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Chapter 25: Creodonts and Carnivores

ADAPTATIONS OF THE CARNIVOROUS MAMMALS

The early mammals that arose from primitive insectivore ancestors evolved along varied lines of adaptive radiation, to occupy the numerous ecological niches that had been vacated by the wide extinctions of reptiles at the end of the Cretaceous period. Several orders of mammals became adapted for feeding on plants, whereas two orders of land-living placental mammals, the creodonts and carnivores, became dominantly specialized for eating other vertebrate animals. Why was not the killing and eating of prey more widely followed among the orders of mammals? Perhaps the answer to this question is that the carnivores specialized as efficient predators at such an early date, and became so widely distributed, that no other mammals were able to compete with them on their own terms. It is an interesting fact that the successful predators outside the orders Creodonta and Carnivora are those mammals that have lived in regions or in habitats where they have been free from carnivore competition, for instance, the carnivorous marsupials in Australia (and in past ages in South America), the insectivores, the bats, and the predatory whales and porpoises.

Adaptations for a predatory mode of life are on the one hand generally less extreme than those required for a life of plant-feeding, yet on the other hand they involve more "evolutionary risks" in the long battle for survival. The plant-eater must possess complicated teeth and digestive organs to gather and convert bulky plant food into energy, but in general the source of food for animals of this type is abundant and readily available. The meat-eaters, on the other hand, depend largely upon their ability to catch other animals. This ability may not require advanced specializations, although often it has resulted in the evolution of highly modified animals, but it does make the carnivore dependent on a very uncertain and variable source of food. Consequently there has been intense competition among carnivorous mammals through the ages, either on the level of species or of individuals.

The adaptations that have been characteristic of both orders of the carnivorous mammals from the beginning of the Cenozoic era to present times may be outlined briefly. These mammals usually have had strong incisor teeth for nipping, and enlarged, daggerlike canine teeth for stabbing. In most carnivores the canines have been the principal weapons with which they kill their prey. Certain cheek teeth in the carnivorous mammals have been commonly transformed into blades that act against each other like the blades of a pair of scissors, for cutting and slicing meat into small pieces that can be swallowed easily and assimilated by the digestive system. These cutting teeth in the carnivores are called the carnassials. Naturally the carnivores have strong jaws, and strong crests and zygomatic arches on the skull for the attachment of powerful jaw muscles.

The carnivores usually have been very intelligent animals, because a great deal of mental alertness and coordinated action are required if other animals are to be overcome and killed. The sense of smell usually has been highly developed as an aid to hunting, and in many carnivores the eyesight has been very keen. The body and limbs generally have been strong and capable of lithe, powerful movement. There has been little reduction of the toes, which have sharp claws. These animals today are frequently fast runners over short distances, or adept climbers.

THE CREODONTS

Fortunately there is a good fossil record for both orders of carnivorous mammals, the creodonts and the carnivores (in the strict sense of the word), so that we can follow their evolutionary histories in considerable detail. For many years these two groups of meat-eating mammals were placed within a single order, the Carnivora, with the creodonts ranked as a suborder-an arrangement based on the view that the creodonts and the other carnivores were closely related, with the former group occupying an ancestral position to the latter group. The work of recent years makes it apparent, however, that the creodonts had a quite separate evolutionary history from the other land-living carnivorous mammals; that the resemblances between them were the results of parallelisms that grew out of similarities in habits and, consequently, in adaptations. In this way, two groups of mammals became carnivores independently of each other; they have been designated as the Creodonta and the Carnivora.

The creodonts constitute the older and the more primitive of the two groups. These mammals appeared in early Cenozoic time and enjoyed the culmination of their evolutionary development during the early phases of Tertiary history. They were rather archaic in morphological adaptations for the chase and the kill, and as long as the herbivorous mammals on which they preyed retained their primitive adaptations-as long as they were relatively clumsy and slow-the creodonts prevailed as the dominant meat-eaters. But with the appearance of advanced herbivores, roughly during the transition from Eocene to Oligocene times, the creodonts were at a disadvantage and were gradually replaced by the more specialized, more adept, and more intelligent Carnivora. A few of the creodonts persisted into late Tertiary times, but for the most part these carnivorous mammals were no match for the "true" carnivores and therefore were replaced by the evolutionary fines of meat-eating mammals that have continued into our modem world.

