EVOLUTION IN CARNIVOROUS MAMMALS

by R. J. G. SAVAGE

Nineteenth Annual Address, delivered 17 March 1976

In tauros Libyci ruunt leones;
Non sunt papilionibus molesti.

(In Africa lions attack bulls;
they do not molest butterflies.) *Martial*

ABSTRACT. Carnivorous mammals are identified on the basis of their carnassial dentition and their predatory preference for vertebrates. Jurassic pantotheres possess a dentition from which arose both carnivore and herbivore specializations. The changes towards carnivorous feeding involved emphasis on the cutting functions of the cheek teeth, with corresponding reduction of the crushing activities. A carnivorous mode of living evolved twice among the marsupials (borhyaenids in South America and some dasyurids in Australia) and twice among the placentals (Creodonta and Carnivora). Characteristics of the post-cranial skeleton in carnivores are mentioned. Features of the jaw mechanics, the brain, and the senses (smell, sight, and hearing) are discussed. Specializations of sabre-like canines and crushing premolars are discussed. The form and function of the carnassial dentition and its evolution are analysed.

THE evolutionary history of elephants and horses is well documented yet, despite a reasonable fossil record, there is surprisingly little information readily available on the evolutionary history of carnivores. Detailed taxonomic accounts of faunas and phylogenetic studies of families abound, but the literature on functional aspects of carnivore evolution is meagre. Three papers are outstanding exceptions to this generalization: Denison (1938) on creodonts, Simpson (1941) on sabre-toothed carnivores, and Crusafont and Truyols (1956) on the evolution of carnassial teeth.

THE LIVING CARNIVORE

Let us examine a lion as a living representative of one of the peaks of carnivore evolution and see what distinguishes it from the herbivorous gazelles it preys upon and also from its shrew-like ancestors of the earliest Tertiary. What in other words, starting from a shrew, would be the modifications required to produce a lion?

To earn a living as a carnivore, the first essential is to locate your victim—before he locates you. This means having very acute sensory receptors (vision, hearing, and smell), and a first-class brain to integrate rapidly and efficiently and to analyse the information. In the lion, as often in carnivores, sight is the most important sense, with the eyes set well forward giving stereoscopy. Hypermetropic vision, and ability to judge distances accurately, enable the lion to locate its victim precisely. The next move is to creep up close stealthily; ability to move silently close to the ground and to take maximum advantage of cover is essential. Then, to make contact, a burst of very high speed is needed; long legs with muscles aligned to give maximum mechanical advantages for speed and physiologically adapted for rapid

[Palaeontology, Vol. 20, Part 2, 1977, pp. 237-271]

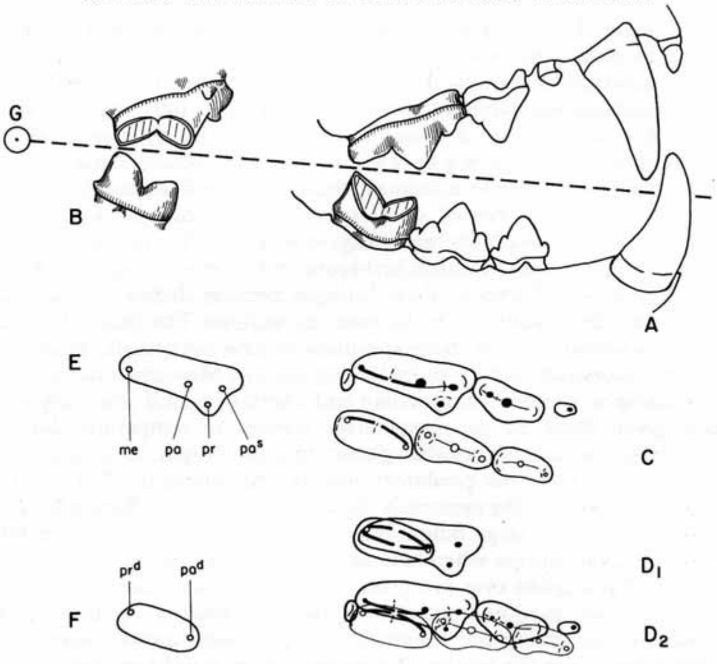
contractions, ensure success. The attack on the victim must be swift to be effective; usually the gazelle is thrown off balance with a sideways crash which enables the lion to plunge its canine teeth into the throat region while holding the prey down with the claws of its forepaws. The carnivore will then rip open the carcass, using incisors and canines. The meat is torn off and cut into chunks, with the powerful closing muscles of the jaws operating the scissor-like carnassial blades of the cheek teeth. But even with all these refinements, the lion has on average only about a one in five chance of success; it is clearly not a game for amateurs.

There is no sharp distinction between insectivore and carnivore. Neither is a single natural order of mammals; they reflect modes of living. There are some ten orders of mammals that are basically insectivorous, and about twenty orders that are essentially herbivorous. There remain only two that are fundamentally carnivorous, the Creodonta and the Carnivora, with the Marsupialia evolving two carnivorous stocks from insectivorous ancestors. In this review we shall omit the Cetacea, which would make the fourth carnivorous order; they are so specialized as marine aquatic mammals that the carnivore specializations are relatively secondary and quite unlike those of land mammals.

The two prime essentials of a carnivore are that its diet include a substantial proportion of vertebrates, and that it possesses a carnassial dentition. By specifying vertebrates, we can eliminate the insectivores, though this also leaves out animals like the mollusc-feeding sea otter *Enhydra*, and, of course, those members of the order Carnivora which have become secondarily herbivorous, such as the pandas and some of the bears. A few herbivores have produced omnivorous stocks that are partially carnivorous; for example, some pigs and the extinct mesonychids have large incisor or canine tusks and may supplement their diet with animal food, but they never achieve a carnassial dentition which is the hallmark of a truly carnivorous land mammal. When one or more pairs of upper and lower cheek teeth develop a blade structure, such that on closing the jaws these blades pass over each other like scissor blades, this is spoken of as carnassial specialization (text-fig. 1). Slicing teeth develop in some herbivores, e.g. pyrotheres, deinotheres, barytheres, and macropodids; these are always on transverse lophs, extend along all or most of the cheek dentition, and are not self-sharpening, so that with wear the dentition becomes flattened. The extinct marsupial *Thylacoleo* is a puzzling exception; it has a 'carnassial' specialization, but otherwise retains many phalanger characters, which makes it difficult to interpret it as anything but a specialized herbivore (Gill 1954).

THE ANCESTRY OF CARNIVOROUS MAMMALS

The mammals of the Jurassic were essentially small insectivorous beasts and probably nocturnal. Multituberculates were the exception in being specialized rodent-like herbivores, but an aberrant sideline destined to leave no descendants. By mid Cretaceous times we can recognize, in the main stream of mammalian evolution, a fork into marsupial and placental stocks. While this cleft is based fundamentally on reproductive differences, some dental characters enable us to detect it; for example, the presence of certain stylar cusps on the outer margin of the upper molars is a marsupial feature unknown in placentals. Though our knowledge is as yet very



TEXT-FIG. 1. Views of the carnassial dentition of *Felis*. A, lateral view, P^4 and M$_1$ in relief; B, internal view of P^4 and M$_1$; C, occlusal view of upper and lower cheek dentition, carnassial blades in heavy lines; D$_1$, carnassial teeth at beginning of occlusion; D$_2$, cheek dentition in full occlusion; E, cusps of P^4: *me* metacone, *pa* paracone, *pa^s* parastyle, *pr* protocone; F, cusps of M$_1$ = *pa^d* paraconid, *pr^d* protoconid; G, position of glenoid jaw articulation with respect to A.

slender, there is evidence that during mid Cretaceous times there were considerable floral changes. Table 1 (after Hughes 1976) shows the proportion of flowering plants (angiosperms) to other megaplants. In the earliest Cretaceous the gymnosperms and pteridophytes share the total in equal proportions. By latest Cretaceous the angiosperms have taken over 90% of the flora, the number of gymnosperms has dropped dramatically, and although the ferns have actually increased in species numbers, their proportion of the total flora is drastically reduced. Angiosperms arose in the early Cretaceous and rapidly expanded; this must surely have lead to a diversification

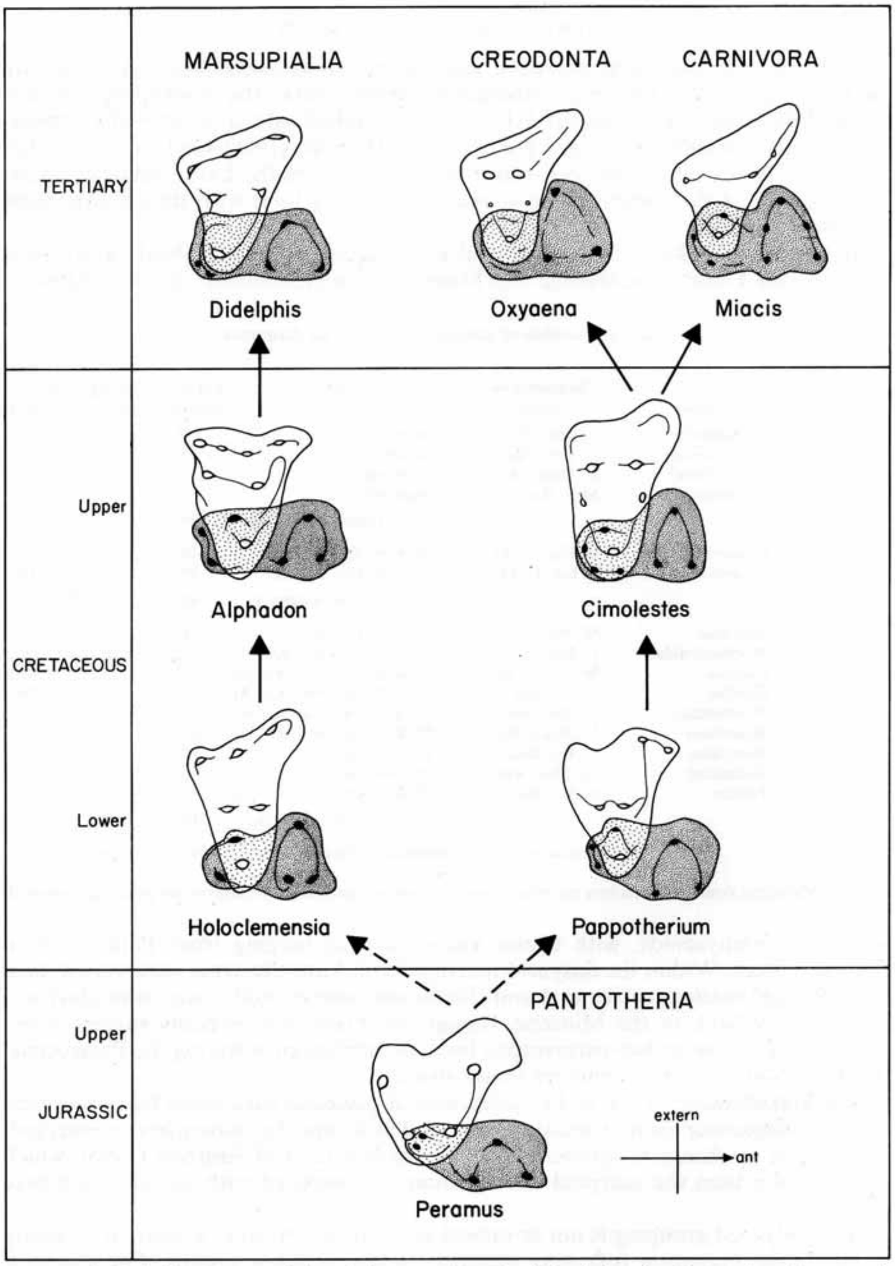
TABLE 1. Estimated number of megaplant species (after Hughes 1976).

	Pteridophyte	%	Gymnosperm	%	Angiosperm	%
Recent	10 000	3·4	640	0·2	286 000	96·4
Latest Cretaceous	2 000	9	500	2	20 000	89
Earliest Cretaceous	1 500	50	1 500	50	0	0

of the insect fauna. The Cretaceous insect record is, however, very poor, and the most that can be said is that when good faunas are next seen, in early Tertiary, they show a major advance on Jurassic faunas, with a much greater diversity (Crowson *et al.* 1967). Insectivorous mammals usually include fruit, nuts, and berries in their diet; the much greater range of these, and probably also of insects, in the Late Cretaceous is likely to have been a critical factor in mammalian radiation.

