PLANTIGRADY AND DIGITIGRADY IN THE FISSIPED CARNIVORANS

by

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The author examines the osteological characters relating to the support of the foot in fissiped carnivorans, and studies actual materials from a variety of plantigrade and digitigrade animals. Enumeration of characters. Interpretation. Application to paleontology: reconstructing the mode of living of some fossil carnivorans.

The Carnivora represents one of the main branches of the class Mammalia, both in the importance of their role in the balance of terrestrial faunas and in the number of their forms and the variety of their adaptations. Not linked to the sorting of a particular floral biotype, they are dependent chiefly on the abundance and ease of capture of prey, and they have adapted over the course of geologic time, little by little, evolving under very different circumstances. They are encountered in the pursuit of very diverse prey, under all climates and all latitudes, and omnivores, insectivores, ovivores, piscivores and herbivores are found besides the purely carnivorous forms. Particular anatomical conformations correspond to each of these ecological adaptations: length of the limbs, development of certain muscles, body proportions, the posture they give to the feet while taking support on the ground during a walk or run. The most purely carnivorous species are thus digitigrade, while those more herbivorous are plantigrade. Between these two poles, the majority of omnivores are either semi-plantigrade or semi-digitigrade.

Having had them in hand, in the course of a revision I made of the fossil carnivorans from the excellent Miocene deposits in Sansan (Gers) concerning the important parts of the carnivore skeleton belonging to subfamilies extinct today and represented by structural forms not found in exact replica in the modern fauna, I attempted to recover their mode of life solely from interpretation of their osteology. Towards this goal, I first looked again at the skeletons of modern carnivorans, given that the mode of movement is well known, and developed significant criteria for distinguishing between plantigrady and digitigrady. I have studied principally the extreme forms, either purely digitigrade or purely plantigrade: various species of *Felis*, animals typically digitigrade and using successive bounds to move rapidly; *Acinonyx jubatus*, the cheetah, a digitigrade runner, the fastest of all mammals and capable at times of a speed exceeding 110 km/hr; *Canis lupus*, the wolf, and *Lycaon pictus*, the hunting dog, types of digitigrade runners, less rapid but more endurable than the cheetah; *Hyaena brunnea*, the striped hyaena, digitigrade but less quick; various bears (*Ursus arctos, Thalassarctos maritimus, Helarctos malayanus, Tremarctos ornatus*), plantigrade; the wolverine/glutton *Gulo luscus*, plantigrade and arboreal; the Old-World/Eurasian badger *Meles meles*, Malay badger *Mydaus javanensis*, hog badger *Arctonyx collaris*, and the honey badger/Cape ratel *Mellivora capensis*, all plantigrade, as well as the lesser and giant pandas, *Ailurus fulgens* and *Ailuropoda melanoleuca*; the crab raccoon *Procyon cancrivorus*, the red coati *Nasua rufa*, the little North American ringtail *Bassariscus astutus* and the fossa of Madagascar *Cryptoprocta ferox*, agile and plantigrade climbers. This last animal merits particular attention: though the anatomy of the internal ear makes it a viverrid, it has the dentition of a felid, with reduction of the anterior premolars, the tuberculoses and the talonid of the inferior carnassial. In it is seen generally a viverrid very engaged in the lifestyle of felids, but still living at an ancient stage comparable to that of the first felids, *Haplogale* and *Proailurus* from the French Oligocene. But the cryptoproct, although like cats it attacks prey of comparable strength (lemurs of the big island), is perfectly plantigrade. Also the anatomical differences that can be observed in comparable limbs in cats would be particularly significant because of their unique relation with the different mode of support for the foot.

Beyond this purely osteological study, a certain number of dissections made on diverse carnivorans (lion, panther, puma, mongoose, polar bear, washer raccoon, and hunting dog) allowed me to realize the exact location of the muscular insertions and of the relations existing between the surfaces occupied by the insertions and the corresponding muscle volumes.

DIFFERENTIAL OSTEOLOGICAL CHARACTERS

I have therefore made notes of a certain number of these characters. All are not of the same merit and certain among them, moreover among the most significant, were already known. Without pretending to present an exhaustive list, I think that it would have been a loss not to mention them. They are:

Plantigrade and digitigrade carnivorans

1) On the humerus of plantigrade carnivorans, the deltoid tuberosity (on which insert the deltoid, mastoidohumeral and pectoralis muscles) is very much more developed than in digitigrade forms, and tends to form a flat surface orthogonal to the sagittal plane of the body.