The term Creodonta is not being used here in the same sense that it was formerly employed. Certain groups of mammals, notably the arctocyonids long regarded as creodonts, are now placed among the most primitive of the hoofed mammals, the condylarths. If this seems like a drastic shift from primitive carnivore to primitive herbivore, it must be remembered that the very early eutherian mammals were quite generalized in morphology, and probably in habits, also. Thus, the distinction between carnivore and herbivore was a small one. The mesonychids, also formerly regarded as creodonts, are now generally placed in a separate order, the Acreodi, as has been noted in the preceding chapter. By removing the above two groups (generally classified as families) from the creodonts, the order becomes restricted to two remaining groups, the hyaenodonts and the oxyaenids.

As mentioned above, the creodonts were archaic carnivorous mammals. The skull was low with a small braincase; the molar teeth were basically tribosphenic, but with various molars frequently modified to form cutting blades. No ossified auditory bulla surrounded the middle ear, as in the advanced Carnivora. The skeleton was generalized; the limbs were generally

rather short and heavy; the tail was long; and the toes terminated in sharp claws.

At an early stage in their evolutionary history the creodonts branched into two phylogenetic lines, the oxyaenids, in which the first upper molar and the second lower molar were the carnassials, or cutting teeth, and the hyaenodontids, in which the second upper and third lower molars were the carnassials. Adaptations were varied among these creodonts. Some were small and slender like the Eocene hyaenodont, *Sinopa.* Others were large and powerfully built, like the Eocene oxyaenids, *Oxyaena* and *Patriofelis*, or the Oligocene hyaenodont, *Hyaenodon.* It is obvious that these creodonts were the arch predators of early Tertiary times and anticipated the divergent evolution that was to take place among the carnivores in later Tertiary times, after the creodonts had become extinct.

After the extinction of all other creodonts at the end of the Eocene epoch the hyaenodonts continued into the Oligocene epoch, and from then through the Miocene and into the early phases of the Pliocene epoch. Evidently these particular creodonts were sufficiently well adapted as beasts of prey so that they could compete successfully with the progressive land-living carnivores, often known as fissipeds, that arose at the end of the Eocene times, to blossom into abundance and great variety during subsequent geologic ages.

THE MIACIDS

The various creodonts that have thus far been described shared their function of early Tertiary predators with still another group of carnivores, the miacids. These carnivorous mammals appeared in Paleocene times, and like many of the creodonts they continued through the Eocene epoch to become extinct at the close of that phase of geologic history. They had certain primitive characters, such as the general archaic structure, with a low skull, elongated body and tail, and short limbs. The miacids, however, were progressive in some very important features. For one thing, they seem to have had a proportionately larger and more highly developed brain than the typical creodonts, a feature that would have been of great advantage to them as beasts of prey. Of particular importance is the fact that in these carnivores the carnassial teeth were more anteriorly placed than in any of the other early Tertiary carnivores, for they consisted of the fourth upper premolar and the first lower molar. The molar teeth were tribosphenic in form, and the last upper molar was absent. These are exactly the conditions typical of carnivores, and for this reason the miacids are regarded by many authorities as the most primitive representatives of the Order. However, two primitive characters distinguish the miacids from the later carnivores to which they were ancestral. In the first place there was no ossified tympanic bulla that in later carnivores (and other mammals) forms a chamber that encloses the bones of the middle ear. And secondly the bones of the wrist were all separate, whereas in later carnivores there was a fusion of the scaphoid and lunar bones to form a single element. These may seem like small features of carnivore anatomy, but they are important in determining relationships, the details of the basicranium being particularly crucial.

The miacids were small carnivores of weasellike form. They were probably forest dwellers, preying upon small animals that lived in the dense undergrowth or in trees. *Viverravus* and *Miacis* were characteristic Eocene genera.