By Late Cretaceous times the mammals show considerable diversity, though still largely within the same niches of small sized insectivorous stocks. Within these faunas, however, we can detect the beginnings of several orders of Tertiary mammals, in particular the early trends towards herbivore and carnivore lineages. By terminal Cretaceous and earliest Tertiary, these lineages became distinct as the mammals invaded the niches left vacant by the dinosaur extinctions. The detailed stages of the take over are not known, though many speculations have been made. Small mammals could compete successfully with reptiles throughout the Mesozoic only by occupying niches unavailable to reptiles. Mammalian endothermy, even if relatively inefficient, would have given them an advantage over reptiles in temperate climates (and temperate climate microniches) enabling them to feed at night, so long as they could hide during the day from the predatory lizards and dinosaurs. The need to hide imposed size limitations on the mammals; furthermore, it is not efficient for an insectivorous mammal to grow large unless bulk food is available. Insects in bulk only became possible food sources when colonial ants and termites evolved, probably in the Oligocene. Mammalian eyes are primarily designed for nocturnal vision, since the receptor cells are predominantly rods; they secondarily became adapted for diurnal vision by increasing the numbers of cones. Here again, mammals would have the advantage over the smaller dinosaurs, which may have been endothermic but are likely to have had poor night vision. When the diurnal niches became available in the terminal Cretaceous, the mammals were ready to invade them. Gradual improvements in their physiology, in particular temperature control and metabolic rates, enabled them to increase in size and to acquire specialized trophic preferences. Tooth adaptations evolved in the herbivore lineages to crush food, and in the carnivores to cut it into chunks small enough to swallow.

Text-fig. 2 illustrates trends in mammalian molar teeth during the Mesozoic. While named genera are chosen as examples, this does not imply that they are on direct lines of descent, only that we can trace likely lineages from the stocks to which they belong. In the Jurassic, a pantothere such as *Peramus* has a cheek dentition with primitive tribosphenic pattern, that is to say upper and lower wedge-shaped triangular teeth that cut against each other. A detailed and lucid analysis of the functional principles of tribosphenic molars is to be found in Crompton and Sita-Lumsden (1970). *Peramus* has a good insectivorous dentition, capable of cutting up small and relatively soft food. From the Early Cretaceous of Texas come *Holoclemensia* and *Pappotherium*, which probably respectively belong to primitive marsupial and placental stocks. Their teeth are rather similar and functionally show a considerable change from those of *Peramus*; they have acquired a protocone cusp on the inner side of the upper molar, and a talonid or basin has developed in the lower molar to receive the impact of the protocone on occlusion. Thus a crushing action is now added to the slicing action of the Jurassic mammals. By the Late



TEXT-FIG. 2. Evolution of carnassial teeth; lower molars stippled and showing the overlap of upper and lower teeth in full occlusion.

Cretaceous, the marsupial *Alphadon* and the placental insectivore *Cimolestes* are in their dental pattern almost unchanged descendants; the marsupials are distinguished by having a broad stylar shelf on the labial side. The ratio of crushing/slicing varies in different taxa. Crompton and Hiiemae (1970) have estimated that in the living opossum *Didelphis*, which differs little from the Late Cretaceous marsupials, 60% of the chewing time is spent on pulping food with their sharp cusps and 40% on cutting.

In the early Tertiary, both marsupial and placental stocks evolved carnivorous lineages (see Table 2 and text-fig. 18). From didelphid marsupials in South America arose the borhyaenids, with twelve known genera ranging from Palaeocene to Pliocene times. Within the dasyurid marsupials of Australia arose carnivorous taxa such as *Sarcophilus* (native cat) and *Thylacinus* (native wolf); we know dasyurid history only back to the Miocene, though its origins are certainly earlier. From placental insectivores two carnivorous lineages differentiated during the Palaeocene, the Creodonta and the Carnivora (*sensu stricto*).

TABLE 2. Families of terrestrial carnivorous mammals.

Orders	Families	Stratigraphic range	Geographic distribution	Extinct genera	Living genera	Total no. of genera
MARSUPIALIA	(Didelphidae)	L. Cret.-Rec.	N. & S. Am., Eu.	(1)		(1)
	Borhyaenidae	U. Pal.-Plio.	S. Am.	25	-	25
	(Dasyuridae)	U. Oligo.-Rec.	Australia	2	2	4
	(Phalangeridae)	Mio.-Rec.	Australia	(1)	-	(1)
			Total MARSUPIALIA	29	2	31
CREODONTA	Oxyaenidae	U. Pal.-U. Eo.	N. Am., Eu., As.	10	-	10
	Hyaenodontidae	L. Eo.-U. Mio.	N. Am., Eu., As., Af.	35	-	35
			Total CREODONTA	45	-	45
CARNIVORA	Miacidae	M. Pal.-L. Oligo.	N. Am., Eu., As.	16	-	16
	Amphicyonidae	U. Eo.-U. Mio.	N. Am., Eu., As., Af.	29	-	29
	Canidae	M. Oligo.-Rec.	N. & S. Am., Eu., As., Af.	22	13	35
	Ursidae	U. Eo.-Rec.	N. & S. Am., Eu., As., Af.	22	6	28
	Procyonidae	L. Mio.-Rec.	N. & S. Am., Eu., As., Af.	14	8	22
	Mustelidae	L. Oligo.-Rec.	N. & S. Am., Eu., As., Af.	65	29	94
	Viverridae	U. Eo.-Rec.	Eu., As., Af.	11	36	47
	Hyaenidae	M. Mio.-Rec.	Eu., As., Af.	8	3	11
	Felidae	U. Eo.-Rec.	N. & S. Am., Eu., As., Af.	31	3	34
			Total CARNIVORA	218	98	316
		Total MARSUPIALIA, CREODONTA and CARNIVORA		292	100	392

Note. Marsupial families in brackets are mainly non-carnivorous, and only the carnivorous genera are counted.

The classification of the higher categories of placental carnivores has undergone major changes over the past decade, and no widely accepted grouping has yet emerged. The degree of change is apparent when the classification of Simpson (1945), which has for long been the accepted classification, is compared with the one used here (Table 3).

The proposed grouping is not as radical as might at first sight appear; it is largely a tidying-up operation following detailed studies on some groups. For almost a decade it has been accepted that the Arctocyonidae and Mesonychidae are condylarths and not creodonts; they lack carnassial specializations and have developed crushing dentitions. The only remaining creodonts are the truly carnivorous oxyaenids and hyaenodontids. The miacids are the accepted ancestral stock of living carnivores and, since both creodonts and miacids can be traced independently back to an insectivore ancestry in the Palaeocene, I consider that the Creodonta and Carnivora should have equal rank as orders. Savage (1957) suggested that the pinnipeds were probably diphyletic. This has been followed up by other authors, and new discoveries, especially that of the new sub-family Enaliarctinae (Mitchell and Tedford 1973), have added greatly to our knowledge of aquatic lineages. Unfortunately the phocids have a poor fossil record compared with the otariids; nevertheless it seems likely that the otariids arose via enaliarctines from canoid ancestors, with odobenines as a side line, while the phocids arose from a mustelid ancestor. Acceptance of this diphyletic origin means the disappearance of the pinnipeds, and so also the need for the term fissiped. I have grouped the carnivore families into five superfamilies; this is a fairly orthodox classification more like that of Gregory and Hellman (1939) than that of Simpson (1945). I cannot identify a mustelid ancestor among the canoids, and the family seems more likely to have arisen directly from a miacid ancestor. It appears equally likely that felids and viverrids have independent origins from miacids. The Eocene faunas of carnivores form a complex of taxa which it is sometimes difficult to assign with certainty to living families.

TABLE 3. Classifications of carnivores.

SIMPSON 1945

Superorder FERAE		
Order CARNIVORA		
Suborder CREODONTA		
Superfamily	Arctocyonoidea	(Arctocyonidae)
	Mesonychoidea	(Mesonychidae)
	Oxyaenoidea	(Oxyaenidae, Hyaenodontidae)
Suborder FISSIPEDA		
Superfamily	Miacioidea	(Miacidae)
	Canoidea	(Canidae, Ursidae, Procyonidae, Mustelidae)
	Feloidea	(Viverridae, Hyaenidae, Felidae)
Suborder PINNIPEDIA		(Semantoridae, Otariidae, Odobenidae, Phocidae)

SAVAGE 1977

Superorder FERAE		
Order CREODONTA		
Superfamily	Oxyaenoidea	(Oxyaenidae, Hyaenodontidae)
Order CARNIVORA		
Superfamily	Miacoidea	(Miacidae)
	Canoidea	(Amphicyonidae, Canidae, Ursidae, Procyonidae, Otariidae)
	Musteloidea	(Mustelidae, Phocidae)
	Viverroidea	(Viverridae, Hyaenidae)
	Feloidea	(Felidae)

THE GEOMETRY OF THE FOSSIL RECORD

There are almost 1000 genera of living mammals, and in trophic terms they can be grouped thus: carnivores 10%, insectivores 23%, herbivores 14%, omnivores 9%, gnawers 38%, and aquatic taxa 6%. Leaving aside the aquatic forms, carnivores today make up about 11% of all land mammal genera. Taking the fossil record into account, we know in all about 3000 mammalian genera, and of these 14% are carnivores; this apparent rise is in part due to smaller mammals (rodents and insectivores) being less well represented in the fossil record. In Table 4 we see an analysis of Tertiary mammal faunas in North America, Africa, and South America. The North American record is good at all periods and shows that carnivores have ranged from 16 to 32% (mean 22%). The African record is much less complete and shows carnivores with a slightly lower range, 12–28% (mean 18%). The South American record yields figures of 3–9% (mean 6%); this much lower range may in part be due to inadequate sampling, but also to the carnivore niche being in part occupied by the large phororhachid birds. If these birds are taken into account, the range for carnivores becomes 3–13% (mean 9%).

TABLE 4. Percentages of carnivores in Cenozoic land mammal faunas.

	North America			Africa		
	Creodonta	Carnivora	Total	Creodonta	Carnivora	Total
Pleistocene	—	21·0	21·0	—	16·0	16·0
Pliocene	—	23·7	23·7	—	28·0	28·0
Miocene	—	31·6	31·6	6·0	6·0	12·0
Oligocene	2·6	13·2	15·8	16·0	—	16·0
Eocene	14·0	5·3	19·3	17·3	—	17·3
Palaeocene	18·4	2·6	21·0	—	—	—

	South America			
	Marsupial carnivores	Placental carnivores	Phororhachoid birds	Total carnivores
Pleistocene	—	9·1	2·4	11·5
Pliocene	4·5	1·8	3·7	10·0
Miocene	6·3	—	7·0	13·3
Oligocene	6·3	—	5·2	11·5
Eocene	3·9	—	—	3·9
Palaeocene	2·6	—	—	2·6

Table 4 also illustrates how the Carnivora gradually replaced the Creodonta in North America, and similarly in Africa, though here the creodonts persisted until the Late Miocene. In South America the early Tertiary carnivores were marsupials; these were supplemented in the Oligocene by phororhachid birds, and finally the placental carnivores invaded that continent in the Pliocene and displaced both native stocks.

Considering now the biomass relationships, the standing crop ratio of predators to prey is around 2–3%; for example, the Ngorongoro crater in Tanzania supports around 25000 large herbivores and around 500 large carnivores. These ratios are fairly constant for endotherms (Bakker 1972); in a Pliocene mammal community in Nebraska analysed by Voorhies (1969), the ratio was around 3%.

Reasonably complete skeletal remains of carnivores are rare, for example the skeletons of only three borhyaenids and six creodonts have been reassembled. A fair number of skulls of most families are preserved, but the majority of taxa are known only from mandibular and maxillary fragments with incomplete dentitions. The Palaeocene record is very weak, with Europe and North America the only continents from which adequate faunas are known throughout the Tertiary.