It is particularly large in the bears and badgers. In *Ursus arctos* and *Ursus spelaeus* it even descends onto the lower third of the bone, a level that it does not reach entirely in *Thalassarctos maritimus* and *Helarctos malayanus*. On the humerus of the badgers, honey badger, and giant panda it is larger than the minimal diameter of the shaft and descends down to the middle of the bone. It is a little less developed in the fossa, coatis, and wolverine. In contrast, in canids, felids, and hyaenas this surface is reduced and oriented very obliquely.

2) Among digitigrade forms, these limbs are much longer than in plantigrade forms. This character has been difficult to appreciate. The size of the epiphysis can still be judged by its relation to the length of the shaft. The distal articular surface of the humerus can serve as a criterion. It is thus very much larger in the fossa than in the caracal, animals which possess humeri of perceptibly the same size and strength.

3) The entepicondyle of the humerus is well-developed, massive (*Meles, Mydaus, Gulo*) and elongated either laterally (*Mydaus, Ailuropoda, Cryptoprocta*) or towards the back (bears) in plantigrade forms, whereas it is very much reduced and compact in digitigrade forms.

4) In the most truly plantigrade animals, the arms and forearms are not pivoted in the same plane but, assuming the axis of the elbow articulation was fixed, the planes in which the humerus and ulna move make a significant angle with each other, exceeding 20° in bears. This angle is a little less (around 15°) in badgers and the wolverine; it hardly reaches 10° in the fossa, 5 to 6° in *Felis* and is practically nil in the running forms, the wolf, hunting dog, dhole, hyaenas, and cheetah.

5) At the top of the olecranon, the surface on which the anconeus profundus tendon slides presents two elevated edges of perceptibly the same importance in digitigrade carnivorans. In contrast, this groove is less profound in plantigrade forms, larger, and these two edges present a strong asymmetry; the lateral edge is nonexistent (honey badger, bears, fossa) or nearly so (badger), whereas the medial edge, without always forming a prominent rim, rises near the top and can extend far forward of the same (*Ursus, Thalassarctos, Mellivora*).

6) Always in plantigrade forms, the posteromedial angle of the top of the olecranon is lengthened on the medial side into a veritable apophysis on which the accessory anconeus (oriented near the top) and the medial ulna (oriented near the bottom) insert. This apophysis is particularly distinct in bears, the honey badger, badgers, and coatis. In the fossa, it is curiously lengthened near the bottom into a small, fairly slight, bony blade. This apophysis is reduced to a simple prominence in digitigrade carnivorans.

7) In bears, which are the most plantigrade of all carnivorans, the ulna shows a strong lateral twisting, best visible in *norma facialis*, on a par with the length of the bone, with the lower part quickly oriented more medially. The angle can reach 15°. *Gulo* and *Mellivora* show the same phenomenon, not mingled with the regular curve of the ulna, which is very elongated into a particularly thin member as in digitigrade forms. In this last case, there is no quick curving to a given level, but a general twisting of the whole shaft which takes the profile of an arc.

8) In *Gulo, Meles, Mydaus, Ailuropoda, Cryptoprocta, Arctictis, Procyon, Nasua* and *Martes*, the articular surface of the scapholunar with the unciform is formed by a portion of this unique curve, allowing relatively ample wrist movement. In *Felis*, this articular surface draws a double curve in the shape of an S, not allowing for any such motion. On the unciform of *Canis* and *Lycaon*, a small backward abutment of the articular surface limits movement of the wrist near the back, but on the contrary assures a greater wrist stability. In *Bassariscus* there also exists a small abutment on the posterior face of the unciform, though situated lower than in the wolf, in such a way that it does not lengthen the superior articular surface and assures a greater stability to the wrist without limiting its range of movement. In bears, the source of the articulation is entirely different. It consists of a kind of thoroughly curved narrow gorge on the scapholunar formed by two smooth surfaces making an acute angle between them, on the sides of which slides the top of the unciform. This combination permits a great freedom of movement.

9) The metapodials are lengthened in digitigrade forms, and short in plantigrade ones. This criterion is one of the best known. It is not infallible, however. The metatarsals of *Procyon* and *Bassariscus* are also proportionally longer than those of digitigrade carnivorans.