THE FISSIPED CARNIVORES [see **Carnivore Taxonomy**]

The fissipeds are the modern and familiar land-living beasts of prey that have been dominant from late Eocene and early Oligocene Superfamily: times to the present day. They are the

dogs and their relatives, the bears, the raccoons and pandas, the varied mustelids such as the weasels, minks, badgers, wolverines, skunks and otters, the Old World civets, the hyenas and the cats. It is probable that at the time the early fissipeds appeared or soon after, the aquatic pinnipeds, the sealions, seals, and walruses, originated. However, the fossil record of the latter carnivores does not extend back beyond the Oligocene epoch.

The twofold division of modern fissipeds into canoids and feloids is based upon various technical details of anatomy, especially the structure of the tympanic bulla that surrounds the middle ear. When fossils are taken into account the distinction between these two groups of carnivores is not very sharp, since some of the primitive forms in each superfamily approach each other closely in structure. On the whole, however, this makes a good practical arrangement for grouping the fissiped carnivores beyond the miacids, and it probably expresses their basic relationships with a fair degree of accuracy.

THE CANOID CARNIVORES

The early canoid and feloid carnivores were, like the miacids, probably forest-dwellers that preyed upon the small game they could catch in the undergrowth and in trees. *Cynodictis,* a late Eocene form, and *Pseudocynodictis* (properly known as *Hesperocyon)* of the Oligocene were among the first canids, and although they retained many characters of their miacid ancestors they showed certain features that were to characterize the evolutionary development among the dogs or canids. There was some elongation of the limbs and feet in these early dogs, and the carnassial teeth were more highly specialized as shearing blades than they had been in the miacids. Also, the brain-case was expanded. Thus we see the early dogs embarking along the evolutionary path of long feet and limbs for running, sharp carnassial teeth for cutting meat, and a large brain, an indication of a high degree of intelligence. In these ways the dogs advanced; in other ways they have remained as comparatively primitive carnivores. For instance, there has been little loss of teeth or change in the form and function of the dentition beyond the stage characteristic of the late Eocene or early Oligocene carnivores.

From the small Oligocene *Hesperocyon* the canids progressed to the Miocene genus, *Cynodesmus,* from thence to the Pliocene *Tomarctus,* and finally to the modem dogs like *Canis* of Pleistocene and Recent times. This sequence represents the "main line" of canid evolution, but as so often happens there were several side lines of canids during Miocene and Pliocene times. *Amphicyon* was a very large, heavy, rather clumsy dog with a long tail.

Borvphagus was another large dog, with a very deep, heavy skull and robust teeth. *Borophagus* and various related genera constituted an important line of Miocene and Pliocene dogs.

In Pleistocene and Recent times the history of the dogs reached its culminating phases in the differentiation of our modern canids, the wild dogs, wolves, and foxes of the northern hemisphere, and various highly specialized dogs of South America and Africa. These are intelligent animals that hunt and live in family groups and packs. For the most part they run down and kill their prey, often pursuing their victims over many miles of terrain. The foxes, however, are more solitary in habits and frequently hunt by stealth or by cunning strategems, for which they are justly famous in folklore.

The social instincts of the wild dogs have made them ideal as companions, and they were

certainly the first animals to be domesticated. Man and dog lived together and worked together as early as Neolithic times, and this relationship has continued ever since, through a period of many thousands of years. It is difficult to make positive statements as to the origin of the domestic dog, *Canis familiaris,* but these friends and companions of home and field are probably in the main of wolf ancestry. Since the dogs are structurally primitive in many respects, they are genetically plastic. The truly astonishing variety of modem breeds of dogs is a proof of this that needs no elaboration in words. Under the guiding hand of man, the domestic dog has indeed departed far from his wild, wolflike ancestor in form and physical appearance, yet psychologically he is still a wolf-an intelligent, friendly canid that likes to run and hunt.

In Miocene times some dogs began to evolve as large, heavy carnivores. From such an ancestry it is probable that the first bears, typified by *Ursavus,* of Miocene age, arose. From *Ursavus* there evolved the Pliocene *Indarctos* and related genera, with massive skulls and robust teeth. In carnivores of this type the carnassial teeth lost their shearing function, and the molar teeth became square in outline, with blunt cusps. At the same time the legs and feet became heavy and the feet short, and the habit of pursuing the prey declined. The tail was reduced to a mere stub. Thus the bears evolved as massive middle and late Cenozoic carnivores. The trend of bear evolution reached its climax in the Pleistocene and recent bears, typified by Ursus. In the modem bears, some of them the largest of all land carnivores, the molar teeth are elongated and the crowns are complicated by a wrinkling of the enamel. This is obviously a specialization for an omnivorous diet and a great departure from the predominantly meat-eating habits of the dogs.