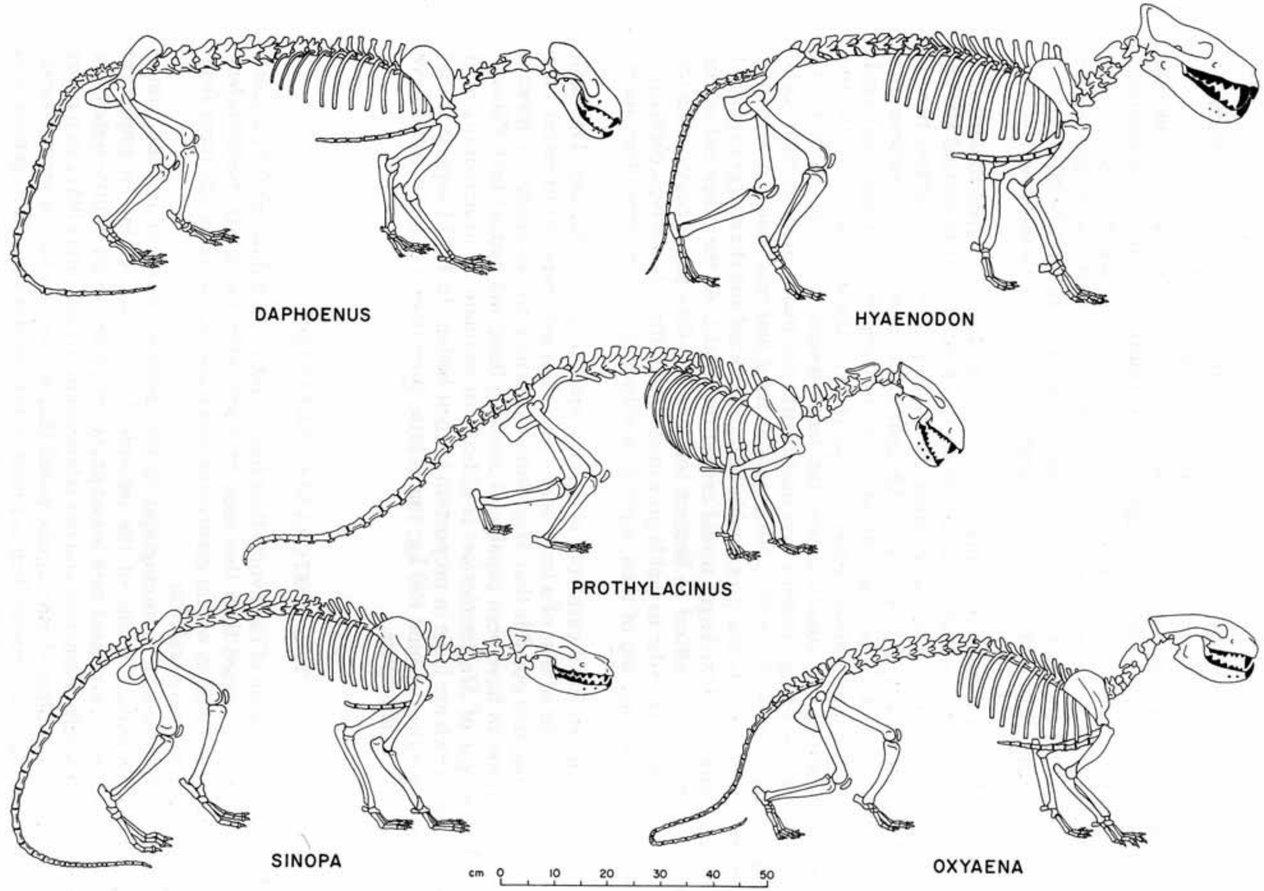
Carnivores have a greater size range than that found in any other mammalian order; they range from a weasel of around 50 gm to a Kodiak bear of around 800 kg. The weasel is about ten times larger than the smallest shrew; the largest bear is about a tenth the weight of an elephant. All small carnivores have to compete with the predatory birds, and the majority of carnivores are small to medium sized. Two-thirds of all living carnivore genera belong to two families, the Viverridae and Mustelidae. Omitting the aquatic otters, the mean weight for mustelids is 4·3 kg and for viverrids is 3·6 kg; rodents and insectivores are major items in their diets. The weasel can cope with small rodents such as mice and rats, but if it were any smaller the range of prey would presumably be too restricted and the energy expended in obtaining small food packages would exceed the intake. At the other end of the scale, carnivores cannot afford to become too large, as they pay a heavy price for this in loss of speed. In order to tackle prey much larger than themselves, carnivores hunt in groups, making use of their superior intelligence to overcome other shortcomings.

The largest known fossil carnivore is the hyaenodont *Megistotherium*. The skull is about twice the size of that of a large bear—and bears are omnivorous rather than truly carnivorous. It is possible that *Megistotherium* was a carrion feeder; it appears from the dentition to have been capable of crushing bone and cutting flesh (Savage 1973). The weight of *Megistotherium* is difficult to estimate as hyaenodonts tend to have heads which are large in proportion to their bodies. In 1973 I suggested that it might have weighed around 880 kg; this is little more than a guess, it could have been half or twice that figure.

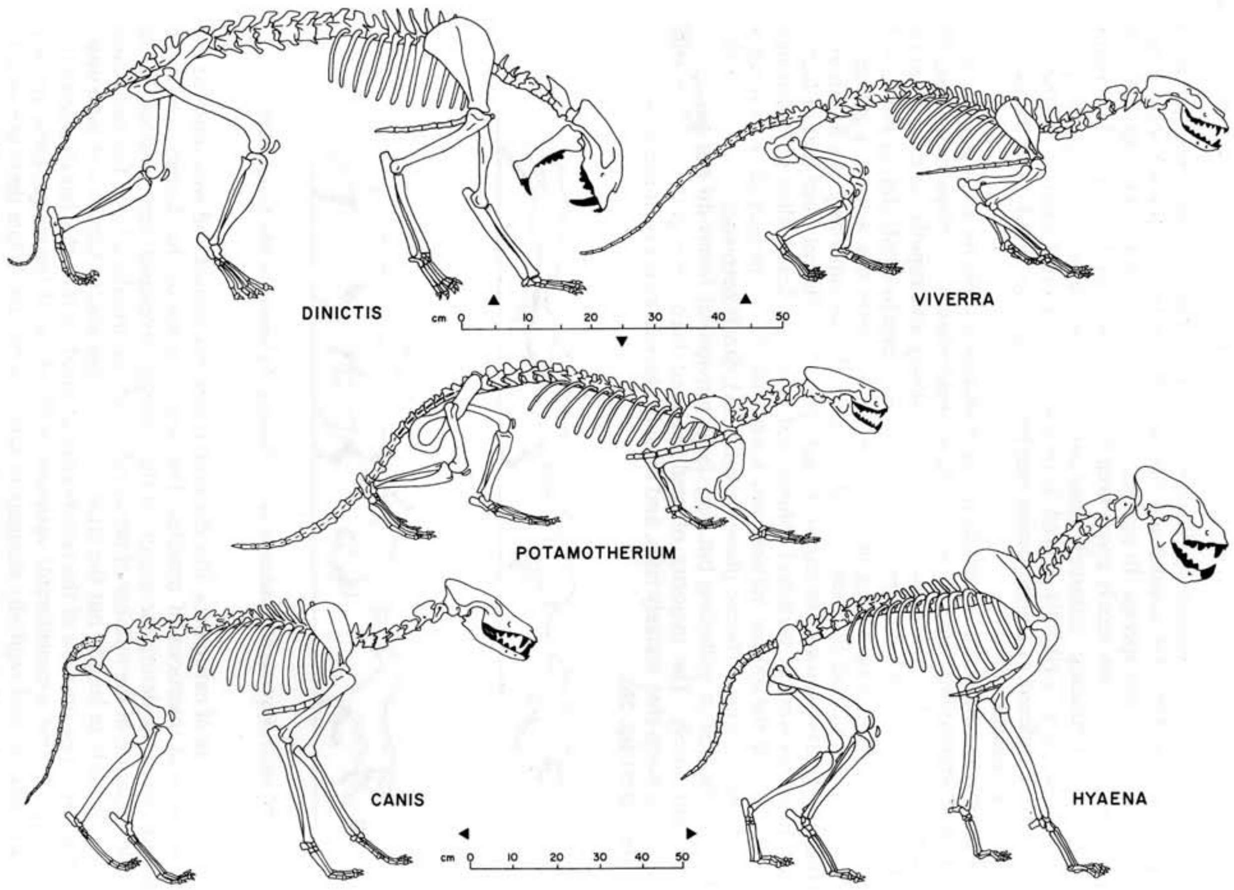
THE POSTCRANIAL SKELETON

The postcranial skeleton of carnivores (text-figs. 3 and 4), excluding the fully aquatic pinnipeds, is less modified than that seen in many other mammals. Nevertheless, there are many differences within carnivores which also show many advances from the primitive insectivore skeleton.

Stromer (1902), in a large monograph on the carnivore vertebral column, stated that the morphological details of the individual vertebrae exhibit no important features consistently correlated with major phyla and therefore are of little systematic importance; they reflect function and not relationship. Hildebrand (1961), in a paper on the body proportions of marsupials, noted that marsupials have a greater variation in postcranial proportions than is found in placental mammals in general and



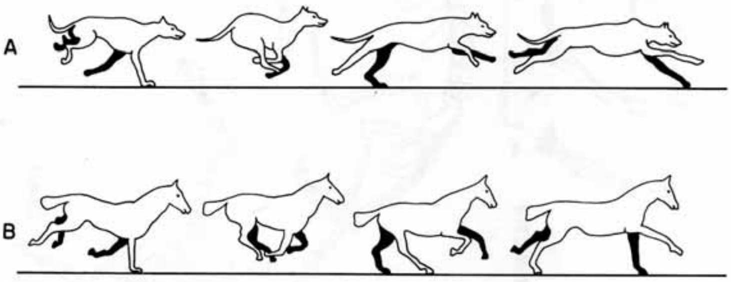
TEXT-FIG. 3. Skeletal reconstructions: borhyaenid *Prothylacinus* (after Sinclair 1906); creodonts *Sinopa* (after Matthew 1906), *Oxyaena* (after Osborn 1900), and *Hyaenodon* (after Scott and Jepsen 1936); amphicyonid *Daphoenus* (after Scott and Jepsen 1936).



TEXT-FIG. 4. Skeletal reconstructions: mustelid *Potamotherium* (after Savage 1957); canid *Canis dirus* (after Merriam 1912); viverrid *Viverra* and hyaenid *Hyaena* (after Blainville 1864); felid *Dinictis* (after Scott and Jepsen 1936).

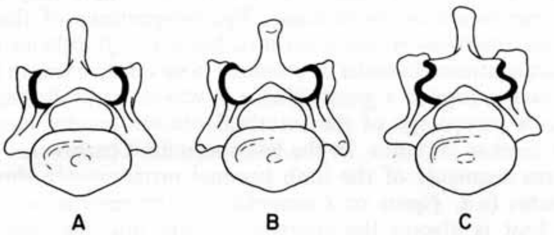
in canids in particular. Within the didelphids there is some correlation between body proportions and habit for aquatic and riparian species, but not for arboreal, semi-arboreal, or terrestrial species. In another paper, Hildebrand (1954) remarked that in the ungulate skeleton nearly every bone has been profoundly modified to adapt the animals for running; although some canids can overtake fast ungulates, none of their bones is so strikingly altered in response to cursorial habit. Nevertheless, most skeletal differences among canids can be attributed to variation in the degree of cursorial specialization.

In carnivores, the prime essentials of the postcranial skeleton are strength, flexibility, and adaptability. Insectivores are scurrying creatures, carnivores are usually cursorial beasts. The carnivores need to move slowly and rapidly, to crouch down and stand up full stretch, to turn rapidly, and sometimes to climb, dig, or swim, and to use the limbs to clasp struggling prey. Most carnivores can achieve a galloping gait, a gait in which all four feet are off the ground simultaneously. As Smith and Savage (1956) have shown, the carnivore gallop is very different from that of herbivores. In carnivores the vertebral column and limbs are flexed, then unfolded like a spring to give the animal vertical and horizontal thrust, projecting it through a parabola with a long airborne phase (text-fig. 5A). Small herbivores may adopt the carnivore method of galloping but very large graviportal forms do not gallop, or do so only rarely. The majority of medium-sized herbivores gallop with a stiff vertebral column that scarcely rises, and most of the energy is expended in swinging the limbs (text-fig. 5B).



TEXT-FIG. 5. Sequence of phases in the gallop of a dog and a horse (after Muybridge 1899).

The vertebrae of carnivores, like the limb bones, are robust and well sculpted for the origins and insertions of muscles. The neural spines of the thoracic vertebrae are long, accommodating the origins of the strongly developed neck muscles. There is little variation in the number of presacral vertebrae, usually 27 ± 1. The neck does not vary greatly in length, but the atlas is often diagnostic to family and sometimes generic level. The position of the vertebrarterial canal on the atlas has characteristic patterns and there is considerable variation in the shape of the wings; these are, for example, narrow and sagittally elongate in sabre-tooth cats. While there are usually 20 thoracic and lumbar vertebrae in carnivores, the proportions vary. The lumbars vary from 4 to 7, though 5 or 6 is normal in both creodonts and living carnivores; the arboreal pandas often have only 4 lumbars. Savage (1957) demonstrated that the zygopophysial articulations of the thoracic vertebrae are orientated to allow great freedom of movement, and in particular to allow the anterior part of the body to twist relative to the posterior. This twisting ability is a uniquely mammalian characteristic, but is poorly developed in herbivores as compared to carnivores. The longer the thoracic region and the more posterior the anticlinal vertebra, the greater is the degree of flexibility. Creodonts have in general a less flexible column than living carnivores. The creodont lumbar vertebrae have tight articulations and very little freedom of movement; this is seen most markedly in *Patriofelis*, which has sigmoidal-shaped zygopophyses (text-fig. 6). Tail lengths are highly variable, even within a species, as is common in mammals, but on the whole they tend to be long. All creodonts and marsupial carnivores have long tails; among living carnivores only bears, giant pandas, and a few hyaenas and cats have notably short tails—and of these bears are omnivorous and giant pandas herbivorous. The cats with short tails are the lynxes and some sabre-toothed cats. Lynxes tend to be slow movers, often living in forests, where they climb in trees and feed on rabbits and hares. The sabre-toothed cat *Smilodon*, with its rather short hind legs, may not have been a fast runner. The marsupial sabre-tooth *Thylacosmilus*, however, appears to have had a reasonably long tail. Tails are used for balance when changing direction at high speed, for swimming in otters, and other occasional uses include its use as a prehensile organ for climbing as in procyonids. In small species, a bushy tail coiled round the body is important in keeping the animal warm.



TEXT-FIG. 6. Posterior view of lumbar vertebrae, showing extent of articulatory surface of posterior zygapophyses in heavy line. A, typical of Carnivora; B, typical of Creodonta; C, as found in *Patriofelis* (after Denison 1938).