10) The differences in size between the metapodials; they are weaker in plantigrade (*Ursus, Helarctos, Thalassarctos, Ailuropoda, Ailurus, Gulo, Meles, Mydaus* or *Cryptoprocta*) than in digitigrade forms. In the latter, digits III and IV are of perceptibly the same size and strength, and clearly go beyond the level of digits II and V in anatomical connection, which equally reach comparable levels from the distal ends. In contrast, in plantigrade forms the distal ends of metapodials III and IV arrive only very rarely at the same level. Metapodials III, IV, and V reach more or less regularly shortened levels in the kinkajou, coatis, badgers, honey badger and wolverine; the first two metapodials are shorter. In the giant panda and bears, the metapodials, as long in the fore limb as in the hind, reach a level very close to one another, sometimes the same on the same line (the foot of *Melursus ursinus*); in general, the absolute height of the metapodials is curved from the first to the last metapodial, but the distal articular blocks reach these levels regularly curved (except the pollex is a little short somewhat, as in the polar bear) up to the fourth metapodial, the fifth being a little shorter than the fourth.

11) The first digits of the hand and foot, well developed in plantigrade forms (the bears, badgers, wolverine, honey badger, pandas, coatis, raccoons, and fossa), are very reduced in digitigrade forms. This is one of the best criteria, along with the preceding one.

12) In the majority of plantigrades the fifth metacarpal is more massive than the other metapodials of the forefoot and its shaft shows a lateral spreading near the exterior along its entire length; it is thus among the forms which I have studied, in *Ursus, Melursus, Helarctos, Thalassarctos, Ailuropoda, Ailurus, Bassariscus, Procyon, Nasua* and *Cryptoprocta*. The fifth metatarsal shows the same phenomenon in the giant panda.

13) The metapodials of the hand and foot of plantigrade forms are spread more or less fully in a fan along the distal edge. In contrast, in digitigrade forms they are tight against one another and form parallel shafts, so as to reduce the supporting surface on the ground as much as possible.

14) In *Ursus, Melursus, Thalassarctos, Helarctos, Meles, Mydaus, Gulo, Mellivora, Arctictis, Ailuropoda, Ailurus, Bassariscus, Potos, Procyon* and *Nasua*, the shaft of the femur is not regular in section from top to bottom as in felids, canids and hyaenas, but shows an distinct narrowing to the level of the base of the upper third of the bone, widening in a cone near the top and bottom from this level. However, the fossa presents the example of a shaft which is very regular and parallel to the edges, as in digitigrades.

15) The femoral insertion of the gluteus maximus, or superficial flexor/abductor, is very weak in the wolf, hunting dog, hyaena, lion, puma, panther, and cheetah, while it is very important and produces a very appreciable projection onto the bone (called the third trochanter) in the bears, Malayan badger, honey badger, pandas, coatis, raccoons, ringtail and fossa.

16) The same seems to be true for the insertion of the scansorius/piriformis (or fourth fessier/abductor, or accessory of the flexor/abductor profundus), which is situated between the first and third trochanters. The placement of this insertion, insignificant in digitigrades, in contrast is large in plantigrades. However, the muscle scar is weak in these same forms, though it is lacking a complete series of dissections in order to to confirm the strength of this character.

17) On the femur of *Canis, Felis*, and *Acinonyx*, the articular surface of the kneecap is narrow, deep, and its two edges are elevated, whereas it is very large, flat, and without projecting edges in *Ursus, Helarctos, Thalassarctos, Ailuropoda, Ailurus, Procyon, Arctonyx, Gulo, Mellivora* and *Cryptoprocta*. An intermediate situation is observed in *Hyaena, Nasua* and *Meles*.

18) The two condyles of the distal end of the femur form two very strong backward projections in the hyaena, wolf, cheetah and cats, whereas in the bears, raccoons, pandas, badgers, honey badger, and wolverine they are much less prominent. The fossa shows a situation a bit intermediate on this point, although closer to that of plantigrade forms.

