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Abstract: In this book about the carnivores of West Africa, a very detailed description of the distribution, general characteristics, skull, habits (sociality, territorial behavior, diet, hunting behavior, speed, handling by humans, climbing capacity, mating behavior, development, and vocalization), taxonomy and measurements of the cheetah are described.

Dans ce livre sur les carnivores d'Afrique de l'ouest, une description très détaillée de la distribution, des caractéristiques générales, du crâne, des mœurs (socialité, comportement territorial, régime alimentaire, techniques de chasse, vitesse, utilisation par l'homme, capacités à grimper, comportement reproducteur, croissance et vocalisations), de la taxonomie et les mesures du guépard sont décrites.

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THE CARNIVORES OF WEST AFRICA

BY

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with 11 plates in colour

by

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and 172 line drawings

by

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TRUSTEES OF
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Genus **ACINONYX** Brookes, 1828

Cheetahs

Acinonyx Brookes, 1828, *A Catalogue of the Anatomical and Zoological Museum of Joshua Brookes Esq.*: 33. Type species *Acinonyx venator* Brookes (= *Felis venatica* Griffith). This was merely a sale catalogue, no descriptions being furnished; the specimen a skeleton, the whereabouts of which does not now appear to be known. The name was probably derived from the Greek *akaina* thorn and *onyx* claw, referring to the appearance of the foot with its unsheathed claws; but it has also been suggested that its origin lies in the Greek prefix *a*—signifying deprivation of, and *kineo* to move, in reference to the commonly held, though mistaken, belief that the claws are incapable of retraction.

Cynailurus Wagler, 1830, *Natürliches System der Amphibien, etc.*: 30. Type species *Felis jubata* Schreber. This name is from the Greek *cyon*, *cygnos* dog, and *ailouros* cat.

Guepardus Duvernoy, 1834, *L'Institut, Paris*, 2: 145, as a subgenus of *Felis*. No actual type species was named but two were cited as appropriate to the subgenus, firstly "le Guépard proprement dit" *Guepardus flavus* (? Duvernoy), and secondly *Felis guttata* Hermann, with *Guepardus fulvus* (? Duvernoy), given as a synonym, Schreber plate 105B. The name is merely a Latinisation of the French *guépard* for the cheetah.

Guepar Boitard, 1842, *Le Jardin des Plantes*: 234. No type specified, but *Felis jubata* Schreber included.

Cynofelis Lesson, 1842, *Nouveau tableau du Règne Animal . . . Mammifères*: 48. No type specified but *Felis jubata* Schreber included. This is a compound of the Greek *cyon*, *cygnos* dog with the generic name *Felis*.

Gueparda Gray, 1843, *List of the Specimens of Mammalia in the . . . British Museum*: 46. A variant of *Guepardus* Duvernoy. Type species *Felis jubata* Schreber.

Taxonomy. *Acinonyx* has, nominally, a wide range, from northern India across western Asia to Africa, and throughout a great part of that continent almost to the extreme south. It is today almost universally regarded as a monospecific genus. At one time, however, the Asiatic and African cheetahs were considered to be specifically separate, this conception originating with Duvernoy (1835). More recently, Hollister (1911) and Hiltzheimer (1913) have been the chief protagonists in a disagreement concerning the most appropriate names for the two reputed species, reaching almost diametrically opposite conclusions. This nomenclatural divergence of view hinged largely on the interpretation of the specific synonymy which follows below in the next section, much of it, as so often in the case of early inadequate descriptions and poor colour reproductions of unrealistic paintings, bound for ever to remain a matter of purely personal opinion. In brief, Hollister held that *jubatus* Schreber referred to the African cheetah and that *venaticus* Hamilton Smith was the proper name for the Indian form, the earlier *guttatus* Hermann being impossible to determine from the curt description. Hiltzheimer, on the other hand, regarded this as a complete misrepresentation of the position, Schreber's *jubatus* plate being obviously that of an Indian animal, this name being thus appropriate to the Asiatic cheetah; while Hermann's *guttatus* was fully identifiable through plate 105B of Schreber's *Die Säugethiere* (see below) and was in consequence the correct name for an African cheetah. At the same time he cited, or erected, a number of other forms at specific level, now regarded as, at most, possible races. Somewhat later, Pocock (1927) described a further very striking African species, *rex* from Rhodesia, in which a large proportion of the dorsal and flank spots coalesced

into narrow bands; but this has for long been regarded as nothing more than an individual mutation, even, subsequently, by the author himself (Pocock, 1939).

Neither Hollister's nor Hilzheimer's view accords with the trend of modern thinking, which is that, as in the parallel case of the leopard, there is but a single species having a continuous range from northern India to southern Africa. This attitude had been adopted by Elliot in 1883; and the possibility of there being separate species in Asia and Africa does not even receive mention in the two most recent taxonomic surveys of the two regions, Ellerman & Morrison-Scott (1951) and Ellerman, Morrison-Scott & Hayman (1953). There is, however, one recent dissentient, Ognev (1962), who not only adopts Pocock's categorisation of the cheetahs as a subfamily, the Acinonychinae, but also regards the Asiatic animals as being separable from those of Africa as *venaticus*, and, further, considers *rex* to be without doubt a good species.

Since it is dealt with herein as comprising a single species all relevant detail concerning the genus will be found below in the account of *jubatus*; but the main points of distinction between *Acinonyx* and the other two feline genera, *Felis* and *Panthera*, and which Pocock considered of sufficient importance to support subfamily status (*vide* page 380), are for convenience briefly re-outlined here. Many other less significant differences of morphology and pattern apart, the most fundamental distinction is that while *Acinonyx* is equipped with the same type of hyoidal structure as *Felis* (and thus differs materially from *Panthera*, as described on page 377) its claws lack the cutaneous sheaths of that genus and, though similarly fully retractile from a forward attitude of aggression, are thus incapable of protective withdrawal from abrasion and view as in all other living cats.

ACINONYX JUBATUS (Schreber)

Cheetah or Hunting Leopard

Felis jubata Schreber, 1775, *Die Säugethiere* . . . , 3: pl. 105; and 1777, text: 392-393. Southern Africa, Cape of Good Hope; but according to Hilzheimer (1913) the illustration is clearly that of an Indian form. The name is the Latin adjective meaning having a crest or mane, with reference to the nuchal crest.

Felis guttata Hermann, 1804, *Observationes Zoologicae*: 38. No type locality was given; it was later stated by Wagner in Schreber's *Die Säugethiere*, Supplement, 2: 503 to be Africa; and Hilzheimer (1913) believed it to be from the Cape. The species was regarded by Hollister (1911) as quite indeterminable, even with Hammer's added editorial notes to Hermann's posthumous work; but Hilzheimer (1913) was firmly of the view that, the inadequate description apart, the species was clearly identifiable from plate 105B published in Schreber's *Die Säugethiere*, Supplement, 3 over the caption *Felis guttata* Herm. and which *vide* Duvernoy (1835) had been specially painted at Hermann's direction from a living animal. The Latin word *guttata* means spotted.

Felis venatica Griffith, 1821, *General and particular descriptions of the Vertebrated Animals* . . . , 2: 93 and plate. Type locality now regarded as India; and the name is taken only as representing the Indian race of *jubatus* Schreber, see the discussion above under the generic head. *Venatica* is the Latin adjective denoting pertaining to hunting.

Acinonyx venator Brookes, 1828, *A Catalogue of the anatomical and zoological museum of Joshua Brookes Esq.*: 33. No type locality given; now regarded as India. The name is the Latin for a hunter.

Felis fearonii A. Smith, 1834, *S. Afr. Q. Jl*, 2: 245. North-east of Natal. It is not clear after whom this was named.

Felis jubata senegalensis Blainville, 1843, *Ostéographie . . . des Mammifères*, Atlas, *Felis* pl. 9 (wrongly indexed as 10). Senegal. Preoccupied by *Felis leo senegalensis* von Meyer, 1826.

