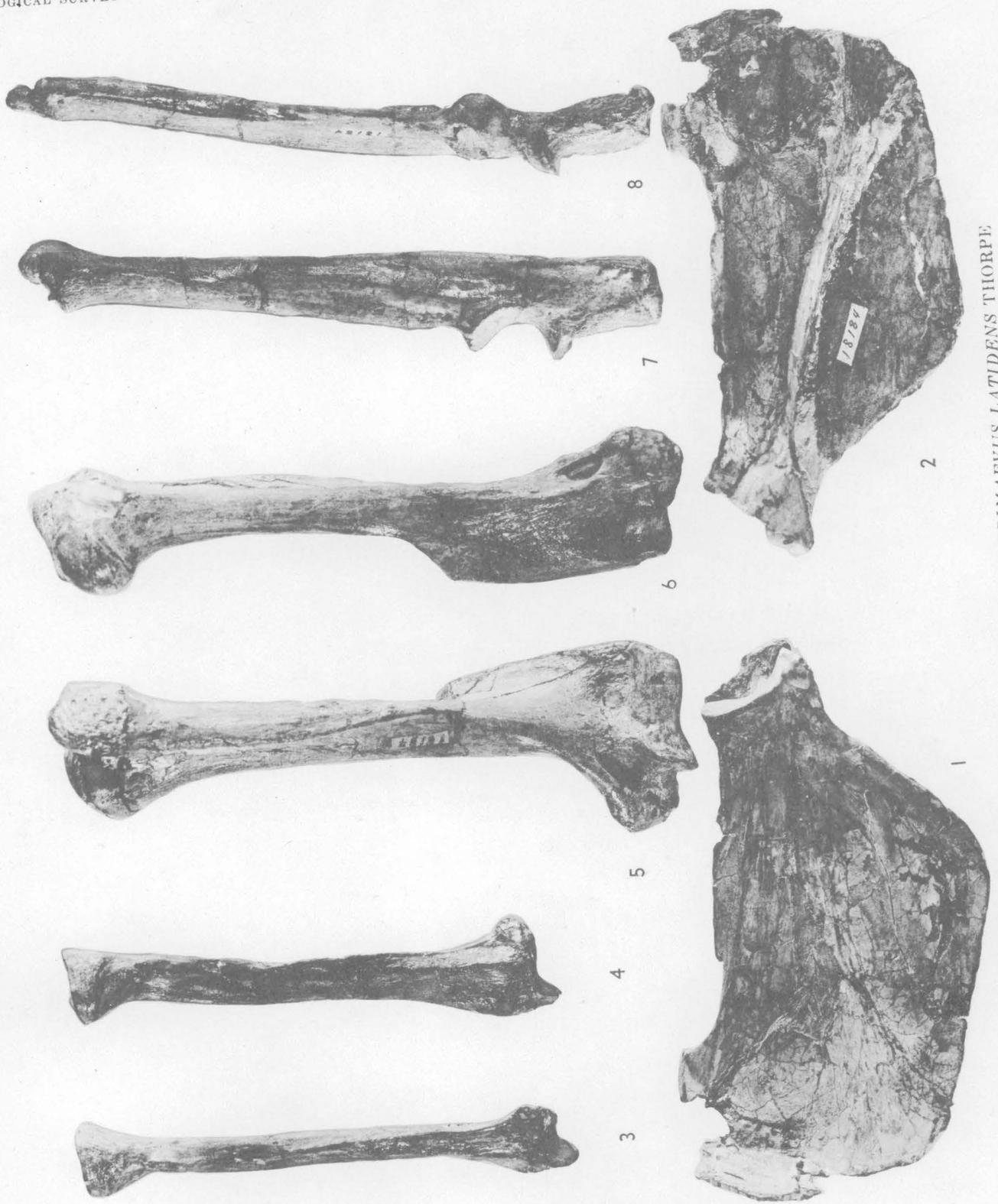
FIGURE 4. Anterior view of radius.

FIGURE 5. Posterior view of humerus.

FIGURE 6. Anterior view of humerus.

FIGURE 7. External view of ulna.

FIGURE 8. Internal view of ulna.



FORE LIMB BONES OF *HOPLOPHONEUS PRIMAEVUS LATIDENS* THORPE

PLATE 30

Hind limb bones of *Hoplophoneus primaevus latidens* Thorpe

[U. S. N. M. 18184]

FIGURE 1. Posterior view of femur.

FIGURE 2. Anterior view of femur.