19) The posterior face of the tibia is occupied by three large insertion surfaces. That of the popliteus occupies the superior medial part, the extra overflowing largely onto the internal face of the bone; that of the external head of the flexor digitorum longus (or external head of the perforant flexor) covers the inferior part and is whittled down near the top extending along the external edge; between these two impressions, the tibialis posterior muscle extends onto a narrow zone, bearing diagonally across the posterior face of the tibia. The relation of the occupied areas to these two last insertions offers one of the best criteria for differentiating plantigrade carnivorans from digitigrade ones: in *Canis, Cuon, Lycaon, Hyaena, Felis*, and *Acinonyx* , the insertion surface of the external head of the flexor digitorum longus is considerably developed and

that of the tibialis posterior strongly reduced. This same disproportion is still more marked in the running types over that in the "bounding" types. In contrast, in *Ursus, Melursus, Thalassarctos, Helarctos, Meles, Mydaus, Arctonyx, Mellivora, Gulo, Ailurus, Ailuropoda, Procyon, Nasua* and *Cryptoprocta*, the insertion of the tibialis posterior is much larger than in the preceding case and extends more distally, thus occupying a larger area, to the sole detriment of the insertion surface of the flexor digitorum longus.

20) The tibiotarsal articular surface draws a small marked curve in plantigrades, more accentuated than in digitigrades. This character, which is difficult to appreciate on the tibia, is very visible on the astragalar pulley, which is deeply excavated and very symmetrical in digitigrades, and shallower, larger, and less symmetrical in most plantigrades (large bears, pandas, ringtail, badgers, honey badger, and fossa). However, in the coatis and raccoons it is deep enough, although large and very slightly asymmetrical. In the Malaysian bears, on the contrary, this pulley is even larger, but very asymmetrical and deep.

21) The posterior articular surface between the astragalus and the calcaneum similarly forms a less pronounced curve in plantigrades (the bears and fossa), than in digitigrades. Only the washing raccoon, among plantigrades, also shows a narrow curvature, like that of cats.

22) The astragalar head in digitigrade carnivorans is basically globular in form; in contrast it is dorsoventrally flat and spread out transversely in plantigrades. An elongate form on the navicular corresponds to this character in plantigrades, but a more square form in digitigrades.

23) The neck of the astragalus is extremely reduced in heavier and more plantigrade carnivorans, namely the bears and giant panda. In contrast, that of the wolf and of *Felis* of small to medium height present a maximum lengthening.

24) In the bears, giant panda, lesser panda, coatis, raccoons, ringtail, kinkajou, wolverine, badgers, honey badger and Madagascan fossa, the calcaneum is a short bone and more stocky in aspect than that of *Felis* and *Canis*, with a more slender aspect. In particular the manubrium, or the part of the body of the bone found in back of the articular surfaces, is very much longer in digitigrades (the cats, hyaenas and wolf), thus offering a more important lever arm to the action of the gemelli of the legs and of the soleus.

25) The sustentaculum tali, a wide apophysis that issues on the internal face of the calcaneum and on which the anterior articular surface of the astragalus is placed, is in a very advanced position in plantigrades, the inverse of that observed in digitigrades where the part situated forward of the astragalar articular surfaces is longer.

26) The accessory of the flexor digitorum longus (or the skin patch of Sylvius), a small fleshy muscle originating on the external face of the calcaneum and moving down rapidly into the flexor longus, leaves a particularly marked imprint on the calcaneum of the bears, lesser panda,

giant panda, coatis, ringtail, honey badger, wolverine, badgers and fossa. The same imprint is in contrast very weakly indicated in the felids, hyaenas, and wolf.

27) On the cuboid of digitigrade carnivorans the astragalar articular surface is noticeably parallel to the articular surface with the fourth metatarsal, whereas these two surfaces form a very pronounced angle between them, which can reach up to 30°, in plantigrades.

Semi-plantigrade and semi-digitigrade carnivorans

We have until now considered the two groups of plantigrade and digitigrade forms. Nature offers the spectacle of a multitude of intermediaries, in which a mixture of the characters of plantigrady and digitigrady are observed, and at the same time a number of more or less important transition characters.

Digitigrade carnivorans

In running digitigrade forms (*Lycaon*, *Acinonyx*) the limbs and metapodials are more elongate than those of bounding digitigrade carnivorans, such as cats. A dissection demonstrated to me that in the hunting dog, the soleus and skin patch of Sylvius (which still showed a certain importance in *Felis*) no longer existed. In the dog, it is known that the soleus has disappeared but that the skin patch of Sylvius still exists. In *Acinonyx jubatus*, the insertion surface on the leg of the soleus, which has become situated at a posterior angle from the proximal extremity of the lateral fibula as in *Felis*, on a dominant tubercle the wide pit whence originates the top of the external head of the flexor digitorum longus, is so reduced that I also believe in the near-disappearance of this soleus muscle.