Cynailurus soemmerringii Fitzinger, 1855, *Sber. Akad. Wiss. Wien*, 17: 245. Kababish, south of Bajuda desert, Kordofan. This name, which Fitzinger queried as possibly originating with Rüppell, not himself, commemorates Ritter Samuel Thomas von Soemmerring, a prominent member of the Senckenberg Natural History Society. The spelling with a single *r* was thus a *lapsus*; both it and the proper attribution of the name to himself were later the subjects of correction by Fitzinger (1869).

Felis megabalica Heuglin, 1863, *Leopoldina*, 4, No. 3: 23. Type locality uncertain: the skin was purchased on the west bank of the Bahr-el-Abiad but was possibly, and in Heuglin's opinion very likely, brought from further inland. The description leaves some doubt as to whether this really was an *Acinonyx*. The name is from the Greek *mega* very much, and *balios* spotted.

Felis jubata var. *africana* Hartmann, 1868, *Z. Ges. Erdk. Berl.*, 3: 56. Africa.

Felis fearonis Fitzinger, 1869, *Sber. Akad. Wiss. Wien*, 59 (1): 664. A substitute, or error, for *Felis fearonii* A. Smith.

Felis lanea P. L. Sclater, 1877, *Proc. zool. Soc. Lond.*: 532. Beaufort West, Cape Colony. The name is the Latin adjective meaning woolly, given in reference to the unusual pelage of the type animal.

Acinonyx wagneri Hilzheimer, 1913, *Sber. Ges. naturf. Fr. Berl.*: 285. Kordofan. This name was erected for possible eventual attachment to the description given by Wagner in Schreber's *Die Säugethiere*, Supplement, 2: 503, intended by him for *guttata* Hermann but which Hilzheimer regarded as depicting some other form which might or might not prove to be different from *soemmerringii* Fitzinger.

Acinonyx hecki Hilzheimer, 1913, *Sber. Ges. naturf. Fr. Berl.*: 288, text-f.1. Senegal. This was named in compliment to Professor Heck in celebration of his 25th year as Director of the Berlin Zoological Gardens.

Distribution and general. Famed as the fastest animal on earth the cheetah is, from its constant exhibition in zoos and illustration in natural history publications, one of the best-known of cats, at least as regards its general appearance. And since it is in habits very largely diurnal besides frequenting the more open types of country it is not so rarely seen in nature as most of the other felines, nocturnal and secretive as they are. Until relatively recent times it had a wide and continuous distribution from the Cape to northern India. It was to be found in most of the more open types of woodlands or semi-desert in Africa, extending its spread to parts of the north Atlantic and Mediterranean countries; thence it ranged across the Arabian peninsula, through Jordan, Iraq, Iran, Afghanistan and Baluchistan to the Ganges in Bengal. Its distribution is, however, with rapid expansion of human population and the opening up of formerly remote and undeveloped areas becoming yearly more restricted and its existence in several regions severely threatened. Pocock in 1939 thought that it was probably already extinct in much of India and the middle east. Its territory has contracted, too, in both northern and southern Africa, but it appears to retain its hold to some extent in the open woodlands of the tropical parts of the continent, being at its most plentiful on the eastern side between Eritrea and Malawi. At the southern end of its African range it no longer occurs at more than about 28° S at most, though in former times it reached practically to the Cape.

The cheetah has always been present, and not uncommon, around the borders of the Sahara, both north and south, and not so long ago even penetrated deeply into those parts of the desert sufficiently favourable to support an adequate supply of addax, gazelle and other acceptable prey (Lhote, 1946); but its optimum range in West Africa has always been the Sahel and Sudan zones of vegetation, where gazelles, crowned duiker, hartebeest and other suitable sources of food exist in reasonable numbers, and

range of vision is not too greatly obstructed by dense ground cover. During the dry-season when the grass has been burnt and antelopes move southwards into the Doka and northern parts of the Guinea woodlands to crop the young fresh green herbage the cheetah follows and for a few weeks is to be found in these zones which it otherwise mostly avoids owing to the difficulty of detecting and pursuing prey in the lush undergrowth that burdens the area throughout the greater part of the year. It avoids marshy ground.

The cheetah reputedly occurs in West Africa throughout the length and breadth of the Sudan and Sahel woodlands from Senegal to Cameroun; but positive records are very few, and there are in the British Museum no more than a single skin from Lake Chad, dating from 1905, one adult skull from Yantumaki (Katsina Division, Nigeria), and a juvenile skull, ex-zoo, from an unspecified locality in northern Nigeria but very possibly the Bauchi Plateau. *Acinonyx* has never been really abundant in West Africa, and there is no doubt that for some time it has become increasingly scarce in most areas; but this paucity of study material must not be taken as an accurate indication of rarity, for the pelt has always been a much-desired trophy with which the hunter is unwilling to part, and in recent years has become of such high commercial value that it has been lifted out of the class of zoological gifts to museums by even the most enthusiastic of amateur collectors. Indeed, this shortage of material does not apply solely to West Africa; for Pocock (1939) in compiling the *Fauna of British India* had to obtain a skin specially sent at his request from India since none existed at the time in the national collection; and he was forced to publish the measurements of African skulls in default of Indian specimens. According to Graham & Parker (1965) the greatest concentration of cheetahs in East Africa is in the Nairobi National Park where they occur at a density of one to about every 5 square kilometres; but a more common figure over the rest of the region is one to 130 sq km. It is unlikely that in West Africa anything higher than the latter density is anywhere attained, and over most of the area, particularly the more southerly portions of the range, it is probably less.

Description. The cheetah is regarded by many as certainly the most elegant of all the cats with its tall, slender form, delicately patterned coat and long, impressive tail, the whole marred only, perhaps, by a head that seems somewhat too small for the body. In its motions it is graceful and deliberate. Only the serval, in Africa, has the same long-legged, svelte build; but that is much smaller besides lacking the authoritative, even disdainful, air that characterises the cheetah. This imposing feline, the smallest of the three African "large cats", nevertheless stands higher at the shoulders than the bulkier leopard, about 760 to 850 mm; and, indeed, the shoulders, accentuated by their erectile crest, are often noticeably the highest part of the profile, the back curving concavely away to somewhat lower hindquarters, and the head and neck not infrequently held inclined downwards. The body, which is extremely slender and held far off the ground by the unusually long thin legs, measures, with the head, in the adult roughly some 1100 to 1300 mm, the tail some 60 to 70 per cent of this in addition. The weight is generally from 50 to 60 kg, the males on the whole being slightly larger than the females. The latter develop a dozen or more mammae.

The coat pattern is simple but very distinctive. In respect of ground-colour the fur

varies in different specimens from buffish to pale red-brown, an ill-defined band along the spine being rather more intense than the rest. On this background is superimposed a pattern of very numerous, clearly defined, usually jet-black spots, which are almost entirely round or slightly oval, mostly between 10 and 20 mm in diameter; but in the only West African skin in the British Museum they are considerably smaller, about 5 to 7 mm diameter. The spots are independent, not grouped in obvious rosettes as in the leopard; and though they can often be traced as clearly running in lines the direction of these is so inconstant that the overall disposition of the spots is in sum irregular. Their black colour resides only in the terminal portion of the hairs forming them. This maculation covers the entire body except for some of the underparts, running from the top of the head over the whole back, flanks, legs and the basal half of the tail; the chin, throat and posterior part of the belly being white, the forward part of the chest and middle region of the belly spotted. In the distal half of the tail the spots tend to unite into irregular transverse bands above; and near the end form about three complete black rings, the tip itself being white. Its whole underside is white or whitish except for these black rings. In general form the tail is subcylindrical; but in the distal half the hair increases in length and with it, consequently, the overall diameter of the structure.