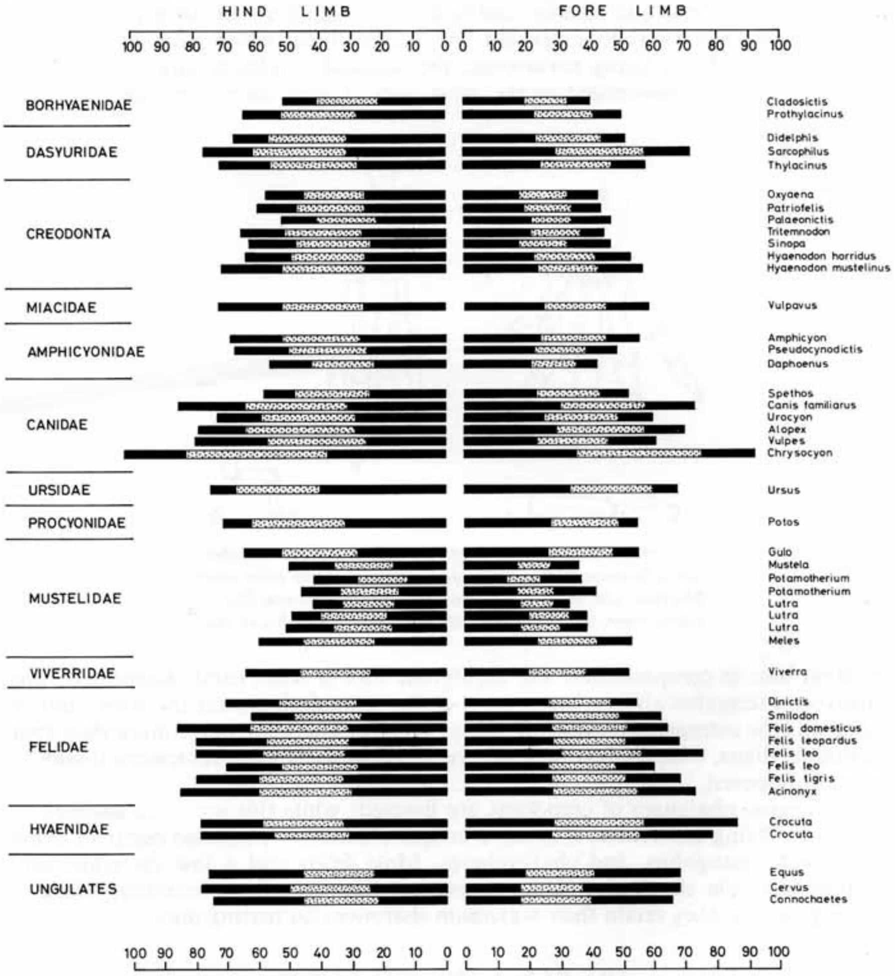
Much more variation is seen in the girdles and limbs than in the vertebral column. The scapula is usually fairly broad, with the supraspinous fossa often equal to or even larger than the infraspinous fossa; in ungulates the supraspinous fossa tends to become much the smaller. The scapular spine, acromion, and metacromion are usually well developed; they serve for the origins of muscles which abduct the limb, and in ungulates, with their specializations towards antero-posterior limb movements, these processes are reduced. The clavicle is vestigial or absent, as would be expected. In the pelvis the ilium and ischiopubis are usually of equal length; in aquatic carnivores the ilium is much shortened and the ischiopubis lengthened, while the opposite trend is seen in ungulates. Smith and Savage (1956) demonstrated that this difference was explicable as an adaptation to powerful limb movements in carnivores and rapid movements in ungulates. The ilium in creodonts is usually expanded dorsally and has a strong longitudinal keel. Since creodonts have three sacral vertebrae as in living carnivores, the heavier ilium was not for greater pelvic rigidity, but rather for more massive gluteal musculature. This, combined with the development in creodonts of a third trochanter on the femur, is indicative of the strong abduction capabilities of the limb.

In carnivores the hind limb is used almost solely for locomotion, but the fore limb has many additional uses—climbing, digging, grooming, tearing, and holding prey. Limbs can never be as specialized as in herbivores, where they are used almost exclusively for one mode of locomotion. The proportions of the limb segments have attracted the attention of many authors, but it is still difficult to provide more than broad generalizations. In order to compare both relative length and proportions of the limbs, I have compiled a graph (Table 5) where the limbs and their segments are expressed as a percentage of the vertebral column length, measured from the atlas to the last lumbar vertebra. In the less-specialized carnivores (e.g. *Mustela* or *Viverra*) the three segments of the limb become progressively shorter distally. In cursorial ungulates (e.g. *Equus* or *Connochaetes*) the reverse is true. In cursorial carnivores the foot is always the shortest element and the other two segments approach equality in length. Hildebrand (1961) concluded that only aquatic adaptations (all segments short) were clearly differentiated on limb proportions. Arboreal and fossorial forms also tend to have short limbs. Hind limbs are usually about 10% longer than the fore limbs; hyaenas are the exception with fore limbs equal to, or longer than, the hind. We might define short-legged carnivores as those whose fore limbs are 40% or less of the vertebral column, and the hind limbs 50% or less; this would include the otters, some *Mustela* species, and the borhyaenid *Cladosictis*. If we define long-legged as 70% or more for the fore limbs and 80% or more for the hind limbs, then the candidates are some species of *Felis* and *Canis*, together with *Acinonyx* and *Chrysocyon*; all these are cursorial and mostly high-speed runners. But *Chrysocyon* is not a particularly fast runner; increase in speed is bought at the expense of power. The very long legs of *Chrysocyon* are an adaptation to living in the long pampas grass.

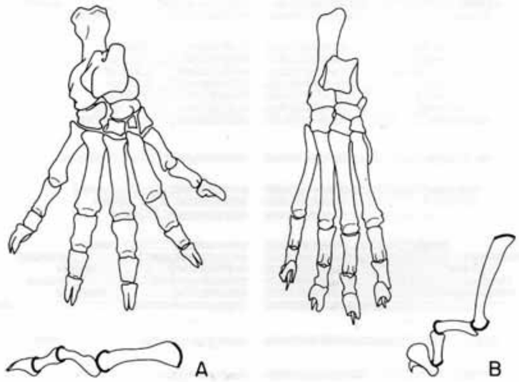
From our knowledge of locomotion in living carnivores, we can look at the fossils and make comparisons on limb proportions. The borhyaenid *Cladosicitis* has limb proportions almost identical with those of the living otter *Lutra*, and both animals are of similar size. *Prothylacinus* has the size and proportions of the living wolverine *Gulo*. Oxyaenids and proviverrines all have shortish limbs, especially the fore limbs; it seems probable that these are primitive character traits rather than aquatic specializations. *Hyaenodon* has longer limbs, though still shorter than those of living cursorial carnivores. The amphicyonids vary from fairly lightly-built forms to very large bear-like varieties.

There are all gradations between plantigrade and digitigrade. On the whole the more primitive carnivores, arboreal, and slower-moving animals, have plantigrade feet, while all cursorial types have digitigrade feet, or are capable of achieving

TABLE 5. Limb proportions of carnivorous mammals, shown as percentages of vertebral column length (atlas to last lumbar vertebra), with those of three ungulates for comparison. First joint (femur or humerus) and pes shown in black. Second joint (tibia–fibula or ulna–radius) stippled.



digitigrade posture, which considerably lengthens the limb and so adds to the mechanical advantage of the lever system. Borhyaenids and early creodonts were plantigrade, but later hyaenodontids were fully digitigrade (text-fig. 7). Plantigrade taxa have short, broad, and widely spread metapodials; in digitigrade taxa the metapodials are long and slender and held close together with strong tendons to give support when the foot is elevated. The scapho-lunar bones never fuse in creodonts, as they do in living carnivores; the unfused condition might have given greater freedom of movement in the wrist joint. Living carnivores have lost this freedom but, in compensation, the digitigrade foot is more firmly supported. The carnivore astragalus always has a good pulley articulation with the tibia, and in creodonts the astragalar foramen is always present. There are never more than four functional digits, with the first variously reduced; in some arboreal species it may be partially opposed.



TEXT-FIG. 7. Right pes of A, plantigrade creodont *Patriofelis* (after Denison 1938) and B, digitigrade carnivore *Felis* (after Merriam and Stock 1932); each pes shown with one digit in lateral view, the articular facets emphasized with heavy line.

The ungual phalanges of creodonts are fissured; while this serves to distinguish them from living carnivores, it is not a unique character—they also occur in living condylarths, pangolins, and chalicotheres. Most felids and a few viverrids have evolved retractile claws; this serves to prevent the claws from becoming blunt in walking, so that they retain their maximum sharpness for tearing prey.

THE BRAIN AND THE SENSES

Until about a decade ago, Edinger's (1929) paper contained almost all that was known of fossil carnivore brains. Piveteau (1961) illustrated thirteen genera, with anatomical notes commenting on the patterns of the sulci and gyri; his conclusion was that larger and more Recent brains tend to be more fissured and more complex.

More recently Jerison and Radinsky have in different ways made significant contributions. Jerison (1961, 1973) took a broad approach to the problems of brain evolution in vertebrates and concentrated mainly on characteristics of brain weight to body weight ratios. In amniotes the brain weight (E) increases as the two-thirds power of the body weight (P), that is $E = kP^{0\cdot 66}$ where k is a constant. Jerison also made use of an encephalization quotient (EQ), which is the ratio of the actual measured brain size to the expected brain size in an 'average' mammal of the same body weight.

The data for carnivores in Table 6 is extracted from Jerison (1973) with the addition of some original data. The estimates of brain weight and body weight can rarely be determined with accuracy, and a good deal of inspired guesswork has gone into the estimates. Nevertheless, the figures are reasonably consistent. Taking living carnivores as having an EQ of 1·10, then the mean (x) for Neogene carnivores is 0·76, that for Palaeogene carnivores 0·61, and that for creodonts is 0·48; that for the marsupial *Didelphis* on this basis is 0·22. That creodonts are about half as intelligent as living carnivores might be a deduction, but the samples are very small and there is considerable overlap in brain size of carnivore families, which is masked by the grouping. When carnivorous mammals are compared with their herbivorous contemporaries, they are seen to be ahead through the Tertiary (Table 7), though the ungulates appear to be steadily narrowing the gap. Radinsky (1975) used a

TABLE 6. Brain and body size estimates in fossil carnivores (after Jerison 1973).

	Genus	Brain weight (E) g	Body weight (P) kg	EQ $\left(\frac{E}{kP^{0\cdot 66}}\right)$	$\frac{EQ}{x}$
Creodonts	*Thinocyon*	5·7	0·80	0·55	
	Cynohyaenodon	8·3	3·0	0·33	
	Pterodon	62	42	0·43	0·48
	Hyaenodon	85	56	0·48	
	Megistotherium	375	354	0·62	
Palaeogene carnivores	*Plesictis*	11	1·3	0·77	
	Potamotherium	50	9·7	0·92	
	Daphoenus 1	49	26	0·46	
	,, 2	66	30	0·54	
	Hesperocyon	15	2·0	0·79	
	Pachycynodon	39	9	0·75	0·61
	Hoplophoneus 1	47	20	0·53	
	,, 2	52	49	0·32	
	Eusmilus	38	21	0·42	
	Herpestes	13	2·1	0·66	
	Amphicyon	110	49	0·64	
Neogene carnivores	*Plesiogulo*	140	38	1·03	
	Mesocyon 1	52	10	0·93	
	,, 2	37	9·5	0·69	
	Cynodesmus	36	13	0·54	0·76
	Tomarctus	58	15	0·80	
	Pseudaelurus	89	43	0·60	

modified EQ relating brain size to the area of the foramen magnum (Table 8). The foramen magnum area is related to body weight (correlation coefficient 0·65) and is a more readily available parameter. Using brain size–foramen magnum area relationships, Radinsky found that the modified EQ (EQA) was higher for carnivores than for mammals in general. While the families have considerable overlap in range, the mean for canids is higher than that for viverrids, and the latter is higher than that for felids.

TABLE 7. Evolution of relative brain size (after Jerison 1973). Means with sample size in brackets.