Bears are very adaptable animals, as are the dogs for that matter, and they are widely distributed throughout the world. The middle Tertiary origin and the evolution of the bears took place in the northern hemisphere. They entered South America during Pleistocene times, but curiously they never invaded Africa.

From the central canid stock there was another evolutionary trend that also led away from the chase and the kill, to adaptations for climbing and an omnivorous diet. This was the line of the procyonids-the raccoons and their allies.

The procyonids; probably diverged from the canids during the Oligocene epoch, for in Miocene times they were well established, as indicated by the genus *Phlaocyon,* a small, climbing carnivore with handlike forepaws, flexible limbs, a dentition in which the carnassials had lost their shearing function, and molar teeth that were square with blunt cusps. The adaptations characteristic of *Phlaocyon* have been continued with little change in the modem *Bassariscus,* the ring-tailed "cat" or cacomistle of Mexico and the southwestern United States. Here we see in effect the structural ancestor of the procyonids, a small carnivore that lives among rocks or in trees, where it eats almost anything it can catch or gather. It is partly a meat-eater, partly a vegetarian.

From *Phlaocyon* the advanced procyonids evolved during late Tertiary times. Many of them have remained relatively small and have been confined to North America, where they originated, or to South America, a region that they invaded. These are the familiar raccoons, *Procyon* and its relatives, the coatis, *Nasua,* and the kinkajou, *Potos*, of South and Central America, and some other forms. All of them are forest-living animals that spend much of their time in the trees or along the banks of streams, where they feed upon a great variety of foods. The catholic diet of the common raccoon of North America is well known to many farmers and

fishermen, who have had their fields, their chicken coops, or their fishing grounds raided by these intelligent little carnivores.

The pandas evolved in Eurasia during middle and late Tertiary times. The lesser panda, *Ailurus,* now lives in the Himalayan region, but fossils show that it once extended as far west as England. It looks very much like an enlarged raccoon, even to the ringed tail and the mask on the face. The giant panda, *Ailuropoda,* was rather widely distributed in Asia during Pleistocene times, but is now confined to a comparatively small area in western China. This animal is as large as a bear, and like a bear is heavily built, with a very short tail. The relationships of the giant panda have been long debated. Some authorities have included it with the lesser panda among the procyonids or raccoons. Detailed studies would seem to indicate, however, that it probably should be regarded as an ursid or bear. The giant panda is interesting because it is a carnivore that has turned completely herbivorous. The molar teeth are low crowned, with blunt cusps, and the enamel is wrinkled, making a broad grinding surface. These decorative and popular animals live exclusively upon green bamboo shoots.

Although the dogs, bears, and procyonids; are closely related, the mustelids, on the other hand, are set apart from the other canoids, and have been a separate phylogenetic line since the time of their origin, at the beginning of the Oligocene epoch. *Plesictis,* one of the first of the mustelids, was a small carnivore of generalized structure, with tribosphenic molars. However, the carnassial teeth were well developed, and the posterior molars were suppressed. The face was short and the braincase long and expanded, characters quite typical of the mustelids. From this ancestry the mustelids evolved with bewildering variety during middle and late Cenozoic times. Their evolution was characterized by the development of several short-lived lines of adaptive radiation, now extinct, which add to the complexity of mustelid phylogeny and make an interpretation of their history particularly difficult. It is not possible at this place to go into the details of mustelid development, but perhaps it may be useful to discuss briefly the modem mustelids, the persisting groups that have emerged from the complex melange of middle and late Tertiary mustelid history.

Generally speaking, there are about five groups of modem mustelids, all of subfamily rank. In the first place there are the primitive mustelids, the mustelines, many of them retaining the characters of their middle Tertiary ancestors. In this group are the weasels, the martens, the minks and their relatives, and the wolverines. These are very active, highly carnivorous animals, living in trees and on the ground in the forests. Some of diem, especially the weasels *(Mustela),* are savage out of all proportion to their size.