On the contrary, the jaguar shows a certain number of resemblaces with plantigrades: for example compare it to the puma, in which the bones and the limbs are shorter and stockier, the superior insertion of the tibialis posterior is more extensive, and the calcaneum is stockier with the part in front of the astragalar surface shorter; the skin patch of Sylvius leaves a slightly more marked imprint on the external face of the calcaneum, and throughout the metapodials are clearly shorter. Now the jaguar is an animal which moves fairly little and does not much pursue its prey, and therefore does not entirely utilize the possibilities offered it by digitigrady. It prefers to wait for its prey in hiding and attack it in a single bound, furthermore with an extraordinary power.

INTERPRETATION OF FACTS

The observations have now been put down and grouped in a purely empirical manner. To order among them these observations and links in a similar logical chain, the following process is proposed: the primitive fissiped carnivorans, from the dawn of the Oligocene, or the same from the end of the Eocene, were all plantigrade. The limbs were short, the gait slow, the forelimb slightly arched. The pentadactyl foot leaned largely on the ground, with the short metapodials spread in a fan and their heights little different from one to another. The first digit of the hand and foot were also noticeably developed over those following; the fifth metacarpal, in contrast, was stronger than the other metacarpals, the animal not holding its feet perfectly flat, but slightly out-of-line near the exterior. The articular surfaces of the hand and foot allowed ample and comfortable movement. Then, little by little, these carnivorans, pursuing prey more and more rapid, invented a new mode of locomotion. They held themselves on the ends of the phalanges. The metapodials lengthened and, to a lesser degree, the arms, forearms, thighs and legs. In the extreme running forms, this elongation of limbs is particularly important. The ampleness of the stride is thus considerably increased. At the same time, the forms improved, the limbs became lighter, more rectilinear and slender, and the bottom of the foot was reduced; the lateral digits regressed, in particular digit I; the metapodials contracted against one another as the fingers of a closed fan. This contraction and the regression of the first digit involved the slight regression of the first cuneiform in the hindlimb, which also was moved and came to lodge almost behind the second cuneiform. In respose, the navicular took a more square form and the head of the astragalus stood less along the medial edge. The contraction of the digits lead them to become all parallel. This movement contributed to make the cuboid take on a rectangular profile. As the gait was more rapid, and the bounds longer, the shocks of landing are more difficult; the articulations must become, at least in the forms of great and moderate size, more solid, and the movements more strictly guided. One sees the scapholunar-unciform articulation is, in digitigrades, more limited but more solid than in the plantigrades. Similarly the kneecap lodges in a more restricted furrow in the femur, retaining more elevated edges, and the tibiotarsal articular surfaces draw curves by a radius of smaller curvature. Finally, the animals were raised on their digits, and the movements of the ankle became more important. The longer calcaneum assured a lesser control of speed to the action of the gemelli of the legs and the soleus, but a larger control of power, allowing more powerful bounds. The tibialis posterior, which produces flexion of the tarsus relative to the tibia, was reduced, and thus also the skin patch of Sylvius, which causes flexion of the phalanges relative to the tarsus. At their expense, the flexor profundus, which flexes the phalanges relative to the tibia, is reinforced.

APPLICATION TO PALEONTOLOGY

The differentiating characters found between modern plantigrade and digitigrade carnivorans may now permit determination of the mode of foot support in fossil fissiped carnivorans. This is limited to citation of some examples:

1. *The phylogenetic line of the genus* Felis

Of all modern carnivorans, *Felis* is that which offers the best knowledge of its paleontological past. The line which can be followed with the most precision is that which ends in the European lynx. It appears in the first part of the Oligocene with *Haplogale media*, from the Phosphorites of Quercy, a small animal to our eyes from the end of the snout, the slender teeth, about the size of the small Indian civet *Viverricula indica*, followed by *Proailurus lemanensis* from the Aquitanian of Limagne, then by *Pseudoailurus* (*Schizailurus*) *lorteti* from the Burdigalian and Vindobonian of France and Spain. The first lynx appeared in the Pliocene of Perpignan.