FIGURE 3. Posterior view of tibia.

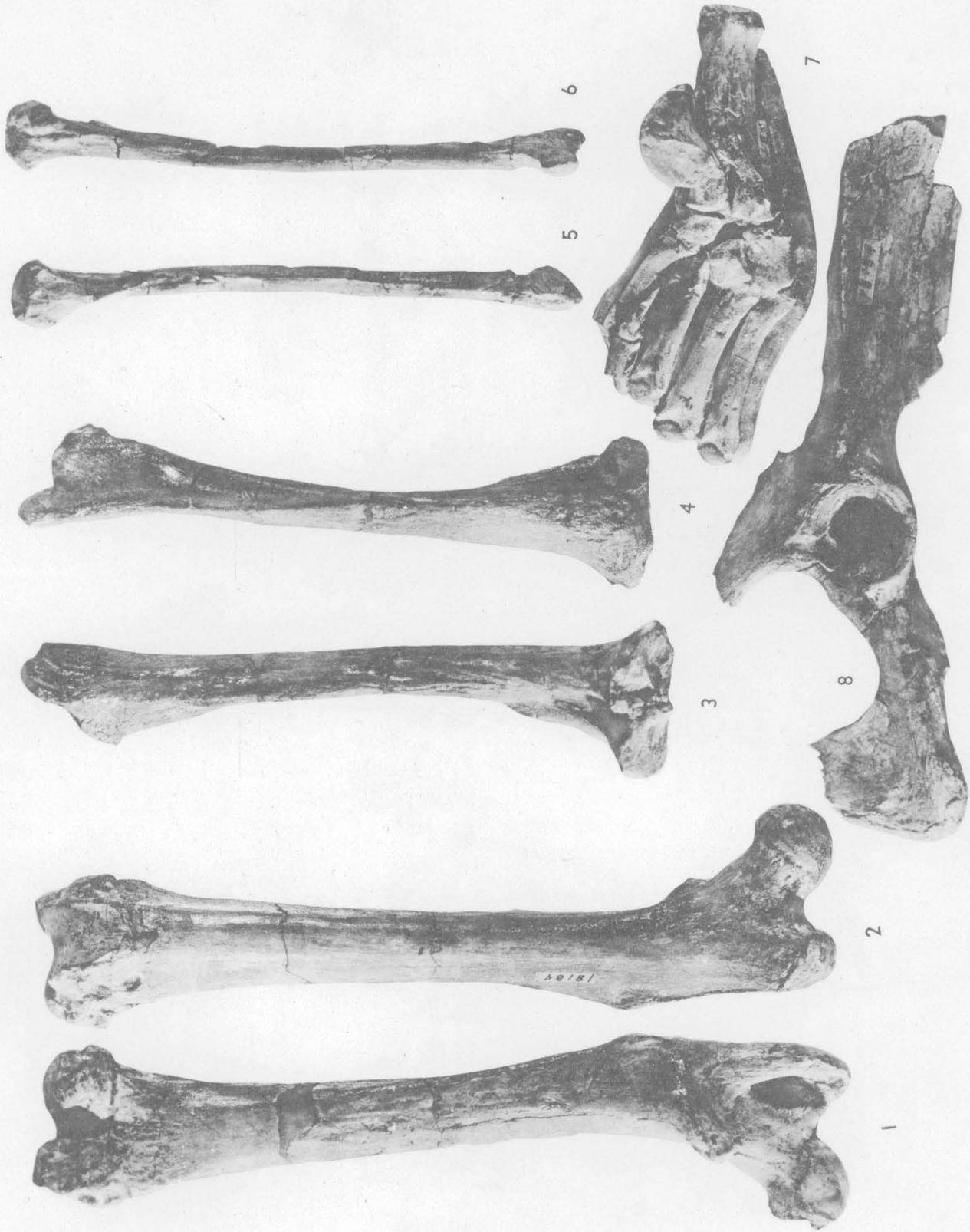
FIGURE 4. Anterior view of tibia.

FIGURE 5. Anterior view of fibula.

FIGURE 6. Posterior view of fibula.

FIGURE 7. Dorsal view of hind foot. (The astragalus and calcaneum are rotated so that the lateral aspect is shown.)

FIGURE 8. External view of pelvis.



HIND LIMB BONES OF *HOPLOPHONEUS PRIMAEVUS LATIDENS* THORPE



*HOPLOPHONEUS PRIMAEVUS LATIDENS* THORPE  
(Side view of vertebral column. U. S. N. M. 18203.)