The insides of the legs are spotted as well as the outsides but the front limbs do not display the clear black "bracelet" bands present in many of the cats; and the hindfeet from toes to ankle are almost entirely devoid of markings. The soles are hairy in between the pads, which are hard and dog-like; the interdigital webs are narrow; the claws not so curved or sharp as in the more typical cats; and though they are retractile they have no cutaneous sheaths to conceal them in this position. The nail of the 1st digit of the forefoot (the "dew claw") is more curved than the others and, since it is raised well off the ground and so freed from wear, often much sharper.

The head is very rounded, the muzzle being short. The ears are small for the size of the body, rounded, not very high and widely separated from each other across the head. On their backs they are intense black in the lower half, the distal portion being more or less of the common ground-colour of the pelage. The crown of the head carries small spots and so do, often, the cheeks; but the chief facial marking is a very conspicuous black stripe curving down from the inner angle of the eye to almost the corner of the mouth. There are rather obscure whitish marks under the eyes, and sometimes above; the pupil is round. The rhinarium is fairly large, with two conspicuous features, the prominent naked area lateral to the nostrils, and the deep vertical groove on its frontal aspect.

The pelage is of variable length and density, probably in accordance with season; but it can be characterized in a general way as short, close-lying, mostly slightly harsh in texture. There is a far more lengthy crest, or even mane, of variable extent in different specimens. At its greatest spread it covers the whole back of the neck with dense woolly fur some 50 to 70 mm long; and this is continued posteriorly down the medial line as a crest to just beyond the shoulders. The broad neck mane is sometimes lacking, but the narrow medial crest is generally present though in some examples relatively poorly developed. The colour may be greyish or, more often in the crest a mixture of ground-colour and wholly blackish hairs. Young cheetah cubs have a markedly different

appearance from the adults in that their dorsal pelage which is sharply divided from the normally coloured lower parts, is not only extremely long but also of a light greyish colour and superficially unspotted. On turning this lengthy fur back the usual maculation is discoverable; and during adolescence this juvenile covering is moulted revealing the normal short, tawny, spotted pelage of the adult. It seems probable that the nuchal "mane" is not developed with age but, quite the contrary is, in fact, the last remnant of this juvenile coat which ultimately disappears leaving only the adult crest. This crest is erectile.

The composition of the pelage is very variable. In some specimens the underfur is short and sparse and plays a relatively minor role compared with the bristle-hairs and long fine-petioled sub-bristles. But in others the underfur is long and abundant and dominates the pelage. This is possibly a question of age or, more probably, season. The black spots in the pelage are composed of precisely the same elements and in the same proportions as the rest of the fur, the only difference being that the hairs are black at the tips.

Skull (figs. 65 and 66). In lateral aspect the skull is highly domed, falling away steeply from a supraorbital summit towards the occiput and towards the short rostrum. The zygomatic arch is broad anteriorly, across the jugum, much narrower posteriorly; it is relatively sharply upcurved compared with most *Felis* species. There is a considerable jugal process but the orbital ring remains widely open. The maxillary process is short and very little salient and does not in any way overhang the infraorbital foramen. This last is, at its full development, tall and narrowly elliptical but is often very much divided, consisting sometimes merely of a number of small canals.

In dorsal view the postorbital processes are very short and blunt, the frontal region having roughly a broad diamond outline, the interorbital width appreciably less than the postorbital constriction. There is a broad, shallow but very marked depression around the fronto-nasal suture, this suture itself being wide and often square or shallowly angular, the nasals not tapering posteriorly to a sharp narrow point as they commonly do in other feline skulls. The vertical branch of the premaxilla protrudes only a short distance between the maxilla and nasal so that these two latter bones are in lengthy contact with each other. The nares are very large, possibly facilitating a great deal of rapid breathing. The braincase is very rounded, and there is usually little evidence of a sagittal crest except at the extreme posterior end adjoining the well-developed but not very wide-spreading supraoccipital crest. A low but quite distinct sagittal crest can, however, sometimes be developed, as some British Museum specimens demonstrate.

Ventrally, the palate is short and broadly triangular. The postdental palate has sharply sloping sides and is not very extensive owing to the great width of the mesopterygoid fossa the anterior margin of which is broadly semicircular, mostly with a medial notch. The hamulars are broad hooks, carried about the mid-length of the pterygoids, the lateral wings of which are well-developed. The bullae, though inflated, are relatively small for the overall size of the skull. One of the most noticeable features of this ventral aspect is the pronounced angle formed by the posterior, basicranial, floor of the skull with the anterior, palatal, portion; in the majority of felines, as well as in other carnivores, the two lying much more nearly in the same plane.

There is nothing remarkable about the mandible except that for a large cat hunting large prey it is not particularly strongly built, the rami being shallow and straight, the anterior end not sharply upturned. The dentition, however, both upper and lower, is distinctive. The cheekteeth are nominally $\frac{3.1}{2.1}$ as in all other African felines except the caracal; but the small anterior upper premolar may not infrequently be lacking. When it is present it completely fills the very narrow space between the canine and the second premolar, being often tightly jammed against the latter. The space between the canine

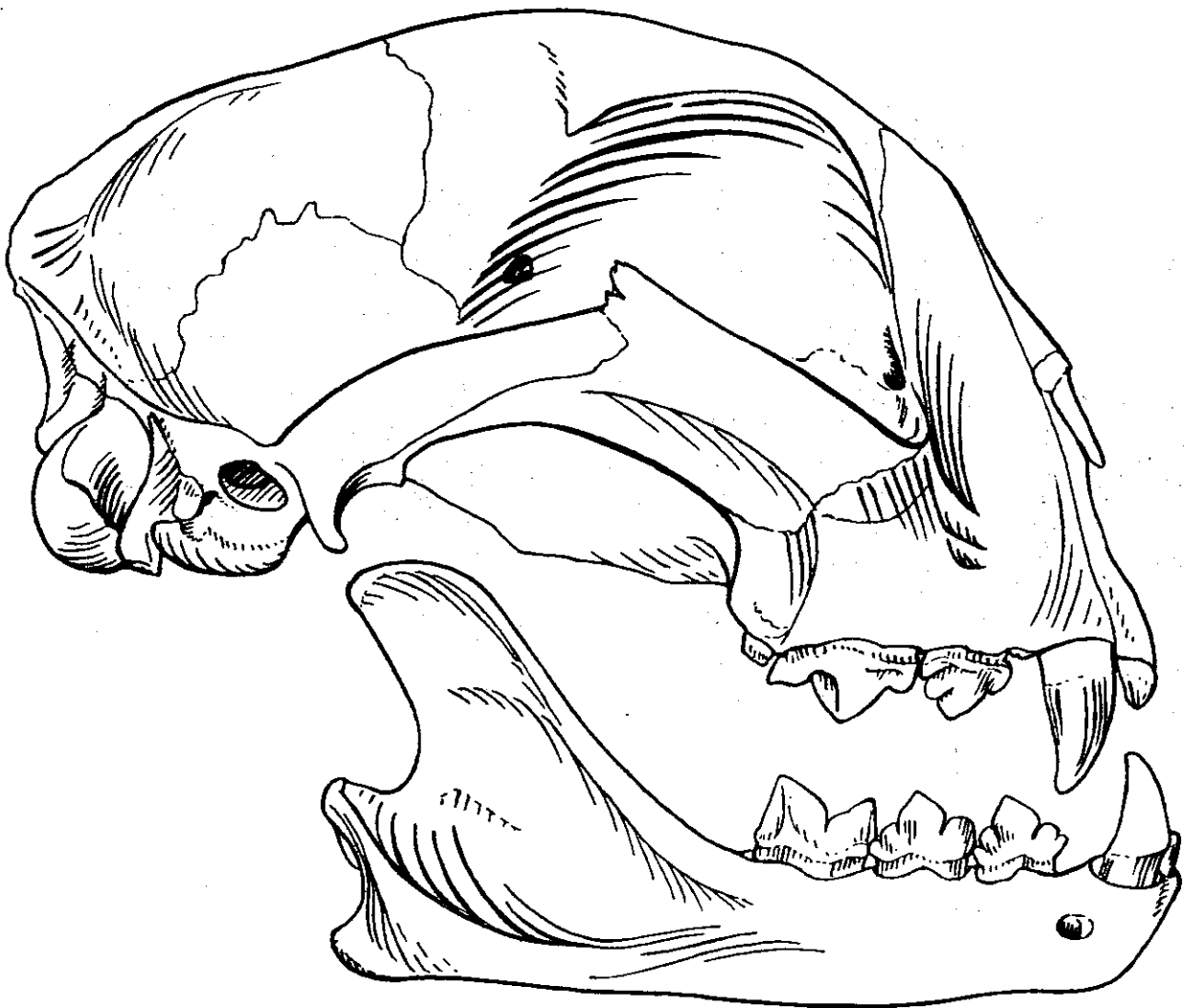


FIG. 65. *Acinonyx jubatus*: skull, B.M. No. 32.12.27.1, ♀, $\times \frac{4}{5}$; lateral view