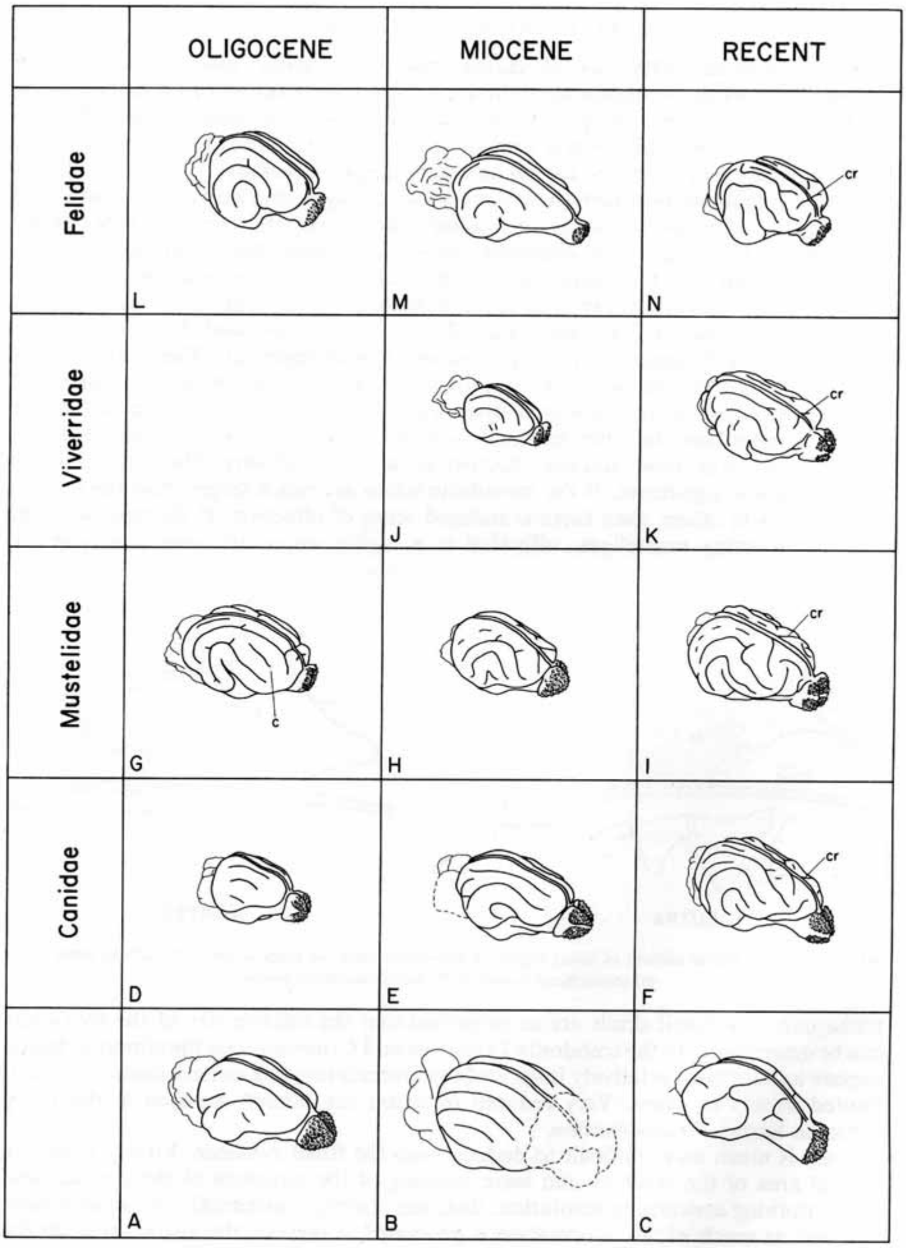
	Ungulates	Carnivores	
Archaic	0·18 (13)	0·48 (5)	Creodonta
Palaeogene	0·38 (26)	0·61 (11)	Carnivora
Neogene	0·63 (13)	0·76 (6)	,,
Recent	0·95 (25)	1·10 (15)	,,

TABLE 8. Relation of brain size (E) to foramen magnum area (A) (after Radinsky 1975). ($EQA = E/E^{a}$ where $E^{a} = 1{\cdot}35A^{1{\cdot}48}$).

	Range	Mean (x)
Canids	1·32–1·70	1·51
Viverrids	0·93–1·58	1·23
Felids	0·98–1·51	1·15
164 species from 5 orders		1·0

A totally different approach to brain studies is that of mapping the cortical areas and tracing the evolutionary changes in the fissure patterns (Radinsky 1968, 1969, 1971, 1973, 1975). Experimental work on living mammals (e.g. Welker and Campos 1963; Welker *et al.* 1964) has shown that the sulci delimit functional areas of the cortex, and to an increasing extent these are becoming identifiable. Radinsky (1968) examined the brain morphology of living otter genera and noted that the coronal gyrus and lateral part of the posterior sigmoid gyrus were usually enlarged. It has been shown that the latter is associated with sensory receptors for the fore limb, while the coronal gyrus is associated with tactile sensitivity in the head region. For otters in water, the efficiency of sight is reduced and that of smell is totally lost; in compensation, otters have increased tactile sensitivity through well-developed vibrissae. The clawless otters feeding on crustaceans and molluscs use their sensitive digits to locate prey. The earliest known lutrine *Potamotherium* has an enormous coronal gyrus, and the bone around the upper lip is densely pitted, strongly suggesting well-developed vibrissae (Savage 1957).

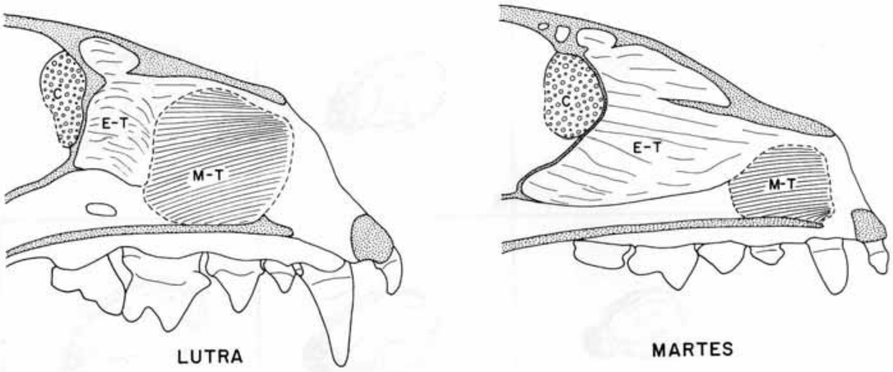
In the evolution of living families of carnivores, Radinsky (1971) has shown that one structure, the cruciate sulcus, has evolved independently at least five times (text-fig. 8); no specific function is yet known for this feature. The brains of living canids are all very similar, except for the prorean gyrus, and canids share with amphicyonids some fissure patterns which suggest a relatively close relationship.



TEXT-FIG. 8. Endocasts of carnivore brains. A, *Daphoenus*. B, *Megistotherium*. C, *Thylacinus*. D, *Hesperocyon*. E, *Mesocyon*. F, *Vulpes*. G. *Potamotherium*. H, *Promartes*. I, *Martes*. J, *Herpestides*. K, *Ichneumia*. L, *Eusmilus*. M, *Proailurus*. N, *Felis*. (B, C, and G original; others after Radinsky 1971). c, coronal gyrus; cr, cruciate sulcus.

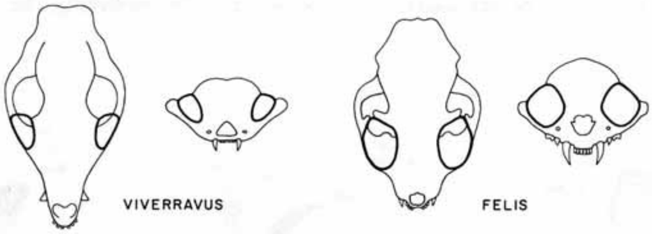
With improved techniques of taking endocranial casts, more information is becoming available. Unfortunately there are very few creodont brain casts known, but there appears to be a progressive increase in relative size through time. *Megistotherium* has relatively the largest known brain for a creodont. The pattern is also highly complex and the brain has an unusually large cerebellum.

From the brain we now turn to the senses—smell, sight, and hearing. The olfactory sense leaves in fossils two traces, the turbinal bones and the olfactory lobes of the brain. Though we have few complete endocranial casts, the trend in carnivores seems to indicate that the relative size of the olfactory lobes has increased with time. Radinsky (1975) has shown that the ratio of the olfactory lobes to total brain volume in living carnivores is 2·9% for felids, 4·7% for viverrids, and 5·0% for canids. Turbinal bones, if preserved, provide a second line of approach. There are two sets of turbinals in the nasal area. An anterior set, the maxilloturbinals, is innervated by the fifth cranial nerve and is concerned with warming and filtering the air. Behind these is a second set, the ethmoturbinals, which is innervated by the olfactory nerve; the air passes over these, and the olfactory sense is located here. The relative size of the turbinals is significant. If the maxilloturbinals are much larger than the ethmoturbinals, as in otters, then there is reduced sense of olfaction. If the reverse is the case, as in many mustelines, olfaction is a highly important sense (text-fig. 9). Unhappily, few fossil skulls are so preserved that the relative size of the two areas can be determined. In the creodonts *Thinocyon* and *Cynohaenodon* the ethmoturbinals appear to have been relatively large and the animals may, like many mustelids, have hunted mainly by scent. Very reduced olfaction can already be seen in the Early Miocene lutrine *Potamotherium*.



TEXT-FIG. 9. Transverse section of nasal region of two carnivores; to same scale. C, cribiform plate; E-T, ethmoturbinal bones; M-T, maxilloturbinal bones.

Sight is much more difficult to deduce from the fossil evidence. Firstly, from the orbital area of the skull we can learn nothing of the structure of the eyeball, and hence nothing concerning resolution, distance, diurnal, nocturnal, or colour vision. Further, as much of the information is processed in the eye, the visual areas on the cerebral cortex do not enlarge or increase in complexity in proportion to visual acuity. But the size of the orbit does provide some clue, and the orientation of the orbits allows us to assess the degree of stereoscopy. Quantitative evaluation of these characters is difficult, but generally in borhyaenids, creodonts, and miacids the eye is proportionately much smaller than in living carnivores. The degree to which the visual fields overlap provides some measure of stereoscopy (text-fig. 10 and Table 9). *Borhyaena* appears to have had the best stereovision among marsupial carnivores; the eyes of *Thylacosmilus* were very small and set facing laterally. Among creodonts, *Patriofelis* had the most forwardly directed eyes, though not as advanced as in living canids, hyaenids, and felids.



TEXT-FIG. 10. Dorsal and anterior views of miacid *Viverravus* and felid *Felis* skulls to illustrate size and orientation of the orbits (in heavy line).

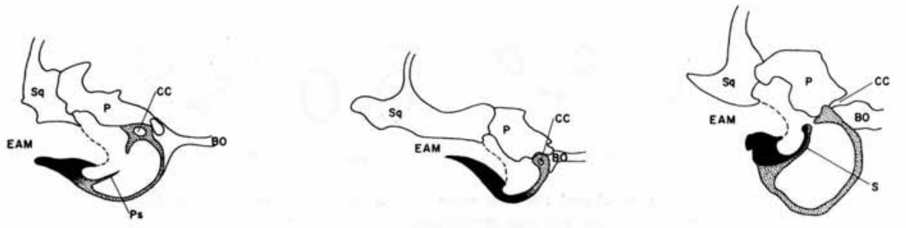
TABLE 9. Degree of stereoscopic vision in carnivores.

	Marsupialia	Creodonta	Carnivora
Low 30°-50°	*Cladosictis* *Prothylacinus* *Thylacosmilus*	Hyaenodontidae	Miacidae
Medium 50°-70°	*Borhyaena*	*Oxyaena* *Palaeonictis*	Amphicyonidae
High 70°-80°		*Patriofelis*	Ursidae Viverridae Mustelidae
Very high 80°-120°			Canidae Hyaenidae Felidae

The auditory sense is both the most important and the least satisfying sense to study. A great deal of information is often preserved, in both the middle- and inner-ear regions; these are frequently described in great detail (e.g. Hough 1948), yet extremely little of functional significance can be deduced. Hearing is certainly important in most carnivores, and in canids in particular—the bat-eared fox and desert foxes have remarkably large ears and their auditory perception is very acute.

The basic taxonomic divisions within the carnivores are based as much on ear structure as on dentitions. For example, the tympanic bulla is never present on any creodont or miacid. An ossified bulla without a true septum demarcates the canoid and musteloid families, and a bulla with a septum distinguishes the viverroid and feloid families. Recently Hunt (1974) has made a detailed study of the auditory bulla in the context of carnivore evolution.

Tympanic bullae are absent in almost all Palaeocene and Eocene mammals. They are absent in early insectivores, rodents, perissodactyls, and artiodactyls. All condylarths and creodonts lack ossified bullae, as do miacids (text-fig. 11). The primitive bulla in carnivores is flat, as seen in the extinct amphicyonids, in ursids, and some mustelids. Inflated bullae develop in canids, procyonids, viverrids, felids, and in some mustelids and hyaenids. The function of the inflated bulla is not entirely clear; many desert mammals, especially rodents, have highly inflated bullae. Sound absorption in air becomes greater with a decrease of humidity and an increase of temperature. So in warm arid environments, selective pressure will favour forms with acute hearing. The increased acuity is achieved by enlarging the middle-ear cavity; this is the principal trend in the evolution of the carnivore ear region and is seen in members of most carnivore families except ursids. The increased space is acquired mainly by the expanded growth of the caudal entotympanic bone, and may be supplemented by invasion of the mastoid bone (some mustelids and hyaenids) or by expansion into the external auditory meatus (amphicyonids). Hunt has further shown how the carotid circulation provides a counter-current heat exchange mechanism to cool the cerebral arterial blood by the development of internal and external carotid retia.