From the Oligocene to the modern epoch, size increased slightly and about regularly, the snout shortened, the number of premolars reduced, and M_2 and the talonid of M_1 disappeared. We know the skeleton of *Proailurus lemanensis* and that of *Pseudailurus*. In the Aquitanian animals, the humerus is more massive, equal in size to that of a *Felis* or a *Pseudailurus*, the distal articular surface is similarly larger, the crista supinatoria more spread out, and the entepicondyle more prominent. The ulna is shorter and presents a more developed insertion crest for the pronator teres than that in the lynx, and at the same time a larger groove for the anconeus profundus tendon. The metapodials are shorter than in *Pseudailurus* and *Felis* (*Lynx*). On the pelvis, the insertion of the scansorius/piriformis is more prominent than on that of these two genera, and on the femur, shorter than that of the caracal, one finds a large area reserved for the insertion of the scansorius/piriformis and a prominent third trochanter with a strong scar left above by the gluteus maximus. The tibia is shorter and possesses in particular an important insertion for the tibialis posterior. Finally the calcaneum has a shorter manubrium and a sustentaculum tali in a more anterior position for the same articular surface size as those of *Felis* and *Pseudailurus*. Except for some detail (entepicondyle of the humerus and a more developed insertion of the tibialis posterior, and slightly longer metatarsals), the anatomy of *Proailurus lemanensis* is extremely similar to that of the fossa. The differences between the lynx and *Pseudailurus* are weak and few in number: only the pit of the olecranon is narrower, the femoral insertion of the gluteus maximus and that of the tibialis posteriorare more developed, and the metapodials are longer in the lynx; in contrast the astragalus and calcaneum are identical. Thus by the Oligocene the first felines are still plantigrade. They had then only to perfect some points of their anatomy to become as fast as the Quaternary *Felis*.

2) *The machairodonts*

These curious felines, characterized principally by the immense size of their upper canines, existed in our country from the Oligocene to the Quaternary and are referred to two different phylogenetic lines: the most ancient are the eusmilines, which we find in the Oligocene of North America (*Dinictis, Hoplophoneus*), in the Phosphorites of Quercy in France (*Eusmilus*) and in the middle Miocene of Europe (*Sansanosmilus*). The machairodonts of the second group, or machairodontines, appeared suddenly in Europe with the great Pontian migration, spreading even into America and becoming extinct at the beginning of the Quaternary. Acheulean man knew the last representatives. Of the eusmilines, we possess the nearly complete skeleton of a small form from the French Miocene, *Sansanosmilus palmidens*. Regarding the humerus, the proportions recall those of the humerus of the jaguar and fossa, the extremities are large, the deltoid crest extremely strong, the crista supinatoria very wide and the entepicondyle, though slight, very spread out laterally, more like that of the fossa; on the femur, the second and third trochanters are very developed, and the articular surface of the kneecap is rather large; the insertion of the posterior tibia very much more prominent than in *Felis*; the astragalus is very short, the head large and flattened, and the pulley very shallow; the calcaneum is short, compact, and the sustentaculum tali occupies a very anterior position there. The metapodials are very short and the first digit well developed. This animal, as strong as a jaguar and the size of a panther, was therefore plantigrade. One of its characteristics is still the possession of an extremely robust forelimb in comparison to the hindlimb, with more developed muscular insertions and more pronounced scars on the bone surfaces. This original disposition, allied to plantigrady and the development of upper canines, evokes a particular hunting mode. The animal must not have run after its prey but waited in hiding, leaping on its victim by surprise, attacking it in a single bound, overthrowing it, immobilizing it by the force of its claws and anterior strength, then stabbing it with its fangs like the blade of a sword.

The Pontian, Pliocene and Quaternary machairodonts display all the characters of digitigrade carnivorans (lionlike humerus, long metapodials, first digit very reduced, Tibialis posterior little developed) and a forelimb considerably stronger and more muscular than the hindlimb. Thus they must have, while pursuing their prey as modern felines currently do, killed them in the same manner as the eusmilines.

3) *The amphicyons*

In the Oligocene and Miocene, the canids were represented principally by the amphicyons, animals showing a number of characters convergent with ursids, and belonging to a subfamily that became extinct during the Pontian. In the Oligocene, many species reached the size of a wolf and, in the Miocene, that of a lion. The skeleton of the amphicyons is well known.