and first premolar of the mandible is also unusually narrow, so that when the jaws of *Acinonyx* are tightly closed there is little sign of any postcanine gap which is so obvious a feature of other felines. This tight closure of the jaws is to some extent facilitated by the great reduction and almost complete evanescence of the antero-internal cusp of the upper carnassial, present in all other West African species. In addition, the anterior and posterior cusps of the premolars, both above and below, are not only unusually well-developed but also in nearly every case doubled by the interposition of a shallow notch.

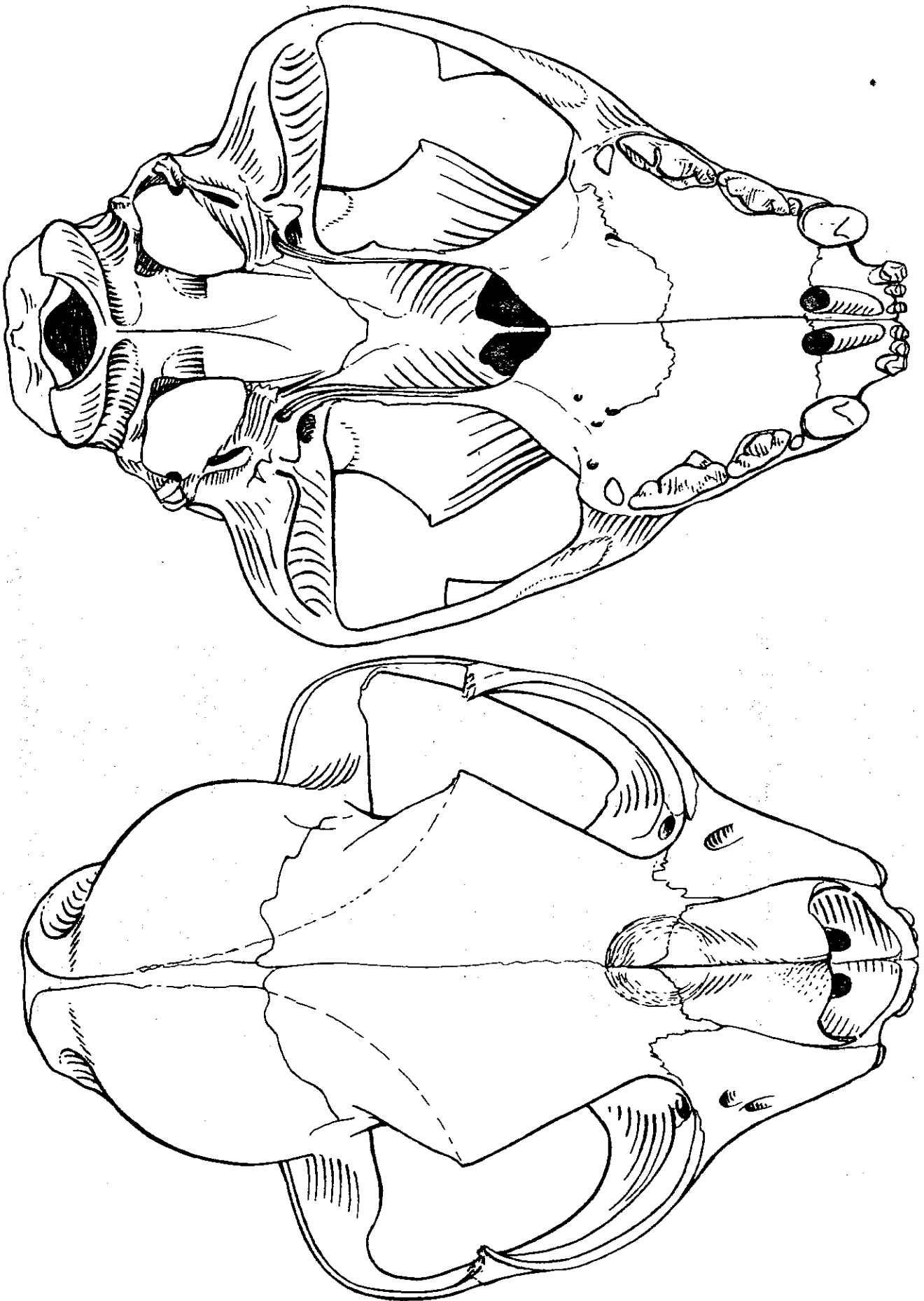


FIG. 66. *Acinonyx jubatus*: skull, B.M. No. 32.12.27.1, ♀, $\times \frac{4}{5}$; palatal & dorsal views

The canines exhibit little or no sign of vertical furrowing usually obvious in other African felines.

Habits. The habits of the cheetah have been more fully recorded than those of most other African felines since it has been under much closer observation for a long time as a commonly captive species; and as it is chiefly diurnal and frequents open country it is more often seen and its behaviour in nature more readily studied than with almost any other cat but the lion. Yet the great majority of such field sightings have in the past been but fleeting glimpses or isolated experiences of different naturalists leading to general deductions and a composite picture, not necessarily accurate or very complete, for the species as a whole. Recently, however, specific and prolonged field studies of the cheetah have been made by Kruuk & Turner (1967) and Eaton (1970a, b & c) using motor vehicles, film-strips, telephotography, tape-recorders and other modern equipment and methods which enable a far more broadly based, complete and less controversial picture to be obtained.

Cheetahs are for the most part active from daybreak, or just a little before, until nightfall; but this does not entirely rule out nocturnal movement, for they may occasionally be picked up deep in the night in the headlights of cars. But their usual method of hunting calls for an initial distant view of possible prey and a final high-speed chase rather than a close-quarters spring as in other cats, and these requirements, as in *Lycan*, postulate daylight or at least rule out all but the most brilliant of moonlight nights. For the same reason the cheetah is forced to frequent open country; and though much of eastern and southern Africa conforms to this description, in West Africa it is only the Sudan, Sahel and Subdesert that for the greater part of the year provide this requisite. Hunting activity has been observed at all times of the day but there is some evidence that morning and evening are preferred, perhaps because of the arduousness of an all-out sprint in the mid-day heat of the tropics.

Acinonyx may be seen singly or in larger associations, either all males or of mixed sexes. Some of these groups are simply a mother with her young, the father never remaining with the family. But where adults alone are concerned Graham (1966) found in East Africa that solitary animals occurred in only 27 per cent of sightings; pairs were the commonest at 34 per cent; groups of three formed 19 per cent, and of four or more 20 per cent. The leader of a group is always a male except, of course, when the association is simply that of a mother with her young cubs; but in this latter case one of the male children eventually, at sexual maturity (about 14 months), becomes dominant, after perhaps first sharing leadership with his mother for a short probationary period (Eaton, 1970b). The size of such a family group of a mother with her offspring generally decreases with the age of the cubs; for the mortality rate is high, nearly 50 per cent of a litter disappearing, mostly taken by lion, leopard or spotted hyaena, within the first 8 months (Graham, 1966; Eaton, 1970b). There appears, apart from very occasional accidental adult losses, to be very little other cause of death but this predation of juveniles.