The second mustelid group is the mellivorines, now represented by the ratel or honey badger *(Mellivora)* of Africa. Specializations here have been toward a ground life and a varied diet. A third group is the melines, the badgers of Eurasia *(Meles)* and North America *(Taxidea).* They are large, heavy mustelids that live in burrows. They are aggressive, but not highly carnivorous.

The fourth modem group of mustelids is the mephitines, the skunks *(Mephitis* and other genera) of North America. These small mustelids are ground-dwellers that burrow, and feed upon a great variety of things- small animals, insects, worms, berries, plants, carrion, and garbage. The skunks are protected by special scent glands that emit a strongly scented liquid, the smell and effects of which need no description for American readers.

Finally there are the lutrines, *Lutra,* and its relatives, the otters. They are aquatic mustelids

specialized for catching fish, or even for feeding upon shellfish. Many of them Eve along the banks of streams, but the sea otters of the Pacific Ocean spend their life almost entirely in the shallow waters along the coasts.

From this brief review it can be seen that the evolution of the mustelids has been highly divergent, and of all the carnivores they certainly show the widest range of adaptive radiation.

THE FELOID CARNIVORES

The most primitive of modem carnivores are some the Old World civets, little modified descendants of the progressive miacids, that may be regarded as essentially late Eocene carnivores living on into modem times. The genet, *Genetta,* now inhabiting the Mediterranean region, is very near to the central stock from which all the civets have evolved. This is a small, forest-living carnivore, with a long body and a very long tail. The limbs are rather short and the feet are provided with claws that can be withdrawn to some extent, like the retractile claws of a cat. The skull is elongated and low, and narrow, the carnassial teeth are sharp, to form efficient shearing blades, and the molars retain the primitive tribosphenic pattern. The last molars are absent. The modem genet has a spotted coat, and it is probable that this is a primitive color pattern that has been retained through the ages. It has specialized scent glands for marking territory and for defense, a characteristic adaptation in the modem civets.

The civets are abundantly represented in considerable variety among the modem faunas of Asia and Africa. From a central, conservative stem. approximated by the genet and its relatives, the viverrids have branched along varied lines of adaptive radiation. One branch is composed of the various African and Oriental palm civets and the binturong or bearcat of Asia, this last one of the largest of the civets. An extreme offshoot of this general line of adaptation is *Eupleres,* the falanouc of Madagascar, in which the teeth have been reduced to relatively simple pegs, as an adaptation to eating ants and insects. Another evolutionary branch is represented by *Cryptoprocta,* the fossa of Madagascar, a very catlike civet. The position of this carnivore, whether a catlike civet or a civetlike cat, has long been debated. It is very possible that the fossa arose from a primitive civet, but near the ancestry of the cats, so that it shares catlike as well as civet characters. Finally, one large branch of the civets is the group of mongooses, small active civets that are famous as predators upon snakes and upon various small mammals.

Civets first appear in sediments of upper Eocene and lower Oligocene age, and are represented by such genera as *Stenoplesictis* and *Palaeoprionodon.* The subsequent epochs of the Cenozoic era reveal very little of the past history of the viverrids, probably because these predominantly tropical, forest-living carnivores were rarely preserved as fossils. The few genera known from Miocene and Pliocene sediments in Eurasia indicate that the viverrids continued as very primitive carnivores during much of Tertiary times. Thus the sequence from *Palaeoprionodon* through middle and late Tertiary forms, of which the Mongolian genus *Tungurictis is* an example, to the generalized modern civets, indicates only a minor amount of evolutionary progress.

In Miocene times one evolutionary branch split from the central civet stock and followed a trend toward increase in size and particularly the development of a heavy skull and very robust teeth. This was the line of hyenas, which share with the bears the distinction of being the youngest among the families of carnivores. Simply stated, the hyenas are very large, heavy descendants of the civets, in which the legs have been elongated for running and the teeth and

jaws usually enlarged for cracking bones. The enlargement of the teeth is concentrated especially on the last two cone-shaped premolars, which are used for breaking the bones of large carcasses on which the hyenas feed. The jaws and the jaw muscles are necessarily very strong. The carnassials are highly specialized shearing blades in the hyenas, and the molars behind the carnassials are reduced to mere remnants.