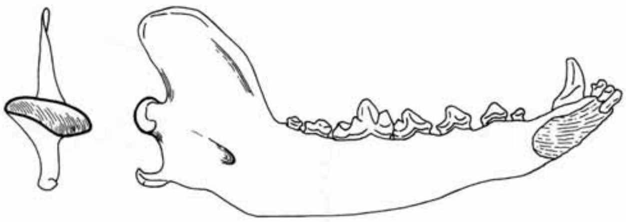


CANIS LUTRA FELIS

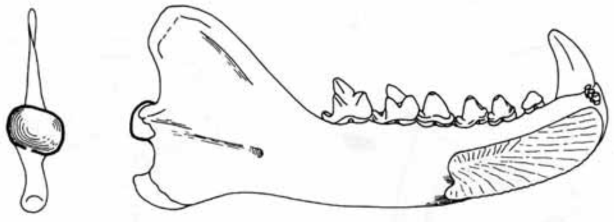
TEXT-FIG. 11. Transverse section of the ear region of three carnivores to illustrate the structure of the tympanic bulla. Ectotympanic black; entotympanic stippled; tympanic membrane (eardrum) dashed line. BO, basioccipital; CC, carotid canal; EAM, external auditory meatus; P, petrosum; Ps, pseudoseptum; S, septum; Sq, squamosal.

JAWS AND DENTITION

Considering the mandibles of creodonts and carnivores, there are a number of consistent differences. Both lineages have evolved large and small taxa, short- and long-jawed types, exclusively carnivorous stocks and others only partially carnivorous. In both lineages the mandibular dentition is narrower than the maxillary, and chewing occurs on one side at a time. The early creodonts (text-fig. 12) with their loose spherical condylar joint and very well fused and long symphysis, could have swung the mandible sideways into action, the transverse ridges of the molars guiding the occlusion of the carnassial teeth. In true carnivores, the tight cylindrical



CANIS



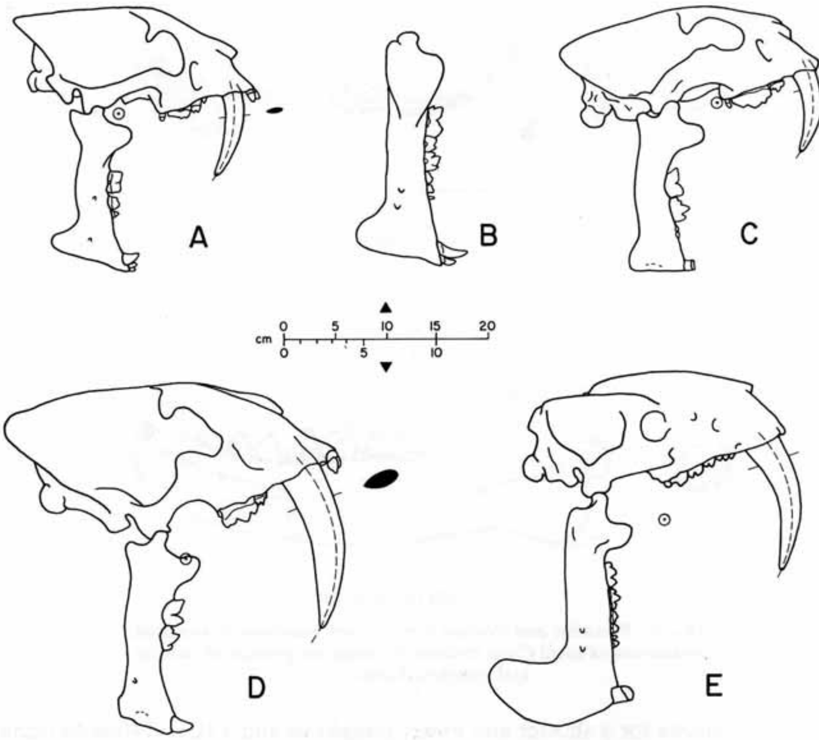
OXYAENODON

TEXT-FIG. 12. Posterior and internal views of left mandible of creodont *Oxyaenodon* and of canid *Canis*, to illustrate shape and position of condyle and symphysial area.

condylar joint allows for a shorter and looser symphysis and a lateral slide to bring the carnassials into occlusion. In both lineages the temporal is the main muscle closing the jaw, whereas in ungulates it is the masseter (Smith and Savage 1959). The temporal is well aligned to provide fast action and derives strength from its massive size.

Incisors and canines. The incisors are never specialized in carnivores and usually all three are present; the upper incisors are reduced in number in some short-faced forms and in those with sabre-like canines.

Canines are always present and usually equally well developed in both upper and lower jaws; they are used for biting, piercing, and holding prey. In some lineages they become massive, that is thick in proportion to their length, as, for example, in amphicyonids, ursids, borophagine canids, and some creodonts such as *Megistotherium*. It is, however, the evolution of sabre-like canines that provides the really startling innovations. These have evolved independently in the marsupials with *Thylacosmilus*, in the creodonts with *Apataelurus*, and several times among the felids (text-fig. 13). Associated with the evolution of sabre teeth are changes in the architecture of the skull and mandible, in the musculature for opening and closing



TEXT-FIG. 13. Skulls and mandibles of sabre-toothed carnivores, showing the arcs and centres of curvature of the canines. Transverse sections of the canines in black. A, *Hoplophoneus*. B, *Apataelurus*. C, *Nimravus*. D, *Smilodon*. E, *Thylacosmilus*. (A, C, and D after Matthew 1910, B after Denison 1938, and E after Riggs 1934).

the jaws, and in the musculature for bringing the head down in a powerful sweep to provide the stabbing action. The face is always short; the nuchal crests rise high above and sweep back beyond the occipital condyles. The condyles are often elevated high above the level of the dentition and there is a massive mastoidal area for the attachment of musculature to pull the head downward. The mandibles are slender with weak coronoid processes and are capable of opening wide to give a gape sufficient to clear the line of action of the sabre canines. A bony flange often develops on the ramus to protect the upper canine when the jaws are closed. In transverse section the sabres are usually ovoid, with the posterior edge more acute. While a circular section would be strongest, it would also offer great resistance to penetration; likewise a very thin tooth which would penetrate easily would be liable to damage. Serrations often develop, especially on the more proximal edges of the blade. Riggs

(1934), describing *Thylacosmilus*, stated that the sabre canines were open rooted and continually growing; their roots extend much further back into the skull than in any other sabre-toothed carnivore. The immediate ancestors of the Pliocene *Thylacosmilus* are unknown, although in all features other than the canines it is a normal borhyaenid. The creodont *Apataelurus* is known only from the mandible and is placed with other less fully sabre-toothed taxa in the subfamily Machaeroidinae of the family Hyaenodontidae. Within the Felidae, lineages are not clear; the Oligocene *Hoplophoneus* does not appear to be ancestral to the Plio-Pleistocene machaerodontines, and so sabre-like canines have evolved at least twice within the felids. The absence of any living sabre-tooth forms makes it impossible to be totally certain of their mode of functioning. Simpson (1941) has very fully analysed the mechanics of sabre-like canines, and only the briefest outline need be given here. He detailed the four theoretical ways in which the sabres could function as stabbing weapons to pierce thick skin and sink deep into the flesh, causing the victim to bleed to death; this he considered the principal function of the teeth. Secondarily they may have acted to slice open the carcass, but neither the outline of the teeth and their leading edges, nor the orientation of the musculature of the head and neck are optimally adapted for this, and slicing without prior stabbing would be virtually impossible.

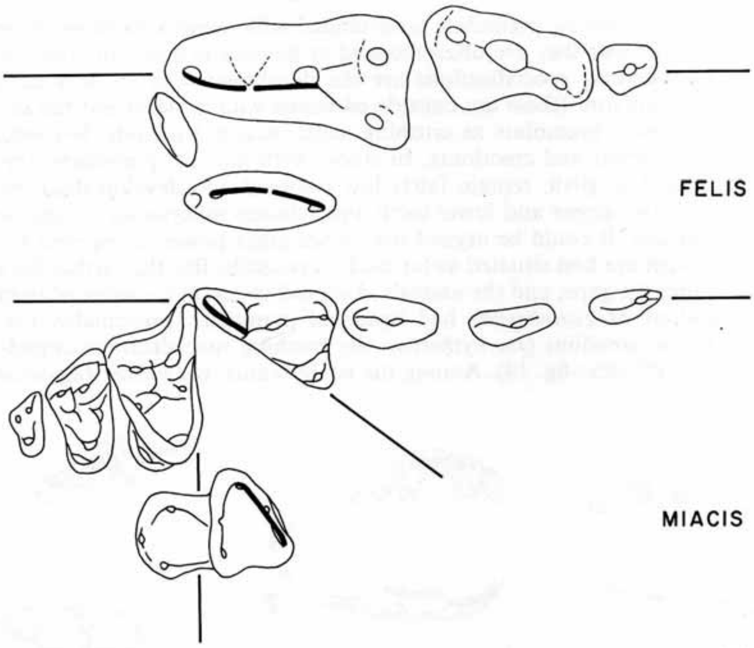
Premolars. In carnivores, premolars have tended with some notable exceptions to remain unspecialized; they are often reduced in number and the anterior ones are lost. The two striking specializations are the development of P^4 as a carnassial tooth in the Carnivora (these are considered below with molars) and the development of very heavy premolars as crushing teeth, seen in hyaenids, borophagines, and some marsupials and creodonts. In stocks with massive premolars, the teeth become enlarged in girth, remain fairly low crowned and develop thick enamel; usually one or two upper and lower teeth, immediately anterior to the carnassials, are thus modified. It could be argued that, since great power is required to crush bone, these teeth are best situated as far back as possible. But the further back they are, the smaller the gape, and the animals also need to retain a carnassial dentition. The hyaenodont *Megistotherium* had hyaenoid premolars, presumably for bone crushing. In the creodont *Quercytherium* the crushing specialization extends over four teeth (P^1–P^4) (text-fig. 14). Among the borhyaenids, the genus *Angelocabrerus*

TEXT-FIG. 14. Occlusal views of upper dentitions and lateral views of lower dentitions to illustrate specialized premolars in creodont *Quercytherium*, canid *Borophagus* and hyaenid *Crocuta*. Not to scale.

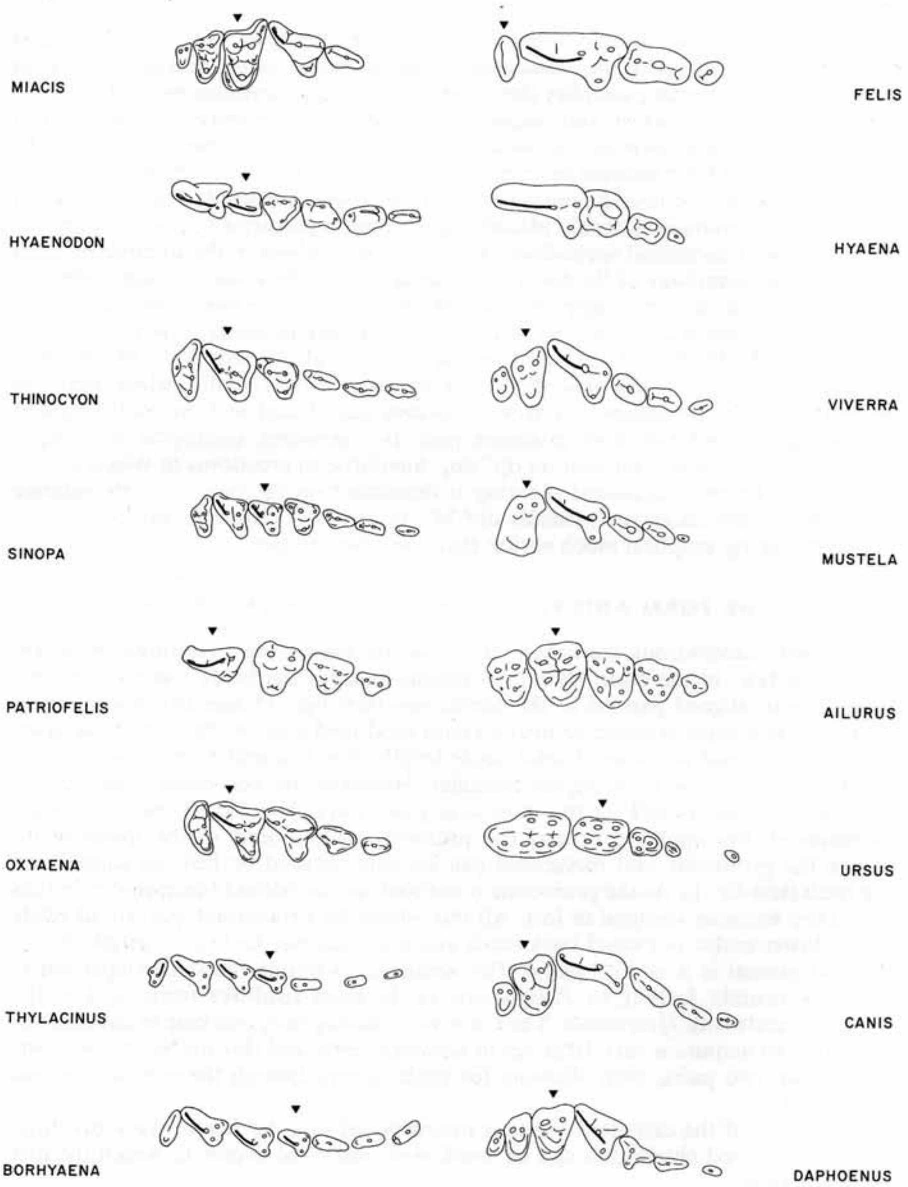
has a massive P_3 and can be regarded as a likely hyaenoid type. The canid subfamily Borophaginae comprises a suite of large hyaenid-like dogs with heavy crushing premolars in the Neogene of North America.