The question of territory in the cheetahs is an interesting one. It has been investigated by Eaton (1970b). It is easy to appreciate that from the low densities of these animals upon the ground, mentioned earlier, that it would be an impossible task constantly to

demarcate the boundaries of the large areas over which they must hunt and effectively defend them against invasion by other groups, as in the manner of the wild dog *Lycaon*. The element of time is therefore introduced; and though different groups of cheetah may roam and hunt over much the same general area they are careful, should their paths cross, not to follow one another but to pursue different directions. This is effected by a system of scent marking the route taken, whose prohibition of trespass is operative for only a period of 24 hours. Marking is effected by backward urination upon especially prominent features such as unusual trees, isolated shrubs, tall herbs, conspicuous clumps of grass, rocks and so forth, objects, in fact, which by some degree of difference from their surroundings, in species, size, shape or isolation, attract visual attention. This marking is carried out at frequent space intervals (30 to 100 metres) by the males, the penis being accurately directable and a few drops of urine sufficing. The tail during micturition is held stiffly straight, almost erect. In Eaton's view urination in the female is purely an excretory function having no territorial significance though, of course, it may serve the purpose of indicating to passing males that she is in season. The situation of desirable marking points may dictate a zig-zag rather than a straight line; but these paths become known not only to one particular group but to all that frequent the area.

When in the course of their journeying a group comes across a mark recently left by another group they all, males and females alike, take a great deal of interest in it and then proceed to mark the same place. Eaton observed them then to scatter somewhat to search the neighbourhood for further marks, the first cheetah to find a site kneeling as an indication to the others, which then join him and do likewise while sniffing and analysing the message. The two marks together thus provide a clue to the line recently taken by the first group; and the second party, having themselves marked the second point, are then careful to move off in a different direction. It will thus be seen that though there is no demarcated territory in the generally accepted sense the different groups avoid clashing and operating in the same area. The scent loses its intensity, and hence its warning or prohibitory effect, in 24 hours; and a second group may thus without hesitation pursue almost precisely the same route, or at least a great part of it, as that taken by another group the previous day. Should two groups pass within sight of each other there is no question of aggressive behaviour as in territorial defence in other animals. The most that happens is that they adopt an attitude of threat, with lowered head, ears drawn back and mouth slightly open.

Cheetahs appear to be strictly carnivorous. There is, indeed, no record of stomach contents; but no observer seems ever to have seen them deliberately taking any kind of vegetable food, nor is there any account of captive cheetahs eating anything but meat. It is, nevertheless, true that like so many of the larger cats that live on herbivores they do, in fact, take in more vegetable food than appears at first sight by reason of consuming the gut of their victims and its grassy content. In general the food consists of freshly killed animals or, less frequently, birds. Cheetahs do not eat carrion, nor do they as a rule return later to their own kills. They have thus sometimes been stigmatised as wasteful predators; but anything that they may leave, of course, provides a welcome meal for other less fastidious feeders. The distaste for stale food renders trapping difficult.

The main food is provided by antelopes, from those of small size to not fully-grown specimens of the larger kinds. The criterion is that the prey must be of no greater bulk than can be knocked over and successfully held down by a predator of the slender build and relatively light weight of the cheetah, lacking the solid mass and the powerful limbs of the lion or leopard. Full-grown and healthy specimens of such things as, in West Africa, eland, roan, waterbuck and the hartebeests are thus excluded; but immature, ailing or otherwise enfeebled examples of these, such as highly gravid females, may be attacked, though not always successfully. All carnivores have a very quick eye for the least sign of incapacity in potential prey. The favourite food species are with little question gazelles; they live in herds and so offer selective opportunity, and they are of such size as to render a knock-down almost certain. With ungulate species that live singly or in pairs, or lead a secretive existence in dense undergrowth, such as duiker, or are of large bulk, such as full-grown hartebeest, the chance of a successful conclusion to a hunt is lessened but may through force of circumstances have to be taken. The problem of feeding is, for the cheetah, altogether more difficult in West Africa than in East Africa, where the terrain is for the most part far more open, the number of community-dwelling species of antelope much higher, and the size of the herds as a general rule incomparably greater. Besides gazelles, other species taken in West Africa are oribi, crowned duiker, bushbuck, addax and young warthog; but other kinds are killed as opportunity offers, and at the lower end of the scale a cheetah which has been unable to find a better meal will readily take simpler fare such as a hare, giant rat, cutting-grass, guinea-fowl, bustard or other ground-haunting bird, even a young ostrich, though the possibility of this last is rare today in West Africa.

Except in the case of these smaller creatures successful hunting involves speed, the precursor to the climax of the kill being always a rapid sprint rather than the sudden and unexpected pounce employed by the majority of felines. The most usual preliminary to this is for the cheetah to detect, from some eminence, potential prey in the distance and then to advance on it at a walk, using every possible bit of cover to enable it to approach within a hundred metres or so. Some observers—but there is disagreement on this—describe it as, in the last stages of this approach, crouching low to the ground, slinking along behind bushes or tufts of grass until the moment comes to reveal itself and the prey takes flight. At once when this happens the cheetah accelerates with astonishing rapidity into a bounding gallop which before long brings it up with the fleeing antelope even though the latter may have had a hundred metres or more start. The cheetah progresses by long bounds, its feet alternately bunched together beneath the belly or widely extended apart as the body flies through the air. As soon as it is sufficiently alongside its prey, during one of these latter outstretchings, it strikes the antelope either across the hindlegs or across the back, thus upsetting the victim's balance and bringing it crashing to the ground on its flank or back. It has been asserted in India (Burton, 1950) that the curved, sharp and powerful dew-claw plays an important role in this striking down, though more recent observers in Africa have made no reference to this or to any gash across the flank thus caused. It would seem, indeed, that no such ripping wound is necessary, the problem of bringing the animal to the ground being purely one of over-balancing it by weight or impetus.

The moment the prey is on the ground the cheetah leaps stiff-legged upon it, rolls it on its back and fastens its jaws into the throat, maintaining this stranglehold without any relaxation until suffocation brings about death. Any other method of killing by an adult cheetah is very unusual, and is never employed for an antelope—no leap onto the back as with the lion or leopard, no rupture of the spinal cord by a bite into the back of the neck, or no severance of the jugular vein as sometimes asserted. But strangulation is of slow effect and may, according to Eaton (1970b) commonly take 5 minutes and not infrequently as long as 25 minutes; and sometimes the victim recovers and has to be suffocated a second or even a third time. During this slow death the doomed animal must be held firmly down. This is one reason why large and powerful ungulates can rarely be successfully tackled; because even if in the course of a gallop they can without much difficulty be thrown off balance and brought to the ground they are too muscular to be held there long enough for throttling to take effect. Moreover, even with moderate-sized antelopes the cheetah must be careful how it positions itself; for were it to place any portion of its body to the rear of its victim's head it might well, in the latter's struggles, receive a serious, if not fatal, wound from the horns. It does, in fact, while fastened to the throat lie at right-angles to its prey, one forelimb across the head, one across the neck or forequarters, pressing the animal to the ground. It is here that the dew-claws might well come into play, assist in pinning down the choking antelope and, by the latter's convulsive movements, cause incidental gashes that may have misled Indian observers. At any rate, Robert Coulthard, at one time game warden in northern Nigeria (personal communication), noticed that the dew-claws played an active role in feeding, the food material being held in place by the side of the forefoot, not the sole.

What has just been described is generally regarded as the normal sequence of hunting—concentrated observation of distant prey from an elevation, or nearer prey from an outlook in the grass; careful approach to within striking distance by stalking, using all available cover; and the final sprint. It is so recorded by many observers of both wild and trained captive cheetahs, including Eaton (1970c) who has as the result of special study given the most detailed account. But Kruuk & Turner (1967) observed a different method. They never saw a cheetah stalk its prey, though it possibly made some use of long grass. For the most part it walked unconcealed across the open plain to its potential prey. A herd of antelope might watch an approaching cheetah with interest, but no apparent alarm, until it was within 50 to 80 metres before they thought of taking flight. Cheetahs might even sometimes walk through the midst of a scattered herd without any sign of offensive action until one of the antelopes more timorous than its companions took to its heels. It was this action that triggered off the predator's response, causing it to break immediately from its leisured gait into rapid pursuit. The rest of the story, the striking down, seizure by the throat and throttling, is the same. Since females are generally more timid than males it is that sex which constitutes the greater number of kills.