Ictitherium, of late Miocene and early Pliocene age, was the first hyena. This carnivore was truly intermediate between the civets and the hyenas, larger and heavier than the former but much lighter and smaller than the latter. The step from *Ictitherium* to advanced and fully modern hyenas was a quick one, and we find fossil hyenas very similar to the modern animals in sediments of early Pliocene age. In effect the hyenas quickly reached the peak of their adaptational. perfection soon after they split from the civets, and they have maintained their specialized form with little change since it was first attained. Hyenas live in Asia and Africa at the present time; but during the Pleistocene epoch they were widely distributed through northern Europe. One modem hyena, *Proteles,* the aardwolf of South Africa, is curiously specialized for eating termites, and the cheek teeth are reduced to small pegs, although the canines remain large.

The cats had an evolutionary history something like that of the hyenas, but it began at an earlier date. Once having split from a viverrid ancestry and, once having departed from the civet stem, the cats very rapidly evolved into fully specialized cats. They have maintained their high degree of specialization without much change for millions of years. The separation of the first members of the cat family from their civet ancestors took place during late Eocene times, and the upper Eocene genus, *Proailurus,* may represent an early step in the evolution of the cats. By early Oligocene times the cats were highly evolved cats, not very different from their modem relatives. Of all land-living creatures, the cats are among the most completely specialized for a life of killing, and for eating meat. They are very muscular, alert, supple carnivores, fully equipped for springing upon and destroying animals as large or larger than themselves. They generally hunt by stealth, and catch their prey with a long bound or a short rush of great speed. The limbs are usually heavy and strong, and the feet are provided with sharp, usually retractile claws that are used for catching and holding their victims. The neck is very heavy to take up the severe shocks imposed by the violent action of the head and the teeth. The teeth are highly specialized for just two functions-stabbing and cutting. The canine teeth are therefore long and strong, and the carnassials are large, perfected shearing blades; the other teeth are reduced or completely suppressed. The smaller cats are adept treeclimbers, but the larger cats spend most of their time on the ground.

All cats are constructed pretty much to the pattern that was established by the cats of early Oligocene times. However, there seems to have been a dichotomy in the evolutionary history of the cats that went back to the time of their definition and continued until the end of the Pleistocene epoch. On the one hand, the cats evolved as active, fast-moving predators, the normal cats with which we are familiar; on the other hand, they developed as the comparatively heavy and slower saber-tooth cats. The ancestry of the normal or "feline" cats is exemplified by *Dinictis* of Oligocene age; that of the sabertooth cats by *Hoplophoneus,* also of Oligocene age.

Both of them were medium-sized cats with long tails. In *Dinictis* the upper canine teeth were large and heavy, and the carnassials were well-developed shearing blades. There were premolar teeth in front of the carnassials, but the molars behind the shearing teeth were greatly reduced. In *Hoplophoneus* the upper canine teeth were elongated sabers, and there

was a flange on the lower jaw to protect these down-pointing swords when the mouth was closed. The carnassials were specialized cutting blades, and the other cheek teeth were greatly reduced or suppressed.

As the feline cats evolved, the canine teeth became relatively smaller than they had been in *Dinictis;* but otherwise the dentition changed very little. As the saber-tooth cats evolved, the canine teeth remained large, as they had been in *Hoplophoneus.* Such trends indicate that the feline cats became increasingly perfected for catching and killing agile animals, while the saber-tooth cats became specialized for killing large, heavy animals.

The culmination of saber-tooth evolution was reached during the Pleistocene epoch, in the large saber-tooth cat, *Smilodon.* This cat was as large as a modem lion, and the upper canines were huge daggers of impressive proportions. Anatomical studies indicate that *Smilodon* was able to open the mouth very wide, thus clearing the way for the large canine sabers to function. In attacking its prey, *Smilodon* evidently struck down very hard with the sabers, using the force of the strong neck and the weight of the shoulders and body to give power to the thrust. This was an effective method of hunting, as long as there were large, comparatively slow animals available. But as the Pleistocene drew to a close, the large animals on which the saber-tooth cats had preyed became extinct, and so did the sabertooth. They mere unable to compete with their agile feline cousins in the chase of speedy animals.