Molars. The main trends which can be distinguished in the evolution of carnivore molars are the simplification of the tooth pattern, the loss of crushing function in the more truly carnivorous types, the loss of the post-carnassial teeth and the increasing efficiency in carnassialization. The most sophisticated carnassials seen in felids are structurally very simple teeth, and it is in no small part due to this simplicity that the carnassial dentition at its most refined is so successful. This is seen most clearly when one looks at the cheek dentition of a primitive miacid and of a living felid (text-figs. 1 and 15).

In insectivorous stocks, shearing and crushing are performed by two parts of the same tooth. On an upper molar, for example, the metacone provides the blade and the protocone the crushing mechanism, while on the lower molar the paraconid-protoconid becomes the blade and the talonid the basin. This arrangement persists in early creodonts, with the blades enlarged at the expense of the crushing function (text-fig. 16). In the Carnivora, however, since the carnassials are only one pair of



TEXT-FIG. 15. Occlusal view of carnassial dentition in a miacid (*Miacis*) and a felid (*Felis*). Carnassial blades in heavy line. *Miacis* has a diagonal blade and transverse guiding ridge formed by post-carnassial structures; *Felis* has a longitudinal blade and lacks any guiding ridge. Not to scale.



TEXT-FIG. 16. Occlusal views of upper cheek dentitions of carnivorous mammals. Carnassial blades in heavy line; M^1 indicated with black triangle.

teeth, the more posterior teeth can take on a crushing function for the smaller pieces of food already cut up by the carnassials. Amphicyonids, canids, mustelids, and, to a lesser extent, viverrids exemplify this trend. Ursids and procyonids have secondarily lost the carnassial function and acquired frugivorous, herbivorous, or omnivorous diets, while the insectivorous hyaenid *Proteles* has only a vestigial dentition. In those stocks that have become more purely carnivorous, such as felids and hyaenids, there is a tendency to lose the post-carnassial teeth, with the result that the shearing blades become more posteriorly placed and so a more powerful bite is achieved.

The study of carnassial specialization involves an analysis of the number of teeth involved, the homology of the teeth, their replacement, the posterior migration, the increase in blade size, the angle of shear, the reduction of the non-shearing parts of the teeth, and the self-sharpening devices. The number of carnassials ranges from three pairs (M^1–M^3/M_2–M_4) in many marsupials, through two pairs (M^1–M^2/M_3–M_4) in many creodonts, to one pair (P^4/M_1) in all Carnivora. Usually, when there are several pairs, the carnassial action is not evenly distributed and one pair tends to be dominant, often the more posterior pair. In Carnivora, carnassial shearing is developed in the milk dentition on dp^3/dp_4. Similarly, in creodonts in which a milk dentition is known, carnassial shearing is developed on the pair of teeth anterior to the permanent successors, usually dp^4/M_1. In creodonts M_1 is invariably heavily worn, indicating eruption much earlier than the other molars.

THE FORM AND FUNCTION OF CARNASSIAL TEETH

In all early carnivorous mammals, the shearing blades are orientated obliquely across the jaw; in the more truly carnivorous lineages the blade tends to become longitudinal, aligned parallel to the dental row (text-figs. 15 and 16). Functionally a longitudinal shear is easier to operate with food held against the side of the jaws, but the price paid is a loss of total shear length (the diagonal being equivalent to the hypotenuse of a right-angled triangle). However, by becoming longitudinal, there is no longer a need for the transverse guide lines provided by the protocone–paracone in the upper teeth and the protoconid–metaconid in the lower teeth. Hence the protocone and metaconid can become reduced or lost, so simplifying the teeth (text-fig. 1). As the protocone is reduced, so the talonid function diminishes and it too becomes vestigial or lost. All this allows the protoconid–paraconid blade of the lower molar to extend backwards and make up for the loss of length due to the realignment in a sagittal plane. This sequence of trends evolved independently in the oxyaenids, leading to *Palaeonictis* as the most felid-like form, and in the hyaenodontids with *Hyaenodon*. The Carnivora, having only one pair of carnassials, were able to acquire a very large set of shearing teeth and this probably functions better than two pairs, even allowing for replacement, though there is no obvious proof of this.

The length of the carnassial blade is proportional to *a* the size of the individual, *b* the size of food chunk that can be swallowed, and *c* the degree to which the diet is carnivorous.

Another interesting feature of carnassial blades is their shape; they are concave in a vertical plane and plano-convex in a horizontal plane (text-fig. 1). On closing, the ends of the blades meet first, and only when almost fully closed do the centres meet. The double guillotine action produced by the concave edges allows the maximum force to be exerted on a very small area at a time, and so increases the efficiency of the blade. The concave arc also ensures that the food is trapped between the blades and does not slide out. The terminal pillars of the blades are massive, and the blade thickness tapers towards the centre, where a slit separates the two halves. Opposite the slit the teeth are deeply excavated on the outer face of the P^4 and on the inner face of M_1; this creates space for the food during slicing and, by its semi-conical shape, helps to retain the chunk of food in position during cutting. A slit in this area is more efficient than a very thin band of enamel, which would be easily damaged.

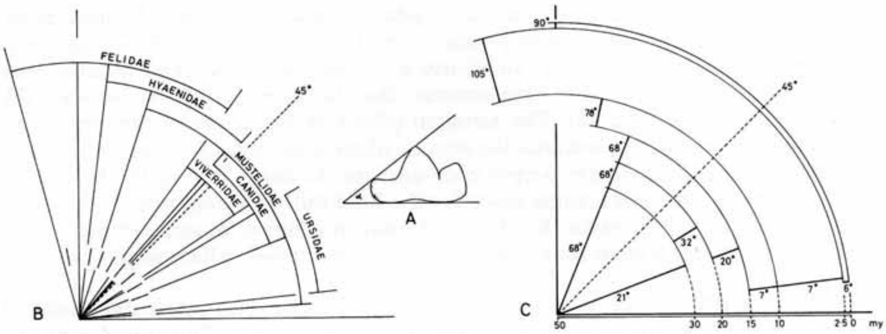
The blade of M_1 is always convex outwards in a horizontal plane; the blade of P^4 is either slightly convex inwards or flat in the same plane. Thus on closing the jaws (text-fig. 1D), contact is made between the two blades at two centrally moving points throughout the traverse. The movement is primarily orthal with a slight medial movement; to allow this, the cylindrical glenoid permits the mandible to slide inwards as it closes, and differential stresses are absorbed in the non-fused symphysis.

Several authors have attempted a quantitative assessment of carnassiality, most recognizing that the trend involves a migration of the shear plane from the diagonal to the longitudinal position. Denison (1938) gave figures for the 'shear angle' (unidentified but presumed to refer to the angle formed by the plane of the paraconid–protoconid shear with the jaw axis). Only three genera were used: *Oxyaena* spp. 60°–30°, *Protopsalis* very low, and *Patriofelis* 0°, i.e. parallel to the jaw. Butler (1946) measured the anterior and posterior (i.e. lateral) borders of the upper carnassial teeth and gave the maximum value of the ratio of posterior edge/anterior edge; this ratio he divided by the number of carnassial teeth to produce his index of carnassial differentiation. His table comprised nine genera of creodonts, ranging from 0·50 in the primitive genus *Sinopa* to 0·90 in the advanced *Patriofelis*.

Crusafont and Truyols (1956) have given an excellent and original account of carnassiality in carnivores, restricting themselves, however, to members of living families of carnivores and omitting creodonts and miacids. The analysis is based on the measurement of the angle of the blade of the upper and lower carnassial teeth for six families throughout the Cainozoic. For example, the angle formed by the protocone–metastyle–paracone is analysed with the following results: Ursidae 26°–52°, Canidae 15°–36°, Mustelidae 19°–44°, Viverridae 18°–25°, Hyaenidae 14°–22°, and Felidae 10°–25°. The smaller the angle, the more reduced the protocone and the more longitudinal the shear on the metastyle. Ursids are seen to be hypocarnivores, felids and hyaenids hypercarnivores, with viverrids, canids, and mustelids occupying a central position. Similar results are obtained for the lower carnassials. The range of angles is seen to increase with time; in the lower carnassial it is 47° in Eocene–Oligocene and 98° in the Late Miocene–Pliocene (text-fig. 17).

The obvious extension would be to apply the Crusafont and Truyols techniques to marsupials and creodonts. However, frequent lack of good reference points made this difficult, and it was found impossible to achieve consistent and reliable results.

Of prime importance for efficient functioning of the carnassial dentition is the



TEXT-FIG. 17. Range of variation of the carnassial angle in M_1 of living families of carnivores. A, measurement of angle α. B, family range of angle α. C, range of angle α through time (after Crusafont and Truyols 1956).

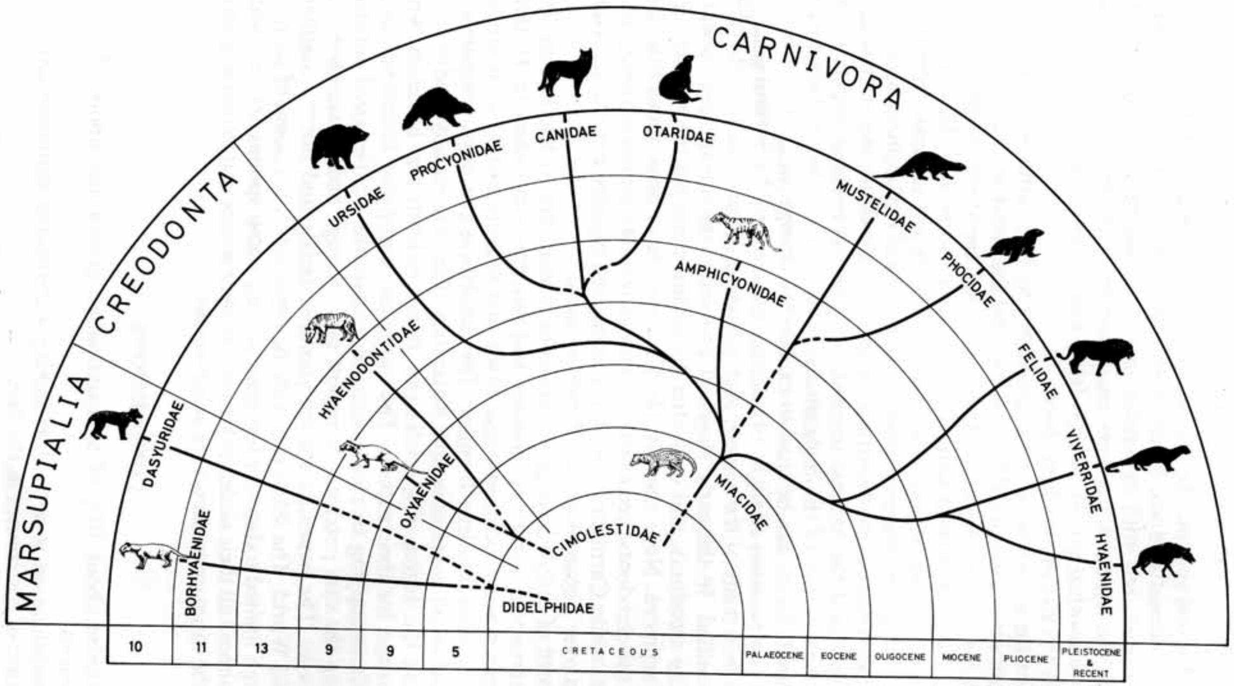
maintenance of a sharp cutting edge, and there are various ways in which this could be achieved. In rodents the incisors maintain a cutting edge by having enamel restricted to one edge so that the softer dentine wears down more rapidly and leaves a sharp edge; this rapid wear is compensated for by continual growth from open roots. In sabre-like canines a serrated edge of enamel is developed, since there is nothing for the tooth to be sharpened against. Neither of these solutions would be efficient in a carnassial dentition. The alignment of the blades is very precise, and the rodent incisor method is unlikely to be adequate. The apposition of two teeth rules out the serrated-edge method, which works only in isolation. This leaves only a self-sharpening device, a process named 'thegosis' by Every (Every and Kühne 1971). The self-sharpening works well on all save a few specialized hyaenodonts which, according to Dr. J. S. Mellett (pers. comm.), continue to enlarge their skulls throughout life and so alter the spatial relationships of the teeth, which turn inward and wear down to the roots in an attempt to counter the effects of size increase.

BIOGEOGRAPHY

The marsupials evolved two successful carnivore lineages. The borhyaenids were the only mammalian carnivores in South America from Palaeocene to Pliocene times; twenty-five genera are known and they range from small otter-like forms to true highly specialized sabre-toothed taxa. Most are poorly known; some reached the size of bears, but none appears to have been truly cursorial. They were only ousted in the Plio–Pleistocene by the invasion of placental carnivores from North America; of these the canids, mustelids, and procyonids have been particularly successful.