I have studied one of a large Miocene form, *Amphicyon major*. The bones of the forelimb show an entirely remarkable convergence with those of ursids, both by their proportions and by smaller details of their anatomy. The humerus has a deltoid crest which is very prominent, large, flat and descends even to the lower third of the bone, also a crista supinatoria as developed as in the bears and more than in the badger and wolverine, an entepicondyle thick in back and also spread out laterally as in the wolverine; the humerus and ulna move by connecting to one another in planes forming a very appreciable angle between them; at the top of the olecranon, the two edges of the groove for the anconeus profundus are very asymmetrically placed and are very unequal lengthwise; the superior articular surface of the unciform is a simple curve and no abutment comes to extend in back, therefore as in *Gulo, Meles* and *Cryptoprocta*; the five metacarpals, robust and short, spread widely into a fan. The forefoot was thus plantigrade. In contrast the pelvis and femur are, in all their important details, of a very lionlike type. On the tibia, the contact between the surfaces for the insertion of the tibialis posterior and the external head of the flexor digitorum longus is intermediate between that which we observe in the bears and in the lion; the astragalus is short, the head widely developed on the medial edge but with a deep pulley; the posterior astragalocalcanear articular surface forms a curve with a large radius of curvature; the sustentaculum tali occupies a very anterior position on the calcaneum, as in the bears, but the manubrium is much longer than in all modern plantigrades that I know and the bone is also thinner and more tapered than in these; the cuboid is very ursoid, with a trapezoidal anterior profile; finally the metatarsals are as short as in the forelimb. The association of all these characters may be surprising. I have concluded that *Amphicyon major* was a plantigrade animal but that it was capable of a relaxation comparable to that of great modern beasts. Not reduced like the bears, too slow, to a vegetarian regime, the amphicyons fed on lively prey - their teeth confirm this - that they must have attacked at the end of a very brief chase, making only some bounds, even a single bound, a little like our modern lions when they attack a beast of great size.

CONCLUSION

The digitigrade and plantigrade forms do not represent fundamentally opposite structural types, but the first are derived of animals having lived according to the mode of the second, and the modern world offers us a rich range of intermediaries. Evolution has adjusted them to speed and according to diverse modes in the different groups. The other part, the case of the machairodonts and the amphicyons shows us that there existed types of pursuit adaptation which are no longer represented today. Other original formulas without doubt still must have existed. Also, if the observation of higher enumerated characters is relatively easy, the interpretation of a structural type from the observed characters on a fossil animal is much more delicate. A set character has independently only the value of a clue. Only numerous characters taken from different parts of the skeleton can permit, in considering them together, a satisfactory interpretation in the end.

SUMMARY

We have tried to separate the osteologic characters related to the digitigrade and plantigrade condition of the fissiped carnivores by seeking out the common characters of carnivores distantly related zoologically but possessing the same mode of progression. Our study material consisted principally of the bear, panda, coati, raccoon, several badgers and *Cryptoprocta* among the plantigrade forms, and the wolf, hyaena, lion, jaguar, cheetah, lynx, and the cheetah among those digitigrade. We have established the following characters in the plantigrade types: limb bones heavier and shorter than those of the digitigrade; a more loose and supple articulation with articular surfaces of a greater radius of action. For example, the scapholunar in rapport with the cuneiform, the patella or tibia with the tarsus, and the astragalus with the calcaneum; humerus with a prominent crista supinatoria and entepicondyle and a wide deltoid imprint descending very low, ulna with a wide neck asymmetrical for the triceps tendon at the top of the olecranon; femur with a strong third trochanter and distal condyles little developed; short calcaneum with a sustentaculum tali very advanced; cuboid trapezoidal in shape; metapods short and spread in a fan; metapods I and V well developed; the fifth metacarpal larger than the other metacarpals.

Working from these basic facts one can deduce the position of the foot, or stance of a fossil carnivore. Thus, in the phylogenetic line of *Felis*, the digitigrade condition is attained in the Miocene with *Pseudailurus*, the more ancient like from the Aquitanian, *Proailurus* being still plantigrade. The same is true in the eusmilines (*Hoplophoneus, Eusmilus, Sansanosmilus*) which are plantigrade, while the machairodonts, appearing in the Pontian, are digitigrade.

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