The feline cats, on the other hand, have continued into modern times with great success. As said above, cats are cut pretty much to one pattern, yet there is a great variety of modem cats, differing mainly in size and in the habitats that they frequent. The modem cats show a distinct division into the typical cats, *Felis* (and related genera), on the one hand, and the swift-running cheetah or hunting leopard, *Acinonyx,* on the other. As for the typical cats, they are found throughout the world except in Australia and on remote islands. There are many small cats, and from some of these, probably from a mixture of the ancient Egyptian wild cat and the European wild cat, our modem domestic cat has descended. The large cats are so familiar as to need no particular description - lions and leopards in Africa, leopards and tigers in Asia, jaguars and cougars in the Americas.

Cats did not enter South America until Pleistocene times, when both feline and sabertooth cats invaded that continent. The invasions of South America by the cougar or puma from the north established one of the widest known ranges for a single species of mammal, except man, for this cat extends from the snows of Canada to the southern tip of South America. A comparable distribution is typical of the Old World leopard, which ranges from the southern portion of Africa into northern Asia.

THE PINNIPED CARNIVORES

The pinnipeds-the sea lions, walruses and seals-appear in the geologic record during the transition from Oligocene to Miocene time, as exemplified by *Enaliarctos,* known from an almost complete skeleton discovered in California. *Enaliarctos,* although undoubtedly a pinniped, retains numerous anatomical characters that indicate its derivation from terrestrial canoid ancestors. Thus the evidence of this earliest known pinniped clearly points to a monophyletic origin for these carnivores, in contrast to the frequently held view that the pinnipeds are diphyletic, with the sealions and walruses derived from canoid ancestors while the seals presumably originated from mustelid progenitors.

In making the transition from life on the land to life in the water, the pinnipeds became streamlined for swimming. However, their adaptations along this line have never been as complete as in some of the totally marine tetrapods, like the ichthyosaurs or the whales, for they have retained a flexible neck and have failed to evolve a dorsal fin or a propulsive tail. Perhaps the tail had been reduced to such a point in the ancestors of the pinnipeds that it was, so to speak, never available for transformation into a propeller. Consequently, the pinnipeds have had to rely on the limbs in combination with body movements for propulsion through the water. In these carnivores all four feet are transformed into paddles, with webbing between the toes. The front paddles are used for balancing and steering, as well as for making propulsive thrusts. The back paddles are turned back and function like a sort of caudal fin when these animals are in the water. In the sea lions *(Zalophus)* and walruses *(Odobenus)* the back flippers can be turned forward or back at will, and are used when on land as aids to locomotion. In the seals (Phoca) the back flippers are permanently fixed in the backward direction, so that when seals are on land or on ice floes they have to move along on their bellies by a "humping" motion of the body.

Sea lions are found today along the Pacific coast, while the walruses are found in both the Pacific and Atlantic oceans. The seals are widely distributed along the seacoasts of the world.

The teeth are greatly modified in all the pinnipeds. The incisors are commonly reduced or suppressed, whereas in most pinnipeds the premolars and molars are secondarily simplified to the form of pointed, cone-shaped teeth, all much alike. Such a dentition is useful for catching fish. The walruses have large canine tusks, and the cheek teeth, reduced in numbers, are broadened into crushing mills, with which these carnivores grind up the oysters and clams on which they feed. The sea lions have small external ears; in the other pinnipeds the external ear lobes or pinnae are completely suppressed.

The seals are more highly adapted to an aquatic life than are the sea lions and walruses. The teeth are highly modified from the primitive carnivore pattern, so that in some seals the teeth behind the canines are distinguished by having accessory "cusps" or points on a midline in front of and behind the principal cusp. Such teeth are very efficient for grasping and holding slippery fish.

Perhaps the most remarkable adaptations among the seals are those allowing them to make deep and prolonged dives, in which respect they are second only to the whales. An integrated series of specializations in the lungs, the heart and the circulatory system, provide some of these carnivores with an ability to dive to depths as great as 600 meters, and to stay submerged for more than an hour. It is probable that such adaptations were present in many of the seals of Cenozoic age.