The dasyurid marsupials in Australia are less well known in the fossil record, with only two truly carnivorous genera in recent times, of which the thylacine closely paralleled *Canis*.

The creodonts successfully occupied the Palaeogene carnivore niches; they did not survive beyond the Oligocene in North America, but continued on into the



TEXT-FIG. 18. Phylogeny of the carnivorous mammals.

early Miocene in Europe and into the late Miocene in Africa and Asia. The oxyaenids were particularly successful in the North American Eocene with seven genera, all relatively short legged, but with carnassial specializations near to those of felids (e.g. *Patriofelis*). The hyaenodonts were more diverse, with long- and short-faced taxa, with a sabre-toothed group, canid-, felid- and hyaenid-like forms. Some of the latter reached the size of very large bears.

The reasons for the replacement of the creodonts by true carnivores are far from clear. Both groups originated in the Palaeocene, and the creodonts rapidly achieved a dominance in the carnivore niches. The specialized creodonts display many of the characters usually associated with the Carnivora—some had digitigrade feet, some had good stereoscopic vision, some had highly efficient carnassial dentitions, and yet others had large and complex brains. The history of replacement is paralleled in those of the replacement of the multituberculates by the rodents, the perissodactyls by the artiodactyls, and the archaic ungulates by the modernized ungulates. The most recent example is that of the replacement in Australia of the thylacine by the dingo. No one single factor can be cited to explain the change; in an intensely competitive field the combination of slight advantages are favoured by natural selection; only a thorough field study of the ecology and behaviour of each stock would enable these to be quantified. In the early stages of evolution, the advantages appear to have lain with the creodonts, and only after 20 million years did the balance tip in favour of the Carnivora. None the less, the Carnivora have been about four times as successful as the creodonts; creodonts are known from 45 genera spanning about 45 million years, while Carnivora, excluding living and aquatic genera, are known from 218 genera over a span of about 55 million years.

The fossil record of early Palaeogene Carnivora is poor, but by late Eocene times nearly all the terrestrial carnivore families had become established in Holarctic realms. The amphicyonids occupied canid, ursid, and hyaenid niches, to be replaced later by stocks of these modern families. The canids are the most ubiquitous of carnivores, found on all continents save Antarctica. They are usually medium sized and never achieve the degree of specialization found in felids and hyaenids, which may in part account for their success. The mustelids, occupying Holarctic realms, and the viverrids, occupying tropical realms, dominate the smaller-sized carnivore stocks, exploiting the vast potential of rodent prey, though usually supplementing it with other foods. The hyaenids are the youngest family and occupy ossifagous niches in the Old World. The felids can truly be regarded as the acme of carnivore evolution; though limited today to a few genera, their many species are very widely distributed. In almost all their skeletal elements, in their senses and dental apparatus, they represent the ultimate in carnivore achievement.

CONCLUSIONS

Carnivores comprise about 10% of all mammalian genera and about 2% of the mammalian biomass.

Carnivore specialization is defined as having a carnassial dentition and a substantial proportion of vertebrates in the diet.

Carnivore stocks evolved twice among the marsupials (borhyaenids and dasyurids) and twice among the placental mammals (Creodonta and Carnivora). Borhyaenids were the only mammalian South American carnivores until the Pliocene, dasyurids filled a similar role in Australia until Recent times. Creodonts were gradually replaced by Carnivora in North America during the Oligocene, and in Africa and Asia during the late Miocene.

The vertebral column of carnivores is strong and flexible, and the tail is usually long. In creodonts the vertebral column was less flexible than in living carnivores.

The limbs of carnivores are multi-purpose organs and do not become highly specialized, though most acquire some cursorial adaptations. They are relatively shorter in the Creodonta than in the Carnivora. Aquatic carnivores always have short limbs, and cursorial forms have long limbs. The foot is usually the shortest element of the three segments of the limb, whilst in herbivores the foot is the longest. Primitive carnivores have plantigrade feet, but advanced creodonts and all cursorial carnivores have fully digitigrade feet.

The brains of creodonts are smaller and simpler than those of living carnivores, but the brains of carnivorous mammals are always relatively larger than those of the contemporary herbivores.

The olfactory sense in creodonts was probably at least as good as in living carnivores. Sight, however, was probably not as good, and fully stereoscopic vision developed only rarely in carnivorous marsupials and creodonts, whereas it is common in canids, hyaenids, and felids. Hearing is acute in canids, felids, and viverrids and is particularly acute in carnivores living in warm arid environments.

The mandibles in most creodonts were loose fitting with long firm symphyses, and the carnassials required transverse guiding ridges to ensure precise occlusion. The mandibles of the Carnivora are tightly fitting with no need for long symphyses and guiding ridges; their carnassial blades have rotated from an oblique angle to a longitudinal position in the most specialized forms (canids, hyaenids, and felids). The most advanced creodonts were more specialized than the primitive Carnivora.

The canine teeth are usually well developed and may become specialized as stabbing sabre-like teeth: this trend evolved independently in three stocks—marsupials, creodonts, and felids.

Premolar teeth in some marsupials, creodonts, and Carnivora have become massively large to function as bone-crushing tools, and in a few cases to act as mollusc-shell crushers.

The principal trend in the evolution of molar teeth is one of simplification, by the reduction or loss of the crushing function and loss of the post-carnassial dentition.

The evolution of the carnassial dentition involves three, two, or one pair of teeth. The most advanced forms have only one pair, which is large and devoted solely to shearing by loss of all other parts of the teeth not concerned with cutting. The cutting edges of the blade are self-sharpening.

REFERENCES

BAKKER, R. T. 1972. Anatomical and ecological evidence of endothermy in dinosaurs. *Nature, Lond.* **238,** 81–85, 2 figs., 2 tables.

BLAINVILLE, H. M. D. DE. 1864. *Ostéographie ou description iconographique du squelette et du système dentaire des mammifères récent et fossiles.* Paris. Atlas Vol. IV.

BUTLER, P. M. 1946. The evolution of carnassial dentitions in the Mammalia. *Proc. zool. Soc. Lond.* **116,** 198–220, 13 figs.

CROMPTON, A. W. and HIIEMAE, K. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. *Zool. J. Linn. Soc.* **49,** 21–47, 10 figs., 1 pl.

—— and SITA-LUMSDEN, A. 1970. Functional significance of the therian molar pattern. *Nature, Lond.* **227,** 197–199, 5 figs.

CROWSON, R. A. *et al.* 1967. Arthropoda. *In* HARLAND, W. B. *et al.* (eds.). *The Fossil Record.* London (Geological Society), pp. 499–534.

CRUSAFONT-PAIRO, M. and TRUYOLS-SANTONJA, J. 1956. A biometric study of the evolution of fissiped carnivores. *Evolution,* **10,** 314–332, 14 figs., 9 tables.

DENISON, R. H. 1938. The broad-skulled Pseudocreodi. *Ann. N.Y. Acad. Sci.* **37,** 163–256, 32 figs.

EDINGER, T. 1929. Die fossilen Gehirne. *Ergebn. Anat.* **28,** 1–249, 203 figs.

EVERY, R. G. and KÜHNE, W. G. 1971. Bimodal wear of mammalian teeth. *In* KERMACK, D. M. and K. A. (eds.). *Early Mammals.* London: Academic Press, pp. 23–27, 1 fig., 1 pl.

GILL, E. D. 1954. Ecology and distribution of the extinct giant marsupial '*Thylacoleo*'. *Victoria Nat.* **71,** 18–35, 12 pls.

GREGORY, W. K. and HELLMAN, M. 1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora, a phylogenetic study of the skull and dentition. *Proc. Am. phil. Soc.* **81,** 309–392, 36 figs., 6 pls.

HILDEBRAND, M. 1954. Comparative morphology of the body skeleton in Recent Canidae. *Univ. Calif. Publs. Zool.* **52,** 399–470, 30 figs., 4 pls.

—— 1961. Body proportions of didelphid (and some other) marsupials, with emphasis on variability. *Am. J. Anat.* **109,** 239–249, 9 figs.

HOUGH, J. R. 1948. The auditory region in some members of the Procyonidae, Canidae and Ursidae. *Bull. Am. Mus. nat. Hist.* **92,** 67–118, 11 figs., 7 pls.

HUGHES, N. F. 1976. *Palaeobiology of angiosperm origins.* Cambridge: Univ. Press, vii+242 pp., 73 figs.

HUNT, R. M. 1974. The auditory bulla in Carnivora. *J. Morph.* **143,** 21–76, 3 figs., 13 pls.

JERISON, H. J. 1961. Quantitative analysis of evolution of the brain in mammals. *Science,* **133,** 1012–1014, 1 fig.

—— 1973. *Evolution of the brain and intelligence.* New York: Academic Press, xiv+482 pp., illustrated.

MATTHEW, W. D. 1906. The osteology of *Sinopa,* a creodont mammal of the Middle Eocene. *Proc. U.S. natn. Mus.* **30,** 203–233, 20 figs., 1 pl.

—— 1910. The phylogeny of the Felidae. *Bull. Am. Mus. nat. Hist.* **28,** 289–316, 15 figs.

MERRIAM, J. C. 1912. The fauna of Rancho la Brea Pt. II. Canidae. *Mem. Univ. Calif.* **1,** 215–272, 43 figs., 5 pls.

—— and STOCK, C. 1932. The Felidae of Rancho la Brea. *Publs. Carnegie Instn,* No. **422,** xvi+231 pp., 152 figs., 42 pls.

MITCHELL, E. and TEDFORD, R. H. 1973. The Enaliarctinae a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bull. Am. Mus. nat. Hist.* **151,** 201–284, 27 figs., 4 tables.

MUYBRIDGE, E. 1899. *Animals in motion.* London: Chapman and Hall, x+264 pp.; illustrated.

OSBORNE, H. F. 1900. *Oxyaena* and *Patriofelis* restudied as terrestrial creodonts. *Bull. Am. Mus. nat. Hist.* **13,** 269–279, 8 figs., 2 pls.

PIVETEAU, J. 1961. Encephales de carnivores fossiles. *Traité de Paléontologie,* **6** (1), 806–820, 19 figs.

RADINSKY, L. B. 1968. Evolution of somatic sensory specialisation in otter brains. *J. Comp. Neur.* **134,** 495–506, 6 figs.

—— 1969. Outlines of canid and felid brain evolution. *Ann. N.Y. Acad. Sci.* **167,** 277–288, 6 figs.

—— 1971. An example of parallelism in carnivore brain evolution. *Evolution,* **25,** 518–522, 4 figs.

—— 1973. Evolution of the canid brain. *Brain Behav. Evol.* **7,** 169–202, 13 figs.

—— 1975. Evolution of the felid brain. Ibid. **11,** 214–254, 12 figs., 2 tables.

RIGGS, E. S. 1934. A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predacious marsupials. *Trans. Am. phil. Soc.* **24,** 1-32, 8 pls., 4 figs.

SAVAGE, R. J. G. 1957. The anatomy of *Potamotherium* an Oligocene lutrine. *Proc. zool. Soc. Lond.* **129,** 151-244, 3 pls., 38 figs., 8 tables.

—— 1973. *Megistotherium*, gigantic hyaenodont from Miocene of Gebel Zelten, Libya. *Bull. Brit. Mus. nat. Hist. Geol.* **22,** 483-511, 20 figs., 4 pls.

SCOTT, W. B. and JEPSEN, G. L. 1936. The mammalian fauna of the White River Oligocene. Pt. I. Insectivora and Carnivora. *Trans. Am. phil. Soc.* **28,** 1-153, 7 figs., 22 pls.

SIMPSON, G. G. 1941. The function of saber-like canines in carnivorous mammals. *Am. Mus. Novit.* No. **1130,** 1-12, 4 figs.

—— 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* **85,** 1-350.

SINCLAIR, W. J. 1906. Mammalia of the Santa Cruz beds: Marsupialia. *Rep. Princeton Univ. Exped. Patagonia,* **4,** 333-482, 9 figs., 16 pls.

SMITH, J. M. and SAVAGE, R. J. G. 1956. Some locomotory adaptations in mammals. *Zool. J. Linn. Soc.* **42,** 603-622, 14 figs., 3 tables.

—— —— 1959. The mechanics of mammalian jaws. *School Sci. Rev.* **141,** 289-301, 8 figs.

STROMER, E. 1902. Die Wirbel der Land-Raubtiere, ihre Morphologie und systematische Bedeutung. *Zoologica,* **36,** 276 pp., 5 pls., 23 tables.

VOORHIES, M. R. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *Contr. Geol. Univ. Wyoming Spec. Paper,* **1,** 69 pp., 29 figs., 11 tables.

WELKER, W. I. and CAMPOS, G. B. 1963. Physiological significance of sulci in somatic sensory cerebral cortex in mammals of the family Procyonidae. *J. Comp. Neur.* **120,** 19-36, 10 figs., 6 tables.

WELKER, W. I., JOHNSON, J. I. and PUBOLS, B. H. 1964. Some morphological and physiological characteristics of the somatic sensory system in raccoons. *Am. Zool.* **4,** 75-94, 23 figs., 1 table.

R. J. G. SAVAGE

Department of Geology
The University
Bristol BS8 1TR

Typescript received 5 July 1976