This behaviour postulates a somewhat random choice of victim. Eaton's observations, on the other hand, appear to indicate that it is the dominant male of a cheetah group that determines not only when hunting shall take place but selects as well both the kind

of prey and the actual individual to be killed. In any case, when more than a single cheetah is concerned, though all take part in the chase one alone leads and does the actual killing. It is obvious that with the method employed, seizure of the victim's throat, it would be difficult or impossible for more than one cheetah to fasten onto the limited area available. The only known West African observation confirms this. The late J. T. Davey of the Locust Research unit (personal communication) came across three cheetahs hunting red-fronted gazelle in the north of Nigeria and followed them in a car at a distance of about 50 metres, the animals being quite unaware of his presence. It was the centre cheetah that dominated the hunt and eventually killed, the other two playing a subordinate role during the chase, lying on the flanks at a distance of about 5 metres. Indifference to motor cars has been noticed by others (e.g. Hanström, 1949).

The only variation in the method of killing would seem to be with warthogs, the throat of these animals being too broad to be successfully seized and compressed by the cheetah's relatively small and not outstandingly powerful jaws. But it is only the young of these that are taken, and death is probably caused by fracture of the thin bones of the immature skull brought about by leaping on the back and the overtopping blow given by the predator's paw. Where it is possible cheetahs like to drag their kill to cover before consuming it; and sometimes before killing it. This is almost certainly because they are not very courageous in defence of themselves or their possessions and are easily driven from their meal by lions or spotted hyaenas. Eaton (1970c) observed that except in the case of young antelopes the head and upper part of the neck were not as a rule eaten and these parts could thus be examined as soon as the cheetahs left their kill in order to determine that the cause of death was, in fact, strangulation and nothing else. Stevenson-Hamilton (1947), on the other hand, describes a lengthy set sequence of consuming the prey which includes eating the meat off the face and neck. This author also states that the victim is generally eaten where killed, not dragged away to shelter; and there are other confusions—all examples of the directly contrary accounts of behaviour commonly occurring in the old and the new literature which sometimes make it difficult to credit that it is the same species whose habits are being described.

Whatever the manner of approach to the prospective prey the cheetah's success depends ultimately upon speed. It does not understand overcoming its victim other than by a toppling thrust given to an animal in the vulnerable equilibrium of an all-out gallop. In order to achieve this overbalancing blow it must often catch up a hundred metres or more in the relatively short space of four or five hundred metres; for no cheetah can maintain its high speed for more than such a distance, and if it fails by then to have come up with its quarry it must stop exhausted and start the whole sequence over again. Cheetahs, therefore, without question travel very fast, for antelopes are by no means slow. But how fast? It is very commonly asserted today that they are capable of 112 km (70 miles) an hour or even more; yet no one has actually timed them at such a speed and there is evidence that such a figure should be regarded with caution.

It is not easy to trace the actual origin of this high estimate of velocity; for practically all those who quote it make no claim to having themselves attempted to confirm it. A. B. Howell (1944) in a book entirely devoted to speed in animals adduced no figures or measurements of any kind for the cheetah but merely the hearsay view that "it

seems certain that it can travel at the remarkable speed of 65, and not unlikely that for a short space even 70, miles per hour". Severin (1957) claimed to have timed a captive cheetah over a short course at about 113 km (71 miles) per hour; but Hildebrand (1959) pointed out that this was invalid due to inexactitudes of timing, distance and calculation. Hildebrand himself (1959 and 1961) attempted to deduce a cheetah's speed by analysis of film strips of an animal in action, and produced a figure of about 90 km (56 miles) an hour. In spite of this, in the summary of his paper (1959) he makes the assertion that cheetahs can sprint at 112 to 120 km (70 to 75 miles) an hour, though there seems, from the main text, to be no more valid ground for this than "a general consensus" and possibly the fact that a pet cheetah in America was once observed to overtake a young pronghorn antelope, someone else at another time having shown by a car speedometer that a pronghorn can under favourable conditions attain 97 km (60 miles) an hour though normally running at 80 km (50 miles) an hour. On the other hand, Bigalke (1964) expressed the view that the cheetah's speed was commonly overstated and that it was more probably about 72 km (45 miles) an hour; and this opinion was supported by Grzimek (1964) who quoted a trial made in England against racing greyhounds. It is possible that under great stimulus a cheetah might be able to exceed such a speed but only for a very short burst. There is no positive evidence at present available that it can reach, let alone maintain, as high a rate as 112 km (70 miles) an hour. And indeed, simple calculation shows that 80 km (50 miles) is adequate. Gazelles as a rule run at something like 60 km (37 miles) an hour; and at this speed if they have from the cheetah 100 metres start the latter can catch them after having run 400 metres, the whole affair being over in less than 20 seconds. Such figures, in fact, accord pretty well with the general run of field estimation of time and distance—two much easier factors to judge than speed. Acceleration from a standing or walking start is necessarily extremely rapid and it seems probable that top speed is achieved in between 2 and 3 seconds, though once again there is no accurate measurement.

The remarkable quality of the cheetah's speed and the thrill though brief, of watching it overhaul a herd of deer or antelope which had been given a long start led to its being kept, in the past, as a spectacular hunting animal by many of the rich potentates of Persia, India and elsewhere. This was no matter of the possession of a single specimen as an unusual curiosity; cheetahs were kept in some numbers with their own special staff of trainers and handlers. When wanted for a hunt they were taken out to the chosen location chained and hooded in special bullock carts without sides; and when they came within suitable distance of the chosen prey, which may also on special occasions have been herded or transported to the site in order to ensure a sufficient spectacle, their eyes were uncovered and they were, from the eminence of the waggon, given a sight of their quarry. They were then unleashed and allowed to leap down from the cart; and the chase, thereafter, followed the pattern outlined above—cautious stalking to within a manageable interval, revelation with consequent alarm and flight, the lightning pursuit, the strike and the stranglehold. The huntsmen usually followed at a short distance on horses, recaptured the cheetah, slew the quarry and rewarded a successful hunt with a bowl of the victim's blood and a joint of its flesh.

Such hunts took place over a period of some hundreds of years, as old literature

makes clear. A first-hand account of their form in India in the early 19th century, together with steel engravings, is to be found in Mundy (1832): and another in Vigne (1842: 41). Today, when in Asia rich potentates, herds of ungulates and the cheetah itself are all virtually extinct, they are things of the past. Yet two important aspects of the life and behaviour of *Acinonyx* are still apparent from this once regal pastime. It was found that cheetahs taken as kittens turned into poor hunters and that real success could be obtained only by their capture as adults. This is because the young, though born with some inherent predatory instinct, have to learn from their mothers the finer arts of hunting and killing (Eaton, 1970c). This they do partly by continual observation over a long childhood lasting about a year, and partly by practice deliberately given to them by their parent. Speed for the chase is inborn; and, as demonstrated by their behaviour in play, so is the striking down action of the paw, which Encke (1960) first saw exhibited in cubs of 11 to 12 weeks old. But the cautious stalking and the rest of the sequence up to the seizing of the throat is learned by watching the mother in action and eventually copying. Kruuk & Turner (1967) observed a female to put a still living fawn before her young and allow them to chase it; and Eaton (1970c) records what appears to be a deliberate segregation of a warthog sow from her litter by a mother cheetah whilst her own cubs practised chasing the young pigs. It is probably not until they are about 6 months old that cheetah cubs are allowed to accompany their mother on a foraging expedition, and certainly not to take any active part until later. They probably attain full skill at the age of about a year.

The second point that emerges from the ancient Asiatic pastime is that adult cheetahs are docile, quite amenable to captivity and handling by humans, lacking the fierce offensive resentment exhibited by the vast majority of carnivores taken after the initial stages of babyhood. While it is true that a cheetah driven into a corner in ultimate defence of its life may, like any other animal, turn on its opponent it does so in no very alarmingly fierce way; and, in fact, aggressive behaviour plays exceptionally little part in its life. It has already been mentioned that when two groups of cheetahs meet in the field there is no challenge or fighting, though Stevenson-Hamilton (1947) does record two cases of fatal combat between males. Eaton (1970b) found that even when a young male is taking over leadership of a group it is done without contest or aggression. It was noted above that cheetahs put up very little defence of their kills, being easily driven off by lions or spotted hyaenas. They are, in fact, sometimes killed by lions (Hardy, 1959); and, though there appears to be no definite record, it is not unlikely that the young are snatched by hyaenas even under the eyes of the mother. In most animals, and especially carnivores, the female is bold and determined in defence of her young; but Ansell (1963) records a case of a cheetah cub being taken by a man, the mother advancing threateningly to within a few paces but making no attack even though the male parent was also present in support. Cheetahs have, indeed, rarely been known deliberately to attack man as lions, leopards and other large cats sometimes do. They are almost without exception docile in captivity; but the exact nature of their relationship with man depends on the degree of association. Where the latter is close and domestic they can pass beyond the initial phase of somewhat indifferent tolerance to

friendliness and even some kind of affection (Florio & Spinelli, 1967 and 1968). When brought up with them they will play with dogs.

Can the cheetah climb? It has very often been asserted that because of its blunt dog-like claws and long rather stiff legs it cannot. The answer depends entirely on the definition of climbing, for this problem is solved in different ways. Many animals, for example squirrels, the domestic and most wild cats, can with complete ease ascend a tree trunk vertically by anchoring their feet in the bark at each step with their sharp curved claws. In this sense the cheetah is unable to climb, at least not once past the young kitten stage; but given a tree with a sloping trunk and conveniently placed branches it can, and does, climb or at any rate get fairly high up by an initial leap onto the stem, a walk up it, a further leap onto a branch, and so on. Trees are, in fact, not infrequently utilized as observation posts for game, affording a more distant view than can be gained from hillocks, termite mounds or other similar and often used vantage points. It would seem, too, that look-out trees are territorially marked; for Hanström (1949) observed a cheetah to defaecate or urinate on a branch, to be followed by a similar action on the same spot by its companion. Cheetahs have been said to "sharpen their claws" on the boles of trees; but this is most likely nothing more than a muscle-stretching action, often seen in cats and dogs.

Intense visual concentration on potential prey is one of the cheetah's leading characteristics, both during its final cautious approach and, earlier, as it makes its initial, more removed, survey of the possibilities, sizing up relevant factors—wind, distance, intervening cover, vigilance of the herd, indications of weaker members, and so forth—before deciding whether a hunt would hold out prospects of success. This observation may be carried out from the branches of a tree, from a hillside, a hillock or even a termite mound, or, not infrequently in suitable terrain, merely while lying hidden in the grass. The cheetah, in fact, spends a good deal of the day lying concealed, watching. To what sort of shelter it retires at night is not so clear; whether merely curled up in a "form" in the grass, or in some more secluded spot as a hole in the ground or amongst rocks is not recorded. And whether a group habitually frequents the same spot for several nights or is wholly nomadic has never been ascertained.

Nor have actual breeding places been often observed. These are sometimes, and perhaps generally, deserted terrestrial burrows, though in suitably rocky country natural cavities between boulders are doubtless used. Nothing has been recorded of breeding habits in the wild; and strangely, in view of this animal's placid nature and semi-domesticity, it has proved to be an exceptionally difficult species to get to breed successfully in captivity. There has been either a refusal to mate or, if coupling has taken place, an almost total mortality amongst cubs. Pournelle (1964), for instance, records that of 4 litters of 3, 4, 3 and 2 only 2 cubs survived. In the last decade or so, however, more success has been met with and more of this important matter is now known thanks to the accounts given by W. D. Thomas (1965), Florio & Spinelli (1967 and 1968), and Manton (1970).

The female comes into season repeatedly at intervals of from 7 to 10 days, each period lasting about 15 days. In the pre-mating phase there is close association between the sexes; but the considerable interest that the male then exhibits sinks at once into

indifference as soon as oestrus comes to an end with conception. Copulation has not been much observed but appears to be repeated during the oestrus period (W. D. Thomas, 1965). In the cheetah's natural surroundings it probably takes place after dark. Gestation lasts 91 to 95 days. There may be from 1 to 4 cubs in a litter in captivity, 2 or 3 being the most usual numbers; but in the wild, litter size appears to go up to 8, 4 not being uncommon. At birth each cub weighs some 250 to 300 grammes; but increase is rapid, and Encke (1960) found his to weigh 370 grammes on the 3rd day; and these reached a weight of $8\frac{1}{2}$ kg at $5\frac{1}{2}$ months. They can start to crawl at the age of about 2 or 3 days; stand up at 10 days; and walk at about 16 days. The date of the opening of the eyes seems to be widely variable. Florio & Spinelli (1968) record one litter in which the eyes started to open only on the 10th day, were not fully open until the 15th day, and started to focus properly about the 28th day; but in a previous cub from the same female (1967) the eyes were open on the 4th day. Manton (1970) tells of a litter of 3 cubs in which the eyes were open on what appears to have been the 6th or 7th day; while both Pournelle (1964) and Encke (1960) found the eyes to open after 8 days. The latter author noticed that the first pupil reflex became obvious on the 20th day.

The first teeth erupt at about 3 weeks; and meat eating normally starts probably when the cubs are about a month old. Nevertheless, one cub ate meat regurgitated by the mother on the 18th day; but though by the time it was 4 months old it was regularly eating meat and chicken heads it still took milk from its mother and even attempted to do so at 6 months. In other litters weaning took place a month earlier than this. The mat of dense grey hair which covers the dorsal aspect of cheetah cubs is moulted gradually from behind forwards and mostly disappears at about 3 months, though it persists rather longer over the shoulders and neck. The claws of the young are very sharp and cat-like, especially those of the forefeet, and can be used effectively for vertical climbing. Sexual maturity is attained in males at the age of about 14 months. In females it is somewhat earlier, the first oestrus period being exhibited at 9 or 10 months. After parturition a female can come into season again at the end of $3\frac{1}{2}$ to 4 months. It is thus possible for a cheetah to have two litters in a year; but whether this actually takes place in nature is another matter. If it did the first litter would be only about 7 months old when the second was born, with a further 5 to 7 months training to undergo with the mother; but there seems to be no evidence of the existence of parties of young cheetahs comprising two distinct age groups. There is, however, some reason to suppose that a litter may stick together for a considerable time, with perhaps occasional absences of a male in order to follow a female whose oestrus scent he has picked up, and to mate. There is possibly not much actual interchange between groups. These may consist of all males or of mixed sexes; but it seems likely that females, once they are sexually mature, tend to be rather more solitary, going apart to mate and thereafter bringing up their families unaided. According to S. S. Flower (1931) a cheetah lived in a zoo to the age of nearly 16 years; but they seldom live in captivity for as much as half this.

The young soon after birth (Florio & Spinelli, 1968) utter a bird-like cheep or whistle. A similarly bird-like sound is made also by adults. Roosevelt & Heller (1915) record that when they first heard this chirp, from captive cheetahs, they could not

believe that such a sound could come from them and looked everywhere for the bird responsible for it. Cowie (1957) says that cheetahs call to each other in the field with a shrill whistle or squeak, more like a bird than a mammal; but according to Eaton (1970b) they do not appear to vocalize to attract mates, this probably being sufficiently effected by the chemical message left in the female's urine. However, he found that a mother could give orders to her cubs when they accompanied her out foraging. A low-pitched "ughh" had the effect of making them remain in one place to await her while she hunted; and a high-pitched "chirp" brought them to the site of the kill. When cheetahs are content they utter a deep vibrant purr; but when angered or alarmed they snarl and spit in the usual cat fashion. Stevenson-Hamilton (1947) describes them as sometimes uttering a cat-like mew.

Cheetahs frequently walk, at a rather stately pace sometimes with the head up sometimes with it lowered and pointed forwards. This gait is used for normal travel, and their approach to game may be initially in this manner. When proximity to their prey calls for care they lower their bodies somewhat and move more deliberately and circumspectly, never removing their eyes for a moment from the potential quarry, watching with deep concentration for the least sign of alarm and for the exact moments to remain stationary or cautiously to advance further. Observers, as so often, differ remarkably. Stevenson-Hamilton (1947) describes the cheetah as crawling along "glued flat to the ground"; Eaton (1970c) says that they never crouch; and this latter, with the proviso that they do to some extent lower their posture and slink, seems the more accurate. Again, Kruuk & Turner (1967) say that the cheetah breaks into a gallop straight from a walk; but Mundy (1832), giving an eye-witness account of a set hunt in India, describes the cat as approaching its prey "at a slow, crouching canter". It seems to be a fact that this species uses the trotting gait so common in this subfamily much less than in the majority of felines. The gallop is a most impressive sight, though difficult to describe succinctly. The action, together with the general movements of the cheetah's body, have been analysed in some detail and diagrammatically depicted by Hildebrand (1959, 1960 and 1961). Omitting details, the stride may be reckoned as starting with the feet close together under the belly, one hindfoot on the ground, the body contracted in length. This hindleg gives a tremendous forward thrust, quickly followed by a second from the other hindleg; the animal then flies through the air, the body stretching out, the forelegs extending to their utmost until one forefoot strikes the ground, shortly followed by the second as the body continues to fly forward over them. The hindlimbs are brought forward again, coming up once more with the forelimbs beneath the belly and overtaking them somewhat; and the sequence is repeated. One such stride covers, on the average, the astonishing distance of about 7 metres. There seems to be no record of the cheetah swimming.

Taxonomy. Arguments relating to the standing of *jubatus* as a species have been dealt with above under the generic head; the question of subspecific division is considered here. It will be seen from the synonymy given earlier that in the past a considerable number of proposals have been made to differentiate forms of *Acinonyx* from one another, chiefly with specific status. It is generally held today, and may be regarded as virtually certain, that there is not, and never has been in recent times, more than a single

species in this genus; and therefore if these various proposed forms have any validity whatsoever it can only be at racial level. Two names alone have been directly associated with West Africa: *senegalensis* Blainville and *hecki* Hilzheimer. The former is unavailable, having been preoccupied; but the latter is related to the same locality, Senegal, and may reasonably be assumed to be synonymous (as in G. M. Allen, 1939). For the rest of the suggested forms, it would seem improbable that those connected with India or with extra-tropical southern Africa would be applicable to the region under consideration in this work. This reduces consideration of proposed names to three possibilities which, though extralimital, have their type localities situated in transcontinental vegetation zones occurring in West Africa. These are *soemmerringii* Fintzinger (Kordofan), *megabalica* Heuglin (? Bahr-el-Abiad), and *wagneri* Hilzheimer (Kordofan). The origins of these, together with *hecki* Hilzheimer (Senegal), though ill-defined or doubtful, are very possibly in the Sahel woodland zone.

The standing and comparison of these forms was discussed fully by Hilzheimer (1913). A great deal depends on the diagnosis of the earliest of them, *soemmerringii*; but as Hilzheimer pointed out it was doubtful whether Fintzinger's very inadequate description of this form, differentiating it from *guttatus* Wagner—longer legs, darker colour, bushier tail and scantier mane—was sufficient to make the name valid. It has, however, been customary to retain it and to synonymise it with *megabalica* Heuglin, almost as obscurely described, and sometimes (G. M. Allen, 1939) also with *wagneri* Hilzheimer. In illustration of the slender basis of much of the taxonomy it is perhaps instructive to draw attention here to that of the last of these, the diagnosis of which was not furnished by Hilzheimer but by Wagner himself, intended purely as a supplement to Hermann's earlier inadequate description of *guttatus* and as a verbal complement to the painting which Hermann had apparently intended to depict that species. Hilzheimer considered Wagner's description to fail in both these respects having been made by him from a stuffed skin of an animal collected by Rüppell in Kordofan, differing in Hilzheimer's opinion from *guttatus* Hermann. In recent years it has been customary to assume that West African animals are of the race *soemmerringii*—e.g. Rosevear, 1953, which was based on oral hearsay from taxonomists at that time reputed to know; and Dekeyser, 1955, which was very probably derived from that work.

The distinctions between various reputed forms of *Acinonyx* often hinge upon slight differences in such characters as the ground-colour of the pelage, in the size, number and colour of the spots, including those of the face, and in the number of rings on the tail. Without doubt differences, and sometimes marked differences, exist between cheetahs; but the study material available is mostly insufficient to say in what degree such variations are due to idiosyncrasy, age, moult or other non-taxonomic factor. Certainly the paucity of museum material makes it impossible to judge what range of local variation may be expected in West Africa itself; but comparison of skins from single areas in other parts of the continent make it clear that ground-colour, spot size and shape can vary in one locality to a degree equal to that which has been thought sufficient for the erection of new forms. The sole West African skin in London, now almost 70 years old, differs clearly from the general run of extralimital specimens both in its pallid ground-colour and its numerous dullish spots of small size; but it is, from its

mane, without doubt a young animal not yet in the full possession of its adult coat, and it is impossible to say into what it would eventually develop.

Whether *hecki* is a valid race requires much more material than Hilzheimer's single specimen to prove. It is in brief according to this author (1913: 290) a small, light-coloured animal with a small number of spots, and soles with pale-coloured hairs. However, whether size can be properly estimated from a single living animal of unknown age; or racial colour in the wild, either of pelage or soles, be satisfactorily judged from one which has been kept for any length of time in a European zoo is open to some doubt. Further, even if *soemmerringii* can be identified from its obscure description it yet remains to be demonstrated that West African specimens conform to it. The fact is that the extent of any real knowledge of the cheetah in West Africa takes us no further at present than the specific name. In any case it seems probable that with such a wandering, wide-ranging species anything in the nature of a true local race is unlikely.

Measurements. The table which follows shows the only measurements available for West Africa. Both specimens are females. The skull, though not of a particularly young animal, is somewhat on the small side and the measurements of a fairly old

Table 31: Numerical data for *Acinonyx jubatus*

	Nigeria:		
	Yantumaki Sudan	Lake Chad Sahel	Uganda ?Sudan
Vegetation			
Number in mean	I	I	I
Condylbasal length	150.5	—	168.8
Basilar length	136.0	—	153.4
Palatilar length	58.2	—	68.7
Zygomatic breadth	116.9	—	131.0
Upper cheekteeth breadth	66.2	—	70.3
Nasals, length	50.6	—	67.5
Interorbital breadth	40.0	—	44.5
Postorbital constriction	52.0	—	57.1
Braincase breadth	69.3	—	69.9
Toothrow ($c-m^1$)	49.1	—	53.4
p^4 length	(19.2)	—	21.8
m^1 breadth	5.8	—	6.8
m_1 length	6.0	—	6.8
Head & body	—	770	—
Tail	—	553	—
Hindfoot	—	237	—
Ear	—	72	—
RATIOS (per cent)			
Tail/head & body	—	72	—
Zygom. br./condylob. l.	78	—	78
Braincase/condylob. l.	46	—	41
Braincase/zygom. br.	59	—	53
Palatilar l./condylob. l.	39	—	41
Interorb./postorb.	77	—	78
$p^4/c-m^1$	39	—	41

female from Uganda are given for comparison. No field body measurements exist on any African skin for comparison with the young Lake Chad specimen.

